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# CARBOHYDRATES IN FORAGE: WHAT IS A SAFE GRASS?

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## Introduction

The ability to accumulate high levels of nonstructural carbohydrates (NSC) confers superior agronomic characteristics to grass. Grass species that accumulate NSC are more persistent under drought stress than species that do not (Boschma et al., 2003). Drought tolerance (Volaire and Lelievre, 1997; Volaire et al., 1998) and the ability to grow under cool temperatures (Brocklebank and Hendry, 1989) are linked to high fructan levels. Grasses that retain higher levels of NSC after grazing or hay production have faster regrowth and better persistence (Donaghy and Fulkerson, 1997). Grasses with larger seeds containing more starch are faster to germinate and establish after planting. Animal preference and better performance of meat- and milk-producing animals are also associated with higher levels of NSC in forage. High sugar concentration in grass allows more efficient utilization of nitrogen in the rumen, preventing excess from being excreted and contaminating the environment (Miller et al., 2001; Lovett et al., 2004). For all of these reasons, high concentration of NSC in grass is a major focus for grass breeders (Humphreys et al., 2006).

While the ruminant livestock enterprises benefit from higher levels of NSC in grass, various forms of carbohydrate intolerance are being recognized in horses. Obesity, laminitis, insulin resistance (Treiber et al., 2006), developmental orthopedic disease (Hoffman et al., 1999), and polysaccharide storage myopathy (Firshman et al., 2003) all involve excess dietary NSC in their etiology. Traditionally, these conditions were attributed to consumption of excess starch from grain; however, recent studies now include NSC in forage as a potential trigger factor (Longland and Byrd, 2006). Hyperinsulinemia may cause laminitis in ponies (Asplin et al., 2007), which implicates carbohydrates that elicit a glycemic response as triggers. Inulin, a form of short-chain fructans found in some broad-leaf plants, may trigger laminitis in horses via mechanisms involving microbial population dynamics (van Eps et al., 2006) and hyperinsulinemia (Bailey et al., 2007). Laminitis may also be induced with inulin in cows (Thoefner et al., 2004). A better understanding of the NSC concentration of various grass species and variation throughout the growing season would be valuable to those managing horses at risk for illness associated with excess carbohydrates.

## **Carbohydrate Source-Sink Dynamics**

An important concept to the understanding of carbohydrate concentration and distribution in grass is the dynamic nature of its production and utilization. A brief overview is presented by Nelson (1995). Plant scientists use the term “source” to indicate where carbohydrate is produced and “sink” to explain where carbohydrate is utilized. Plant organs can be either source or sink depending on stage of growth and environmental conditions. In early spring, carbohydrates stored in seed, crown, stem base, root, or rhizome tissues are the source for carbon and energy utilized in the formation of the first new leaves, which in this case are the sink. When enough leaf area has formed, such that the surface area has sufficient photosynthetic capacity to produce more carbohydrate than that required for growth, that leaf then becomes a source of sugar. Once the leaf is fully extended, the sink for growth is removed. Thereafter, sugars produced in excess of respiratory needs are available for translocation to sinks in other parts of the plant. Meristematic tissues, which are undifferentiated growth points throughout a plant, have priority for allocation of NSC. The sink for excess NSC might be new leaf, tiller, root, stem, or seed production. During the stem-elongation phase, the developing reproductive organs inside the stem are the sink. During seed filling, the stem is then the source and the seed is the sink. If adverse conditions limit seed filling, excess sugars may be left over in the stem. During germination, the seed is once again the source for NSC. High respiratory rates in cool-season grasses during hot weather may become a sink, burning up sugars that might otherwise go towards growth or seed production. In some winter-hardy types of perennial grass, onset of freezing temperatures may trigger translocation of sugars back to stem bases or underground storage organs. Leaf tissue in this case is the source; the storage organs are the sink. The source-sink relationship between various plant organs is dynamic, and can change hourly as environmental conditions affect photosynthetic capacity, respiration, and growth. Polysaccharides are too large for transport, so they are hydrolyzed to sugars for translocation. Much of the translocation of sugars from source to sink occurs in stem tissue. This is why stems are often higher in sugar concentration than leaves.

When growth slows or stops due to cold temperatures or a lack of water or other nutrients, the sink is removed. As long as there is still green leaf tissue and adequate sunlight to allow production of photosynthates, accumulation may occur whenever carbohydrate production exceeds utilization.

