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Defoliation frequency affects morphophysiological traits in the bunchgrass *Poa ligularis*

La frecuencia de defoliación afecta las características morfofisiológicas en la gramínea perenne *Poa ligularis*

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Abstract. *Poa ligularis* is an important forage in Patagonian rangelands. Populations of this perennial bunchgrass have been severely affected by overgrazing. We propose that increased defoliation frequencies will decrease (1) aerial- and belowground dry matter production, (2) root survival, and (3) concentration and content of total non-structural crown + root carbohydrates, and (4) increase root mortality. Five defoliation frequencies (plus 1 control) were applied in a representative grassland of the Occidental District in Patagonia during two consecutive growing seasons. All four hypotheses were rejected. Aerial and belowground dry matter production increased from one to two or three defoliations. Root production and dynamics were not affected by the study defoliation frequencies. Total non-structural carbohydrate (TNC) concentration (%) and content (g/plant) in crown + roots were increased when defoliations augmented from three to five times (%, 2002-2003), or from two to three times (% and g/plant, 2003-04) during the growing cycle, but TNC contents in 2002-03. These results suggest that TNC availability in crown and roots, and plant vigor on *P. ligularis* in dry Patagonia are favored by light to moderate defoliation frequencies (no more than two or three defoliations annually) immediately before internode elongation to 5 cm stubble height each.

Keywords: Aerial dry weight; Defoliation frequency; Perennial grasses; *Poa ligularis*; Root dynamics; Total non-structural carbohydrates.

Resumen. *Poa ligularis* es una forrajera importante en los pastizales de la Patagonia. Las poblaciones de esta gramínea cespitosa perenne han sido afectadas severamente por el sobrepastoreo. En este estudio proponemos que incrementos en la frecuencia de defoliación reducirán (1) la producción de materia seca aérea y subterránea, (2) la supervivencia de raíces, y (3) la concentración y contenido de carbohidratos no estructurales totales (CNET) en coronas + raíces, e (4) incrementarán la mortalidad de raíces. Se aplicaron cinco frecuencias de defoliación (más un control no defoliado) en un pastizal representativo del Distrito Occidental en Patagonia durante dos estaciones de crecimiento consecutivas. Las cuatro hipótesis fueron rechazadas. La producción de materia seca aérea y subterránea se incrementó de una a dos o tres defoliaciones. La producción y dinámica de raíces no fueron afectadas por las frecuencias de defoliación estudiadas. La concentración (%) y en contenido (g/planta) de los CNET en coronas + raíces se incrementaron cuando la frecuencia se incrementó de tres a cinco defoliaciones (%, 2002-2003), o de dos a tres defoliaciones (%, 2003-2004) durante el ciclo de crecimiento, excepto los contenidos de CNET en 2002-2003. Estos resultados sugieren que la disponibilidad de carbohidratos en coronas + raíces, y el vigor de las plantas de *P. ligularis* en la zona árida de Patagonia son favorecidos por frecuencias de defoliación bajas a moderadas (no más de dos o tres defoliaciones anuales), a 5 cm desde el nivel del suelo, inmediatamente antes de la elongación de los entrenudos.

Palabras clave: Peso seco aéreo; Frecuencia de defoliación; Gramíneas perennes; *Poa ligularis*; Dinámica de raíces, Carbohidratos no estructurales totales.

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INTRODUCTION

It is widely known that defoliation frequency can affect plant growth in perennial grasses (Briske & Richards, 1995). Plant growth might be affected by reductions in (1) size and viability of axillary meristems (buds), (2) growth and aerial biomass production, (3) concentration and content of total nonstructural carbohydrates, and/or (4) growth and dynamics of the root system.

The potential capacity of leaf area replacement is partly determined by the number and degree of physiological activity of the apical, intercalary and axillary meristems which remain in the plant after a defoliation event (Briske & Richards, 1995). Factors which diminish the availability, metabolic activity and/or growth capacity of these meristems [i.e., increases in defoliation frequency: Newton et al. (1992) in *Trifolium repens*] might compromise persistence of affected rangeland plants (Briske & Richards, 1995).

Carbohydrate pools play an important role in initiating plant growth when photosynthetic capacity is severely limited (Briske & Richards, 1995). High defoliation frequencies can reduce concentration and/or content of total soluble nonstructural carbohydrates in crowns and roots, thereafter reducing vigor and productivity of defoliated plants (Sosebee et al., 2004). Content of total nonstructural carbohydrates was reduced concomitantly with increases in defoliation frequency in *Andropogon gerardii* (Forwood & Magai, 1992), *Panicum virgatum* (Anderson et al., 1989), and *Pennisetum* spp (Spitaleri et al., 1994).

Growth and functioning of roots are dependent upon the energy provided by photosynthesis (Briske & Richards, 1995). After a defoliation event, the root system continues functioning as a carbon sink, depending on a continuous supply from the photosynthetically-active aerial plant parts (Briske & Richards, 1995). As a result, removal of aerial plant parts may affect root growth (Briske & Richards, 1995). Various studies have reported that grass defoliation reduces root biomass (Holland et al., 1996) and root relative growth rate (Becker et al., 1997b). Successive defoliations have reduced grass root growth in *Bouteloua gracilis* (Bekele et al., 1974) and *Aristida ramosa* and *Danthonia linkii* (Harradine & Whalley, 1981). Flemmer et al. (2002) reported that total root number decreased as defoliation frequency increased in three perennial grass species.

