

Ecology and Management of Annual Rangeland Series Part 5: Range Plant Growth and Development

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The annual plants that dominate annual grasslands and the understory of oak woodlands have different life cycles from perennials, which dominate most of the world's rangelands. Focusing on California's annuals-dominated rangelands in the Coast Range and the foothills of the Sierra Nevada mountains, this publication will discuss morphological and physiological changes associated with annual and perennial life cycles, photosynthesis and carbohydrate storage, and the effect of grazing on individual plants.

SEASONALITY AND LIFE CYCLES

First, let's define some common terms such as *annual*, *perennial*, *grass*, *forb*, and *shrub*. An annual plant is one that starts from seed each year and completes its life cycle in 1 year. A perennial plant survives and grows for several years. While perennials may produce seeds, they invest a certain amount of energy in the



Figure 1. Seedlings of monocotyledonous (A) and dicotyledonous (B) plants.

storage of carbohydrates in roots and crowns for use in respiration during dormant (cold or dry) periods and initial support of regrowth at the beginning of a new growing season.

Grasses are monocotyledonous plants (monocots), usually herbaceous plants with narrow leaves growing from the base. Monocots are one of two major groups of flowering plants (angiosperms) that are traditionally recognized, the other being dicotyledonous plants, or dicots. Monocot seedlings typically have one cotyledon (seed leaf), in contrast to the two cotyledons typical of dicots (fig. 1). Graminoids include the grasses of the Poaceae family, sedges of the Cyperaceae family, and rushes of the Juncaceae family (fig. 2). Grasses dominate most of the world's grasslands, but they also include cereals, bamboo, and turf grasses that are cultivated for food, fiber, and recreation. Sedges include many wild marsh and grassland plants, as well as some cultivated ones such as water chestnut (*Eleocharis dulcis*) and papyrus sedge (*Cyperus papyrus*).



Figure 2. True grass (A), sedge (B), and rush (C).

Forbs are herbaceous flowering plants that are not grasses, sedges, or rushes. Forbs are dicotyledonous (dicots) and nonwoody. The term *forb* is frequently used in vegetation ecology, especially in relation to grasslands. *Shrub*, or *bush*, is a horticultural term rather than a strict botanical category of woody plant, distinguished from a tree by its multiple stems and lower height, usually less than 15 to 20 feet tall. Many shrubs can be trees or vice versa, depending on the particular growing conditions (fig. 3).

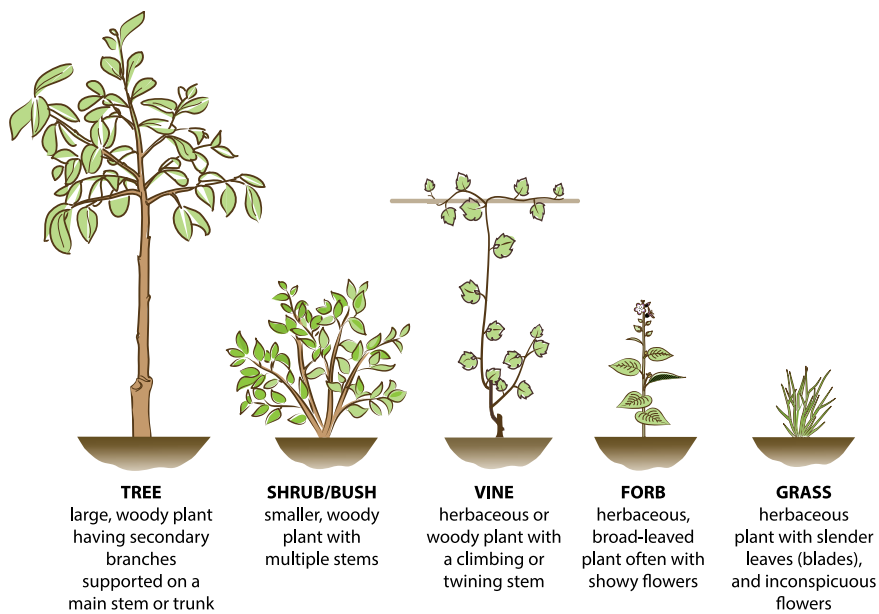


Figure 3. Perennial herbaceous plants include grasses and forbs, and woody plants include shrubs and trees. Vines may be herbaceous or woody.

Life Cycles

Phenology is the progression of periodic plant life cycle events, and it is influenced by seasonal and interannual variations in weather. Examples of life cycle events include germination, seedling emergence, flowering, and seed set. A list of phenological stages normally includes vegetative, flowering, and dormancy stages for perennials. Table 1 gives a list of 12 phenological stages, or stages of maturity, that have been used to study seasonal changes in forage quality of annual grasses (George and Bell 2001).

Table 1. Numerical stage of maturity used to predict protein, crude fiber, phosphorus, and calcium content of annual grasses, filaree, and bur clover

Stage number	Stage description
1	Germinated
2	Early vegetative
3	Late vegetative
4	Early bloom
5	Midbloom
6	Full bloom
7	Late bloom
8	Milk stage
9	Dough stage
10	Mature
11	Dry
12	Dry leached

Source: George and Bell 2001.

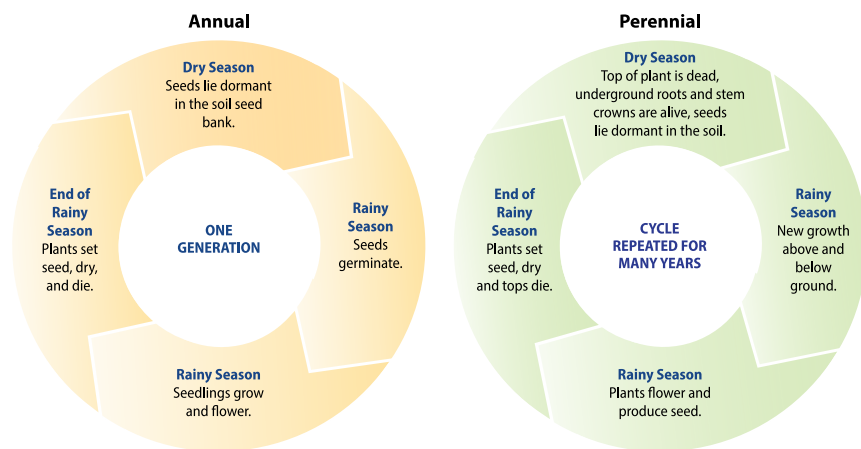


Figure 4. Annual and perennial plant life cycles.

Each year, annual plants germinate, become established, and progress through vegetative and reproductive stages (fig. 4). During the winter, when moisture is adequate but temperatures are low, photosynthesis and plant growth are slow. With the arrival of spring, photosynthesis and plant growth rates increase. As soil moisture is depleted, plants begin to dry and die, becoming litter. Variation in seasonal temperatures and precipitation influences the seasonality of plant growth.

Perennial plants live for more than 1 year and regrow each year (see fig. 4). Therefore, you will be managing the same plant year after year. Perennials reproduce from seed or vegetatively with tillers, stolons, and/or

rhizomes. Short-lived perennials last 3 to 5 years, whereas properly managed long-lived perennials can survive much longer. Woody perennials can live for decades or even centuries. In temperate regions, many perennial plants enter dormancy to survive the freezing winter temperatures. In Mediterranean regions, where there is a pronounced dry season in summer and mild winter temperatures, perennial grasses and forbs may enter a dry-season dormancy, regrowing with the fall rains. Much of the aboveground biomass of perennial grasses and forbs dies as the cold or dry season approaches. The remainder of the aboveground and near-surface portions of these plants enter a dormant phase until the cold or dry season is over. During cold dormancy (winter), soil moisture is stored in the soil throughout rainy periods and snow melt. As spring approaches and temperatures increase, these plants use this soil moisture to begin growth. These perennial plants remain vegetative for several weeks but eventually flower and develop seeds. As the growing season progresses, seed is set and eventually dispersed. With cooling temperatures, the plants begin to enter dormancy, and much of the aboveground biomass dies. Most perennial grasses and forbs in the western United States follow this winter dormancy life cycle pattern.