## **Concentration of Various Forms of Carbohydrate in Grass**

### **SUGAR**

All types of grass contain sugar. Under simulated conditions of 10° C days/5° C nights, some selections of both C3 and C4 grasses had sucrose concentrations ranging from

12-15% DM (Chatterton et al., 1989). Drought stress may increase sugar concentration. The ratio of sugars to starch in a drought-stressed plant can be different depending on whether the drought came on suddenly or developed slowly. In setaria (*Setaria sphacelata*), a C<sub>4</sub> tropical grass, the relationship between sucrose, hexoses (glucose and fructose), and starch was studied after dramatic short-term drought of exposed leaf discs, and a long-term drought of 45-day duration. While short-term water loss caused a reduction of sucrose and starch, presumably due to increased respiration, a long-term gradual drought caused sucrose to increase twofold to almost 50% of the dry matter; glucose and fructose increased significantly; and starch decreased (da Silva and Arrabaca, 2004). When sugar concentration reaches a threshold, formation of storage polysaccharides commences.

## FRUCTANS

C<sub>3</sub> cool-season grasses generally, but not always, store fructans. Chatterton et al. (1989) suggested that accumulation of fructan in most cool-season grasses did not occur before a threshold value of 15% NSC. Other studies showed that tall fescue may accumulate fructan when NSC level is lower than that. Highest mean level of fructan across the growing season in Idaho for eight varieties of tall fescue over the growing season was 119 g NSC kg<sup>-1</sup> DM (equivalent to 11% total dry matter) (Shewmaker et al., 2006). Tall fescue and perennial ryegrass tend to have the highest levels of fructans when compared to other grasses under the same conditions. Fructan is stored in vacuoles inside cells throughout the plant where it is readily available as needed. In some species of grass, the lower part of the stem is a carbohydrate-storage organ.

Extrapolation of dosage of inulin, given as a bolus, necessary to induce laminitis in a clinical setting would require 28% DM fructan in grass and high intake rates over the course of a full day (Longland and Byrd, 2006). While this level has been documented in stem tissue and whole plants or excised leaves grown under artificial, controlled conditions, this concentration of fructan in whole-plant grass samples grown under field conditions is not supported in existing published literature. As per Chatterton (personal communication), maximum concentration of fructan in grass under field conditions is around 20% (DM), although dandelions may have more fructan than grass.

## STARCH

C<sub>4</sub> warm-season grasses store starch in chloroplasts in leaf tissue. While they do not contain fructans, they may contain small amounts of short-chain fructooligosaccharides (FOS) (Chatterton et al., 1991). C<sub>4</sub> grasses have different respiratory mechanisms than C<sub>3</sub> grasses, allowing them to conserve energy under hot conditions when C<sub>3</sub> grasses

may burn off carbohydrates. Under high heat in growth chambers (32.2° C days/26.7° C nights), vegetative growth from two tropical grasses accumulated high levels of starch (16-19% DM), while the NSC of perennial ryegrass stayed fairly low (Wilson and Ford, 1971). C4 grasses such as Bermuda, paspalum, and Rhodes grass grown under heat stress may contain considerable starch content in leafy tissue. When hays made from C4 grasses are fed to carbohydrate-intolerant horses, analysis for starch is recommended even if no seed heads are present.

### **Environmental Factors Trigger Genetic Potential**

Appropriate environmental conditions are necessary to trigger the genetic potential for higher NSC concentration. Cool temperatures, short day length, intense sunlight, drought, and limited nutrients may cause NSC to accumulate. If a required stimulus is lacking, the mechanisms that produce excess carbohydrate are not initiated. Varieties of ryegrass considered “high sugar” in the United Kingdom did not express this characteristic when grown under field conditions in New Zealand. Further investigations in controlled environment chambers found that sugar production was triggered by temperatures below 10° C for 14 days, especially if followed by 10 weeks at 5° C, and accompanied by short day length (Parsons et al., 2004). These same ryegrass varieties were higher in sugar than local commercial standard varieties when grown in Oregon (Downing, 2007). Sometimes, varieties developed in the United Kingdom and considered high in sugar do not express the trait when grown there (Lovett et al., 2004). In orchard grass grown in a Mediterranean climate, drought stress triggered accumulation of WSC in leaf bases and increased as the drought progressed through the summer (Volaire and Lelievre, 1997). Crested wheatgrass is known as a fructan accumulator but fructans were not detected when grown at temperatures optimum for growth (20° C days/15° C nights). Only at cool temperatures (10/5° C) did fructan accumulation occur (Chatterton et al., 1986). In the intermountain region of the United States, where winters are subfreezing and grass becomes dormant, fructan concentrations in crested wheatgrass were least in midwinter when daily maximum temperatures were near 0° C, and greatest in spring and fall. When temperatures increased above freezing, fructan accumulation increased, reaching maximum concentrations when the ambient temperatures reached 15° C and then declining during the summer when optimum growth allowed full utilization of the NSC produced (Chatterton et al., 1988). The total concentration and ratio of NSC components may vary even in the same species depending on slow or rapid onset of cold temperatures, which affects enzymatic activity for first- and second-stage cold hardening (Livingston and Henson, 1998). First-stage cold hardening in cool-season perennial grasses triggers fructan accumulation when temperatures dip below 5° C. Second-stage hardening occurs with onset of prolonged hard freezing, generally causing fructans to hydrolyze to simple sugars. Rapid freezing without a long enough first-stage hardening period to accumulate fructan to use as a substrate for energy

through a long winter may affect winter hardiness, even in species that have the genetic potential to accumulate high levels of fructan under optimum conditions.