Poa ligularis is considered one of the major forages in Patagonia, and it is widely distributed in rangelands of Argentina (Fernández & Busso, 1999). This species is a native, caespitose perennial grass, of high competitive ability and defoliation tolerance (Giorgetti et al., 2006). This is a key species in management of Patagonian rangelands. Its abundance, vigor, height and degree of defoliation are indicators of rangeland condition. The genus *Poa* is spread worldwide (Canada: Scotter, 1972; Peru: Bryant & Farfan, 1984; U.S.A.: Andariese & Covington, 1986; China: Bedunah & Schmidt, 2000); although genotypes of this genus are very likely quite different in (1) growth characteristics and (2) natural habitats to extrapolate these results to a world-wide-scale, they might be useful overseas to gain knowledge on its response to various defoliation frequencies under arid conditions in Patagonia. This tussock perennial grass is highly grazed by domestic livestock in rangelands of Patagonia. As a result, it has seriously been affected by overgrazing (Busso, 1997). *Poa ligularis* is resistant to drought and moderate grazing (Latour, 1979). However, factors which might limit re-establishment of a photosynthetic surface because of variations in defoliation frequency are unkown. The hypotheses of this study are that increases in defoliation frequencies on *Poa ligularis* (1) reduce aerial and root biomass production, (2) root survival, and (3) concentration and content of total nonstructural carbohydrates in crown + roots, and (4) increase root mortality. The objective of this study was to investigate the effect of various defoliation frequencies on (1) production of aerial and root biomasses, (2) rates of root increase and mortality, and (3) concentration and content of total nonstructural carbohydrates in crown + roots of *P. ligularis*.

MATERIALS AND METHODS

Study site. Studies were conducted at the experimental field of INTA EEA Bariloche (41°10'S 70°41'W, 1000 m.a.s.l., NW Patagonia, Argentina), located 80 km from San Carlos de Bariloche, during two consecutive growing seasons (2002/03 and 2003/04). Climate is arid, cold temperate and is characterized by a lightly positive hydric balance during the winter months, and a large water deficit during the warmest months. Mean annual precipitation is 280 mm (Bustos & Rocchi, 1993). Mean temperature of the warmest month is 15 °C (January) and of the coldest month is 2.1 °C (July) (Bustos & Rocchi, 1993). An automatic meteorological station located at the study site provided the climate data during the study period (Fig. 1).

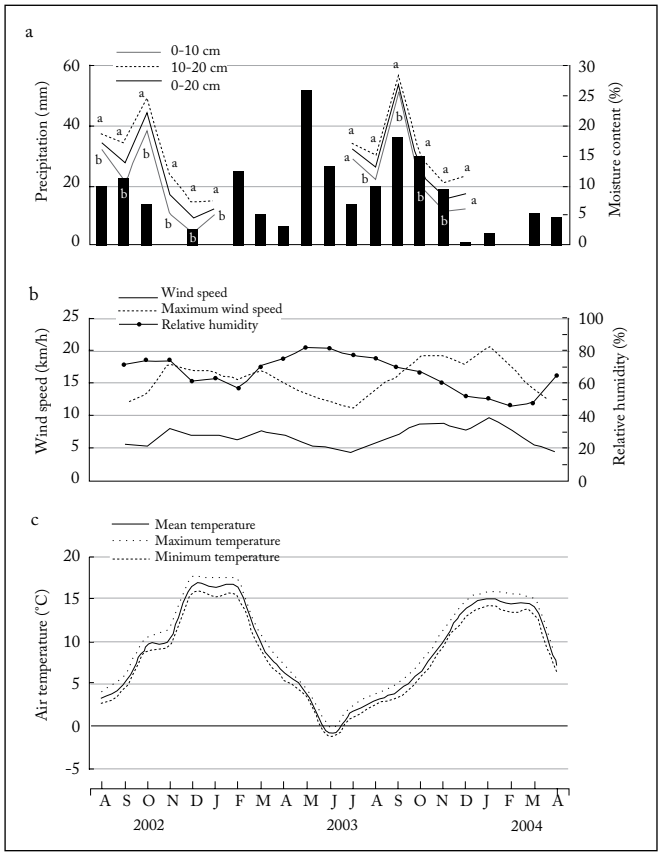
Vegetation is a shrubby-gramineous steppe dominated by *Mulinum spinosum*, *Adesmia campestris*, *Poa ligularis* and *Stipa speciosa*. Soils are of the xerophilous - Haplargid type (Lores et al., 1983). Grazing is extensive in this region, and stocking rate used by land managers varies between 1 and 0.25 sheep/ha.

The species. It has a long dormancy period from mid-summer (January-February) to July-August (mid- to late winter), during which it appears to be dry. Its main forage production is in spring (September-November). It flowers towards the end of spring (November-December) and seed dispersal occurs during summer (January-February) (Giorgetti et al., 2000).

Measurements

Soil moisture content. Soil moisture content was determined gravimetrically. During both growing seasons, 20 samples were randomly taken once monthly: 10 samples were obtained from a depth of 0 to 10 cm, and the other 10 from 10 to 20 cm depth from the soil surface.