Seed Banks

When thinking about seed banks in California's annual rangelands, it is important to make a distinction between short-term (i.e., transient) seed banks and long-term (i.e., persistent) seed banks. *Transient seed banks* refers to the seeds that spend a short time in the soil, usually the time between their production and dispersal in late spring and their subsequent germination with the onset of fall rain. In contrast, *persistent seed banks* refers to seeds that remain in the soil for multiple years; in fact, some seeds can remain viable in the soil for many decades. The degree of difference between the species composition of the aboveground grassland community and the community hidden underground in the seed bank can be quite striking, and it varies among species and grassland types.

Although the relative contribution of different grassland species to transient and persistent seed banks can vary widely, some general trends exist. Grasses, although they are often the dominant component of transient seed banks, are much less likely to contribute to persistent seed banks. The seed of many grass species germinates in the year of its production and rarely survives more than 1 or 2 years in the soil (Young et al. 1981). Even when focusing specifically on transient seed banks, the relative contribution of annual and perennial grasses to these short-lived seed banks can be very different. A study of a mixed annual and perennial (*Stipa* sp.) grassland in the Central Valley of California found that, even in areas dominated by perennial grass cover, there were essentially no perennial seeds in the soil seed bank. In contrast, annual grasses had a well-developed transient seed bank, even in areas where they were a very minor component aboveground (Major and Pyott 1966).

Compared with grasses, forbs have a tendency to produce a more persistent seed bank. A 5-year study in a California annual grassland indicated that seed carryover rates (a measure of seed bank persistence) were more than 10 times greater for forb species than for annual grasses (Young et al. 1981). Among forbs, legumes frequently have the greatest rates of seed carryover and thus can often form very long-lived, persistent seed banks. Seed coat impermeability to water (hard seed) is a form of persistent seed dormancy that is widespread in legumes and is further described below in the section "Germination." Seed longevity may explain the dominance of legumes in persistent seed banks in grasslands. Hull (1973) compared germination rates for a number of North American rangeland species that had been stored in unheated sheds for 14 to 41 years. Seeds of legumes retained their viability longer and had much higher rates of germination than any of the grass and forb species tested, regardless of length of storage.

Spatial variation in the longevity of soil seed banks can depend on the frequency of soil disturbance and the formation of gaps in both plant canopy and litter layers. Germination cueing represents the capacity of a seed to

detect a potential opening for establishment and may involve a number of physical cues such as light quality or soil temperature fluctuations. For example, Rice (1985) reported that diurnal temperature variation among three types of microsites in annual grassland (under grass litter, in bare soil, and in gopher mounds) significantly affected rates of dormancy release in broadleaf filaree (*Erodium botrys*). Microsite variation in soil temperature germination cues in this hard-seeded forb might have a strong influence on seed bank depletion and longevity by affecting the loss rate due to germination.

Germination

Seed germination (fig. 5) initiates a series of changes that ultimately lead to a mature plant and reproduction of the species. Favorable temperature and moisture are essential for successful development of the seedling during the first critical stages of growth. Rapid germination and growth results in high demand for light, moisture, nutrients, and other plant growth requirements.

Fully developed seeds contain an embryo and food reserves, wrapped in a seed coat. Under favorable conditions, the seed begins to germinate and the embryonic tissues resume growth, developing toward a seedling. Some plants produce varying numbers of seeds that

lack embryos; these are called empty seeds, which never germinate.

While water is required, temperature, oxygen, and light quality may also influence germination. Mature seeds are often extremely dry and need to take in significant amounts of water, relative to the seed dry weight, before cellular metabolism and growth can resume. The uptake of water by seeds is called imbibition, which leads to the swelling and the breaking of the seed coat. When seeds are formed, most plants store a food reserve with the seed, such as starch, proteins, or oils. This food reserve provides nourishment to the growing embryo. When the seed imbibes water, hydrolytic enzymes are activated, which break down these stored food resources into metabolically useful chemicals. After the seedling emerges from the seed coat and starts growing roots and leaves, the seedling's food reserves are typically exhausted. At this stage, photosynthesis provides the energy needed for continued growth, and the seedling now requires a continuous supply of water, nutrients, and light. When a seed germinates, the new seedling leaf grows toward light. This is called phototropism.

Oxygen is required for respiration during germination. Oxygen is found in soil pore spaces. However, if a seed is buried too deeply

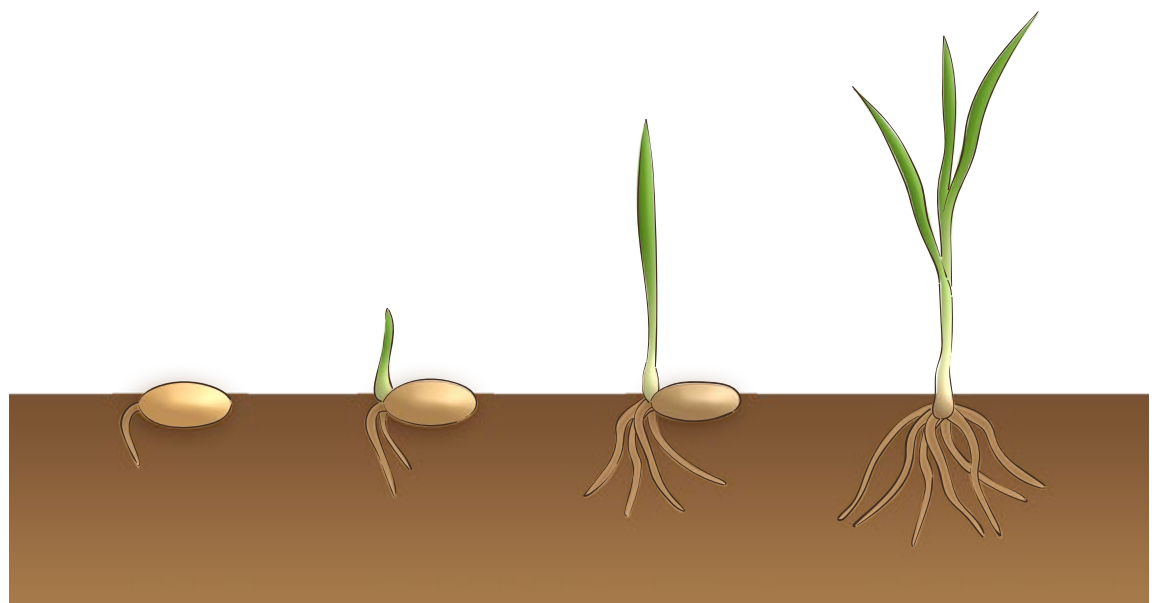


Figure 5. When moisture and temperature are favorable, seed germination starts and results in root and shoot emergence and development of a new plant.

within the soil or the soil is waterlogged, the seed can be oxygen starved. Some seeds have impermeable seed coats that prevent oxygen from entering the seed, causing a type of physical dormancy that is broken when the seed coat is worn away enough to allow gas exchange and water uptake from the environment. Hard seed produced by some legumes, such as rose clover, can survive in the soil for more than 20 years.

Temperature also influences germination. Seeds from different species and even seeds from the same plant typically can germinate over a wide range of temperatures. Seeds often have a temperature range within which they will germinate, and they will not do so above or below this range. Many seeds germinate at temperatures slightly above room temperature (60° to 75°F), while others germinate just above freezing or germinate only in response to alternating warm and cool temperatures. Some seeds germinate when the soil is cool (28° to 40°F), while others germinate when the soil is warm (76° to 90°F).

Some seeds require exposure to cold temperatures (vernalization) to break dormancy. Seeds in a dormant state will not germinate, even if conditions are favorable. Some seeds will only germinate following hot weather, and others must be exposed to high temperatures during a forest fire, which cracks the seed coat. Germination in many seeds, especially small ones, is regulated by light. Many seeds, including species found in forest settings, will not germinate until an opening in the canopy allows sufficient light for seedling growth. Some seeds need to pass through an animal's digestive tract to weaken the seed coat to allow the seedling to emerge.

