Carbohydrate Reserves of Grasses: A Review

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Highlight: *Carbohydrate reserves are nonstructural carbohydrates. Sucrose and fructosan are the predominant reserve constituents of temperate-origin grasses; sucrose and starch, of tropical-origin grasses. Nitrogenous compounds are used in respiration, but probably are not alternately stored and utilized as are carbohydrate reserves.*

Most carbohydrate reserves are stored in the lower regions of the stems—stem bases, stolons, corms, and rhizomes. Nonstructural carbohydrates in the roots of grasses are probably not used directly in herbage regrowth following herbage removal.

Plant development stage, temperature, water stress, and nitrogen fertilization can drastically change the reserve level. The seasonal variation of carbohydrate reserves is often different for the same species when grown in different environments.

The level of carbohydrate reserves in the lower regions of the stems apparently affects the regrowth rate for the first 2 to 7 days following herbage removal. Following the initial period, plant regrowth rate depends on other factors, such as leaf area and nutrient uptake. This initial effect from the level of carbohydrate reserves can be maintained during subsequent exponential growth.

Grazing may be more detrimental than clipping if it removes herbage from some plants and not others. The ungrazed plants may take the available nutrients and water away from the grazed plants. However, grazing may be less detrimental than clipping if grazing leaves ungrazed tillers on a plant while removing others, thus allowing for the transfer of carbohydrates.

Carbohydrate reserves are thought to be used by plants as substrate for growth and respiration. Adequate carbohydrate reserves are important in perennial plants for winter survival, early spring growth initiation, and regrowth initiation after herbage removal, when the photosynthetic production is inadequate to meet these demands. Many pasture and range management practices are based upon knowledge of how various environmental factors and herbage removal treatments affect carbohydrate reserves. This understanding helps managers to maintain high yields of desirable species and to control undesirable species.

May and Davidson (1958) and May (1960) questioned the importance of carbohydrate reserves in controlling herbage regrowth rate because only indirect evidence supported the role of reserves. However, research has shown recently that, under certain conditions, the herbage regrowth rate depends on the level of carbohydrate reserves. The following is a brief review of the functions of carbohydrate reserves in grasses with emphasis on recent findings. Earlier findings were summarized in the following reviews: Graber et al. (1927), Graber (1931), Weinmann (1948, 1961), Troughton (1957), May (1960), Priestley (1962), Jameson (1963), Cook (1966), and McIlroy (1967).

Reserve Constituents

Graber et al. (1927) first defined reserve energy constituents as "... those carbohydrates and nitrogen compounds elaborated, stored, and utilized by the plant itself as food for maintenance and for the development of future top and root growth." These carbohydrates, termed *total available carbohydrates,* are those available as energy to the plant (Weinmann, 1947). Smith (1969) suggested that the term *total nonstructural carbohydrates* (TNC) be used, because it is more applicable to both animal and plant investigations.

Nonstructural carbohydrates—reducing sugars (glucose and fructose), nonreducing sugar (sucrose), fructosans, and starches—are the major reserve constituents. Structural carbohydrates—hemicellulose (pentosans and hexosans) and cellulose—are not considered to provide significant reserves (McCarty, 1938; Sullivan and Sprague, 1943; Weinmann, 1948). Type, distribution in the plant, and relative proportions of individual carbohydrate reserve components vary among and within grass species and under various climatic conditions during the growth season. Predominant carbohydrate reserves stored by temperate-origin grasses are sucrose and fructosans, whereas those of subtropical- or tropical-origin grasses are sucrose and starch (Cugnac, 1931; Weinmann and Reinhold, 1946; Smith, 1968; and Ojima and Isawa, 1968). The *Hordeae, Aveneae,* and *Festuceae* grass tribes store fructosan as short- or long-chain units. Genera of the *Hordeae* and *Aveneae* tribes store predominantly short- and long-chained fructosans, respectively, while some genera of *Festuceae* tribe characteristically store long-chained fructosans and others store short-chained fructosans (Smith, 1968).

