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Grassland Section

Range Plant Growth and Development Are Affected by Environmental Factors

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Range plant growth and development are controlled by internal regulators that are modified according to environmental conditions. The long-term climatic conditions for a region determine the type of vegetation in that region, and regional environmental factors affect growth and development of the plants. The three most ecologically important environmental factors affecting rangeland plant growth are temperature, water (precipitation), and light. These factors require consideration during the development of long-term rangeland management strategies (Manske 2000).

Temperature

Temperature, an approximate measurement of the heat energy available from solar radiation, is an important factor because most plant biological activity and growth occur within only a narrow range of temperatures, between 32F (0C) and 122F (50C) (Barbour et al. 1987). High temperatures limit biological reactions because the complex structures of proteins are disrupted or denatured. Although respiration and photosynthesis can continue slowly at temperatures well below 32F if plants are physiologically "hardened", low temperatures limit biological reactions because when it is frozen and because available energy is inadequate.

Low temperatures define the length of the active growing season. The growing season for annually seeded plants corresponds approximately to the frost-free period, the number of days between the last day with minimum temperatures below 32F (0C) in the spring and the first day with minimum temperatures below 32F (0C) in the fall (Ramirez 1972). Perennial plants maintain physiological processes throughout the year. Winter dormancy in perennial plants is not total inactivity but reduced activity (Leopold and Kriedemann 1975). Perennial grassland plants can grow actively beyond the frost-free period if temperatures are above the level that freezes water in plant tissue and soil. Perennial plants begin active growth more than 30 days before the last frost in spring and continue growth after the first frost in fall; the growing season for perennial plants is considered to be between the first 5 consecutive days in spring and the last 5 consecutive days in fall with mean daily temperature at or above 32F (0C), generally from mid April through mid October. Low air

temperature during the early and late portions of the growing season and high temperatures after mid summer greatly limit plant growth (Jensen 1972).

Different plant species have different optimum temperature ranges. Cool-season plants, which are C_3 photosynthetic pathway plants, have an optimum temperature range of 50 to 77F (10 to 25C). Warm-season plants, which are C_4 photosynthetic pathway plants, have an optimum temperature range of 86 to 105F (30 to 40C) (Coyne et al. 1995).

Large fluctuations in seasonal and daily air temperature occur in the Northern Great Plains. The large diurnal change in temperature during the growing season, which has warm days and cool nights, is beneficial for plant growth because warm days increase the photosynthetic rate and cool nights reduce the respiration rate (Leopold and Kriedemann 1975).

Water (Precipitation)

Water, an integral part of living systems, is ecologically important because it is a major force in shaping climatic patterns and biochemically important because it is a necessary component in physiological processes (Brown 1995). Water is the principal constituent of plant cells, usually composing over 80% of the fresh weight of herbaceous plants. Water is the primary solvent in physiological processes by which gases, minerals, and other materials enter plant cells and by which these materials are translocated to various parts of the plant. Water is the substance in which processes such as photosynthesis and other biochemical reactions occur and a structural component of proteins and nucleic acids. Water is also essential for the maintenance of the rigidity of plant tissue and for cell enlargement and growth in plants (Brown 1977, Brown 1995).

Water Deficiency

The climatic conditions in the Northern Great Plains cause frequent periods when plants experience water stress. Rain deficiency periods in which 75% or less of the long-term mean precipitation is received are called droughts. Periods of drought conditions can last for a full year or a complete growing season, but water deficiency periods of one month are long enough to limit herbage production greatly. Water deficiency conditions during May, June, and July are not frequent. These months constitute the primary period of production for range plant communities. August, September, and October experience water deficiency conditions more than half the time and are not dependable for positive water relations. The water relations during this latter portion of the growing season limit range plant growth and herbage biomass accumulation (Manske 2000). Frequent late-season water deficiency limits shrub and tree growth more than grass growth.

Water Stress

Temperature and precipitation act together to affect the physiological and ecological status of range plants. The balance between rainfall and potential evapotranspiration determines a plant's biological situation. Precipitation-evapotranspiration levels interact and influence the rates of the carbon and nitrogen cycles. Evaporation rates are dependent on temperature: as average temperature decreases, evaporation rate decreases; as temperature increases, evaporation rate increases. The mixed grass prairie region has greater evapotranspiration

demand than precipitation. The tall grass prairie region has greater precipitation than evapotranspiration demand.

The native vegetation in the Northern Great Plains comprises a mixture of cool-season and warm-season species. The relationship between temperature and evaporation levels affects the ratio of cool-season to warm-season grasses in the plant species composition. The northern portion of the region has lower average temperature and lower evaporation rate; these conditions result in a higher percentage of cool-season species. The southern portion of the region has higher average temperature and greater evaporation rate; these conditions result in a higher percentage of warm-season species. A mixture of cool- and warm-season species is highly desirable because the herbage biomass production remains more stable over wide variations in seasonal temperature, precipitation, and evaporation levels.

During periods when rainfall is lower than evapotranspiration demand, a water deficiency exists. Under water deficiency conditions, the rate of water loss from transpiration exceeds the rate of water absorption by the roots, and plants undergo water stress. Water stress can vary from a small decrease in water potential (as in midday wilting on warm clear days) to the lethal limit of dessication. Although range plants have mechanisms that help reduce damage from water stress, water deficiency conditions lasting a month cause plants to experience water stress severe enough to reduce herbage production (Brown 1977, Brown 1995). The annual variation in temperature, precipitation, and evaporation affects the severity and duration of water deficiency, which in turn affect the levels of water stress.