Photosynthetic rate response to temperature and the resulting carbohydrate levels may vary by grass species within the same genus (Borland and Farrar, 1987). NSC concentration of cultivars within the same species can vary significantly (Shewmaker et al., 2006). In a study conducted in the Netherlands during summer, perennial ryegrass cultivars differed up to 37% in WSC concentration under the same field conditions (Smit et al., 2005). In a growth chamber study, a new, improved cultivar of Italian ryegrass had 16% higher NSC under warm conditions and 22% higher NSC under cool growing conditions when compared to a standard commercial cultivar (Hopkins et al., 2002).

Because of confounding factors, many studies comparing NSC content of various grass species have been conducted in growth chambers or greenhouses where factors can be controlled. While these studies are valuable to assess genetic potential to accumulate NSC under controlled conditions, they do not provide information about the NSC content of individual grass species and how it may vary under fluctuating field conditions.

## Seasonal Variation

The temperatures and day length that trigger accumulation of NSC are specific for each genus, species, and variety of grass. Generally, when night temperatures are below 5-10° C, NSC will begin to accumulate. Care must be taken to avoid extrapolating data on seasonal variation of NSC to areas with different climatic conditions. The United Kingdom has mild winters with temperatures frequently just above freezing, so grass stays mostly green, although growth may slow or stop during a cold spell. These conditions are similar to spring in the northern half of the United States, and midwinter conditions in the southern regions. Yet, it is common worldwide to associate “spring grass” with laminitis. Since the theory that fructan may be involved in grass-associated laminitis has received so much attention, it is often assumed that fructan is highest in spring. Seasonal patterns of fructans concentration in four major species of C3 pasture grasses grown in England had greatest fructan concentrations in midwinter (Pollack and Jones, 1978). Fescue in Idaho had highest fructan levels in July (Shewmaker et al., 2006). Periods corresponding to times when NSC fluctuates are about weather, not season, especially in a global perspective. Recommendations for low-NSC forage must be qualified with information about specific growing conditions.

## Growth Rate

It is often incorrectly assumed that fast-growing grass or a “new flush” of grass is high in NSC concentration. The first two to three leaves of new growth are generally

low in NSC concentration as reserves are depleted to accomplish the growth. New growth is a carbohydrate sink. The first new shoots do not have enough surface area for the photosynthetic capacity to function as a source of carbohydrate. When grass is growing the fastest in midsummer warmth, NSC is at the lowest concentration of the year. Accumulation of sugars occurs when growth is slowed such that the products of photosynthesis exceed demand for growth.

In Tasmania, warm temperatures cause rapid growth and increased respiratory rate while cloudy conditions decrease photosynthetic rate. These conditions necessitate intensive management of grazing land based on cool-season grasses. Dairymen must hold off grazing until the critical stage when grass starts accumulating carbohydrates to replenish reserves. If the sink (new growth) is continually removed, the carbohydrate source will be exhausted and grass will die. New growth of perennial ryegrass switched from sink to source at the three-leaf stage (Fulkerson and Donaghy, 2001), and orchard grass at the four-leaf stage under these growing conditions (Rawnsley et al., 2002). It is likely that these critical stages to maintain sustainable grazing would differ in regions with different environmental conditions.

So why is it recommended that horses prone to laminitis avoid rapidly growing grass? While concentration of NSC per mouthful of grass is lower when growth rate is high, the amount of NSC per acre is increasing. Rainfall or application of fertilizer increases carbohydrate per acre (Belesky et al., 1991). Limitations to intake may be removed by the sheer abundance of grass available when growth rate is high. The horse suddenly has the opportunity to overeat. If laminitis is associated with a new “flush” of green grass that grows rapidly and steadily during warm weather, factors other than high NSC concentration should be considered.

## **Maturity**

Sometimes it is incorrectly assumed that very mature forage is safer for horses with metabolic problems. Stage of growth is but one factor in the NSC concentration of grass. Generally, later stages of maturity are considered less nutritious, but care should be taken when interpreting such general terms in the context of NSC. Nutritionists generally quantify fractions as a percentage of total dry matter, which might lead to thinking that an increase of one fraction leads to a decrease of the others. While this may be true of ground feedstuffs, it is not true of carbohydrate fractions found in separate parts of a plant cell.