Although Graber et al. (1927) originally defined reserve constituents as including nitrogenous compounds, most investigators have only considered carbohydrates. Recent studies indicate that proteins may be involved. Davidson and Milthorpe (1966b) concluded that nonstructural carbohydrates formed only a part of the labile pool which provided substrates for respiration and new growth of orchardgrass (*Dactylis glomerata*) in a growth chamber during the first 2 to 4 days following severe herbage removal. They suggested that other labile substances, presumably proteins, must have remobilized because the amount of nonstructural carbohydrates was inadequate to account for the respiration and new growth of roots and shoots. Dilz (1966) in studying perennial ryegrass (*Lolium perenne*) concluded that proteinaceous material should be regarded as reserve constituents.

Most investigators generally have found that proteins are used in respiration but there is not a net utilization (Hackett, 1959). Proteinaceous sources accounted for 27% of the CO_2 released by respiration in phloem explants from the storage root of a carrot (*Daucus carota* var. *sativa*) (Steward et al., 1958; Bidwell et al., 1964). Breakdown products from protein turnover contributed to the storage pool of amino acids and supplied carbon products for direct use in respiration, but carbohydrates were used preferentially over stored amino acids in synthesizing new proteins.

Studies show that even though nitrogenous compounds are used in respiration they still are not as important as carbohydrate reserves in supporting regrowth. Smith and Silva (1969) found that pro-

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portionally fewer nitrogenous compounds than TNC (1:18) were translocated from the roots of alfalfa (*Medicago sativa*) for production of new top growth after cutting in greenhouse trials. Alberda (1966) pretreated perennial ryegrass for a short period to change the plant's level of reserves. Plants with low TNC were obtained by placing them in a nutrient solution in the dark at 30 C, and plants with high TNC were obtained by placing them in water at 15 C in continuous light. The pretreatment changed the amount of nonstructural carbohydrates, but did not change the amount of organic nitrogenous compounds.

In summary, reserve constituents are those nonstructural carbohydrates which include reducing sugars, nonreducing sugars, fructosan, and starch. The predominant reserve constituents of temperate-origin grasses are sucrose and fructosan; of tropical-origin grasses, sucrose and starch. Nitrogenous compounds are used in respiration, but are not alternately stored and utilized as are carbohydrate reserves.

Storage Organs of Perennial Grasses

Nonstructural carbohydrates may be stored temporarily in all plant parts. Many scientists in the past concluded that underground organs were the major storage region for carbohydrate reserves (Weinmann, 1948; Troughton, 1957). Many other studies, however, have shown that the major storage region is generally in the stem bases (which includes stolons, corms, and rhizomes), not in the roots per se (Sampson and McCarty, 1930; Smelov and Morazov, 1939; Sullivan and Sprague, 1943; Baker and Garwood, 1961).

The decrease of carbohydrate reserves in the roots of orchardgrass, grown in growth chambers, after severe herbage removal only accounted for less than one-tenth of root respiration (Davidson and Milthorpe, 1966b). They concluded that transfer of carbohydrate reserves from the shoots, remobilization of other substances in the roots, or both, must have occurred to account for root respiration. Marshall and Sagar (1965), using autoradiographs and labeled CO_2, found that nonstructural carbohydrates in the roots of Italian ryegrass (*Lolium multiflorum*) were not mobilized to the shoots to support regrowth following herbage removal, nor were labeled compounds translocated to the roots from the shoots when a part of the herbage was removed from all tillers. They concluded: "The classical view of a transference of compounds from the root to shoot following defoliation (Troughton, 1957) . . . seems unlikely . . . in perennial grasses without special storage organs."

In summary, the major storage areas of carbohydrate reserves are usually the lower regions of the stems—stem bases, stolons, corms, and rhizomes. These reserves are used as an energy source to initiate new growth until photosynthesis is sufficient to sustain plant respiration. Nonstructural carbohydrates in the roots of grasses are probably not used directly in herbage regrowth following herbage removal. However, more research using labeled carbon is needed to determine if nonstructural carbohydrates in the roots are translocated aboveground for respiration or as structural components of regrowth following herbage removal.