Plant Water Stress

Plants experiencing water stress conditions respond at different inhibitory levels in relationship to the severity of the water deficiency. Early stages of water stress slow shoot and leaf growth. Leaves show signs of wilting, folding, and discoloration. Tillering and new shoot development are reduced, but root production may be increased. Senescence of older leaves is accelerated. Cell wall formation, cell division, and protein synthesis are reduced. As water stress increases, enzyme activity declines and the formation of necessary compounds slows or ceases. The stomata begin to close, and rates of transpiration and photosynthesis decrease. Respiration and translocation are substantially reduced as water stress increases. When water stress becomes severe, most functions nearly or completely cease and severe damage occurs. Leaf and root mortality induced by water stress progresses from the tips to the crown, its rate increasing with increasing stress. If water stress is prolonged or becomes more severe, the condition can be lethal. Plant death occurs when the meristems become dehydrated beyond the limits required to maintain cell turgidity and biochemical activity (Brown 1995).

Plants in water stress have limited growth and reduced photosynthetic activity. Plant vigor is decreased, carbohydrate storage is reduced, and root biomass is reduced. Plant height and herbage biomass accumulation are reduced. Leaf senescence increases and as a result, nutritional quality of forage decreases. The rate of sexual reproduction is diminished as a result of a decrease in seed stalk numbers and height and a reduction in numbers of seeds in the seed heads. Rate of vegetative reproduction is reduced because the number of axillary buds and the number of secondary tillers decrease.

Basal cover is reduced because of mortality of entire plants or portions of plants, and open spaces in the plant community increase because of a decrease in plant numbers. The species composition shifts to an increase in species with advanced water-stress resistance

mechanisms and a decrease in drought-susceptible species. Occurrence of some forbs and weedy species increases because of their ability to exploit the open spaces. Quantity and quality of wildlife habitat diminish. Livestock performance decreases because of the reductions in the quantity and quality of available forage, which in turn cause a reduction in milk production and a corresponding reduction in calf rate of gain and weaning weight. During extended periods of water stress, stocking rates generally need to be reduced.

Light

Light is the ultimate source of energy and the most important ecological factor affecting plant growth. Variations in guality, intensity, and duration of light affect plant growth. Light is necessary for photosynthesis, the process that converts light energy into chemical energy. The rate of photosynthesis varies with different wavelengths, but the guality (wavelength) of sunlight does not vary enough in a given region to have an important differential effect on the rate of photosynthesis. The intensity of sunlight (measurable energy) and duration of sunlight (length of day or photoperiod), however, do vary sufficiently to affect plant growth. Light intensity varies greatly with season and time of day because of changes in the angle of incidence of the sun's rays and the distance light travels through the atmosphere. Light intensity also varies with the amount of humidity and cloud cover because atmospheric moisture absorbs and scatters light rays. However, the greatest variation in intensity of light received by range plants results from the various degrees of shading from other plants. Because most range plants require full sunlight or very high levels of sunlight for best growth, shading can reduce or limit growth of range plants. Duration of sunlight (day-length period or photoperiod) is one of the most dependable cues by which plants time their activities in temperate zones. The buds or leaves of a plant contain sensory receptors, specially pigmented areas that detect day length and night length and can activate one or more hormone and enzyme systems that bring about physiological responses. The phenological development of rangeland plants is triggered primarily by changes in the length of daylight, although other environmental factors produce secondary effects and may cause slight variations in the pattern of phenological development. The tilt of the earth's axis in conjunction with the earth's annual revolution around the sun produces the seasons and changes the length of daylight, which increases from the beginning of the growing season until mid June then decreases to the end of the growing season. Photoperiod (day-length period) for a given date and locality remains the same from year to year (Odum 1971, Daubenmire 1974, Barbour et al. 1987).

Changes in day length (photoperiod) function as the timer and trigger that activates or stops physiological processes initiating growth and flowering and activates the process of hardening for resistance to low temperatures in the fall and winter. Vegetative growth is triggered by photoperiod and temperature (Langer 1972, Dahl 1995), and reproductive initiation is triggered primarily by photoperiod (Roberts 1939, Leopold and Kriedemann 1975, Dahl 1995) but can be slightly modified by temperature and precipitation (McMillian 1957, Leopold and Kriedemann 1975, Dahl and Hyder 1977, Dahl 1995). Cool- and warm-season plants respond to changes in photoperiod differently. Generally, most cool-season plants are long-day plants, and most warm-season plants are short-day plants. Long-day plants reach the flowering stage after exposure to a critical photoperiod and during the period of increasing daylight between the beginning of active growth and mid June, usually flowering before 21 June. 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, usually flowering after 21 June. Short-day plants are technically responding to the increase in the length of the night period rather than to the decrease in the day length (Weier et al. 1974, Leopold and Kriedemann 1975).

Management Implications

The combined influences of light, temperature, and precipitation affect the quantity and quality of plant growth in the Northern Great Plains and can limit livestock production if not considered during the planning of long-term grazing management strategies. Strategies based on phenological growth stages of the major grasses can be planned by calendar date after the relationships between growth stage of the grasses and date have been determined with consideration of a possible variation of about $\frac{3}{12}$ 7 days to accommodate annual potential modification from temperature and precipitation (Manske 1980). Implementation of such strategies has the potential to maintain the stability of the grassland ecosystem, enhance quantity and quality of herbage, and sustain livestock production.

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