Carbohydrate reserves of green needlegrass (Stipa viridula Trin.) as affected by clipping and fertilization
by Larry Melvin White

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree of DOCTOR OF PHILOSOPHY in Crop and Soil Science
Montana State University
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Abstract:
Nitrogen (N) fertilization and frequent clipping have sometimes reduced grass stands by reducing the carbohydrate reserves. We applied N and imposed clipping treatments to determine their effect on the seasonal variation of total nohstructural carbohydrates (TNC) in stem bases of dryland green needlegrass (Stipa viridula Trin.) during 1969. Ammonium nitrate was broadcast at 0, 70, and 140 kg of N/ha in November 1968. Green needlegrass was either left unclipped in 1969 or clipped to a 5-cm height five times — May 7 and 28, June 17, July 8 and 29 — at approximately 21-day intervals.

A preliminary study showed that live stem bases of green needlegrass contained twice as much TNC as live roots. The coefficient of variation of TNC in live stem bases from individual plants was 20% compared to 37% for live roots.

Seasonal variation of TNC in stem bases of clipped and unclipped plants were similar, but clipped plants had a lower TNC content at all sampling dates. The TNC in non-fertilized, unclipped plants decreased from 18 to l4% from growth initiation after winter dormancy (April 5) until after second leaf formation (April 28). The TNC increased after second leaf formation to 19% on May 20 just before boot stage, decreased slightly at heading (May 29) then increased to 18% at first anthesis (June 9). Following first anthesis, TNC decreased to 9% on July 22 just prior to completion of seed dissemination, increased to 19% in late September, decreased to 16% by November. The percentage of TNC in clipped plants was 3 to 5 units lower at all sampling dates and the terminal value in November was 13%. Clipping in 1969 reduced yields significantly in 1970 and tended to reduce yields in 1971- Nitrogen increased TNC content of stem bases during mid-July and again in late autumn, apparently as a result of new tiller development and increased photosynthesis. Nitrogen decreased the TNC only from growth initiation until the second leaf formation. Application of N in November 1968 increased yields in 1969, 1970, and 1971.

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AS AFFECTED BY CLIPPING AND FERTILIZATION

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ABSTRACT

Nitrogen (N) fertilization and frequent clipping have sometimes reduced grass stands by reducing the carbohydrate reserves. We applied N and imposed clipping treatments to determine their effect on the seasonal variation of total nonstructural carbohydrates (TNC) in stem bases of dryland green needlegrass (Stipa viridula Trin.) during 1969. Ammonium nitrate was broadcast at 0, 70, and 140 kg of N/ha in November 1968. Green needlegrass was either left unclipped in 1969 or clipped to a 5-cm height five times -- May 7 and 28, June 17, July 8 and 29 -- at approximately 21-day intervals.

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INTRODUCTION

Green needlegrass (<u>Stipa viridula</u>) is a palatable, productive range grass (Dubbs, 1966) and constitutes an important component of climax vegetation on many sites in the northern Great Plains. Improper grazing has reduced the population of this species on millions of hectares and has concomitantly reduced forage production on these ranges. Information about the effects of nitrogen (N) fertilization and clipping on carbohydrate reserves of green needlegrass is needed to improve its management.

Adequate carbohydrate reserves are important in perennial plants for winter survival, initiation of early spring growth, and initiation of regrowth after herbage removal until photosynthesis is adequate to meet plant needs. Low carbohydrate reserves limit plant growth during the first 2 to 7 days following herbage removal and this slower recovery lowers production during subsequent exponential growth (Davidson and Milthorpe, 1966b). Furthermore, tillers will die if carbohydrate reserves are decreased below the critical level (Alberda, 1966).

Although N fertilization of grasslands in the northern Great Plains generally increases forage production, it sometimes decreases production. Applications of 50 to 200 kg of N/ha on grasslands in the northern Great Plains during some drought years or frequent herbage removal reduced stands of native grasses (Klipple and Retzer, 1959), crested

wheatgrass (<u>Agropyron</u> <u>desertorum</u>) (Rogler and Lorenz, 1969; Seamands and

Lang, 1960), and intermediate wheatgrass (<u>Agropyron</u> <u>intermedium</u>)

(Lawrence, 1963). These stand reductions were attributed to exhaustion

of carbohydrate reserves. High rates of N (200 to 400 kg of N/ha) on

grasslands in the eastern United States in conjunction with frequent

clipping, low soil water, and high temperature reduced stands and

carbohydrate reserves of orchardgrass (<u>Dactylis</u> <u>glomerata</u>) (Drake et al.,

1963; Colby et al., 1965) and tall fescue (<u>Festuca</u> <u>arundinacea</u>) (Hallock

et al., 1965).