Variation of Carbohydrate Reserves

Diurnal and Seasonal

The accumulation of carbohydrate reserves in plant tissue is a dynamic system of energy balance. The level of carbohydrate reserves (hexoses and sucrose) of four grasses at Ayr, Scotland, showed marked diurnal variation (Waite and Boyd, 1953). In Indiana, bromegrass (*Bromus inermis*) utilized almost one-third of the TNC in the herbage during the night, but diurnal fluctuations for other grass species were less (Holt and Hilst, 1969). For the grass species studied, TNC concentration in the herbage was lowest at 6 A.M. and increased linearly to a high at 6 P.M.

The seasonal variation of carbohydrate reserves differs among grass species. In many grass species, the reserve level is lowest when the second or third leaf emerges (about one month after the start of plant growth), but in other species, the reserve level is lowest after seed ripening (Jameson, 1963). Carbohydrate reserves of Colorado wildrye (*Elymus ambiguus*) and mountain muhly (*Muhlenbergia montana*) in Colorado decreased during fast growth and increased during slow growth (McCarty, 1935). However, temperature and the availability of water and nutrients also affect the seasonal variation of carbohydrate reserves.

The accumulation of carbohydrate reserves in plant tissue depends upon the balance between photosynthesis and respiration. The carbohydrate reserves of orchardgrass and bermudagrass (*Cynodon dactylon*) grown in growth chambers decreased when growth and respiration demands were greater than photosynthetic rate and increased when growth and respiration demands were less than photosynthetic rate (Blaser et al., 1966). The level of reserves is determined by growth rate, plant development stage (Hyder and Sneva, 1959), and environment (Troughton, 1957).

Temperature

The effect of temperature on the percentage of carbohydrate reserves in the stem bases is influenced by the origin of grass species. Optimum temperatures for growth and net photosynthesis by temperate-origin grasses are about 20 to 25 C, whereas those for tropical-origin grasses are about 30 to 35 C (Evans et al., 1964; Treharne and Cooper, 1969). This difference in temperature optima for growth of two temperate species [oat (*Avena sativa*) and perennial ryegrass] and two tropical species [maize (*Zea mays*) and buffelgrass (*Cenchrus ciliaris*)] resulted from differences in temperature optima of the major CO_2-fixing enzymes (Treharne and Cooper, 1969). The activity of ribulose-1,5-diphosphate carboxylase is higher in temperate-origin grasses while the activity of phosphoenolpyruvate carboxylase is higher in tropical-origin grasses. Temperate-origin grasses contain only the Calvin (C_3) photosynthetic pathway, while tropical-origin grasses contain both the C_4 (Hatch and Slack) and C_3 photosynthetic pathways. In tropical-origin grasses, the C_4 pathway is located in chloroplasts of mesophyll tissue, whereas the C_3 pathway is located in chloroplasts of bundle sheath tissue (Berry et al., 1970; Kortschak and Nickell, 1970).

Temperature markedly affects the seasonal variation of carbohydrate reserves. Seasonal variation of total fructose in stem bases of orchardgrass (Fig. 1) was different when grown in Massachusetts, USA, than in Hokkaido, Japan (Colby et al., 1966). The total fructose level of orchardgrass grown in Hokkaido increased following heading, whereas in Massachusetts, it decreased. High June temperatures in Massachusetts apparently caused the decrease following heading. Smith and Jewiss (1966) showed that high day and night temperatures decreased the percentage of water-soluble carbohydrates in the stem bases of timothy throughout a growing season. Smith (1970) showed that changing timothy plants at inflorescence emergence from a cool to a warm regime decreased water-soluble carbohydrate content in the stem bases at early anthesis.