Variability in the germination rate exists between and within species. Seed size has been shown to be a critical factor for promoting seedling vigor for some plants. For some legumes and other forbs, seed coat hardness or impermeability often retards germination but spreads germination over years, which is a survival advantage for the species. In general, germination is reduced with increasing seed age.

Seedling Establishment

With the emergence of the radical during germination, seedling establishment begins. However, it may not be considered successful until an adequate root system and leaf area has developed to sustain growth (McKell 1972). While there is no single attribute that influences seedling vigor and establishment, seed size and weight, rapid germination, seed age, high levels of biochemical and physiological activity, and rate of root and shoot growth are all potential indicators of seedling vigor. Rapid root growth is fundamental to the establishment and development of annual rangeland plants. Individual plants and species may gain an advantage over competitors if they are able to maintain both rapid root and top growth. In California, annual grasses frequently exhibit greater root growth rates than native perennial grasses (Aanderud et al. 2003). This is one of the reasons why native perennial grass establishment is so difficult in California's annual rangelands.

Seasonal Growth Rates

Growth rates in the annual rangelands following germination can be rapid if temperatures are warm but can be slow if they are cold (table 2, fig. 6). The average germination date at the UC Sierra Foothill Research and Extension Center (UC SFREC) in Yuba County, California, is October 20, and the average standing crop on December 1 is 404 pounds per acre, or less than 14 percent of average standing crop in May. During the winter, growth is slow. The average standing crop at UC SFREC on March 1 is only about 700 pounds per acre, which is less than 25 percent of the average peak standing crop of 2,971 pounds per acre. Thus, daily growth rates typically average about 5 pounds per acre per day from October 20 to March 1. During rapid spring growth, the average growth rate is about 37 pounds per acre per day, resulting in an average standing crop on May 1 of 2,886 pounds per acre. On average, little production occurs during May at UC SFREC, resulting in only small differences between average standing crop on May 1 and average peak standing crop.

Table 2. Thirty-one years of monthly standing crop estimates for annual rangeland at the University of California Sierra Foothill Research and Information Center

Year	Germinating rain	Dec 1	Jan 1	Feb 1	Mar 1	Apr 1	May 1	Peak crop	Peak % of avg
1979–80	10/20	—	—	—	500	1,300	—	1,670	56%
1980–81	11/30	—	—	—	350	1,385	—	2,560	86%
1981–82	9/24	—	—	—	550	1,357	—	2,770	93%
1982–83	9/17	—	—	—	800	2,142	—	4,630	156%
1986–87	9/18	—	—	—	204	810	—	1,486	50%
1987–88	10/23	—	—	—	214	793	—	1,071	36%
1988–89	11/8	—	—	694	—	—	—	2,527	85%
1990–91	11/25	—	—	162	—	691	—	2,565	86%
1991–92	10/26	—	383	—	—	—	—	2,984	100%
1992–93	10/21	—	—	367	631	2,260	—	4,696	158%
1993–94	10/15	—	—	—	410	1,282	—	2,767	93%
1994–95	10/4	—	547	—	569	1,521	3,074	3,213	108%
1995–96	12/7	—	350	664	950	1,075	3,089	4,123	139%
1996–97	10/25	—	623	583	1,590	2,827	3,201	3,201	108%
1997–98	10/8	280	—	341	438	956	2,073	2,797	94%
1998–99	9/27	—	211	254	316	604	1,463	1,746	59%
1999–00	10/27	592	807	737	1,040	1,954	3,580	3,580	120%
2000–01	9/2	—	—	573	1,082	1,951	3,082	3,082	104%
2001–02	10/30	384	407	385	447	1,475	2,740	2,754	93%
2002–03	12/12	335	567	735	960	1,739	3,386	4,348	146%
2003–04	10/31	—	596	689	848	1,886	2,831	2,831	95%
2004–05	10/20	—	482	517	1,077	2,742	4,107	4,410	148%
2005–06	11/7	404	838	983	1,458	2,540	3,858	4,122	139%
2006–07	11/2	229	426	430	609	2,082	2,977	2,977	100%
2007–08	9/30	—	413	544	531	1,278	1,847	1,847	62%
2008–09	10/4	205	199	284	500	1,117	2,815	2,815	95%
2009–10	10/13	601	641	578	650	1,573	3,176	3,176	107%
2010–11	10/1	—	502	494	703	1,441	2,941	3,794	128%
2011–12	10/3	—	412	338	496	566	2,389	2,389	80%
2012–13	10/23	609	533	873	861	1,679	2,881	2,881	97%
2013–14	11/21	—	52	98	400	1,033	2,218	2,300	77%
Average		404	473	515	685	1,519	2,886	2,971	100%

On rangelands of the intermountain region of the western United States, grass growth begins with warming temperatures after a period of winter dormancy. For example, in northeastern California little or no grass production occurs from October through February or March. Only about 10 percent of the annual production occurs in April as plants begin to grow. Growth in May and June is rapid, often accounting for 50 to 75 percent of annual production. Growth slows for the remaining portion of the summer, with increasing temperatures in July and reductions in soil water availability (see fig. 6).

In California's annual rangelands, the grasses and forbs produced during the growing season dry and become litter as the growing season comes to an end. The University of California has published guidelines for how much litter, or residual dry matter (RDM), should be left at the end of the grazing season for soil protection and to provide mulch to protect germinating seeds (Bartolome et al. 2006).

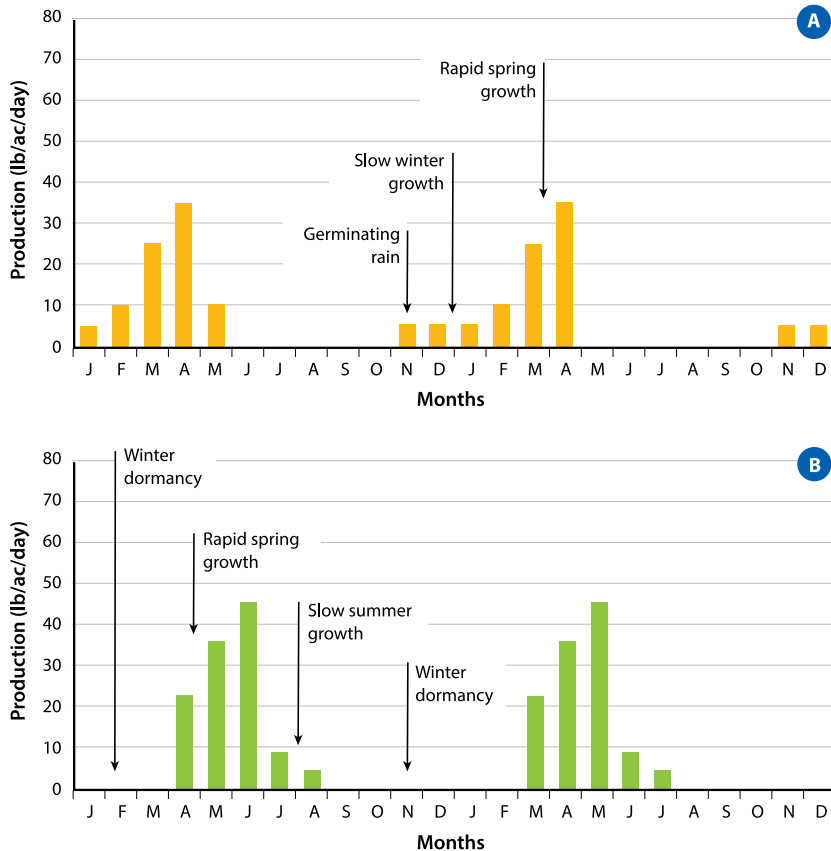
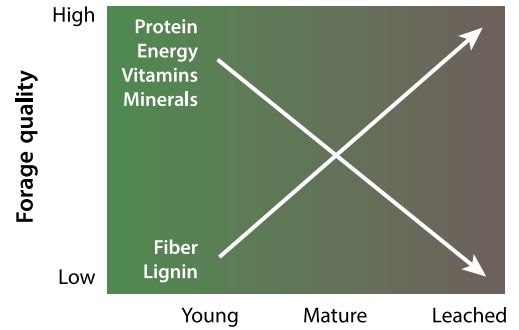


Figure 6. Seasonal forage production on California annual rangelands (A) and intermountain rangelands (B).