Cellulose, hemicellulose, and lignin concentrations increase with increasing maturity and are found in cell walls. NSC concentration is more a function of environmental conditions. NSC is found in storage organs inside plant cells. Apoplastic sugars are found between plant cells. Since fiber and NSC are found in different parts of a plant cell, they are not mutually exclusive. High levels of NSC may be found in very mature, high-fiber forage when grown under environmental conditions conducive to its accumulation.

Plant scientists generally quantify nonstructural dry matter as a ratio of structural dry matter ( $\text{mg gSDM}^{-1}$ ), fully acknowledging that they vary independently (Chatterton et al., 1989). Sometimes this is referred to as adjusted dry weight (ADW) (Shewmaker et al., 2006). The following example shows how to convert ADW to % total dry matter:

$333 \text{ mg gSDM}^{-1} = 333 \text{ mg nonstructural dry matter} + 1000 \text{ mg structural dry matter}$   
 $= 1333 \text{ mg total dry matter. } 333 \text{ mg}/1333 \text{ mg} = 25\% \text{ NSC (total DM).}$

When NSC are expressed as ratio to ADW, plant scientists show that NSC vary significantly independently from structural dry matter (fiber), even over the course of a single day. In Idaho, daily carbohydrate accumulation in tall fescue was studied. Rates of daily NSC gain varied over the season, with the highest rate of increase from dawn to dusk in September at  $30.8 \text{ g kg}^{-1}$  ADW, or nearly 3% of total dry matter in one day (Shewmaker et al., 2006).

## Stage of Growth vs. Environmental Conditions

To investigate whether environmental conditions were more important than stage of growth as a factor of NSC concentration, a study was conducted comparing early- and late-planted oat hay. The spring planting was subjected to freezing temperatures at early stages of growth, and the adjacent summer-planted oats were subjected to freezing temperatures as they matured in late fall. The study was conducted at Rocky Mountain Research & Consulting, Inc. in Center, Colorado. The site is a high alpine desert at 7700 ft altitude with usually cloudless skies, a relatively short growing season, and wide diurnal temperature fluctuations. Samples were cut at seven different stages of growth and air-dried, with four replications. The spring-planted oat hay had peak NSC concentration at boot stage, with 29% NSC (total DM) and 36% NDF, averaged over two growing years. The summer-planted oat hay had peak NSC concentration at soft dough stage, with an average of 27% NSC and 49% NDF. Maximum fructan concentration was near 12% and occurred at boot stage in the second year of spring planting following a period of near-freezing night temperatures. Peak NSC concentration followed trends in temperature more closely than stage of growth (Chatterton et al., 2006). Maturity is a factor in the NSC concentration of forage, but environmental conditions may override stage of growth, producing very mature forage with high NSC concentration.

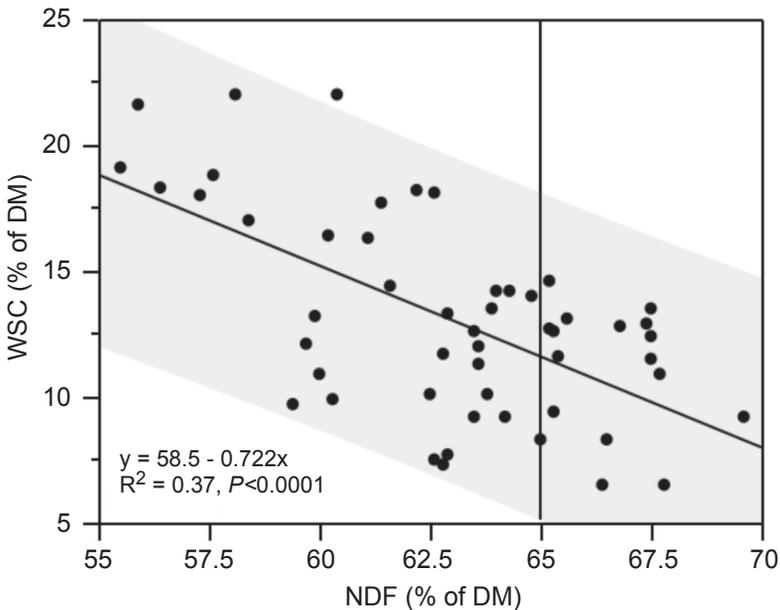
At the same Colorado site, thirteen perennial grass varieties from a randomized block with four replications were cut in late July, a full month after the optimum time for hay production. All were headed out. Samples were frozen immediately and shipped frozen to Dairy One (Ithaca, New York) for analysis. Correlation ( $r$ ) between WSC and NDF was  $-0.61$  ( $P < 0.0001$ ) and between NSC and NDF was  $-0.66$  ( $P < 0.0001$ ). A scatter plot of the data (Figure 1) for means presented in Table 1 illustrates