The effect of high day temperatures is

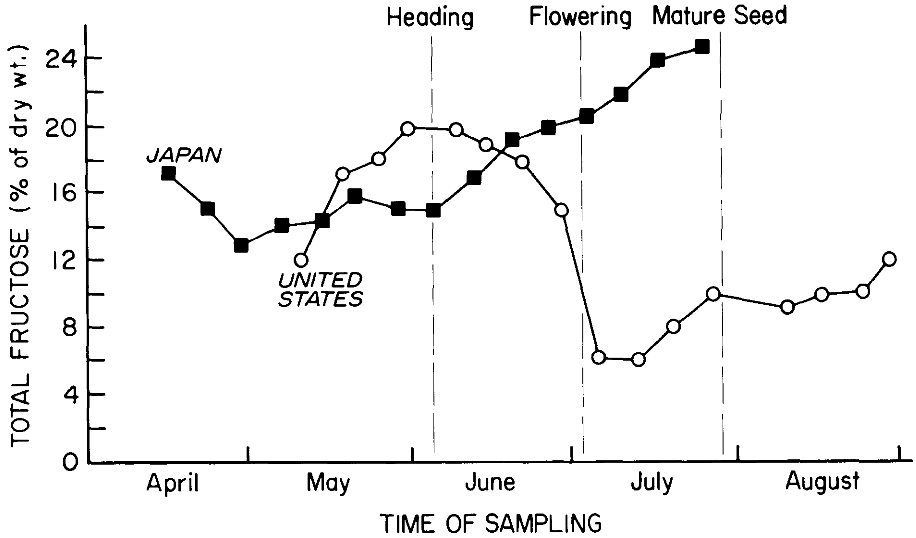

Fig. 1. *Percentage of total fructose in stem bases of orchardgrass plants grown in Massachusetts, USA, and Hokkaido, Japan (Colby et al., 1966).*

different from that of high night temperatures. High night temperatures in a growth chamber decreased reserves of temperate-origin grasses, such as timothy (*Phleum pratense*), bromegrass, orchardgrass, and Kentucky bluegrass (*Poa pratensis*), more than high day temperatures (Baker and Jung, 1968). Increasing the day temperature, if below optimum, increases both respiration and net photosynthesis; whereas increasing the night temperature increases only the respiration rate and, thereby, decreases the reserve level. The level of carbohydrate reserves during the season may be more characteristic of climatic factors than of individual species.

Water

Eaton and Ergle (1948) in a review article noted that the effect of water stress on carbohydrate reserves varies. Some scientists have reported that drought increased the carbohydrate reserves in several grass species (Julander, 1945; Brown and Blaser, 1965; Blaser et al., 1966); others have reported that drought decreased carbohydrate reserves (Bukey and Weaver, 1939; Brown, 1943).

The degree of water stress and the plant growth stage during which it occurs will variably affect carbohydrate reserve levels. Orchardgrass under increasing water stress in a growth chamber showed a decrease in both net photosynthetic and respiration rates (Murata and Iyama, 1963). The photosynthetic rate, however, decreased much more rapidly than respiration, thus lowering carbohydrate reserves. If water stress stops stem elongation and has only minor effects on photosynthesis, as reported by Wardlaw (1968), carbohydrate reserves would then increase. Brown and Blaser (1970) suggested that the buildup of carbohydrate reserves and inorganic nitrogen in plants under water stress results from the transformation of carbon-containing nitrogenous substances.

Nitrogen

The effects of nitrogen (N) fertilization on carbohydrate reserves are complex and variable. Weinmann (1948) in a review article noted cases where N fertilization caused no effect, increased, or decreased carbohydrate reserves. Generally, N applied at low to moderate rates increases carbohydrate reserves. Nitrogen applied at high rates decreases carbohydrate reserves (Adegbola and McKell, 1966). The physiological reasons why N variably affects carbohydrate reserves are not well understood.