Fig. 1. Climate data during the study growing seasons in 2002/03 and 2003/04, (a) Monthly precipitation (black histograms) and soil moisture content (%) at 0-10 (grey solid line), 10-20 (dotted line) and 0-20 cm soil depth (black solid line), (b) Monthly average wind speed (solid line), Monthly average maximum wind speed (dotted line) and Monthly average air relative humidity (solid symbols), (c) Monthly average mean temperature (solid line), and monthly average minimum (large dashed line) and maximum (small dashed line) temperatures. Different letters between sampling depths (0-10 versus 10-20 cm) within each sampling date during mid-winter through early summer in 2002/03, and mid-winter through summer in 2003, indicate significant differences ($p<0.05$) in soil moisture content.
Fig. 1. Datos climáticos durante las estaciones de crecimiento de 2002/03 y 2003/04, (a) Precipitación mensual (histogramas negros) y contenido de humedad del suelo (%) a 0-10 (línea sólida gris), 10-20 (línea punteada) y 0-20 cm de profundidad del suelo (línea sólida negra). (b) Velocidad del viento promedio mensual (línea sólida), velocidad del viento máxima promedio mensual (línea punteada) y Humedad relativa del aire mensual promedio (símbolos sólidos), (c) Temperatura mensual promedio (línea sólida) y promedios mensuales de temperaturas mínimas (línea cortada larga) y máximas (línea cortada corta). Líneas diferentes entre las profundidades de muestreo (0-10 versus 10-20cm) durante cada fecha de muestreo desde mediados del invierno hasta principios del verano 2002/03, y mediados del invierno hasta el verano en 2003, indican diferencias significativas ($p<0,05$) en el contenido de humedad del suelo.



*Aerial Dry matter production***.** Within an exclosure (1 ha) to domestic livestock and small mammals, 160 plants (80 for each study growing cycle) of *P. ligularis* were randomly selected and marked. Before initiation of the study in 2002/03 and 2003/04, during the dormant season (July-August), all study plants were defoliated to 5 cm stubble height such that only growth produced during each growing season was included in the measurements. Within each growing cycle, the 80 plants were assigned to 5 defoliation treatments groups (n=16 per group). Each group contained eight plants to be defoliated and eight plants to be used as Controls (i.e., undefoliated). Plants were defoliated 1, 2, 3, 4 or 5 times during each growing season. Time intervals between the defoliation frequencies varied between 30 to 51 days depending on timing, frequency and growing season of defoliation. Defoliations were always conducted leaving 5 cm stubble each time regrowth reached 10 cm height from the soil surface. Plants of the second growing cycle had also been defoliated during the first study growing season. In this way, the cumulative effect of the different defoliation frequencies was evaluated. During the second study growing cycle, regrowth production allowed to conduct 3 out of the 5 study defoliation frequencies (i.e., plants corresponding to defoliation frequencies 4 and 5 were unable to reach 10 cm height beyond the third defoliation).

*Root system dynamics***.** Thirty of the study plants of *P. ligularis* were randomly selected to study their root system dynamics for each studied defoliation frequency in 2002/03 and 2003/04. Selected plants were from the five defoliation treatments and one undefoliated control in each study growing season. A root periscope similar to that used by Becker et al. (1997b) allowed direct observation of root appearance (a measure of growth) and disappearance, and root spatial distribution in the soil (Flemmer et al., 2002). Glass tubes 0.5 m length and 3.5 cm internal diameter were buried from the plant periphery in an angle (15 to 20° with respect to the vertical: Becker et al., 1997b) such that the bottom part of the glass tubes reached approximately the center of the plant crown. Holes were made using an auger up to 30 cm soil depth. Fifteen centimeters of each tube were left over the soil surface area. This tube extension was covered with dark tape and a piece of PVC pipe such that light entrance into the tubes was avoided. Roots exposed to light can inhibit their growth (Levan et al., 1987). Previous to placement, horizontal circumferences perpendiculars to each tube were engraved every 3 cm tube length, except the tube portion over the soil surface. Root observation was conducted up to 30 cm soil depth. This was because more than 70% of the root system biomass is located in the first 30 cm soil depth in various native perennial grasses at the study site (Fernández & Busso, 1999).

This technique allowed a periodic root monitoring. It was possible to (1) conduct a root mapping at each sampling time, and (2) know if roots had disappeared, or new roots appeared, between successive samplings using a root color scale. Sampling times were: (1) 2002/03: 4 and 31 October, and 5 December in 2002, and 31 January in 2003, and (2) 2003/04: 14 August, 22 October, and 19 November in 2003, and 21 January and 25 April in 2004. It means that samplings were conducted mostly every 30 to 60 days. Four color categories were considered: (1) transparent white (more recent roots),

(2) light brown, (3) brown, and (4) dark brown (a result of initiation of root cortex cell death). This information was used to determine root percentage (as a fraction from here on) increase (Ri) and mortality (Rm) rates [root percentage either increase or death per unit time (day), respectively] during any given study period.

Root increase rates were estimated as:

Ri= Sr + Rr,

where Sr [i.e., the root percentage survival per unit time (day) between any two consecutive sampling dates] and Rr [i.e., the percentage of new roots which appeared per unit time (day) between any two consecutive sampling dates] represent the root survival (S) and recruitment (R) rates (r), respectively. Unit for both parameters is percentage root/d. Survival rate (Sr) was determined as:

$Sr = Survivors_{(t)}/[N_{(t-1)} * L]$

where $Surivors_{(t)}$ is the number of roots which survived during two consecutive samplings, $N_{(t-1)}$ is the number of roots at time $_{t-1}$ (first sampling during the study period), and L is study period length (L: days during any one sampling and the following). Recruitment rate (Rr) was estimated as:

$Rr= New_{(t)}/[T_{(t)} * L]$

where $New_{(t)}$ is the number of new (N) roots at time $_t$ (those which appear between the first and second samplings of any study period), $T_{(t)}$ is the Total (T) number of roots at time $_t$, and L is the length (L) of the study period, already defined for calculating Sr. Roots must show a white color and a swollen aspect to be considered as new (category 1 in color).