36 Carbohydrates in Forage

**Table 1.** Overmature fresh grass NSC vs. NDF (DM).

Variety	NSC	WSC	NDF
Roadcrest crested wheatgrass	20.2	19.2	61.6
Garrison meadow foxtail	19.9	19.2	57.3
Climax timothy	17.2	15.9	59.6
Potomac orchardgrass	15.5	14.4	61.9
NewHy Crested wheatgrass	15.1	14.1	64.0
Cache meadow brome	13.8	12.2	66.5
Sherman big bluegrass	13.4	12.6	67.5
Regar meadow brome	13.0	12.1	64.7
Ginger Kentucky bluegrass	12.8	11.5	63.8
Fawn tall fescue	12.8	9.5	62.3
Wideleaf orchardgrass	12.4	11.3	61.9
Manchar smooth brome	12.0	8.3	63.3
Redtop	10.7	9.5	64.5
LSD (P=0.05)	3.6	3.5	3.4

Mean of 4 reps, Analysis by Dairy One, Ithaca, NY



**Figure 1.** Even when NDF was as high as 65%, WSC concentration was up to 15%.

that even when NDF was as high as 65%, WSC concentration was up to 15%. For a forage entry similar to the sample population evaluated, one would expect that 95%

of the time an entry with 65% NDF would have a WSC value that would fall within a range of about 5 to 17.5% WSC. Fresh grass forage samples (n=3500) submitted to Dairy One (online database through April, 2007) have a mean of 10.4% WSC (DM), and 13.1% NSC (DM). High-fiber grass can still have a considerable amount of WSC under certain conditions.

Purposely allowing grass to become overmature does not necessarily result in low NSC content. Photosynthetic capacity diminishes in mature leaf tissue, but as growth ceases, sugar production may still exceed utilization, especially under cloudless skies and cool night temperatures. While protein and mineral concentrations decrease consistently with increasing maturity, sugar and fructan contents are more closely linked to environmental conditions. Until appropriate studies on availability of NSC in various fiber matrices are conducted in horses, it may be prudent to avoid assuming NSC are unavailable for fermentation or absorption even when fiber content is considered high.

## Inverse Relationship Between NSC Concentration and Yield

When breeders select for more productive varieties of grass, management practices for maximum production are implemented. This may inadvertently select for those varieties that require higher management inputs, such as higher amounts of fertilizer or water. If these are not supplied as needed, the grass will be under stress. Stressed grass is higher in NSC. Far too frequently, horse owners overgraze and neglect pastures. When grass is perceived as the enemy, it seems intuitive to many owners of carbohydrate-intolerant horses to discourage its growth or vigor. Benign neglect becomes the prevailing pasture management practice. If “lush” grass to be avoided, they believe that dry, sparse grass is safer. This may be counterproductive. While NSC per acre may be less, the NSC per mouthful of grass can be greater with nutrient stress. Nitrogen has an inverse relationship with NSC (Lovett et al., 2004). An irrigated paddock of Paddock meadow brome (*Bromus riparius*) and Garrison meadow foxtail (*Alopecurus arundinaceus*) in Center, Colorado was divided into a randomized complete block with four replications. A moderate rate of ammonia nitrate decreased NSC concentration significantly compared to the unfertilized grass (Table 2). Dry matter production increased threefold on the fertilized plots, resulting in a large increase in NSC per acre (Watts, 2005a). In a study conducted in Georgia, fescue fertilized with nitrogen was also lower in carbohydrate concentration, with carbohydrate yield per acre higher on fertilized grass. Higher carbohydrate yield per acre tended to correspond to lower carbohydrate concentration, especially after high rainfall. In the same study, ungrazed fescue had higher carbohydrate yield per acre than fescue after grazing (Belesky et al., 1991). In fescue grown under simulated short-term drought conditions, sucrose levels in leaf bases increased 258% (Spollen and Nelson, 1994). While rapidly growing grass is lower in NSC concentration, sheer volume may remove limitations to intake imposed

by overgrazing, drought, or neglect. Weeds that thrive when grass is stressed may be higher in sugar than grass (Watts, 2005b). While we cannot control the weather, we can do a better job correcting nutrient deficiency and controlling high-sugar weeds to decrease carbohydrate concentration per mouthful. Limiting intake when grass is in abundance seems a more useful approach than purposely stressing grass by ignoring good agronomic practices.