If N is deficient, application of moderate amounts of N can increase plant growth when carbohydrates, water, and other nutrients are available and environmental conditions are favorable. Increased plant growth from N application was associated with increased leaf area, chloroplast protein, and chlorophyll content which increased photosynthesis (Murata, 1969). The increased photosynthetic activity can then, theoretically, increase carbohydrate reserves.

Excess N tends to decrease carbohydrate reserves when other nutrients and environment do not limit plant growth. In this case, N fertilization stimulates the synthesis of amino acids and amide compounds to the detriment of carbohydrate reserves (Prianishnikov, 1951). Carbohydrate reserves are used as the carbon-skeleton for protein synthesis (Prianishnikov, 1951).

Application of high rates of N fertilizer (200 to 400 kg N/ha) in conjunction with frequent clipping, low soil water, and high temperatures reduced stands and carbohydrate reserves of orchardgrass in Massachusetts (Drake et al., 1963; Colby et al., 1965) and tall fescue (*Festuca arundinacea*) in Virginia (Hallock et al., 1965). Applications of high rates of N also reduced stands of orchardgrass and tall fescue in Maryland (Alexander and McCloud, 1962).

Scientists also reported that application of 50 to 200 kg N/ha reduced severely the grass stand, especially when associated with drought or frequent herbage removal on native range in Colorado (Klipple and Retzer, 1959) on crested wheatgrass (*Agropyron desertorum*) in Wyoming (Seamands and Lang, 1960) and North Dakota (Rogler and Lorenz, 1969), and on intermediate wheatgrass (*Apropyron intermedium*) in Saskatchewan (Lawrence, 1963). These scientists assumed that carbohydrate reserves were reduced. Frequent clipping, with or without N fertilization, decreased the percentage basal ground cover of non-irrigated green needlegrass (*Stipa viridula*) in Saskatchewan (Heinrichs and Clark, 1961). In contrast, N fertilization (0 to 375 kg N/ha) did not increase the winterkill of intermediate wheatgrass under irrigation in Saskatchewan, although frequent and close clipping did (Lawrence and Ashford, 1969).

High rates of N should not be applied under the combined conditions of drought and high temperatures. Under these conditions, clipping or grazing could deplete carbohydrate reserves below a critical level, and cause stand reduction and poor growth recovery.

In summary, the interaction of the plant with the environment and the balance between photosynthesis and respiration determine the variation of carbohydrate reserves during the growing season. In some grass species, a low reserve occurs when the second or third leaf emerges; in other grasses, it may occur just before or after seed ripening. The seasonal variation of carbohydrate reserves can differ for the same species grown in different environments. Above-optimum temperatures, especially during the night, decrease carbohydrate reserves; whereas water stress can either increase or decrease reserves depending on the degree of stress and stage of plant growth.

Studies to date generally show that N applied at low to moderate rates increases carbohydrate reserves, but that N at moderate to high rates decreases reserves. Excess N applied during periods of water stress and high temperatures, coupled with frequent herbage removal, often reduces stands and growth rate. More research is needed to fully understand the effects of N fertilization on carbohydrate reserves.

Regrowth After Partial Herbage Removal

Clipping

The effects of herbage removal on plant regrowth has been classified into three simplified categories. Herbage removal reduces (1) amount of carbohydrate reserves, (2) root growth, and (3) leaf area (Alcock, 1964). Many other factors, however, also affect the regrowth rate of a sward following herbage removal (Jameson, 1963).

The importance of carbohydrate reserves in controlling regrowth rate following herbage removal is a controversial topic in grassland management. The results of many field studies show that carbohydrate reserves decreased in both stem bases and roots of grasses after cutting (Graber et al., 1927; Troughton, 1957) until sufficient leaf area developed that carbohydrates produced in photosynthesis equaled those used in respiration and growth. This observation led to the general belief that, following herbage removal, some reserves are converted to structural components of the new and expanding cells, and thus the reserve level affects the regrowth rate. However, May (1960) stated that the "... specific role for carbohydrate reserves in initiating regrowth, and in determining the rate or ultimate extent of regrowth, cannot yet be considered as firmly established."

