Clipping and long-term grazing effects on biomass and carbohydrate reserves of Indian ricegrass

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Abstract

Long-term heavy grazing had little effect on root and crown biomass of Indian ricegrass (*Oryzopsis hymenoides* [Roem. and Schult.] Ricker), nor did it significantly affect the total nonstructural carbohydrate (TNC) reserve levels or the seasonal cycle of reserves in this grass. Fifty years of protection from livestock use had not resulted in ecotypic differentiation in Indian ricegrass for these variables. Clipping reduced crown biomass more than root biomass and removal of 90% of the aboveground biomass resulted in more than a 50% reduction in crown biomass and reserve carbohydrate pool.

Two commercial strains of Indian ricegrass ('Nezpar' and 'Paloma') were compared with native Chaco Canyon strains in a uniform garden study. The Nezpar strain was superior to Paloma and the Chaco Canyon strains in production of crown biomass and TNC reserves at the more mesic garden site. The native strains from the more arid Chaco Canyon site were superior to both cultivated strains in production of roots. The native Chaco Canyon strains were little affected by clipping and have promising genetic potential for tolerance of drought and heavy grazing.

Key Words: Indian ricegrass, *Oryzopsis hymenoides*, heavy grazing, ecotypic differentiation, belowground biomass, carbohydrate reserves

A plant is considered to be a source-sink system where active photosynthetic tissue produces compounds which are used for maintenance and growth, stored in situ, or translocated to other sites of utilization or storage (Burt 1964, Maggs 1964, Neales and Incoll 1968). Deregibus et al. (1982) stated that a reduction of carbohydrate reserves resulting from defoliation after the peak growth period might be caused by a reduction in the leaf area and assimilate production after active aboveground growth had ceased, when meristematic activity was low, and when there were other demands for assimilates below ground. They pointed out that this was at a time when carbohydrates were normally being produced in excess of demand, hence they could be transported to belowground structures for root growth or maintenance, or be converted to long-chain carbohydrates for future growth demands.

Labile carbohydrate reserves are a major source for carbon for regrowth after defoliation (Graber 1931, Cook 1966, Youngner 1972, White 1973, Trlica 1977, Deregibus et al. 1982). However, some researchers have been critical of the role of reserve carbohydrates for regrowth following defoliation (May and Davidson 1958, Moore and Biddiscomb 1964, Davidson and Milthorpe 1965, Caldwell et al. 1981). Studies that utilized radioactive carbon have given some supportive evidence for the use of storage carbohydrates in regrowth (Pearce et al. 1969, Smith and Marten 1970, Chung and Trlica 1980), but reserves may only be needed for a short time to produce the first few leaves.

Several researchers have found that carbohydrate reserve storage in grass species was not significantly affected by grazing or defoliation treatments if the grazing or defoliation was discontinued in time to allow plants to grow up and replenish reserves before fall quiescence (Sampson and McCarty 1930, McCarty and Price 1942, Hyder and Sneva 1963, Paulsen and Smith 1968, Menke and Trlica 1983). This was partially true in the case of Indian ricegrass (Trlica and Cook 1971).

Effects of grazing or defoliation may not only be seen in terms of total nonstructural carbohydrate (TNC) concentration, but also in terms of weight of the storage organs per se (Weinmann 1952). Therefore, determination of total amount of carbohydrate pools in the storage organs (pool = % TNC × biomass of the plant part analyzed), rather than just the concentration of TNC reserves, may be important in assessing regrowth potential of plants (Buwai and Trlica 1977b, Santos and Trlica 1978). Some researchers have contradicted the traditional view that grass crowns represent the major organ for storage of soluble reserves based on determination of soluble carbohydrate pools in crowns (Caldwell et al. 1981, Richards and Caldwell 1985, Richards et al. 1987). These researchers have found little correlation between crown and stem base TNC concentration or carbohydrate pools with regrowth following defoliation.

Crowns of Indian ricegrass (*Oryzopsis hymenoides* [Roem. and Schult.] Ricker) may provide a better indication of TNC storage reserves and defoliation effects than do roots, if crown mass and reserve levels are large. Coyne and Cook (1971) found that crowns of Indian ricegrass had higher TNC concentrations than did roots. Trlica and Cook (1971) found that crown TNC concentration in Indian ricegrass was usually more affected by defoliation than was root TNC concentration.