**Table 2.** NSC content of fertilized vs. nonfertilized pasture.

	<i>NSC*</i> <i>% dry matter</i>	<i>Yield tons</i> <i>DM/acre</i>	<i>NSC</i> <i>lb/acre</i>
35 lb N/acre nitrogen as AmNO <sub>3</sub>	17.88	0.6	631
No nitrogen	23.10	1.8	285
LSD (P=0.05)	2.33	0.8	274

Mean of 4 reps

Analysis by Dairy One, Ithaca, NY. \*NSC=WSC + starch.

## Growing Low-NSC Grass May Be Difficult

It will be easier to grow low-NSC grass in warm, cloudy climates, and more difficult in sunny, cool climates. The most commonly used grasses in horse pasture in regions with hard winters must have a genetic potential for high levels of NSC in order to be productive throughout a long grazing season and to withstand the stress of intensive grazing, cold, and perhaps drought. High-NSC grasses grow in spite of the abuse and neglect that is too often the case in horse pastures. Warm-season C4 grasses tend to be lower in NSC concentration than C3 cool-season grasses, especially under cool growing conditions (Chatterton et al., 1989). When subjected to frost that dramatically raises NSC concentration in C3 cool-season grasses, C4 warm-season grasses go dormant. While these may be a viable lower NSC alternative in subtropical regions, in temperate regions their growth season is very short. They will not break dormancy until the soil temperature is above around 10° C, and are productive only during summer months with adequate rainfall or irrigation. As they tend not to store as much NSC reserves as cool-season grasses, they would not be sustainable under yearlong intensive grazing by horses outside of their region of adaptation. A possible strategy for utilizing some of the more winter-hardy, warm-season grasses in temperate regions might be to set aside a paddock that is grazed only in spring or fall as standing hay, when many cool-season grasses are peaking in NSC content. Keeping invasive indigenous cool-season grasses from taking over the less competitive low-sugar grasses will be a challenge. Many of the low-sugar grasses native to the intermountain region spring up quickly

after snowmelt or summer rains. They remain dormant during times of drought, so they don't have to hoard NSC to stay alive. They will not be competitive when grown where sod-forming grasses thrive. Even in their preferred habitat, they are not sustainable without intensive management that includes rotational grazing and destocking when conditions are suboptimal. Horse owners are generally not willing to withhold access to grazing for the sake of the grass. These low-NSC native grasses comprise a large part of the diet of free-ranging feral horses and wildlife in the intermountain region of the United States. Assessments of the condition of rangelands are done continuously by range managers to determine carrying capacity and assure sustainability. It is unlikely these native grasses will provide a viable alternative for grazing horses confined on small parcels of land, even in areas where they are well-adapted.

A more successful approach to growing low-sugar forage may be to choose a grass species that is well-adapted to the growing area, and apply best management practices for minimizing stress and optimizing growth. Stress causes accumulation of NSC, and growth utilizes NSC. Management systems for individual grass species in specific regions have been developed to facilitate utilization of grass when carbohydrate concentrations are maximized without depleting carbohydrate reserves beyond that which is necessary for optimum regrowth and sustainability of the sward (Fulkerson, 2001). Cutting or grazing grass when NSC are lowest depletes energy reserves (Nelson, 1995). It will be more difficult to manage grass for low NSC content sustainably. Field studies to develop grazing management strategies when NSC are lowest need to be conducted. Studies will be necessary for each type of grass in each bioregion. A rotational grazing plan that allows grass to replenish carbohydrate reserves after grazing will be necessary to sustain the grass sward.

## Summary

The NSC content of a grass species at any given time is dependent upon a complex array of interacting factors. Clearly we cannot consider the concentration or ratio of various NSC fractions in any given grass species without considering the environmental conditions under which it was grown. Horses that cannot tolerate any grass when weather is sunny and cool may be at less risk during warm or cloudy weather. Unstressed regrowth after mowing or intensive grazing when weather is warm will have far less NSC content than grass that is heading or is subjected to cold, drought, or nutrient stress. Overmature grass is not always lower in NSC. While some native grasses are lower in NSC than those adaptable to continuous grazing, a very large acreage per animal, a climate suitable to each species of grass, and intensive management utilizing sophisticated agronomic science will be required to graze such grasses sustainably. Lower productivity will likely be associated with grass species that have relatively lower NSC content than currently popular species. If lower sugar alternatives to the types of grass traditionally recommended for horse pasture are

deemed necessary, appropriate studies to determine suitable varieties and to develop sustainable management systems should be conducted in each bioregion. All the most commonly recommended varieties of grass have the potential to have high levels of NSC under certain conditions. Rather than recommending a different grass, my best current advice for safer grass is to manage existing stands for lower NSC concentration and limit access, or restrict access when this is not possible.