This study was initiated during the autumn of 1968 to determine the

effects of N fertilization and clipping of green needlegrass. This

thesis reports the effects of these treatments on the seasonal variation

of carbohydrate reserves. White et al. (1972) reported the effects of

the treatments on the development, growth, dry matter yield, and forage

quality of green needlegrass and White and Brown (1972) reported the

effects on the seasonal variation of evapotranspiration, water-use

efficiency, and fertilizer N recovery.

LITERATURE REVIEW

Importance of Carbohydrate Reserves

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 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 orchard-grass in a growth chamber during the first 2 to 4 days following severe herbage removal. They suggested that other labile substance, 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 percent 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

used 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

proportionally less 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 carbo-

hydrates 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 orchard-grass, 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 that "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 of 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 AM and increased linearly to a high at 6 PM.

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 is dependent 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 in 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
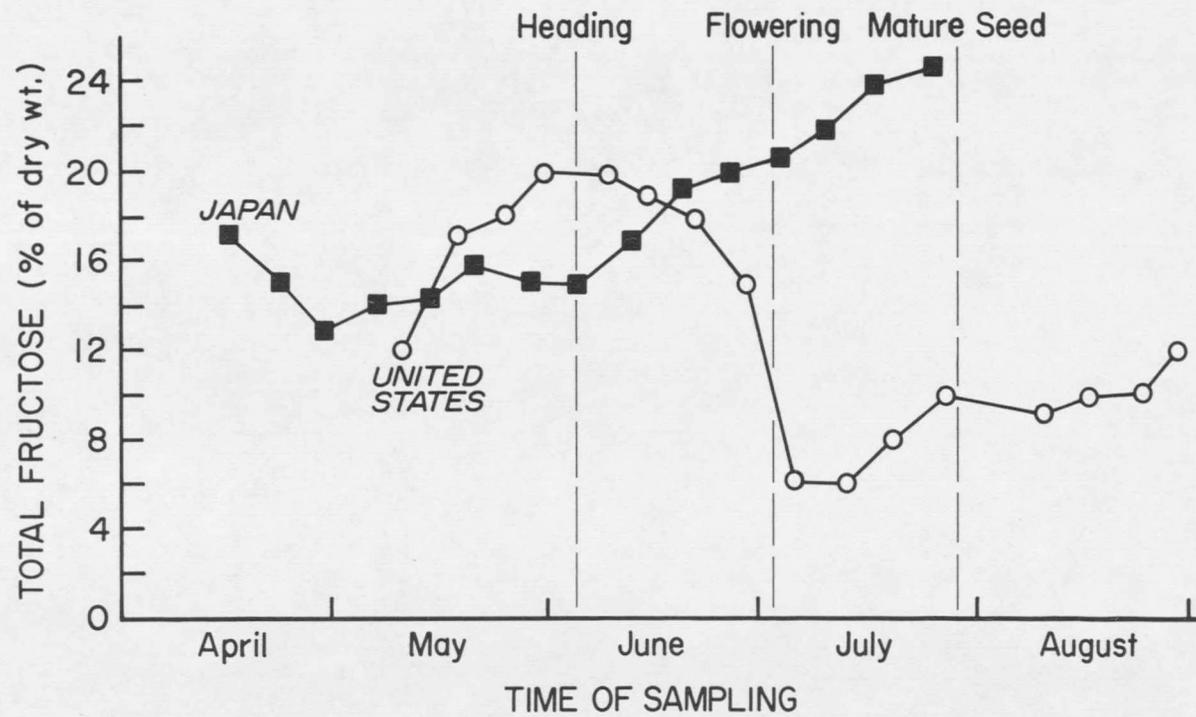
Fig. 1. Total fructose in the stem bases of orchardgrass plants grown in Massachusetts, USA, and Hokkaido, Japan (Colby et al., 1966).

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 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. Orchard-grass 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 build-
up of carbohydrate reserves and inorganic nitrogen in plants under
water stress results from the transformation of carbon-containing
nitrogenous substances.