Root mortality (Rm) rates were estimates as:

$Rm= D_{(t)}/[N_{(t-1)} * L]$

where $D_{(t)}$ is the number of dead roots (D) at time $_t$ (i.e., roots which disappeared between the first and second sampling of any study period), $N_{(t-1)}$ is the Number (N) of roots at the previous sampling time (i.e., $_{t-1}$) time, and L is the period length (L). Only roots which disappeared between two consecutive sampling times are considered dead, because even though root cortex cells start dying (showing a dark brown color), the stele remains active (Deacon, 1987). In addition, water and nutrient uptake occurs in these roots after epidermis and cortex cells have died (Eissenstat & Yanai, 1997).

Total non-structural carbohydrates. For each defoliation frequency, plants were dug up from the soil and taken to the laboratory. This was conducted at two times: immediately before defoliation [n=4 defoliated plants (before defoliation) and 4 controls], and two to three weeks thereafter (n=4 defoliated plants and 4 controls; Table 1). Two to three weeks after defoliation on each defoliation frequency, defoliated and non-defoliated plants were extracted from the soil using a shovel, obtaining soil blocks of 0.5 x 0.5 x 0.5 m (length, width, height, respectively; soil volume: 0.125 m^3). For example, when plants were defoliated 3 times during a growing season, 4 defoliated and 4 non-defoliated plants were harvested immediately before the third defoliation, and 4 defoliated and 4 non-defoliated plants were harvested after the third defoliation (Table 1). At the laboratory, any harvested plant was separated into aerial biomass (defoliation to the soil surface level), and crown + roots. Production of accumulated aerial biomass (g dry matter per plant); crown + root biomass (A) (g dry matter per plant), and concentration of total non-structural carbohydrates in crown + roots (B) were determined on each plant. Total non-structural carbohydrate content per plant was obtained as AxB (Richards & Caldwell, 1985). Aerial biomass samples were dried in an oven at 70°C for 72 h before weighing. For each defoliation frequency, production of accumulated (dry matter coming from previous defoliations plus dry matter production at the time plants were dug up from the soil) aerial biomass gives a measure of the

Table 1. Experimental design to study the effects of various defoliation frequencies [undefoliated controls, plus plants defoliated once (1), twice (2), three times (3), four times (4) or 5 times (5) during the growing season of 2002-2003] on total non-structural carbohydrate concentration and content in plants of *P. ligularis*. Abbreviations are as follows: D= Defoliated; U= Undefoliated; B= Before defoliation; A= After defoliation. The same experimental design was repeated during the 2003-2004 growing season on a different set of 80 plants which received those same defoliation treatments during 2002-2003.

Tabla 1. Diseño experimental para estudiar los efectos de varias frecuencias de defoliación (controles no defoliados, más plantas defoliadas una vez (1), dos (2), tres (3), cuatro (4) o cinco (5) veces durante la estación de crecimiento de 2002-2003) sobre la concentración y contenido de carbohidratos no estructurales totales en plantas de *P. ligularis*. Las abreviaturas son como sigue: D= Defoliada; U= no defoliada; B= antes de la defoliación; A= después de la defoliación. El mismo diseño experimental se repitió durante la estación de crecimiento de 2003-2004 en un grupo diferente de 80 plantas, que recibieron los mismos tratamientos de defoliación aplicados durante 2002-2003.

Defoliation frequency	1				2				3				4				5			
Number of plants	16				16				16				16				16			
	8 D		8 U		8 D		8 U		8 D		8 U		8 D		8 U		8 D		8 U	
	4 B	4 A	4 B	4 A	4 B	4 A	4 B	4 A	4 B	4 A	4 B	4 A	4 B	4 A	4 B	4 A	4 B	4 A	4 B	4 A

effects of any defoliation frequency on total plant dry matter production until that time. Previous aerial biomass measures did not include stubble since immediately prior to the study initiation all study plants had been defoliated leaving 5 cm stubble height, and we wanted to know dry matter production from that height in all defoliation treatments. However, when plants were dug up from the soil on each defoliation frequency, dry matter production from the soil surface up to 5 cm height was also quantified. Defoliation was not conducted at the soil surface level at any time, but when plants were dug up from the soil, since stem bases are a source of TNC reserves (Briske & Richards, 1995).

Crown + roots were (1) washed out of the soil using a 60-mesh-screen (Busso et al., 1990), (2) dried in an oven at 70 °C until constant weight, (3) weighed, and (4) ground using a 60- mesh-size screen (Busso et al., 1990). From these samples, subsamples of 100 mg each were taken by duplicate. Concentration of total non-structural carbohydrates in crown + roots was determined by acid hydrolisis following Morris (1948). Acid extraction allows a 2 to 3 greater carbohydrate digestion than extraction using boiling water (Richards & Caldwell, 1985). Twenty ml of ammonium oxalate at 0.5% (w/v) were added to each subsample, and digestion was conducted for 2h. This material was then filtered and washed. Two ml were taken from this solution, which were combined with the reactive Antrona. Thereafter, samples were heated to 97 °C for 15 to 20 min in test tubes. Total non-structural carbohydrate concentration was measured using a spectrophotometer (absorbance) at 612 nm. Standard glucose solutions were used as controls. Total non-structural carbohydrate concentration was estimated by comparing each sample with the glucose standards to a known concentration (standard curve). Such concentration (%) was calculated for each plant following Murphy (1958):

$$\text{Total non-structural carbohydrates (\%)} = \frac{[\text{Sample absorbence}] \times 100}{0.27}$$

where 0.27 is the standard absorbance.