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## References

- Asplin, K.E., M.N. Sillence, C.C. Pollitt, and C.M. McGowan. 2007. Induction of laminitis by prolonged hyperinsulinaemia in clinically normal ponies. *Vet. J.* 174:530-535.
- Bailey, S.R., N.J. Menzies-Gow, P.A. Harris, J.L. Habershon-Butcher, C. Crawford, Y. Berhane, R.C. Boston, and J. Elliot. 2007. Effect of dietary fructans and dexamethasone administration on the insulin response of ponies predisposed to laminitis. *J. Amer. Vet. Med. Assoc.* 231:1365-1373.
- Belesky, D.P., S.R. Wilkinson, and J. A. Stuedemann. 1991. The influence of nitrogen fertilizer and *Acremonium coenophialum* on the soluble carbohydrate content of grazed and non-grazed *Festuca arundinacea*. *Grass and Forage Sci.* 46:159-166.
- Borland, A.M., and J.F. Farrar. 1987. The influence of low temperature on diel patterns of carbohydrate metabolism in leaves of *Poa annua L.* and *Poa X jemtlandica* (ALMQ) Richt. *New Phytol.* 105:255-263.
- Boschma, S.P., M.J. Hill, J.M. Scott, and G.G. Rapp. 2003. The response to moisture and defoliation stresses, and traits for resilience of perennial grasses on the northern tablelands of New South Wales, Australia. *Aus. J. Ag Res.* 54:903-916.
- Brocklebank, K. J., and G.A.E. Hendry. 1989. Characteristics of plant species which store different types of reserve carbohydrates. *New Phytol.* 112:255-260.
- Chatterton, N.J., P.A. Harrison, and J.H. Bennett. 1986. Environmental effects on sucrose and fructan concentration in leaves of *Agropyron* spp. In: *Phloem Transport* p. 471- 476, Alan R. Liss, Inc.
- Chatterton, N. J., P. A. Harrison, J.H. Bennett, and K. H. Assay. 1989. Carbohydrate partitioning from 185 accessions of gramineae grown under warm and cool temperatures. *J. Plant Physiol.* 134:169-179.

- Chatterton, N.J., W.R. Thornley, P.A. Harrison, and J.H. Bennett. 1988. Dynamics of fructan and sucrose biosynthesis in crested wheatgrass. *Plant Cell Physiol.* 29:1103-1108.
- Chatterton, N.J., W.R. Thornley, P.A. Harrison, and J.H. Bennett. 1991. DP-3 and DP-4 oligosaccharides in temperate and tropical grass foliage grown under cool temperatures. *Plant Physiol. and Biochem.* 29:367-372.
- Chatterton, N.J., K.A. Watts, K.B. Jensen, P.A. Harrison, and W.H. Horton. 2006. Nonstructural carbohydrates in oat forage. *J. Nutr.* 136:2111S-2113S.
- da Silva, J.M., and M.C. Arrabaca. 2004. Contributions of soluble carbohydrates to the osmotic adjustment in the C4 grass *Setaria sphacelata*: A comparison between rapidly and slowly imposed water stress. *J. Plant Physiol.* 161:551-555.
- Donaghy D.J., and W.J. Fulkerson. 1997. The importance of water-soluble carbohydrate reserves on regrowth and root growth of *Lolium perenne* (L.). *Grass Forage Sci.* 52:401-407.
- Downing, T. 2007. Nonstructural carbohydrates in cool-season grasses. Oregon State University. Ext Serv. Spec. Report 1079-E.
- Firshman A.M., S.J. Valberg, J.B. Bender, and C.J. Finno. 2003. Epidemiologic characteristics and management of polysaccharide storage myopathy in Quarter Horses. *Amer. J. Vet. Res.* 64:1319-1327.
- Fulkerson, W.J., and D.J. Donaghy. 2001. Plant-soluble carbohydrate reserves and senescence- key criteria for developing an effective grazing management system for ryegrass-based pasture: A review. *Austral. J. Exper. Agric.* 41:261-275.
- Hoffman, R.M., L.A. Lawrence, D.S. Kronfeld, W.L. Cooper, D.J. Sklan, J.J. Dascanio, and P.A. Harris. 1999. Dietary carbohydrates and fat influence radiographic bone mineral content of growing foal. *J. Anim. Sci.* 77:3330-3338.
- Hopkins, C., J.P. Marais, and D.C.V. Goodenough. 2002. A comparison, under controlled environmental conditions, of a *Lolium multiflorum* selection bred for high dry matter content and nonstructural carbohydrate concentration with a commercial cultivar. *Grass Forage Sci.* 57:367-372.
- Humphreys M.W., R.S. Yadav, A.J. Cairns, L.B. Turner, J. Humphreys, and L. Skøt. 2006. A changing climate for grassland research. *New Phytol.* 169:9-26.
- Livingston, D.P., and C.A. Henson. 1998. Apoplastic sugars, fructans, fructan exohydrolase, and invertase in winter oat: Responses to second-phase cold hardening. *Plant Physiol.* 116:403-408.
- Longland A.C., and B.M. Byrd. 2006. Pasture nonstructural carbohydrates and equine laminitis. *J. Nutr.* 136:2099S-2102S.
- Lovett, D.K., A.P. Bortolozzo, P. Conaghan, P. O'Kiely and F.P. O'Mara. 2004. In vitro total and methane gas production as influenced by rate of nitrogen application, season of harvest and perennial ryegrass cultivar. *Grass Forage Sci.* 59:227-232.
- Miller, L.A., J.M. Moorby, D.R. Davies, M.O. Humphreys, N.D. Schollan, J.C. MacRae, and M.K. Theodorou. 2001. Increased concentration of water-soluble

