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Seasonal variation in root carbohydrate reserves of three shrubs in the Chaco Occidental (Argentina)

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*In the phytogeographic area known as Chaco Occidental (Argentina), agroforestry systems applying different ways of management are under evaluation. To increase the capacity of an area to support more animals per unit area, shrubs are removed by clearcutting at ground level. Among these shrubs are atamisqui (**Capparis atamisquea** O. Ktze., **Capparidaceae**), jarilla (**Larrea divaricata** Cav., **Zygophyllaceae**), and teatín (**Acacia furcatispina** Burk., **Leguminosae**). These shrubs are remarkable because they have high density, frequency and coverage, high resprouting capability and fast biomass recovery. However, there is very little information about them. The evaluation of the carbohydrate dynamics in native shrubs of the Chaco Occidental region has not been studied yet. Knowledge of seasonal variation of root carbohydrates in these species may be an important aspect to consider in the timing of clearcutting practice. In this study, three individuals of each species were sampled monthly, and starch and soluble sugars were determined. Starch plus soluble sugar comprise the total non-structural carbohydrate (TNC) fraction. Results showed that the minimal TNC was observed during flowering for atamisqui and teatín, and during fruiting for jarilla, which coincided with the high rainfall of the early Summer. There were significant ($P<0.01$) differences in the TNC levels between dry- and wet season- atamisqui (257 and 183 µg/mg dry weight), jarilla (196 and 135) and teatín (303 and 231), respectively. Therefore, the time of low TNC and consequently the best time to cut occurs during the time of highest precipitation, when plants have exhausted carbohydrate reserves from their roots to resprout and flower.*

***Key terms**: **Acacia furcatispina**, **Capparis atamisquea**, carbohydrate reserves, **Larrea divaricata**, root, shrubs.*

INTRODUCTION

Important problems facing mankind are shortage of food, uncertainties in energy supply, and soil erosion. One important solution to these problems may lie in the field of agroforestry, a land management system involving trees, agricultural crops and domestic animals in any or all combinations (Shankarnarayan *et al*, 1987). In the phytogeographic area known as Chaco Occidental (Argentina), which comprises approximately 100 million hectares (Adamoli & Neuman, 1972), these types of systems are under evaluation. To increase the capacity of an area to support

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more animals per unit area, trees and grass are preserved, while shrubs are cut at ground level. Among these shrubs are atamisqui (*Capparis atamisquea* O. Ktze.), jarilla (*Larrea divaricata* Cav.), and teatín (*Acacia furcatispina* Burk.). These shrubs have high density (Brassiolo, 1997), frequency and coverage, high capacity of regrowth, and can recover original biomass in five years (Morello & Saravia Toledo, 1959; W Gräffe, personal communication). Controlling the regrowth of these species has been largely unsuccessful, possibly due to poor timing in clearcutting practices.

The energy for resprouting of shrubs, once they are cut at soil level, depends primarily on root reserves. Shrubs can store considerable carbohydrate reserves in their belowground parts, which they can reallocate to aboveground material when necessary (Bryant *et al*, 1983). However, there are no reports concerning the evaluation of the carbohydrate dynamics of native shrubs of the Chaco Occidental region. Knowledge of seasonal variation of root carbohydrates in these species may be an important aspect to consider in timing of clearcutting practices.

Total non-structural carbohydrates (TNC) concentration generally includes both soluble and insoluble substances (Loescher *et al*, 1990). Environmental conditions greatly influence the translocation of TNC, water availability being the most important (Simpson & Barton, 1991). Hallgren *et al* (1991) describe an increase in carbohydrate concentration in roots of *Pinus taeda* as a response to drought. Some aspects of seasonal changes of starch, the main insoluble storage carbohydrate, and soluble sugars have been documented; the maximum content of carbohydrates, especially starch, in trees and shrubs occurs in Autumn, Winter or early Spring, and the minimum in Spring-Summer, when the active growing period is reestablished (Nambiar, 1987; Harrington, 1989; Gholz & Cropper, 1991; Renaud & Mauffette, 1991; Zasada *et al*, 1994). In an attempt to begin delineating important aspects in timing of clearcutting practice, this work aims to: i- examine changes in TNC in roots of atamisqui, jarilla, and teatín throughout the year; and ii- compare TNC variations between dry and wet seasons.