The main objective of this study was to determine effects of previous long-term heavy grazing and clipping on root and crown biomass and nonstructural carbohydrates in crowns of Indian ricegrass. Another objective was to compare biomass and TNC variables of native and commercial strains of this species in a uniform garden environment to assess the genetic potential of the strains.

Methods and Materials

Root and Crown Biomass

Chaco Canyon In Situ Study

An experiment was conducted within and adjacent to the Chaco Canyon Culture National Historical Park (Chaco Canyon) in northwestern New Mexico. Plots were located on a hilltop, hillside, and in a swale on both heavily grazed and protected (ungrazed) pastures at about 580 m elevation as described by Orodho et al. (1990) and Trlica and Orodho (1989). The 0.4-ha

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plots located outside the National Park on lands managed by the Bureau of Land Management (BLM) were fenced in April 1984 to prevent livestock grazing during 1984 and 1985, when the study was conducted. National Park Service and BLM records indicated that this area had been heavily grazed year long by cattle, sheep, goats, and horses for more than 50 years. The area within the National Park was fenced 50 years ago to prevent livestock use within the Park. Two adjacent plots with similar soils, slope, exposure and vegetation were selected at each of the 3 topographic positions. One of the plots at each site was located within the protected area of the National Park, while the other was located on the adjacent, heavily-grazed area managed by the BLM. Plots were located at least 200 m from the Park boundary fence in both the grazed and protected areas at each of the 3 sites to reduce genetic exchange among the grazed and protected sites.

The long-term average annual precipitation recorded at the headquarters of the National Park was 240 mm. Precipitation at the Chaco Canyon site was 110 and 130% above normal in 1984 and 1985, respectively. Most of the precipitation comes during the summer and fall months. The mean monthly temperature ranges from 5 to 35° C and the monthly mean minimum temperature ranges from -11 to 11° C. Soils at the study area are a sandy loam.

Two shrubs, winterfat (*Eurotia lanata* [Pursh] Nutt.) and fourwing saltbush (*Atriplex canescens* [Pursh.] Nutt.) were dominant in the overstory vegetation at the Chaco Canyon study site. The most common grasses were Indian ricegrass, galleta (*Hilaria jamesii* [Torr.] Genth.), blue grama (*Bouteloua gracilis* [H.B.K.] Lag. ex Steud.), and bottlebrush squirreltail (*Sitanion hystrix* [Nutt.] J.G. Smith). *Eriogonum* spp. and Russian thistle (*Salsola kali* L.) were common forbs in the area. Orodho et al. (1990) found that previous heavy grazing at this research area had resulted in a reduction of fourwing saltbush; however, there had been little effect on grass cover, density or production. Density of Indian ricegrass at the Chaco Canyon study site was only 1.5 plants/m^2, whereas density of plants in the uniform garden study were 6–9 plants/m^2. However, Indian ricegrass plants were much larger and grew in association with a number of other species at the Chaco Canyon study site, so competition within the community could have affected results of the in situ field study (Mueggler 1972).

The experiment was a randomized block design which consisted of 2 former grazing intensities (heavily grazed and ungrazed for 50 years) and 4 defoliation intensities (0, 30, 60, and 90% removal of photosynthetic tissue-estimated). The 3 topographic sites served as replications. Four plants within each plot assigned to each defoliation treatment were randomly selected at each date of sampling. Four additional plants were selected from each defoliation intensity for sampling in 1985 at the quiescence stage. Defoliation was done at anthesis in either early June 1984 or late May 1985 for those plants that would be sampled at quiescence in late November 1985. The 4 selected plants were excavated and only crown material was retained during the 1984 sampling. These plants were collected at the second leaf stage (late April), anthesis (early June), maturity (late July), and quiescence (late November) phenological stages in 1984. The fifth sample period was at quiescence in late November of 1985, when roots as well as crowns were sampled with a 13- × 24-cm coring device. These last samples were collected using the same technique and equipment described in the next section to assess root and crown weights in the Cortez uniform garden study.