Forage Quality

Forage quality decreases as plants progress through their yearly life cycle (fig. 7). During the early vegetative stage of growth, before stem elongation and flowering, forage quality is greatest because cell contents and nutrient concentrations in metabolically active tissues are greater and contain less cell-wall



Stages of growth

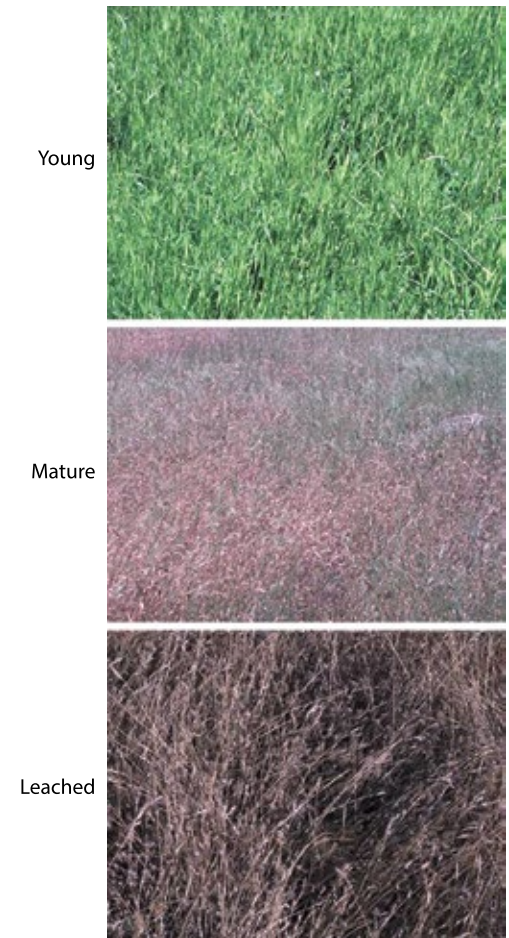


Figure 7. Protein, energy, vitamins, and minerals decrease as plants mature, while fiber and lignin increase (George et al. 2001).

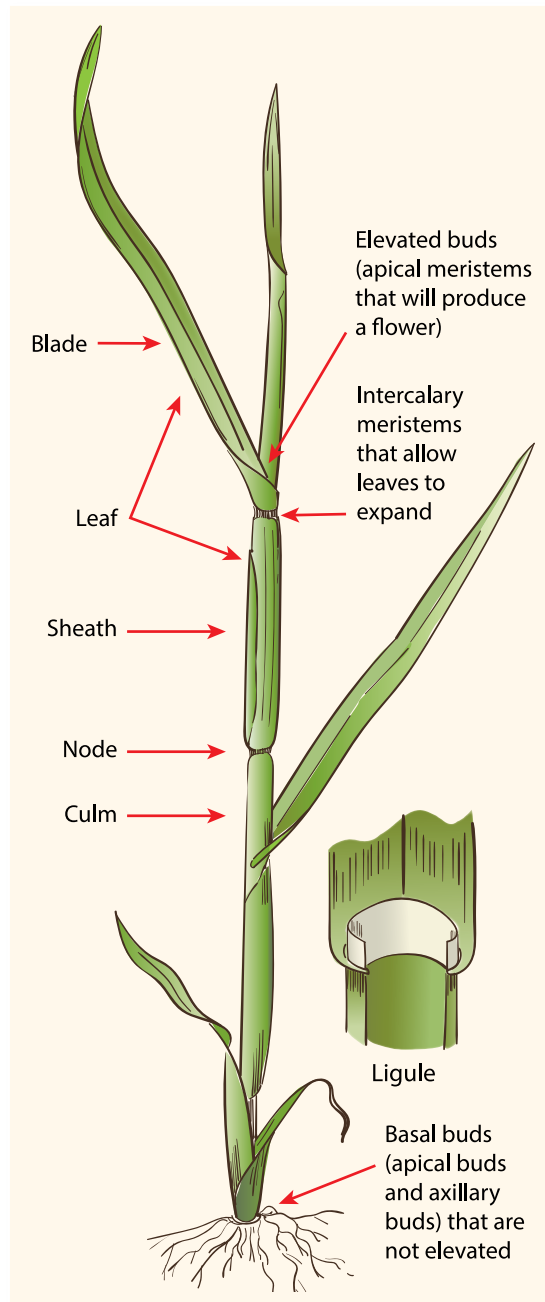


Figure 8. Location of basal, intercalary, and elevated meristems in relation to grass parts (blade, leaf, sheath, node, culm and ligule). *Source:* UC Bulletin 724, 1951.

structure. For annual plants, this stage follows germination. For perennial plants, this is the new plant growth following dormancy or regrowth following harvest. As the season progresses, cell wall increases and cell content decreases resulting in a gradual decline in protein content and digestibility.

In the late vegetative stage, when stems are beginning to elongate just before flowering,

nutrient concentrations are usually lower than at early vegetative stages. This occurs during the adequate-green season's spring flush of growth. As plants begin to flower, nutrients are being translocated to the flowers, and nutrients in the forage continue to decline. By the late-flowering stage, when the dough stage in grass seeds occurs, nutrients have accumulated in flowers and seed, resulting in a loss of nutrients in leaves and stems. This stage occurs late in the adequate-green season (Bentley and Talbot 1951).

As plants mature and begin to dry, seeds are dispersed, and forage quality has declined to such an extent that it does not meet the nutritional requirements for some kinds and classes of livestock. In the dry stage, plants are cured, seed has been dispersed, and weathering is in progress. Plant nutrients are low, and fiber is high. Weathering is accelerated by rainfall, which leaches nutrients from the dry residual forage. This is the dry leached stage, when forage quality is lowest.

MORPHOLOGY AND DEVELOPMENT

Grass Anatomy

In this section, we will discuss the morphology and development of grasses, forbs and woody plants, and plant reproduction.

Several growing points occur on a grass plant (fig. 8). Apical meristems, or buds, develop into the flower and are elevated during the flowering process. Axillary buds give rise to tillers, rhizomes, and stolons. Intercalary meristems allow leaves to expand following grazing or mowing. Buds near the ground are less likely to be grazed or mowed, but some buds become elevated as the season progresses, increasing the risk of removal during grazing or mowing. Delaying bud elevation reduces the risk of bud removal.