MATERIALS AND METHODS

Study area.

The study was conducted in a semi-arid region of northwestern Argentina, at "La María" Agricultural Research Station of the National Institute of Agricultural Technology (INTA). The research center is located at 28° 03' S, 64° 15' W and 169 m elevation. A 10 ha research area was located within a stand of native trees and shrubs. The climate is characterized by wet and dry seasons. Rainfall distribution is often erratic within the wet season in Summer (Boletta, 1988). Soils at the research center are well-drained Entisols (fine-loamy, mixed hyperthermic) with 7.5 pH, 1.7% organic C in the first 14 cm of soil.

Plant material.

Two evergreen species (atamisqui and jarilla) and one deciduous species (teatín) were studied. Three individuals of each species were sampled monthly from December 1991 to December 1992 (except in October 1992), choosing the most frequent size class of shrubs, those no more than 2 m high. At each sampling, a lateral root (1 cm in diameter) of each shrub was taken from the base of the shrub out to a distance of 0.5 m. The root segments were packed in ice until laboratory processing on the same day.

Chemical analysis.

The root samples were superficially scraped and ground with an electric saw. Carbohydrates concentration was determined using the method described by Ciha and Brun (1978) with some modifications. Samples of 100 mg were weighed for fresh weight determination. Dry weight was determined to constant weight at 100° C. Fresh tissue (100 mg samples) was immersed in liquid nitrogen and homogenized with 10 ml of extracting solution (glacial acetic acid: methanol: water, 1:4:5 v/v/v). The homogenate was centrifuged for 10 min at 3000 rpm and the supernatant was decanted. The residue was resuspended in 10 ml of extracting solution and centrifuged another 5 min at 3000 rpm. The supernatant was decanted, combined with the original extract and made up to 50 ml with water. Two 0.5 ml aliquots were removed for determination of total soluble sugar concentration. Starch was extracted by adding 20 ml of 0.2 N sulfuric acid to residue in the centrifuge tube and mixing. The mixture was then heated in a boiling water bath for 1 hour, cooled, filtered through Whatman N° 1 paper, and the filtrate adjusted to 50 ml with water. Two 0.5 ml aliquots were removed for starch determination. For measurement of starch and total soluble sugar, a modified phenol-sulfuric acid assay was used (Dubois *et al*, 1956). A volume of 0.5 ml of 5% (v/v) phenol solution and 2.5 ml of concentrated sulfuric acid were added to 0.5 ml aliquots. The mixture was shaken and cooled to room temperature. The absorption was then determined by spectrophotometry (Shimadzu model UV-120-02 spectrophotometer) at 490 nm. The contents of starch and soluble sugars were determined through standard curves of glucose. TNC was defined as the sum of starch and soluble sugar concentration. Although TNC may be overestimated with this method (Ward & Deans, 1993), this fact is not significant for the comparative purpose of this work.

Experimental design and statistical analysis.

The field was sorted at random in plots, each assigned to a different month of the study. Within each plot three random individuals per species were used for each determination. Each sample was processed twice and its mean used. Collected data were analyzed by ANOVA. Differences in TNC and soluble sugars between dry and wet season were determined by orthogonal contrasts using the Scheffe test (Steel & Torrie, 1980).

RESULTS

The rainfall from December 1991 through December 1992 was 973 mm (Fig 1). The dry season –less than 20 mm mean monthly rainfall– began in May and lasted until September.

Phenological stages for each species are shown in Figure 2. Teatín was deciduous on July and leaves were replenished during October. Flowering and fruiting occurred from December to March for atamisqui, from October to December for jarilla, and from December to February for teatín.