Since May's (1960) conclusion, new research techniques have provided evidence that carbohydrate reserves are used for regrowth following herbage removal. Carbohydrate reserves assimilated as labeled CO_2 by bahiagrass (*Paspalum notatum*) were used to help form leaves for 6 days after herbage removal (Ehara et al., 1966). Labeled nonstructural carbohydrates in alfalfa (labeled by $^{14}CO_2$ assimilation) which were initially stored in the root and crown were utilized after herbage removal as substrate for respiration of both roots and tops and as structural components for top growth (Pearce et al., 1969; Smith and Marten, 1970).

The dry weight of perennial ryegrass with high carbohydrate reserves did not increase for 4 days following clipping because respirational losses exceeded photosynthetic gain; but the weight of plants with low carbohydrate reserves did not increase for 7 days (Alberda, 1966). Davidson and Milthorpe (1965, 1966a, 1966b) after measuring both respiration and photosynthetic rates of orchardgrass grown in growth chambers, concluded that regrowth following clipping depended upon carbohydrate reserves for only the first 2 to 4 days. During this period, stored carbohydrates were used for regrowth and respiration. Afterwards, regrowth depended on other factors, such as photosynthetic rate and nutrient uptake. Milthorpe and Davidson (1966) demonstrated that, even though carbohydrate reserves influenced the regrowth rate for only the first few days, the initial stimulus due to the level of reserves was maintained during subsequent exponential growth. Measurement of the initial response attributable to the level of carbohydrate reserves during the exponential phase of orchardgrass regrowth is difficult because complex interrelationships frequently obscure the response (Davidson and Milthorpe, 1966b).

Ward and Blaser (1961) concluded that carbohydrate reserves of orchardgrass in Virginia stimulated dry matter production for the first 25 days after partial or complete herbage removal; thereafter, regrowth rates were dependent on leaf area. Davidson and Milthorpe (1966b) re-examined Ward and Blaser's data and concluded that the relative rate of leaf expansion of plants with high and low levels of carbohydrate reserves was the same and the effect of carbohydrate reserve levels was confined only to the initial stage of regrowth.

Weinmann (1948) stated that clipping does not always reduce carbohydrate reserves, and Jameson (1963) stated that regrowth rate does not always depend upon the level of carbohydrate reserves. Such discrepancies may be due to any of the following factors: (1) variation in amount of capacity of photosynthetic tissue remaining after herbage removal; (2) sampling for reserves too late after clipping, when the reserves have already been restored; and (3) sampling the wrong plant part.

Photosynthetic capacity remaining after herbage removal depends on height of cutting, growth habit of the plant, and age of remaining leaves. The photosynthetic rate of the sheath of young orchardgrass tillers grown in growth chambers was about one-third the rate of the blades (Davidson and Milthorpe, 1966b). The maximum photosynthetic rate of a leaf occurred when the leaf blade first emerged from the sheath and this rate then decreased with age in tall fescue (Jewiss and Woledge, 1967) and orchardgrass (Treharne et al., 1968). The life span of an orchardgrass leaf in Kentucky, after it reached full extension, was only about 28 days (Taylor and Templeton, 1966). Thus leaf blades older than about 28 days after full extension would be of little value in maintaining the photosynthetic rate of a sward.

In summary, the level of carbohydrate reserves in the lower regions of the stems apparently affects the regrowth rate for 2 to 7 days following herbage removal; but this initial support from carbohydrate reserves can be maintained during subsequent exponential growth. Following the initial period, plant regrowth rate depends on other factors, such as leaf area and nutrient uptake.

Grazing Versus Clipping

The effects of grazing and clipping are similar but not identical. Clipping removes all herbage above a given height from all plants, whereas grazing removes herbage at heights varying from plant to plant and even within the same plant. Hormay and Talbot (1961) reported that grazing of Idaho fescue (*Festuca idahoensis*) by cows in an opening of ponderosa pine (*Pinus ponderosa*) in California was not uniform from plant to plant. When the overall utilization of Idaho fescue herbage was 43%, 40% of the plants were grazed to a 2.5-cm stubble height; 29%, to 5.1-cm; 13%, to 7.6-cm; 3%, to 10.2-cm or taller; and 15% were not grazed at all.