Grasses and other herbaceous plants progress through a vegetative phase, an elongation (transition) phase, and a reproduction phase (fig. 9). In the vegetative phase, grass shoots are mostly leaves. Leaf blade collars remain nested in the base of the shoot, and there is no evidence of sheath elongation or culm development. In response to day length,

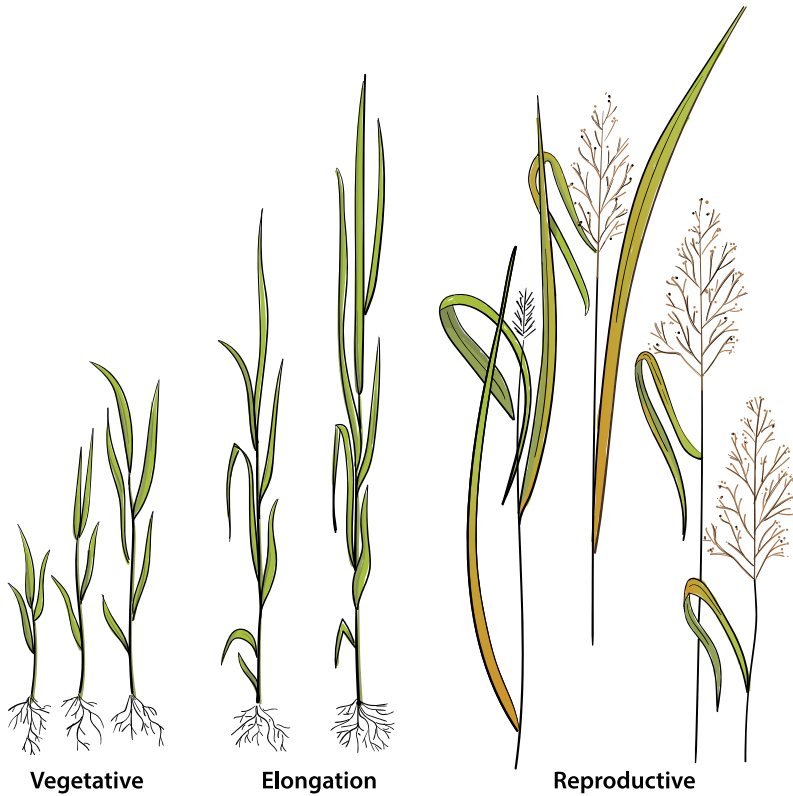
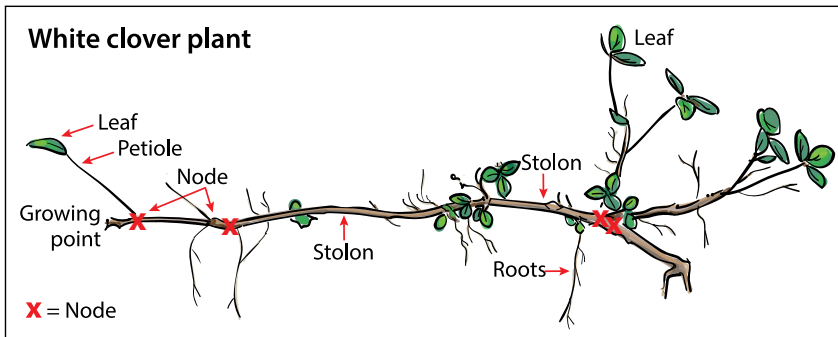


Figure 9. Vegetative, elongation, and reproductive stages of annual plant life cycle.

temperature, or other environmental variables, the apical meristem gradually transitions from a vegetative bud to a floral bud. This is called floral induction. During this phase, leaf sheaths begin to elongate, and culm internodes also elongate, raising the floral buds and leaf bases to a grazeable height. During the reproductive phase, the conversion from vegetative to floral bud production is completed, and the unseen inflorescence emerges from the leaf sheath. Just before the inflorescence emerges, it is covered by the leaf sheath, and this is commonly called the “boot stage” of development. Successful regrowth following defoliation depends on productive plant meristems, or buds. Plant species with growing points elevated are more susceptible to grazing than plants that keep their growing points close to the ground.

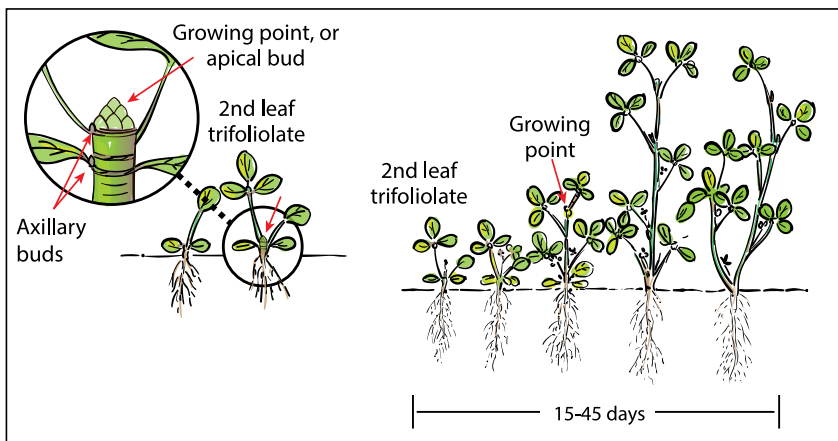
Forb Anatomy

Forb anatomy varies among species. This diagram of legumes identifies some common forb plant parts (fig. 10). Similar to grasses and other plants, forbs have apical buds that may develop into flowers and axillary buds that produce stems, rhizomes, and stolons.



Woody Plant Anatomy

Woody plants have apical and axillary buds similar to those of forbs. They also have buds on the root crown or roots that resprout following damage or loss of the aboveground stems, as occurs during fire or following wood cutting. Chamise (*Adenostema fasciculatum*) and some oaks (*Quercus* spp.) are strong resprouters following fire or top removal.



Reproduction

The reproductive phase is triggered primarily by photoperiod (Leopold and Kriedemann 1975; Dahl 1995), but it can be modified by temperature and precipitation. Some plants are long-day plants and others are short-day plants. The long-day plants reach the 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 are long-day plants and reach flower phenophase before June 21.

Figure 10. Location of growing points on a clover plant.

Short-day plants are induced to flower by day lengths that are shorter than a critical length, which occurs 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 (Leopold and Kriedemann 1975). Generally, most warm-season plants are short-day plants and reach the flowering phase after June 21. The annual pattern of 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). Annual plants are dependent on sexual reproduction (seed) each year for survival. Likewise, short-lived perennials depend on seed production. 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). The frequency of true seedlings is low in perennial 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 readily available to support the growing seedling. Sexual reproduction is necessary for a population to maintain genetic diversity to withstand large-scale changes (Briske and Richards 1995).

Reproductive shoots are adapted for seed production rather than 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 remain vegetative (Branson 1953).

PHOTOSYNTHESIS AND CARBOHYDRATES

Factors That Influence Photosynthesis

When considering grazing and plants, it is important to remember that (1) plants are the only source of energy for grazing animals, (2) the formation of sugars, starches, and proteins



Josh S. Davy

is dependent on photosynthesis, (3) plants do not obtain food from the soil but rather water and nutrients needed for photosynthesis and subsequent growth, and (4) when leaves are removed from plants, photosynthesis and growth capacity are reduced.

Photosynthesis is the bonding together of CO_2 (carbon dioxide) and H_2O (water) to make $\text{C}_6\text{H}_{12}\text{O}_6$ (sugar) and O_2 (oxygen), using the sun's energy. The sugar contains the stored energy and serves as the raw material from which other compounds are made. Respiration is the opposite of photosynthesis, whereby the stored energy in the sugar is released in the presence of oxygen, and this reaction releases the CO_2 and H_2O originally bonded together by the sun's energy.

Stomata are the pores in leaves (and stems) through which CO_2 is taken in and O_2 is released during photosynthesis. Plants control when stomata are open or closed and the width of the opening. The width of the opening is controlled by two guard cells that expand and contract to open and close the space between them. Transpiration is the process of water loss (evaporation) through the stomata when these cells are open. This pulls more water and nutrients to the top of the plant, but it causes the plant to lose water and potentially dehydrate. Water use efficiency (WUE) refers to how efficient the plant is at fixing carbon dioxide in photosynthesis compared to the

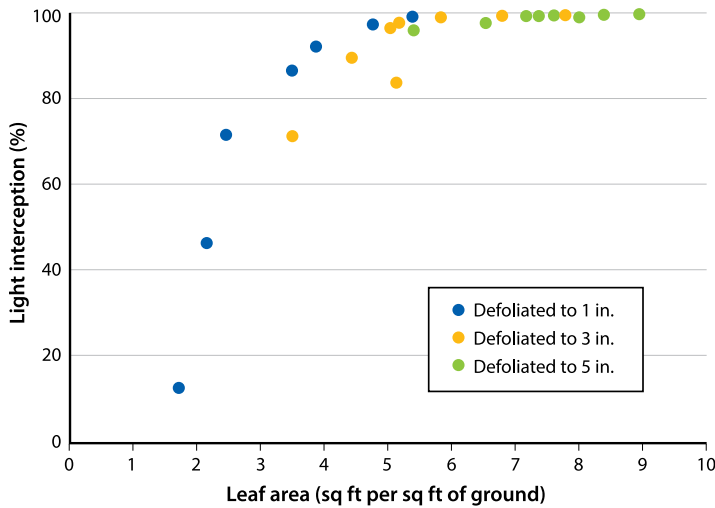


Figure 11. Relationship between light interception and leaf area (Brougham 1956).