Figure 3 shows the TNC variation for the three spcies during the year. The minimal concentration of TNC was observed during early Summer (December), when the highest precipitation took place (Figs 1 and 3). Thereon, TNC increased during Autumn and reached its highest peak in the Winter time. The maximal TNC for teatín correlated with the abscission of foliage.

From orthogonal contrasts using the Scheffe test, there were significant statistical differences ($P<0.01$) in TNC between dry and wet season for all three analyzed species, respectively: 257 and 183 for atamisqui, 196 and 135 for jarilla, and 303 and 231 µg/mg dry weight for teatín. Soluble sugars show less seasonality (data not shown). Differences between dry and wet season in soluble sugars were only significant ($P<0.05$) for jarilla: 63.4 and 52.3 µg/mg dry weight, respectively. Sugar seasonality followed the same direction as starch.

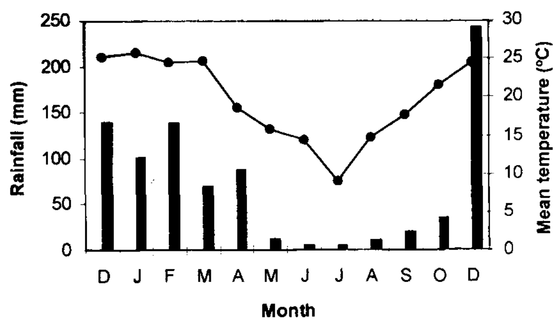

Fig 1. Mean temperature (circles) and rainfall (bars) in the region throughout the experimental period (December 1991-December 1992).

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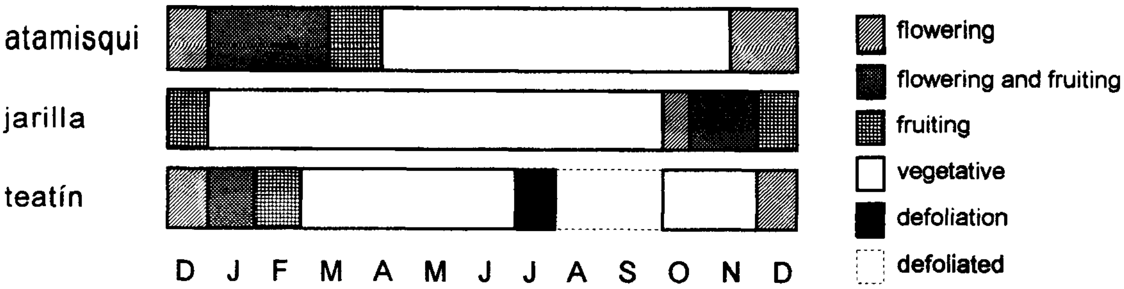

Fig 2. Phenological stages of shrubs throughout the experimental period (December 1991-December 1992).