Cortez Uniform Garden Study

The Cortez study site used for the uniform garden experiments was located at the Southwestern Colorado Research Center near Yellow Jacket, Colorado, which is about 24 km north of Cortez. The Center is located in the dryland farming region of the southwestern corner of Colorado at about 2,130 m elevation. The Center receives annual precipitation of about 360 mm, half of which falls as snow during the winter months. Precipitation in 1984 and 1985 was 105 and 120% of normal, respectively. There is a frost-free period of 120 days. The monthly mean maximum temperature for this area is normally under 33° C, while the monthly mean minimum temperature is above -12° C. This is quite similar to the temperature regime at Chaco Canyon, but precipitation is much greater at the Cortez site.

The principal soil series at the Cortez study site is representative of major acreages of the agricultural land in the area and is silty clay loam soil. These soils have a high water-holding capacity and store winter moisture upon which success of agriculture in the basin is dependent. Topography of the region consists almost entirely of rolling hills and the dominant vegetation types are grassland and pinyon-juniper woodland.

Two strains of Indian ricegrass were obtained from the Chaco Canyon study site. Transplants were excavated from 3 heavily grazed sites adjacent to exclosures on the hilltop, hillside, and swale locations. The transplants from each of the 3 topographic locations were combined in equal proportions to constitute the grazed strain. Similarly, transplants from sites adjacent to plots within the Chaco Culture National Historical Park were combined in equal portions from similar topographic positions to constitute the ungrazed strain.

Grazed and ungrazed plots were located approximately 400-m apart to reduce pollen and seed transport between the 2 populations. Two other strains tested in the uniform garden experiments, 'Paloma' and 'Nezpar', are commercially released cultivars of Indian ricegrass. Paloma transplants were obtained from agronomic plots at the Cortez study site, while Nezpar transplants were obtained from a seed production field near Dolores, Colorado, approximately 25 km northeast of the Cortez study site.

All transplants were excavated in April of 1984, reduced to approximately the same basal area (135 cm^2), and potted before being transported to the Cortez study site. Each plant was subdivided into 4 equal-sized bunches and immediately planted into a well-prepared seedbed at 30-cm plant and row spacings. Weeding was done periodically by hand. We assumed that little intra-plant competition would occur during the 2 years of study.

The uniform garden experiment was a split-split-plot design having factorial arrangement of treatments with 4 replications. Two nitrogen (N) treatments (0 and 50 kg/ha) composed the main plots, 2 clipping treatments (90% of active photosynthetic material clipped and unclipped) made up the sub-plots, and the 4 strains of Indian ricegrass were the sub-sub-plots. Five transplants of each strain of Indian ricegrass were planted in a row within each treatment. Nitrogen was applied in early June of 1984 and in late May of 1985, while clipping was done at the anthesis stage of phenological development in both years. The nitrogen fertilizer application had no significant ($P>0.05$) effect on any measured parameter; therefore it will not be discussed further in this paper.

Root and crown samples were collected in early August at the end of the growing season immediately following the 1985 aboveground biomass harvest. One of 5 plants was selected at random from each treatment in each replication to be collected. A cylindrical sampling core of 13-cm diameter and 24-cm long, with a sharp cutting edge, was placed directly over the selected plant crown and hammered into the ground. We estimate that this core would sample approximately 60–80% of the individual plant root biomass and 100% of the crown biomass, with little contamination of root biomass by neighboring plants. The roots and crowns within the core sample were obtained by digging around the metal core and excavating it. The crowns were separated from the roots, with obvious decayed materials being discarded, and the live crown tissue was washed with tap water and placed into a glass jar. The crown tissue was covered with 95% ethanol immediately following washing to reduce enzymatic activity, and then sealed tightly.

Crown samples were taken to the laboratory where jars were placed, with their lids open, in a forced-draft oven at 60° C. Ethanol was evaporated and the samples completely dried before they were weighed and then ground in a Wiley mill to pass through a 0.5-mm screen. The ground samples were kept in sealed polyethylene bags prior to laboratory analysis.