Grazing reduces plant vigor more than clipping at the same degree of herbage removal because grazing often removes herbage from one plant and not from the surrounding vegetation. In Montana, clipping of individual Idaho fescue plants and not the surrounding vegetation reduced yields of clipped plants more the following year than when the surrounding vegetation was also clipped (Mueggler, 1970). Unclipped plants competed advantageously with clipped plants for nutrients and water.

Grazing, however, can be less detrimental to plant vigor than clipping by leaving ungrazed tillers in a plant. Carbohydrate reserves of tall fescue in Missouri (as indicated by greater etiolated regrowth) increased as the percentage of unclipped tillers per plant increased from 0 to 30% (Matches, 1966). Carbohydrate reserves of dallisgrass (*Paspalum dilatatum*) in Mississippi also increased as the percentage of unclipped tillers increased from 0 to 10% (Watson and Ward, 1970).

Carbohydrate compounds were transferred from unclipped to clipped tillers only for the first few days following cutting and only in small plants. When a single unclipped tiller remained, it initially transported labeled carbon products to defoliated tillers within the same plant (Marshall and Sagar, 1965). However, transfer of assimilates from an unclipped tiller to clipped tillers did not occur beyond the third day after cutting. More mature tillers of Italian ryegrass were independent because leaf blades fed labeled CO_2 transported labeled assimilates only to the root system of that tiller (Marshall and Sagar, 1965). Tillers of large plants of weeping lovegrass (*Eragrostis curvula*) in Maryland apparently were not completely connected by vascular connections at the crown because partial clipping of a group of tillers stopped root growth only of clipped tillers (Crider, 1955). Leaving unclipped tillers not only increased production because of the transfer of carbohydrates but also because of leaving photosynthetic tissue and carbohydrate reserves stored in the stems.

In summary, the effect of grazing on herbage regrowth rate can be more or less detrimental than clipping, depending on circumstances. Grazing may be more detrimental than clipping if grazing removes all herbage from some plants and not others, because ungrazed plants take available nutrients and water away from grazed plants. However, grazing may be less detrimental than clipping if grazing leaves ungrazed tillers on a plant while removing others, thus allowing for the transfer of carbohydrates from ungrazed to grazed tillers.

Management Implications

Various management practices—range readiness, season of use, degree of utilization, and grazing systems—are partially based upon how they affect carbohydrate reserves of grasses (National Research Council, 1962). Effects of a particular management practice often can be evaluated in a single year by observing carbohydrate reserve levels and variation. The effects of various management practices on plant vigor can be partially measured objectively and quantitatively with the percentage of TNC (Cook, 1966; National Research Council, 1962).

The seasonal variation of carbohydrate reserves of many grasses has not been determined. Knowledge of the seasonal variation of carbohydrate reserves and the effects of climate and management practices on them will help pasture and range managers improve present management practices. Factors other than carbohydrate reserves—leaf area, light interception, root area, nutrient uptake, competition and other morphological and physiological factors—also influence the effects of herbage removal.

Cook (1966) stated that "Proper management . . . does not necessarily imply that a maximum level of carbohydrate reserves be maintained, but care must be taken . . . that these reserves do not fall below a critical level" or tillers will die. More research is needed to determine critical levels of carbohydrate reserves at which some tillers die. Perennial ryegrass grown in growth chambers was unable to use carbohydrate reserves below 6% of dry weight, the amount required for normal cell function; and at the 6% level, reserves inadequately supported the existing tiller population and some tillers died (Alberda, 1966; del Pozo, 1963). The critical level of carbohydrate reserves can be different among grass varieties (Davies, 1965) and species and is probably affected by fertility, management, environment, and season.

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