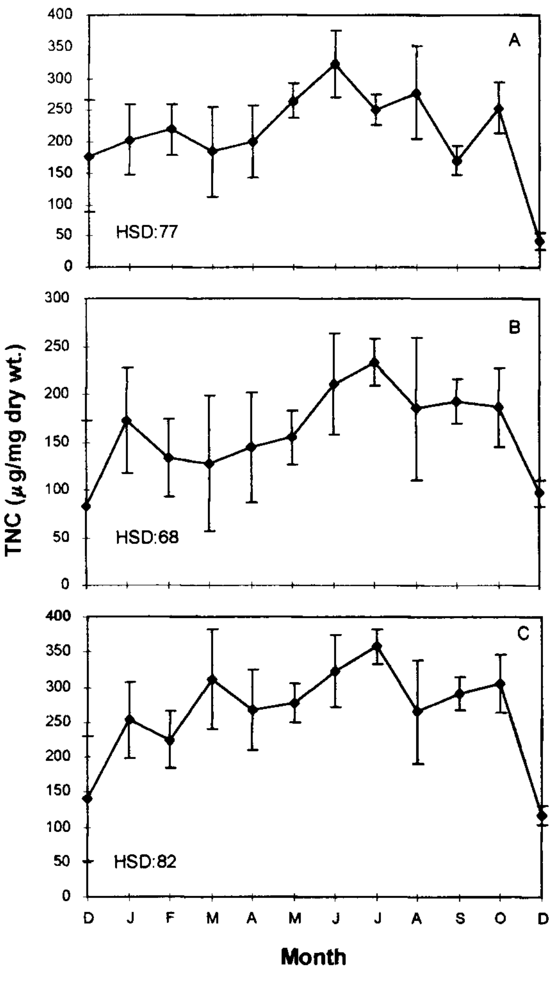

Fig 3. Seasonal changes in the total non-structural carbohydrates (TNC) in roots. **A**, atamisqui (*Capparis atamisquea* O. Ktze); **B**, jarilla (*Larrea divaricata* Cav.); C, teatín (*Acacia furcatispina* Burk.). Diamonds, means of three replicates ± SD. **HSD**: Tukey's Honestly Significant Difference (P < 0.05).

DISCUSSION

The rainfall throughout the experimental period was almost twice the year average –550 mm per year according to Boletta (1988)– but its distribution maintained the typical pattern described by Boletta *et al* (1989).

The variability in TNC among individuals was large probably because of genetic characteristics, external environment (both site and climate), and fruiting/flowering processes (Saranpää & Höll, 1989; Simpson & Barton, 1991). The minimal TNC was observed during flowering for atamisqui and teatín, and during fructification for jarilla, when maximal temperature and rainfall were registered. Total non-structural carbohydrates reaching its minimum during the growth period has been documented (Harrington, 1989; Loescher *et al*, 1990; Renaud & Mauffette, 1991; Zasada *et al*, 1994); however, the exact timing depends on environmental conditions. Harrington (1989) compared his results with those of other authors who also worked in Gamble oak (*Quercus gambelii* Nutt). Carbohydrates measured in oak roots had similar trends. However, low points and subsequent peaks sometimes appeared at different times during the growing season. This could be partially explained by climatic differences from year-to-year, which affect plant phenology and the resulting TNC trends (Harrington, 1989). Loescher *et al* (1990) reported that, after reaching a minimal reserve, most tissues usually begin to accumulate reserves immediately. In some cases, like atamisqui's in the present assay, this accumulation is interrupted during the period of fruit ripening. The increases in TNC during Autumn may be due to the fact that environmental conditions were still favorable for the production of photosynthates after the species had flowered and fructified. Moreover, TNC may increase under deficit irrigation, as a consequence of the decrease in respiration rate caused by lowering temperatures (Loescher *et al*, 1990). This increase in TNC during the time plants are subjected to low temperatures and water stress (Winter) would enhance their ability to tolerate unfavorable conditions (Sakai & Larcher, 1987; Hallgren *et al*, 1991). In agreement with Loescher *et al* (1990), the maximal TNC for teatín correlated with the abscission of foliage.

The less seasonality exhibited in soluble sugars was also mentioned by other authors in *Pinus elliottii* (Gholz & Cropper, 1991). Similar direction in seasonality is shown by sugar and starch –as described by Loescher *et al* (1990). This is probably due to the considerable interconversion between starch and soluble sugars which could take place in stems (Yamashita, 1990), but not in roots.

In contrast to Kozlowski and Keller's (1966) findings, the three species we studied behaved similarly, independently of their condition of evergreen or deciduous foliage. This undifferentiated behavior may be due to the presence of a clear dry season.

As a preliminary conclusion, to support a feasible agroforestal system in Chaco Occidental, the time of low TNC appears to be the most adequate time for cutting. According to our study, this time of low TNC occurs during the high rainfall season, when plants have exhausted carbohydrate reserves from their roots to resprout and flower. However, further research should be conducted to establish this fact definitively.