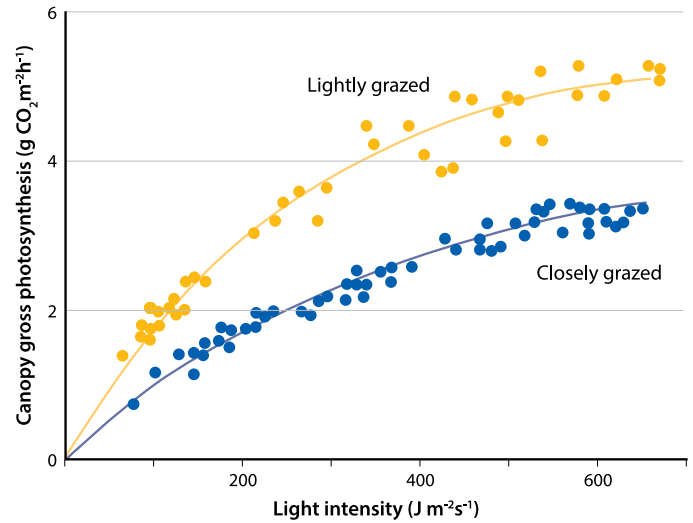


Figure 12. Photosynthesis increases with increasing light intensity (Parsons, Leafe, Collett, Stiles 1983).

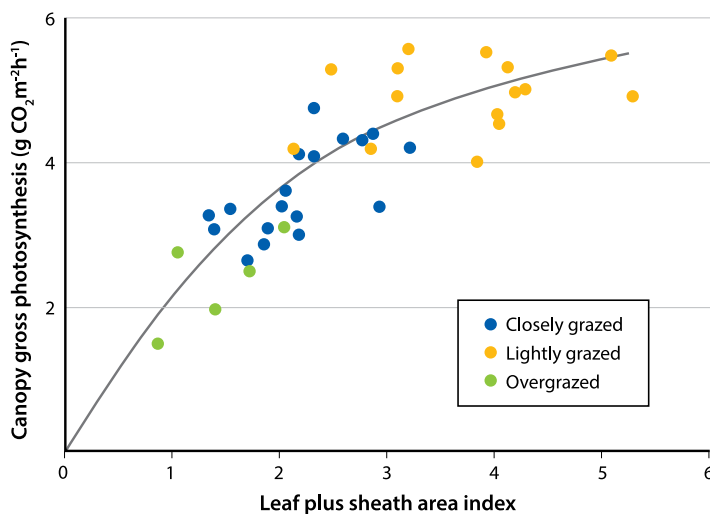


Figure 13. Photosynthesis increases with increasing leaf area (Parsons, Leafe, Collett, Penning, et al. 1983).

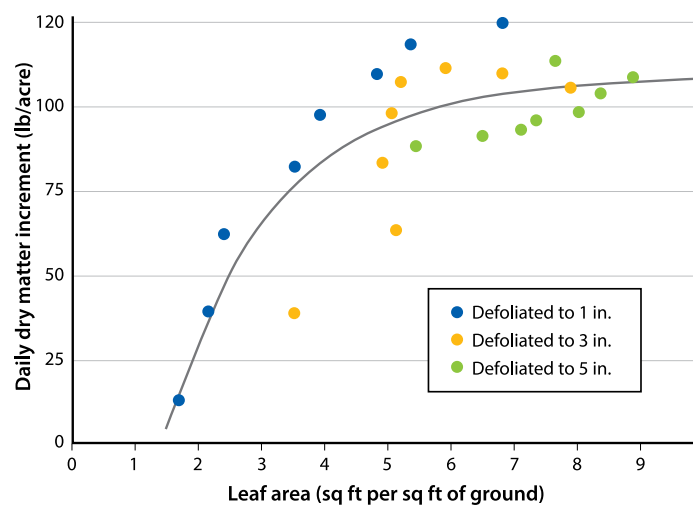


Figure 14. Relationship between herbage yield and leaf area (Brougham 1956)

amount of water lost through its stomata. More specifically, it is the ratio of carbon dioxide intake to water lost through transpiration.

Numerous factors influence photosynthesis, including leaf area, light intensity and quality, carbon dioxide content of the air, physiological efficiency, soil nutrients, water supply and temperature, and other factors. Light interception increases with leaf area (fig. 11). Photosynthesis increases with increasing light intensity (fig. 12). Thus, photosynthesis increases with increasing leaf area (fig. 13), which results in increases in forage yield with increased leaf area (fig. 14).

Production resulting from photosynthesis can be expressed as gross primary production (GPP). Net primary production (NPP) is GPP minus respiration (R). GPP and NPP initially increase as leaf area increases; however, as upper leaves begin to shade lower leaves, respiration increases, which results in decreased NPP (fig. 15).

Carbohydrates and Carbohydrate Allocation

Carbohydrates stored in roots and stems are the “savings account” in many perennial forage plants. A portion of these carbohydrates are energy stores used for survival during

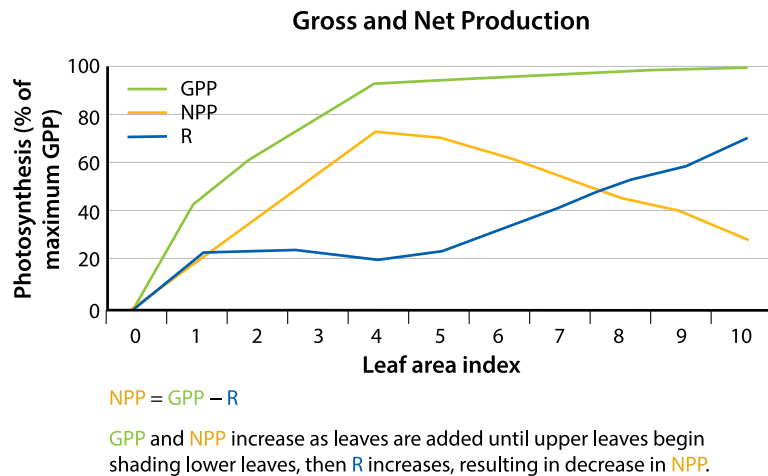


Figure 15. Change in gross primary production (GPP), net primary production (NPP), and respiration (R) with increasing leaf area.