Nitrogen. The effects of 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 photo-
synthesis (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 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 in Wyoming (Seamands and Lang, 1960) and North Dakota (Rogler and Lorenz, 1969), and on intermediate wheatgrass 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 in Saskatchewan

(Heinrichs and Clark, 1961). In contrast, N fertilization (0 to 375 kg N/ha) did not increase the winter-kill 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 effect 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 determing 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 (<u>Paspalum</u> <u>notatum</u>) were used to help form leaves for 6 days after herbage removal (Ehara et al., 1966). Those 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. Measure-

ment 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 carbo-
hydrate 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 or 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 of 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 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 after herbage removal; but this initial support from carbohydrate reserves can be maintained during subsequent exponential growth. After 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; and 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 advantegeously 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 are 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 together
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 photo-
synthetic 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 carbo-
hydrate reserves can be different among grass varieties (Davies, 1965)
and species and is probably affected by fertility, management,
environment, and season.

STUDY AREA

This study was conducted from 1968 through 1971 on a solid stand
of green needlegrass seeded in 1961. The site is 11 km north of
Culbertson, Mont. on the Soil and Water Conservation District
Research Farm. The soil is a Williams loam (sandy loam) derived from
glacial till, sloping from 4 to 6% to the south. In July 1968, 44.8 kg
of phosphorus/ha was boradcast uniformly, since the soil is normally
deficient in phosphorus. After application of phosphorus, the soil
contained over 5 ppm of available phosphorus to a depth of 30 cm (White,
1971). The results of chemical analysis of this soil are shown in
Table 1. The study area is classified as a sandy 25.4- to 35.6-cm
precipitation zone range site. Prior to 1969, green needlegrass
herbage was harvested annually for hay when the first seeds ripened.

Weeds in the stand, primarily volunteer alfalfa, were controlled
by spraying with 1.1 kg/ha of active ingredient 2,4-D amine on May 12,
1969. From 1969 through 1971, leaf spot disease, Alternaria tenuis,
infected the entire second leaf and the distal half of the third leaf
during the middle of May causing light to moderate damage. Subsequent
infections did not occur during the growing season of any year.

The experimental site normally receives 32.6 cm of precipitation
annually, 26.0 cm of precipitation during the growing season (April

Table 1. Summary of soil analysis data (July 1968) before applications of N-P fertilizer.

Depth	pH	Soil texture	Con-ductivity	Organic matter	Available P (Bray-HCL)	Avail-able K	Available nitrate*
cm			mmhos/cm	%	ppm	ppm	ppm
0 - 7.5	7.4	sl	0.8	2.1	23	390	1.3
7.5 - 15	7.1	sl	0.7	1.5	6	250	1.4
15 - 30	7.2	sl	0.7	1.2	6	160	1.2
30 - 60	7.7	sl-cl†	1.1	1.1	4	130	1.1

*Average of values measured in May and August 1969 (nonfertilized plots).

†Sandy loam-clay loam.

to September), 114 frost-free days, and the mean annual air temperature

is 5.2 C. During the 1969 growing season, above-normal precipitation

supplied adequate soil water from August 1968 through April 1969, and

from June 25 through early August 1969. However, below-normal

precipitation and above-normal temperatures caused drought stress which

retarded the growth rate in plants from the last of May through June 24

and again from mid-August through mid-September 1969 (White and Brown,

1972). Precipitation during the 1970 growing season was above normal

except for the last three weeks of May and first two weeks of June.

Precipitation during the 1971 growing season was below normal and

herbage production was only about one-third of normal.

METHODS

Experimental Design and Treatments

Factorial combinations of three levels of N and two levels of clipping were assigned to plots in a completely randomized split-plot design with four replications. Ammonium nitrate was broadcast on main plots (17 by 5 m) in November 1968 at 0, 70, and 140 kg of N/ha. The two clipping treatments applied on subplots (8.5 by 5 m) were (A) plants undisturbed until sampled (unclipped) and (B) plants clipped to a 5-cm height at about 21-day intervals on May 7 and 28, June 17, July 8 and 29, 1969.

Total Nonstructural Carbohydrates

A preliminary study was conducted during October 1968, to determine the plant part and number of samples required to adequately determine the percentage of TNC in green needlegrass. Samples included stem bases to a 5-cm height aboveground and roots in a 15-cm diameter by 15-cm deep core. Individual cores were washed free of soil and the plant material was separated as stem bases or roots and as either live or dead. Material from 35 individual plants was analyzed for TNC to determine the variability among plants. Also, ten plants from each subplot were composited and analyzed for TNC to determine the variability of composited samples.