Plant roots were separated from crowns immediately after they were obtained from the field. Roots were removed from soil by a floatation method (McKell et al. 1961) using 0.05-mm screens. The root samples were oven-dried at 60° C and weighed.

Carbohydrate Analysis

The prepared crown samples from the Cortez and Chaco Canyon study sites were taken to a laboratory for TNC analysis. TNC was extracted from each 0.5-g plant sample with 0.2 N sulphuric acid (Smith et al. 1964). The extracts were then used to determine TNC concentration on a glucose-equivalent basis by using an iodometric titration developed by Heinze and Murneek (1940), but using modified reagents as suggested by the Association of Official Analytical Chemists (1965). Standard curves were determined for each stock solution. The TNC percentages were multiplied by the weight of the plant organ to determine carbohydrate pool quantity.

Data Analysis

All data on root and crown weights, TNC concentration, and carbohydrate pools were analyzed using analysis of variance procedures (Steel and Torrie 1980). The calculated F-values were tested at the $\alpha = 0.05$ level of probability, and if significant ($P \leq 0.05$) interactions were found, then analysis within levels of a factor were conducted. When significant ($P \leq 0.05$) differences were detected, Duncan's New Multiple Range Test was used to separate significant ($P \leq 0.05$) means.

Results and Discussion

Root and Crown Biomass

Long-term heavy grazing (i.e., greater than 50 years) did not significantly affect root biomass of Indian ricegrass in the top 24 cm of soil at the Chaco Canyon study site (data not shown). There were, however, significant differences in root biomass (Fig. 1)

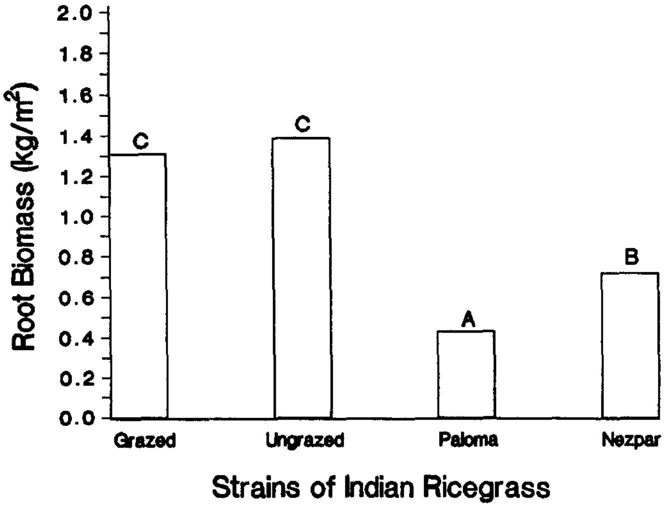

Fig. 1. Root biomass for 4 strains of Indian ricegrass at the Cortez common garden site in August 1985. Values are the average over replications, fertilization, and clipping treatments. Means labeled with similar letters are not significantly different ($P > 0.05$).

among the 4 strains of Indian ricegrass transplanted into the uniform garden at the Cortez site. No significant differences in root biomass among the grazed and ungrazed strains of Indian ricegrass from the Chaco Canyon study site were found. It should be noted that these 2 strains had greater root biomass than did either of the 2 cultivated strains of Paloma and Nezpar (Fig. 1). Paloma had the lowest root biomass among the 4 strains of Indian ricegrass tested in the transplant garden at the Cortez study site. Greater root biomass for the 2 native strains of Indian ricegrass should be advantageous under droughty conditions.

Defoliation at 30, 60, or 90% removal of photosynthetic tissue at anthesis in early June had little effect on root biomass of in situ Indian ricegrass at the Chaco Canyon study site. Clipping Indian ricegrass at anthesis in the Cortez uniform garden also had little effect on root biomass and there was no significant clipping-x-strain interaction. The present research supported earlier work reported by Buwai and Trlica (1977a), who found no change in total root weights of blue grama and western wheatgrass (*Agropyron smithii* Rydb.) after defoliation. Results of this research did not support that reported by Deregibus (1983), who found a reduction of root biomass in *Paspalum dilatum* (Poir) as a result of defoliation. Santos and Trlica (1978) also found that the biomass of crowns and roots of blue grama and the root biomass of western wheatgrass were reduced by frequent defoliation. A number of other researchers have also reported reduction or stoppage of root growth following defoliation (Crider 1955, Oswalt et al. 1959, Jameson 1963, Davidson and Milthorpe 1965).