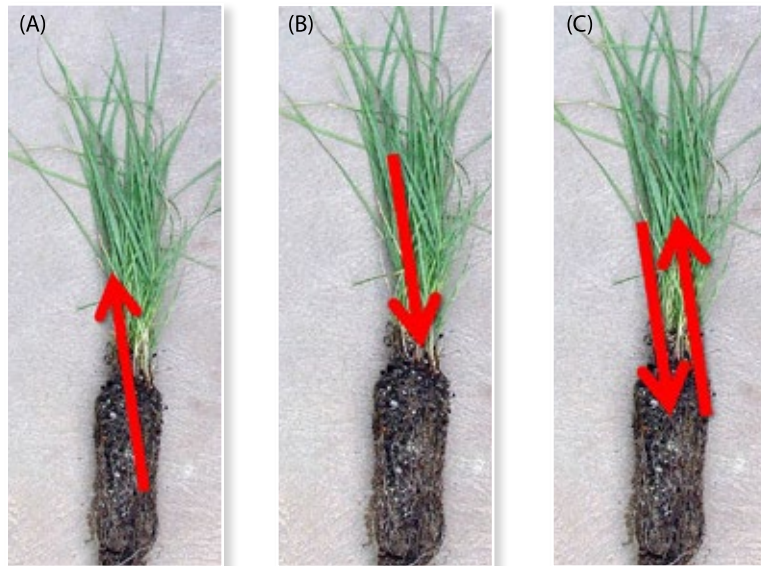


Figure 16. (A) In early spring, a portion of the carbohydrates stored in seed, crowns, stem bases, roots, or rhizomes is a source for carbon and energy used in the formation of the first new leaves, which are initially a sink. (B) Once photosynthesis begins, sugars are produced in excess of respiratory needs fairly rapidly, and excess sugars are translocated to sinks in other parts of the plant (new leaves, tillers, roots, stems, or seeds). (C) The source-sink relationship between various plant organs is very dynamic, and it can change hourly as environmental conditions affect photosynthetic capacity, respiration, and growth.

dormancy and to initiate growth following dormancy, although photosynthesis takes over relatively rapidly. Sugars produced during photosynthesis can be used as an energy source immediately, or stored, or converted to starch and then stored. A portion of these stored carbohydrates can be used as an energy source

that the plant can draw on when photosynthesis is inadequate to meet current plant energy needs. Dormancy is one period when photosynthesis is low or nonexistent. Thus, the plant can draw on these reserves to start growth when dormancy ends. This energy can be used by the plant for root replacement, leaf and stem growth following dormancy, respiration during dormancy, bud formation, and regrowth following top removal.

Plant scientists use the term *source* for tissues where carbohydrate is produced and *sink* for tissues where carbohydrates are utilized. Plant organs can be either sources or sinks, depending on their stage of growth and the particular environmental conditions.

In early spring, carbohydrates stored in seed, crown, stem base, root, or rhizome tissues can be a source of carbon and energy used in initial leaf formation, which in this case would be the sink (fig. 16A). When enough leaf area has formed such that the surface area has sufficient photosynthetic capacity to produce more carbohydrate than required for growth, that leaf then becomes a source of sugar. As the leaf becomes more fully extended, the leaf can translocate sugars in excess of its growth and respiratory needs to sinks in other parts of the plant (fig. 16B). Meristematic tissues, which are undifferentiated growth points throughout a plant, have priority for allocation of sugars. These tissues include new leaves, tillers, roots, stems, or developing seeds. During stem elongation, the developing reproductive organs inside the stem are sinks. During seed filling, leaves and leaf sheathes are sources of sugars and seeds are the sinks. If adverse conditions limit seed filling, excess sugars may accumulate in the stem. High respiratory rates in cool-season grasses during hot weather utilizes sugars for respiration, which might otherwise be used for growth or seed production. When growth slows or stops due to cold temperatures or lack of water or nutrients, the sink for growth is eliminated. As long as green leaf tissue and adequate sunlight are available for photosynthesis, sugars may accumulate whenever sugar production exceeds utilization.

The source-sink relationship between various plant organs is very dynamic, and it can

change hourly as environmental conditions affect photosynthetic capacity, respiration, and growth (fig. 16C). Complex sugars are too large for transport, so they are hydrolyzed to simple sugars for translocation. Much of the translocation of sugars from source to sink occurs in stem tissue, which is why stems are often higher in sugar concentration than leaves.

Water and Nutrient Uptake

Roots take up water containing nutrients (nitrogen, phosphorus, potassium, sulfur, calcium, etc.) from the soil. When soil water content exceeds the permanent wilting point of the plant, water is available to plants, and nutrient uptake occurs. In crop plants, the permanent wilting point is about 15 atm of tension. However, many arid land plants can extract soil water well below the permanent wilting point for crop plants. Most nutrient uptake occurs during periods when soil moisture exceeds 15 atm of pressure. Complex interactions involving decomposition of rocks, organic matter, animals, and microbes take place to form inorganic nutrient ions in soil water. Roots absorb these mineral ions if they are readily available. However, minerals can be bound with other elements or by alkaline or acidic soils. Soil microbes also assist in ion uptake.

Mycorrhizae are a mutualism between plants and fungi. The plant provides the fungus with sugars and carbohydrates, and the fungus helps the plant obtain nutrients from the soil, such as phosphorus and nitrogen, which often limit plant growth. While fungi can absorb nitrogen and phosphorus from the soil, they cannot produce sugars or carbohydrates, which are essential for fungal growth.

Secondary Compounds/Toxins

Secondary products, or metabolites, are compounds produced by plants that appear to have no function in photosynthesis, respiration, solute transport, translocation, protein synthesis, nutrient assimilation, differentiation, or the formation of carbohydrates, proteins, and most lipids. However, secondary compounds have important ecological functions in plants. They protect plants against herbivores and pathogens, and they attract pollinators and seed-dispersing animals.

Secondary compounds have been divided into three groups: terpenes, phenolics, and nitrogen-containing compounds. Terpenes are the largest class and include diverse substances that are generally insoluble in water. Terpenes defend against herbivores in many ways. Pyrethroids are monoterpenes that occur in leaves and flowers of the *Chrysanthemum* species and exhibit insecticidal activity. Thus, they are sometimes ingredients in commercial insecticides. Conifers accumulate monoterpenes in the resin ducts of the needles, twigs, and trunk. These compounds are toxic to many insects. Some terpenes are associated with odors that repel herbivores and toxins that are poisonous to herbivores.

Phenolic compounds from leaves, roots, and decaying litter are sometimes the source of allelopathic compounds that reduce germination and growth of nearby plants. Lignin is a complex phenolic compound found in cell walls of xylem and other conducting plant tissues. While lignin strengthens and protects plants, it deters feeding by animals because it is relatively indigestible. Flavenoids are a large class of phenolic compounds that attract animals for pollination and seed dispersal. Some isoflavenoids in legumes have antiestrogenic effects that result in infertility of sheep with clover-rich diets. Tannins are also phenolic compounds that are common in woody plants. Tannins are general toxins that may significantly reduce growth and survivorship of many herbivores when added to their diets. Cattle and deer commonly avoid plants and plant parts with high tannin contents. Tannins and other phenolics can bind dietary protein in cattle and other animals. However, tannins also have been shown to be beneficial in alleviating gastro-intestinal problems in some grazing animals.

Nitrogen-containing compounds include alkaloids and cyanogenic glycosides, which are toxic to humans and other animals. Most are biosynthesized from common amino acids. Large numbers of livestock deaths are caused by ingestion of alkaloid-containing plants such as lupines (*Lupinus* spp.), larkspur (*Delphinium* spp.), and groundsel (*Senecio* spp.). Likewise, cyanogenic glycosides are widely distributed in the legume family, sorghum (*Sorghum* spp.),

and corn (*Zea mays*), as well as some species in the rose (*Rosa*) family.

Some secondary compounds inhibit growth of other plants. Allelopathy is the inhibition of the growth and development of one plant by another. Plants use allelopathy as a means to guard their own space and protect their resources. Allelopathy is a strategy to reduce competition. For example, one way for a tree to protect its root space is to make other trees' roots die using allelopathy. The tree can then take up more water from the soil for itself. Many ecologists have argued that the effects of allelopathy cannot be distinguished from competition between two or more organisms for limited resources. Researchers' attempts to distinguish between competitive and allelopathic effects remain inconclusive (He et al. 2012).

GRAZING AND PLANT GROWTH

Detrimental Grazing Effects

Grazing removes leaves where photosynthesis occurs. Photosynthesis is required for growth of new buds, leaves, stems, and roots, as well as for production of seeds and storage of carbohydrates. Consequently, the removal of photosynthetic tissue by grazing animals can have detrimental effects, including reduced carbohydrate production and storage, reduced leaf and stem growth, reduced seed production, and reduced root growth. Reduced growth can result in reduced competitive ability.

Grazing effects on the productivity of a plant are influenced by the season, intensity, frequency, and duration of grazing. Competition from neighboring plants can also influence the productivity of individual plants. A grazed plant whose neighbors are not grazed may be at a competitive disadvantage. Thus, grazing of surrounding plants can influence the productivity of an individual plant.