Statistical analyses. Data analysis was conducted using the program Statistica 6.0 (2001; Statsoft, Tulsa, OK, USA), using the General Linear Model (GLM). Within each year, data were analyzed using a nested ANOVA design to evaluate the following factors: Defoliation frequency (5 levels: 1 to 5 defoliations) and Treatment (2 levels: Defoliated and Non-defoliated). This latter treatment was nested within the first one. The test HSD (Honestly Significant Difference) of Tukey (Tukey, 1953) was conducted whenever F tests were significant at $p<0.05$. Homogeneity and normality of variances were tested using the Levene (Levene, 1960) and Shapiro Wilks (Shapiro et al., 1968) tests. Growth rate (gr ms/day=slope of the relationship) was determined using simple linear regression between that biomass and days from study initiation. At the same time, the analysis of assumptions (i.e., normality, homocedasticity and residue independence) involved in the construction of linear models was conducted. Differences between regression lines for each treatment were tested following Neter & Wasserman (1974).

Comparison of root increase, survival, recruitment, and mortality rates was conducted using repeated measures ANOVA. Factors were (1) days between consecutive sampling dates, (2) defoliation treatments (6 levels: T1, T2, T3, T4, T5 and undefoliated Control), and (3) sampling depth from the soil surface (9 levels: 3-6-9-12-15-18-21-24-27 cm). The sphericity assumption was evaluated using the test of Mauchly (Mauchly, 1940); when this test did not fit the assumption, the multivariate approach was used through the statistic of Wilks (Wilk´s lambda) (Wilks, 1932).

Values of total non-structural carbohydrate percentages during the first year, and content of non-structural carbohydrates in the second year were transformed to *ln* for analysis.

RESULTS

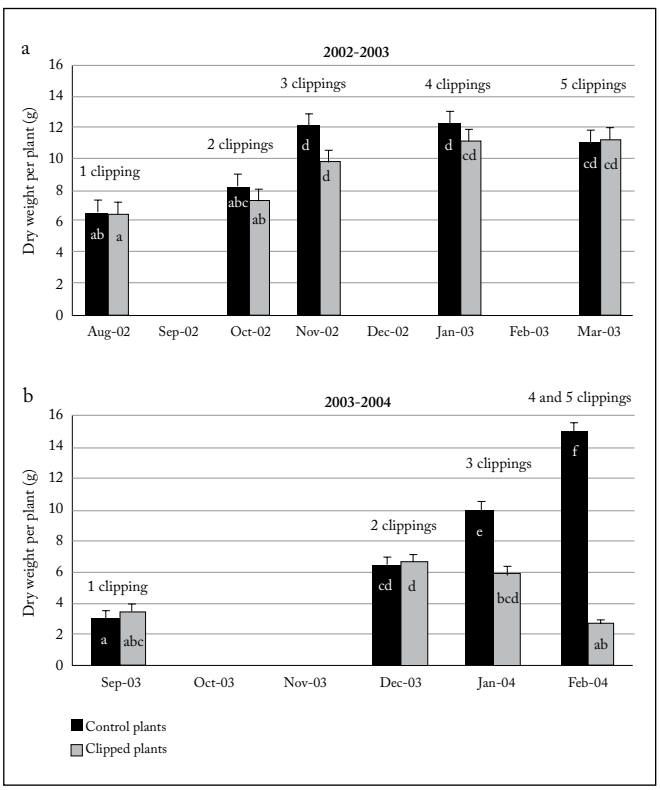
Soil moisture content. The greatest and lowest soil moisture contents at both study depths occurred in October and December, respectively, during 2002/03, and September and November, respectively, during 2003/04 (Fig. 1). Soil moisture content was often greater ($p<0.05$) deeper than shallower with respect to the soil surface level (Fig. 1).

Aerial dry matter production. During 2002/03, defoliated and undefoliated plants showed a similar ($p>0.05$) dry matter production within each defoliation frequency (Fig. 2a). At the same time, plants defoliated at least three times had a greater ($p<0.05$, Fig. 2a) dry matter production than those defoliated once or twice during the growing season; from November to March samplings, dry matter production on Controls (which describe the accumulation of aerial biomass in time in undisturbed plants) was greater ($p<0.05$) than that earlier in the season (Fig. 2a).

During the 2003/04 growing season, the interaction between defoliation frequencies and treatments was significant ($p<0.05$, ANOVA results not shown). Advancement of the growing season increased ($p<0.05$) dry matter production on undefoliated controls. Defoliated plants increased ($p<0.05$) dry matter production until plants were defoliated twice, when maximum values were reached; these values diminished ($p<0.05$) about 59% when plants were defoliated four times. From the third to the fifth defoliation frequency, dry matter production of undefoliated controls was greater ($p<0.05$) than values on defoliated plants (Fig. 2b). Plants that were defoliated either four or five times during 2002/03 only produced dry matter production until the third defoliation frequency in the next (2003/04) growing season; regrowth height of these plants after the third defoliation in 2003/04 did not allow to make further defoliations.