Any defoliation caused significant reductions in crown biomass of Indian ricegrass at the Chaco Canyon study site compared with unclipped plants (control) (Fig. 2). Although there were no differ-

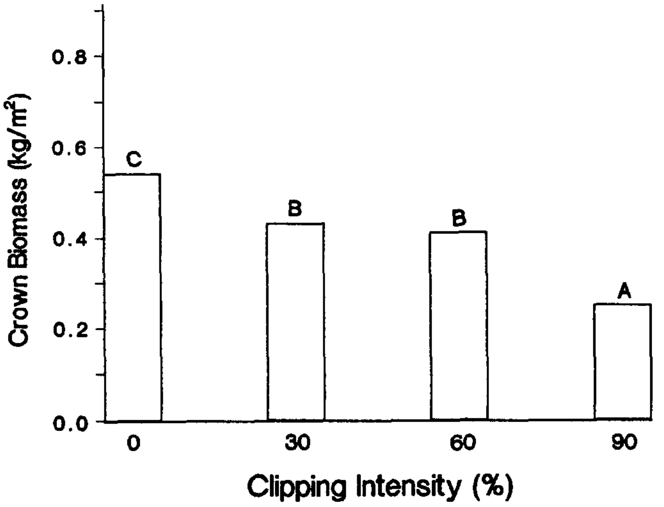

Fig. 2. Crown biomass for in situ Indian ricegrass at the Chaco Canyon study site as affected by defoliation intensity. Values are the average over slope position and previous grazing history. Means for the defoliation intensity labeled with the same letter are not significantly different ($P > 0.05$).

ences in crown weights of plants defoliated at 30 and 60%, plants defoliated at 90% had significantly lower crown weights.

Clipping of Indian ricegrass at anthesis resulted in a significant increase in crown biomass of Nezpar, but did not cause any significant change in crown weights of Paloma or the 2 native strains taken from the Chaco Canyon study site (Fig. 3). This significant clipping-x-strain interaction was caused mainly by the reaction of the Nezpar strain to the single defoliation. These findings were not in agreement with results obtained from the defoliation treatments at the Chaco Canyon study site, where several intensities of defolia-

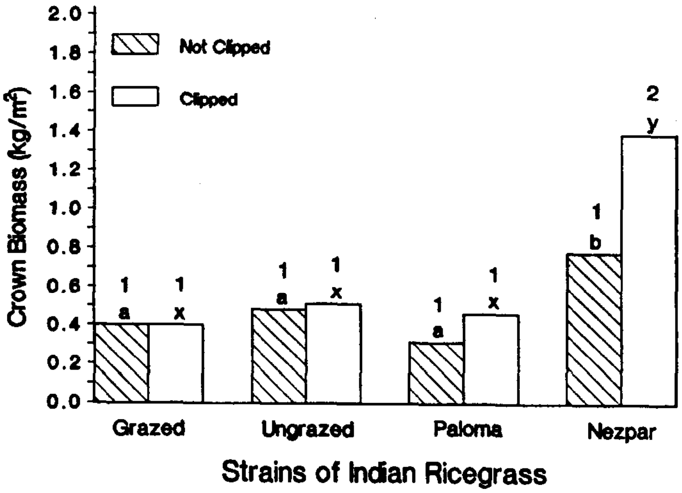

Fig. 3. Crown biomass for 4 strains of Indian ricegrass at the Cortez common garden site as affected by clipping treatment. Values are the average over replications and fertilization treatments. The clipping treatment across the 4 strains labeled with a similar letter is not significantly different ($P>0.05$). The clipping treatment within each strain labeled with a similar number is not significantly different ($P>0.05$).