Annuals

Grazing of annual grasses often results in reduced flowering and seed production (Gutman et al. 2001), with little detrimental effect on vegetative components of the plants. Greater tillering following defoliation often compensates for the loss of photosynthetic

tissue following defoliation in many grasses. The large investment of annual plants in seeds ensures their annual regeneration under moderate grazing and, possibly, even under intense grazing in the vegetative phase. However, intense grazing during the reproductive phase can severely reduce the survival of annual grasses and subsequent seed production (Noy-Meir and Briske 1996).

Season of defoliation can influence the productivity of annual grasses. Leaf elongation in soft chess (*Bromus hordeaceus*) is complete by the time the leaf blade emerges from the sheath. Removal of emerged leaves is not followed by regrowth of the leaf. Instead, only young leaves that have not emerged from the sheath regrow following clipping. If clipping is delayed until flowering, removal of the terminal bud will result in cessation of growth of that shoot. If a portion of the terminal bud remains, the shoot continues to grow (Laude 1957). While other grasses and forbs may react differently to clipping during the vegetative and flowering period, this illustrates the importance of season of defoliation.

The growing season on annual rangelands is short. Annual plants move from the vegetative state to flowering and maturity rapidly during the growing season. The effects of rest following grazing depend on the particular phenological stage of the plant and the amount of time remaining in the growing season. Cold weather may slow regrowth following winter grazing. During rapid spring growth, regrowth following grazing is rapid. However, by the time a normal rest period is over, the plants may have flowered and begun to mature as they near the end of the growing season.

Perennials

Holechek et al. (2004) reviewed several North American grazing studies and concluded that perennial grasses can be grazed without damage if 50 to 70 percent of the leaf and stem material by weight is left intact as a metabolic reserve to support regrowth. Without this amount of remaining material, plant productivity and growth can be reduced. Grazing that is too close and too frequent can slow recovery from grazing, and in the long run it is detrimental to plant productivity,

competitive ability, and survival. Grazing that is close, but followed by an adequate rest period that allows for regrowth and recovery, is not detrimental; but each plant species differs in its tolerance to the intensity and frequency of grazing. Rotational grazing provides rest following grazing. Long grazing periods that result in grazing of regrowth shortly after it is produced can suppress regrowth and recovery rates, especially when stubble or residue following grazing is short. Long or continuous grazing periods that maintain adequate leaf area can be tolerated by many perennial grasses and forbs. The three ryegrass plants in figure 17 illustrate the effect of frequency and intensity of defoliation on individual plants, as follows:

- Plant A was allowed to grow for 3 months without grazing. Note the healthy root system.
- Plant B was clipped to 3 inches every 3 weeks for 3 months. It also has a relatively healthy root system.
- Plant C was clipped to 1 inch every week for 3 months. Note the weak root system.
- Plant B was properly managed. It was not clipped too intensely (closely), and it had a 3-week regrowth or recovery period between each clipping.

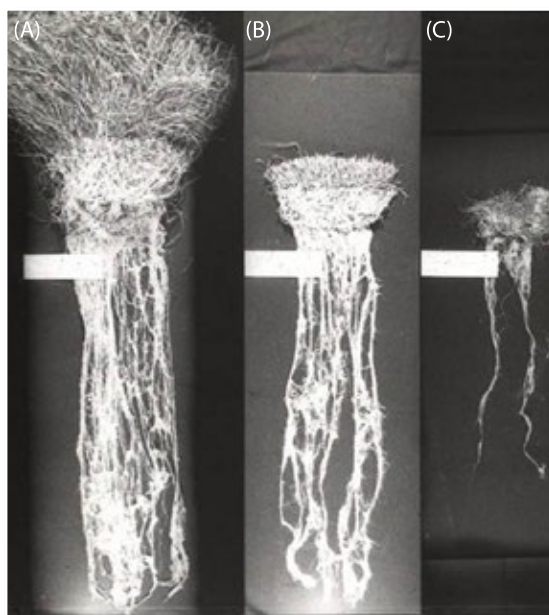


Figure 17. Effect of different frequencies and intensities of clipping on productivity.

- Plant C was clipped too closely and too frequently to maintain adequate rooting depth and may not survive a drought.

Plants that are grazed or clipped too closely, leaving little or no residual leaf material and removing growing points from tillers, are slow to regrow, as illustrated by the purple needlegrass (*Nassella pulchra*, or *Stipa pulchra*) plant in figure 18. This results in delayed regrowth and may result in the use of stored carbohydrates. Root growth may stop in response to heavy grazing, and flowering may be suppressed. Reduced root growth and root death can result in reduced tolerance to drought. The purple needlegrass plant in figure 19 illustrates that leaving adequate residual leaf area following grazing or clipping supports regrowth. This plant was clipped to a stubble height of 4 inches, leaving adequate leaf area for regrowth (George et al. 2013).



Figure 18. Regrowth of purple needlegrass following weekly clipping to ground level for one growing season.



Figure 19. Regrowth of purple needlegrass following weekly clipping to 4 inches.

Season of grazing can influence productivity following grazing. Regrowth rates change as plants progress from vegetative states to flowering, seed production, and maturity. Regrowth rates are faster during the vegetative state but are often slowed during flowering and seed production. Regrowth rates slow with the approach of dormancy. Dormant-season grazing is usually not detrimental. For perennial plants with long growing seasons, grazing followed by rest may be beneficial to plant productivity, competitive ability, and survival. Long growing seasons occur in regions with dependable moisture throughout the year and short cold or dry seasons, such as New Zealand and in irrigated pastures in California.

Most rangelands have short growing seasons. For perennial plants with short growing seasons, the effects of rest following grazing may not be realized within the same growing season because regrowth is slowed as the plant matures and approaches the end of the growing season. In other words, the growing season is too short for rest to be as effective as in a longer growing season.

Grazing at intensities and frequencies that reduce plant growth may also reduce the competitive ability of the plant, especially if the competitor is not being grazed. Grazed plants may be shaded by adjacent competitors. Grazed plants with diminished root systems may be less capable of extracting water and nutrients than an adjacent ungrazed plant. Grazed plants may produce fewer seeds. Vegetative reproduction from tillers, stolons, and rhizomes may be suppressed by grazing.

Compensatory Growth

Increased photosynthesis, compensatory growth, and utilization of stored reserves are some of the mechanisms exhibited by plants to tolerate grazing (Tiffin 2000). Under certain grazing regimes, researchers have found increased growth rates for clipped or grazed plants compared with ungrazed plants (Briske 1993). These findings have typically occurred following clipping or grazing in highly productive and intensively managed systems (Barolome 1993). Proponents of certain grazing systems have referred to compensatory growth

as one of the benefits of the grazing system. However, it has been well documented that compensatory growth does not occur in all species or ecosystems. These divergent findings have contributed to the sometimes heated debate among ecologists and grazing managers regarding the beneficial and detrimental impacts of grazing practices and grazing itself. The impacts of any grazing regime must be judged in light of the four grazing principles of season, intensity, frequency, and duration of grazing. These principles are further explored in the “Grazing Management” publication in this series.

SUMMARY

Intensity of grazing or stocking rate is a fundamental variable determining the sustainability and profitability of rangelands. The negative effects of prolonged, heavy grazing can be summarized as follows:

- decreased photosynthesis
- reduced carbohydrate storage
- reduced root growth
- reduced seed production
- reduced ability to compete with ungrazed plants
- reduced accumulation of litter or mulch, which can increase water runoff and decrease infiltration and retention and lead to increased soil erosion

Conversely, the positive effects of light or moderate grazing can be summarized as follows:

- plant productivity may increase
- tillering may increase
- shading of lower leaves may be reduced
- transpiration losses may be reduced
- ability to compete with ungrazed plants may be improved
- soil-protecting litter will accumulate; however, excessive accumulation can be detrimental to seedling establishment

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