Fig. 2. Aerial dry matter production (g dry matter/plant) for each defoliation frequency (1 to 5 defoliations) on Control (solid histograms) and defoliated (grey histograms) during the study (2002/03 and 2003/04) growing seasons. Each histogram is the mean of n=8. Different letters indicate significant differences (p<0.05) between treatments (with or without defoliation) and defoliation frequencies. Vertical bars represent 1 standard error of the mean.

Fig. 2. Producción de material seca aérea (g materia seca/planta) para cada frecuencia de defoliación (1 a 5 defoliaciones) en plantas Control (histogramas sólidos) y defoliadas (histogramas grises) durante las estaciones de crecimiento estudiadas (2002/03 y 2003/04). Cada histograma es el promedio de n=8. Letras diferentes indican diferencias significativas (p<0,05) entre tratamientos (con o sin defoliación) y frecuencias de defoliación. Las barras verticales representan 1 error estándar de la media.



It was determined that growth rates on plants defoliated twice or three times during the 2002/03 growing season were 20% greater (p<0.05) than those on control plants, when slopes of the regression lines between dry matter production (y) versus time (x) were compared among treatments (Table 2). In the second year, plants defoliated one, two or three times showed slopes 40 to 50% lower (p<0.05) than those registered on control plants (Table 2). At the same time, reductions (p<0.05) in slope values were from 70 to 80% on plants defoliated four or five times compared with values on undefoliated controls (Table1). Slope values were greater (p<0.05) on plants defoliated one, two or three times than on those defoliated four or five times. Slope values within any of the defoliation frequencies were greater (p<0.05) in the first than in the second study growing season (Table 2)*:* such reduction was 60% in the undefoliated controls; 80% on plants defoliated one, two or three times; and 90% on plants defoliated four or five times.

Root biomass. During 2002-03, the interaction between frequency and defoliation treatments was not significant (p>0.05). Plants defoliated three times during the growing season had the greatest (p<0.05) crown + root biomass compared to the other defoliation frequencies in both treatments (with and without defoliation, Fig. 3a). The interaction between frequency and defoliation treatments was again not significant (p>0.05) during 2003/04. The greatest (p<0.05) crown + root biomasses in the second growing season were obtained on plants defoliated two or three times in both defoliation treatments (Fig. 3b).

Fig. 3. Biomass of roots + crown (g dry matter/plant) for each defoliation frequency (1 to 5 defoliations) on Control (solid histograms) and defoliated (grey histograms) plants during (a) 2002-2003 and (b) 2003-2004. Each histogram is the mean of n=8. Different letters indicate significant differences (p<0.05) between treatments (with or without defoliation) and defoliation frequencies. Vertical bars represent 1 standard error of the mean.

Fig. 3. Biomasa de raíces + coronas (g material seca/planta) para cada frecuencia de defoliación (1 a 5 defoliaciones) en plantas Control (histogramas sólidos) y defoliadas (histogramas grises) durante (a) 2002-2003 y (b) 2003-2004. Cada histograma es el promedio de n=8. Letras diferentes indican diferencias significativas (p<0,05) entre tratamientos (con o sin defoliación) y frecuencias de defoliación. Las barras verticales representan 1 error estándar de la media.

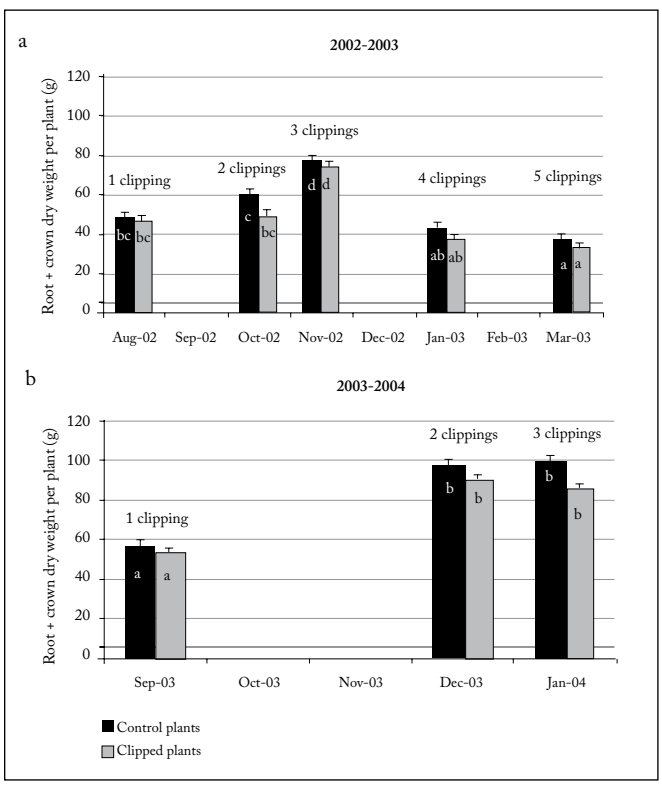
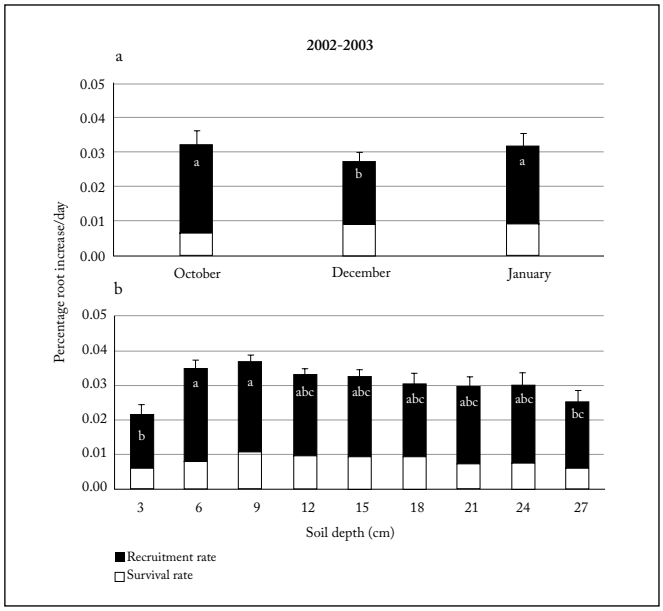