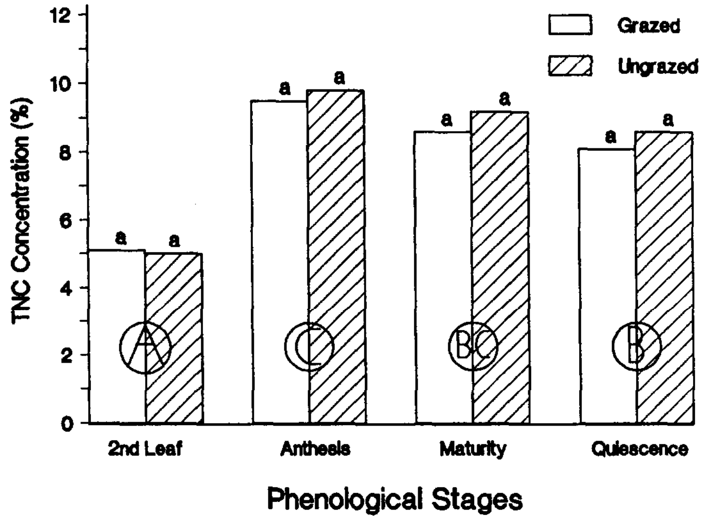

Fig. 4. Total nonstructural carbohydrate (TNC) concentrations in crowns of Indian ricegrass at the Chaco Canyon study site during 1984 as affected by long-term heavy grazing and phenological stage of development. Means for phenological stages labeled with the same capital letter are not significantly different ($P>0.05$). Means for previous grazing treatments within each phenological stage labeled with the same small letter are not significantly different ($P>0.05$).

tion resulted in a decrease in the crown weights of a grazed and ungrazed strain of Indian ricegrass. This may have resulted from possible differences in soil moisture and plant competition (Meuggler 1972) at the 2 study sites. Plants grown at the Cortez uniform garden site had higher soil moisture and relatively less competition from other plants and exhibited more growth, tillering, and increase in crown biomass as compared with in situ plants at the Chaco Canyon study site. The Chaco Canyon study site had low soil moisture after plants were defoliated, which also affected plant growth (Orodho et al. 1990).

Total Nonstructural Carbohydrate Concentrations and Pools

The seasonal TNC concentration trend of depletion during initial growth followed by replenishment of reserves in crowns was shown for both grazed and ungrazed strains of Indian ricegrass at the Chaco Canyon study site (Fig. 4). There were no significant differences in seasonal trends in crown TNC between grazed and ungrazed plants, which indicated that long-term heavy grazing had not significantly affected these trends. There was also no significant interaction for TNC among grazed and ungrazed plants with different phenological stages of development. Similar seasonal trends in carbohydrate reserves have been described for other range species by a number of authors (Sampson and McCarty 1930, Troughton 1957, Hyder and Sneva 1959, Weinmann 1961, Coyne and Cook 1971, Trlica and Cook 1972, Menke and Trlica 1981). However, no previous work was found on seasonal trends in carbohydrate reserve cycles of grasses under different grazing histories.

Results of this study did indicate that there were significant differences in TNC concentrations among in situ Indian ricegrass plants within the different intensities of defoliation at Chaco Canyon. There were no differences in TNC concentrations of plants in the 30% and 60% defoliation intensities (Fig. 5a). Greatest TNC concentrations were found in the crowns of these plants as compared with plants from either the control or 90% defoliation intensity. As expected, plants that had been subjected to 90% defoliation had the lowest TNC concentrations. Cook and Child (1971) noted that Indian ricegrass that had undergone previous defoliations showed good recovery with rest, except for those