REFERENCES

ADAMOLI J, NEUMAN R (1972) Salteño alluvial Chaco. INTA, Buenos Aires. RIA, series 3, vol 9, N° 5

BOLETTA PE (1988) Climate. *In*: FAO (eds) Clear and habilitation of lands in Chaqueña semiarid region. Chile. pp 7-15

BOLETTA PE, ACUÑA LR, JUAREZ DE MOYA ML (1989) Analysis of the climatic characteristics in Santiago del Estero, and behavior of weather under the drought during 1988-1989. INTA-UNSE, Santiago del Estero, Argentina

BRASSIOLO M (1997) Zur Bewirtschaftung degradierter Wälder im semiariden Chaco Nordargentiniens unter Berücksichtigung der traditionellen Waldweide. Doktorarbeit. Albert-Ludwigs-Universität, Freiburg, Germany

BRYANT JP, CHAMPIN FS III, KLEIN DR (1983) Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos 40: 357-368

CIHA AJ, BRUN WA (1978) Effect of pod removal on nonstructural carbohydrate concentration in soybean tissue. Crop Sci 18: 773-776

DUBOIS M, GILLES KA, HAMILTON JK, REBERS PA, SMITH F (1956) Colorimetric method for determination of sugars and related substances. Anal Chem 28: 350- 356

GHOLZ HL, CROPPER WP Jr (1991) Carbohydrate dynamics in mature *Pinus elliottii* var. *elliottii* trees. Can J For Res 21: 1742-1747

HALLGREN SW, TAUER CG, LOCK JE (1991) Fine root carbohydrate dynamics of loblolly pine seedlings grown under contrasting levels of soil moisture. For Sci 37: 766-780

HARRINGTON MG (1989) Gambel oak root carbohydrate response to spring, summer, and fall prescribed burning. J Range Manage 42: 504-507

KOZLOWSKI T, KELLER T (1966) Food relations of woody plants. Bot Rev 32: 293-380

LOESCHER WH, McCAMANT T, KELLER JD (1990) Carbohydrate reserves, translocation, and storage in woody plant roots. Hort Sci 25: 274-281

MORELLO JH, SARAVIA TOLEDO C (1959) El bosque chaqueño. Rev Agronóm Noroeste Argent. Vol III, 1-2

NAMBIAR EKS (1987) Do nutrients retranslocate from fine roots? Can J For Res 17: 913-918

RENAUD JP, MAUFFETTE Y (1991) The relationships of crown dieback with carbohydrate content and growth of sugar maple (*Acer saccharum*). Can J For Res 21: 1111-1118

SAKAI S, LARCHER W (1987) Cold acclimation in plants. In: BILLINGS WD, GOLLEY F, LANGE OL, OLSON JS, REMMERT H (eds) Ecological studies. Vol 62. Berlin: Springer-Verlag. pp 97-137

SARANPÄÄ P, HÖLL W (1989) Soluble carbohydrates of *Pinus sylvestris* L. sapwood and heartwood. Trees 3: 138-143

SHANKARNARAYAN KA, HARSH LN, KATHJU S (1987) Agroforestry in the arid zones of India. Agr Syst 5: 69-88

SIMPSON LA, BARTON AFM (1991) Time dependence of starch levels in the sapwood of *Eucalyptus diversicolor* (Karri) as: standing trees, stored saw-logs, ringbarked trees and trees felled without lopping. Holzforschung 45: 253-257

STEEL RGD, TORRIE JH (1980) Principles and Procedures of Statistics: A Biometrical Approach. 2nd ed. New York: McGraw-Hill

WARD E, DEANS JD (1993) A simple method for the routine extraction and quantification of non-structural sugars in tree tissues. Forestry 66: 171-180

YAMASHITA T (1990) Variations in amounts of carbohydrates, amino acids and adenine nucleotides in mulberry tree (*Morus alba* L.) stems during transitional phases of growth. Tree Physiol 6: 191-200

ZASADA JC, TAPPEINER JC III, MAXWELL BD, RADWAN MA (1994) Seasonal changes in shoot and root production and in carbohydrate content of salmonberry (*Rubus spectabilis*) rhizome segments from the central Oregon Coast Ranges. Can J For Res 24: 272-277