- carbohydrate in perennial ryegrass (*Lolium perenne* L.): Milk production from late-lactation dairy cows. *Grass Forage Sci.* 56: 383-394.
- Nelson, J.C., 1995. Photosynthesis and carbon metabolism. Page 40 in *Forages: An Introduction to Grassland Agriculture*. Iowa State University Press, Ames, Vol. 1.
- Parsons, A.J., S. Rasmussen, H. Xue, J.A. Newman, C.B. Anderson, and G.P. Cosgrove. 2004. Some “high sugar grasses” don’t like it hot. In: *Proc. New Zeal. Grassland Assoc. Conf.* 6:265-271.
- Pollock, C.J., and T. Jones. 1978. Seasonal patterns of fructan metabolism in forage grasses. *New Phytol.* 83:9-15.
- Rawnsley, R. P., D.J. Donaghy, W.J. Fulkerson, and P.A. Lane. 2002. Changes in the physiology and feed quality of cocksfoot (*Dactylis glomerata* L.) during regrowth. *Grass Forage Sci.* 57:203-211.
- Shewmaker, G.E., H.F. Mayland, C.A. Roberts, P.A. Harrison, N.J. Chatterton, and D.A. Sleper. 2006. Daily carbohydrate accumulation in eight tall fescue cultivars. *Grass Forage Sci.* 61:413-421.
- Smit, H.J., B.M. Tas, H.Z. Taweel, S. Tamminga, and A. Elersma. 2005. Effects of perennial ryegrass (*Lolium perenne* L.) cultivars on herbage production, nutritional quality and herbage intake of grazing dairy cows. *Grass Forage Sci.* 60:297-309.
- Spollen, W.G., and C.J. Nelson. 1994. Response of fructan to water deficit in growing leaves of tall fescue. *Plant Physiol.* 106:329-336.
- Thoefner, M.B., C.C. Pollitt, A.W. van Eps, G.J. Milinovich, D.J. Trott, O. Wattle, and P.H. Andersen. 2004. Acute bovine laminitis: A new induction model using alimentary oligofructose overload. *J. Dairy Sci.* 87:2932–2940.
- Treiber, K.H., D. S. Kronfeld, and R.J. Geor. 2006. Insulin resistance in equids: Possible role in laminitis. *J. Nutr.* 136:2094S-2098S.
- van Eps, A.W., and C.C. Pollitt. 2006. Equine laminitis induced with oligofructose. *Equine Vet J.* 38(3):203-208.
- Volaire F., and F. Lelievre. 1997. Production, persistence and water-soluble carbohydrate accumulation in 21 contrasting populations of *Dactylis glomerata* L. subjected to severe drought in the south of France. *Aust. J. Agric. Res.* 48:933-944.
- Volaire, F., H. Thomas, and F. Lelievre. 1998. Survival and recovery of perennial forage grasses under prolonged Mediterranean drought. *New Phytol.* 140:439-449.
- Watts, K. 2005a. Nitrogen-deficient grass is higher in nonstructural carbohydrates than grass fertilized with ammonium nitrate. In: *Proc. Equine Nutr. Physiol. Soc. Symp.*
- Watts, K. 2005b. A review of unlikely sources of excess carbohydrates in equine diets. *JEVS.* 25:338-344.
- Wilson, J.R., and C.W. Ford. 1971. Temperature influences on the growth, digestibility, and carbohydrate composition of two tropical grasses, *Panicum maximum* Var. *Trichoglume* and *Setariasphacelata*, and two cultivars of the temperate grass *Lolium perenne*. *Aust. J. Agric. Res.* 22:563-571.