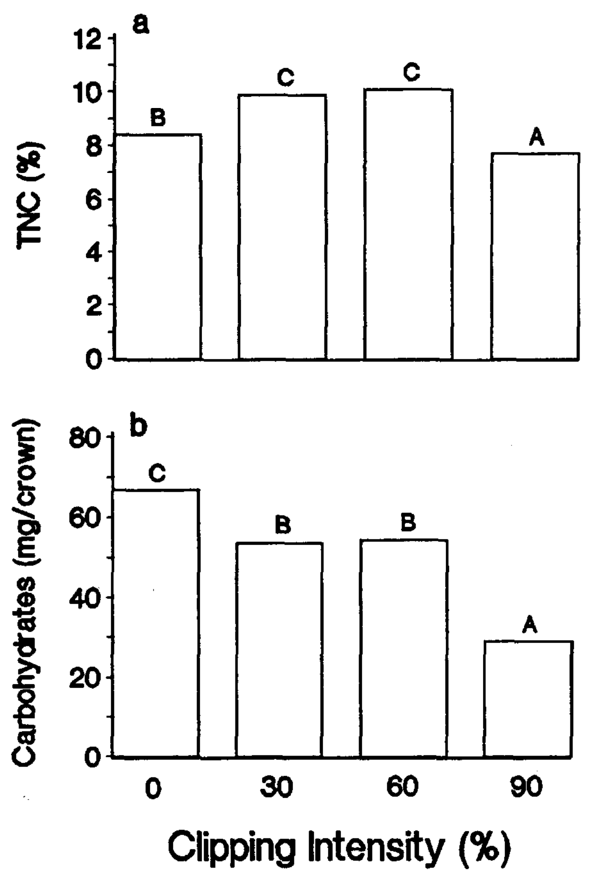

Fig. 5. Total nonstructural carbohydrate (TNC) concentrations (a) and total nonstructural carbohydrate pools (b) in crowns of Indian ricegrass at the Chaco Canyon study site as affected by clipping intensity. Values are the average over slope position and previous grazing history. Means for defoliation intensities labeled with the same letter are not significantly different ($P>0.05$).

clipped at 90%. Trlica and Cook (1971) reported that TNC reserves in both roots and crowns of Indian ricegrass were usually higher among control plants than they were for heavily defoliated plants. They noted that TNC concentrations were significantly lower when defoliation occurred during late spring or near maturity in the summer.

The total carbohydrate pools in crowns of Indian ricegrass at the Chaco Canyon study site following defoliations are illustrated in Fig. 5b. Defoliation at 90% resulted in the lowest total carbohydrate pool in crowns of Indian ricegrass, whereas the greatest carbohydrate pools were found in control plants. There were no significant differences in total carbohydrate pools among plants from the 30 and 60% defoliation treatments.

There appeared to be little correlation between TNC concentration and the total carbohydrate pool in crowns of Indian ricegrass (Fig. 5a & b). The trend observed for total carbohydrate pools in crowns was more correlated with crown weights following defoliation (Fig. 2) than with TNC concentrations (Fig. 5a). Santos and Trlica (1978) found that TNC concentration in blue grama was little affected by clipping, but that total carbohydrate pools were less because of a reduction in mass.

A single clipping in the uniform garden study had no significant effect on TNC concentrations in crowns of grazed and ungrazed strains of Indian ricegrass from the Chaco Canyon study site (Fig. 6a). On the other hand, clipping resulted in a significant increase in