Table 2. Slopes, standard errors (S.E.) and confidence intervals of the regression lines between dry matter production (y) versus time (x) in the various defoliation frequencies and the control during the study years.
Table 2. Pendientes, errores estándar (E.E.) e intervalos de confianza de las líneas de regresión entre la producción de materia seca (Y) versus tiempo (X) en las varias frecuencias de defoliación y en el control durante los años de estudio.

Treatments	2002-2003				2003-2004				2002-2003 vs. 2003-2004
	Slope (b)	S. E.	Confidence interval -95%	Confidence interval +95%	Slope (b)	S. E.	Confidence interval -95%	Confidence interval +95%	
1	0.095 ab	0.009	0.076	0.114	0.015 b	0.004	0.016	0.024	*
2	0.099 b	0.006	0.087	0.110	0.020 b	0.002	0.015	0.025	*
3	0.099 b	0.005	0.089	0.108	0.016 b	0.001	0.013	0.018	*
4	0.093 ab	0.004	0.085	0.101	0.007 c	0.000	0.006	0.008	*
5	0.087 ab	0.004	0.079	0.095	0.009 c	0.001	0.007	0.011	*
Control	0.081 a	0.002	0.077	0.086	0.032 a	0.001	0.029	0.035	*

Different letters in the slope column indicate significant differences in dry matter accumulation with time in the various defoliation frequencies and the undefoliated control at p<0.05. * significant differences at p<0.05.
Letras diferentes en la columna correspondiente a las pendientes indican diferencias significativas en la acumulación de materia seca con el tiempo en las varias frecuencias de defoliación y las plantas no defoliadas a p<0,05. * diferencias significativas a p<0,05.

Fig. 4. Proportion [percentage (as a fraction) per day] increase rate in the number of roots, and components of the increase rate (survival rates and recruitment rates), at the various sampling dates (a) and sampling soil depths (b) during the study period 2002/03. Each histogram is the mean of n=5. Different letters in the histograms for the various sampling either dates or soil depths indicate significant differences (p<0.05). Vertical bars represent 1 standard error of the mean.
Fig. 4. Tasa de incremento en proporción [porcentaje (como fracción) por día] en el número de raíces, y componentes de la tasa de incremento (tasas de supervivencia y tasas de reclutamiento), en las fechas de muestreo (a) y profundidades de muestreo del suelo (b) durante el período de estudio 2002/03. Cada histograma es el promedio de n=5. Letras diferentes en los histogramas para las fechas de muestreo o profundidades de suelo indican diferencias significativas (p<0,05). Las barras verticales representan un error estándar de la media.