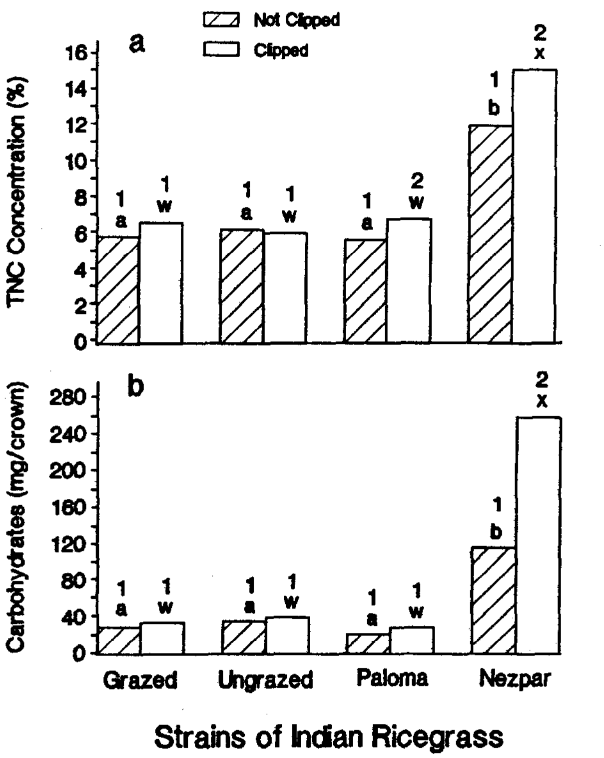

Fig. 6. Total nonstructural carbohydrate (TNC) concentration (a) and total carbohydrate pools (b) in crowns of 4 strains of Indian ricegrass at the Cortez uniform garden study as affected by clipping. Values are the average over replications and fertilization treatments. The clipping treatments across the 4 strains labeled with a similar letter are not significantly different (P>0.05). The clipping treatment within each strain labeled with a similar number is not significantly different (P>0.05).

TNC concentration in crowns of the Paloma and Nezpar strains. Clipped Nezpar plants had more than twice the TNC concentration as the other 3 strains studied. No differences were found for TNC concentrations between the clipped and unclipped plants for the grazed and ungrazed strains of Indian ricegrass.

Clipping resulted in a significant increase in the total carbohydrate pool in crowns of Nezpar, but had no significant effects on the other strains of Indian ricegrass tested (Fig. 6b). Carbohydrate pools among grazed, ungrazed, and Paloma strains were quite similar. Nezpar had the greatest carbohydrate pool in crowns of both clipped and unclipped plants compared with any of the other 3 strains tested in the uniform garden. The carbohydrate pool averaged about 5 times greater for this strain and the carbohydrate pool more than doubled with clipping. Again, carbohydrate pool size was affected more by crown weight than TNC concentration. There was a lack of correlation between TNC concentration and total carbohydrate pool in Paloma following clipping. Clipping resulted in a significant increase in TNC concentration in crowns of Paloma (Fig. 6a), but did not affect the total carbohydrate pool size of this strain (Fig. 6b).

Summary and Conclusions

Long-term heavy grazing had no significant effect on root and crown biomass of Indian ricegrass at the Chaco Canyon study site, nor did it significantly affect TNC reserves in this grass. This indicated that 50 years of protection from heavy livestock grazing pressure had not resulted in significant selection and differentiation of Indian ricegrass into an ecotype with different root and crown biomass or TNC reserve concentrations. We also found that other morphological and chemical characteristics of this grass had not been affected by long-term protection from livestock grazing (Trlica and Orodho 1989). Either long-term heavy grazing in this area has eliminated or greatly reduced nonresistant genotypes, or Indian ricegrass employs high regrowth capacity rather than defense mechanisms to overcome intense herbivory (Meijden et al. 1988, Olson and Richards 1988).

Crown biomass of Indian ricegrass was affected more by defoliation than was root biomass. Defoliation intensities affected TNC concentration and carbohydrate pools in crowns of Indian ricegrass. A 90% defoliation intensity resulted in more than a 50% reduction in the carbohydrate reserve pool. A seasonal trend of carbohydrate reserve depletion during initial growth and subsequent replenishment of reserves at a later growth stage was evident in Indian ricegrass. This pattern of the TNC cycle and amount of carbohydrate reserves were not affected by long-term heavy grazing.

Significant variations in root and crown biomass and in TNC concentrations existed among the 4 strains of Indian ricegrass and in response to clipping. Nezpar was superior to all other strains of Indian ricegrass tested at the more mesic Cortez uniform garden site with respect to crown biomass and carbohydrate reserves. Clipping resulted in greater crown biomass and TNC concentration of Nezpar, while clipping had little effect on the Chaco Canyon strains. This indicated that Nezpar was a better strain of Indian ricegrass to be recommended in the Cortez area with higher elevation and annual precipitation above 360 mm.

The 2 strains of Indian ricegrass from Chaco Canyon were not different from each other but were superior to Paloma. Their superiority was particuarly evident in their greater root biomass. These 2 strains from Chaco Canyon have promising genetic potential in their tolerance to drought and long-term heavy grazing. It is recommended that these Chaco Canyon strains be further evaluated for these traits and constituted into a single improved cultivar for use in revegetation of more arid regions (precipitation less than 250 mm) and at lower elevations in the western United States.

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