Root system dynamics

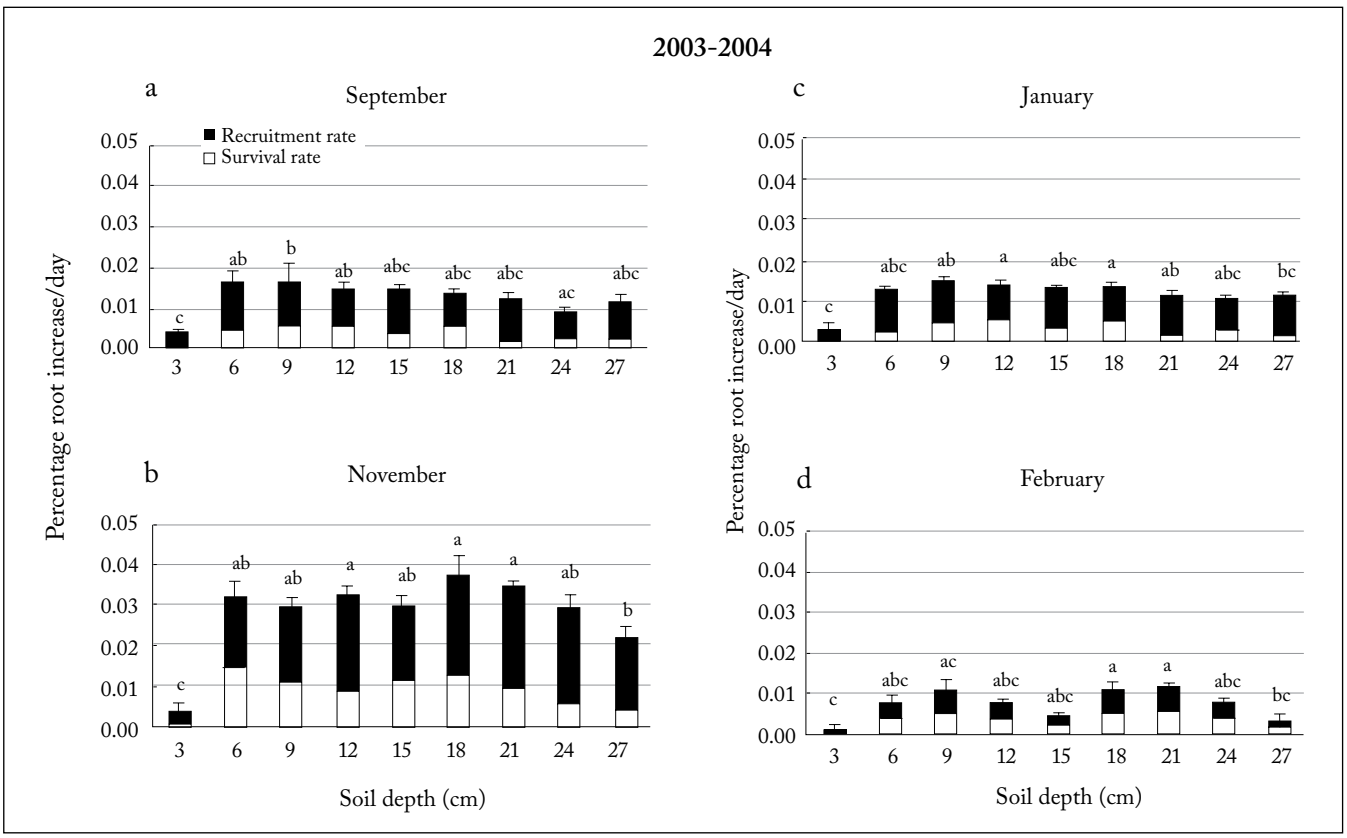
Root increase rates. Root increase rates were similar (p>0.05) between defoliation treatments in 2002/03 and 2003/04. Sampling dates showed significant (p<0.05) differences in root increase rates during 2002/03. Root increase rates were 25% lower (p<0.05) in October and January than December (Fig. 4a) as a consequence of reductions (30%) (p<0.05) in root recruitment rates and no differences (p>0.05) in root survival rates. At the same time, root increase rates of the root system were lower (p<0.05) at 3 cm than at 6 and 9 cm soil depth (Fig. 4b). Root survival rates did not show significant differences (p>0.05) among dates. Also, root increase rates were greater (p<0.05) at 6 and 9 than at 27 cm soil depth (Fig. 4b).

During 2003/04, both sampling dates and depths interacted significantly (p<0.05; ANOVA results not shown). In September, root increase rates were lower (p<0.05) at 3 than at 6, 9 and 12 cm soil depth (Fig. 5a). In addition, such rates were greater (p<0.05) at 9 than at 24 cm soil depth. During this month, no significant differences (p>0.05) were found either for survival or for recruitment rates among soil depths.

During November, January and February, lowest (p<0.05) root increase rates, in general, were shown at 3 cm soil depth in comparison to the other study soil depths (Fig. 5 b, c and d). In November, root survival rates were lower (p<0.05) at 3 than 6 cm soil depth. In January, root survival rates were lower (p<0.05) at 3 and 27 than at 18 and 21 cm soil depth (Fig. 5c). In February, root survival rates at 3, 24 and 27 cm soil depth were lower (p<0.05) than those at 6, 9, 12, 15, 18 and 21 cm soil depth. In November, lowest (p<0.05) values in root recruitment rates were shown at 3 cm soil depth, while in January and February there were no significant differences (p>0.05) among soil depths (Fig. 5).

Fig. 5. Proportion [percentage (as a fraction) per day] increase rate in the number of roots, and components of the increase rate (survival rates and recruitment rates) at the various soil sampling depths during 2003/04: (a) September (14 Aug. to 22 Oct.), (b) November (22 Oct. to 19 Nov.), (c) January (19 Nov. to 21 Jan.) and (d) February (21 Jan. to 25 Apr.). Each histogram is the mean of n=5. Different letters in the histograms indicate significant differences (p<0.05). Vertical bars represent 1 standard error of the mean.

Fig. 5. Tasa de incremento en proporción [porcentaje (como fracción) por día] en el número de raíces, y componentes de la tasa de incremento (tasas de supervivencia y tasas de reclutamiento), en las profundidades de muestreo del suelo durante el período de estudio 2003/04: (a) Septiembre (14 Agosto a 22 Octubre), (b) Noviembre (22 Octubre a 19 Noviembre), (c) Enero (19 Noviembre a 21 Enero) y (d) Febrero (21 Enero a 25 Abril).
Cada histograma es el promedio de n=5. Letras diferentes en los histogramas dentro de cada fecha de muestreo indican diferencias significativas (p<0,05). Las barras verticales representan 1 error estándar de la media.



Root increase rates at 3 or 27 cm soil depth showed no significant differences (p>0.05) among sampling dates (Fig. 5 a and b). However, the remaining soil depths showed greater (p<0.05) root increase rates in November than at the other sampling dates.

Root mortality rates. Root mortality rates were similar (p>0.05) between defoliation treatments during 2002/03 and 2003/04. During 2002/03, there were no significant differences (p>0.05) in root percentage mortality rates among sampling dates (mean± 1 standard error; 0.012±0.002) or soil depths (0.013±0.01). During 2003/04, there were significant differences (p<0.05) among sampling dates: root mortality rates were 3-4 times greater (p<0.05) in November than in October, January and February (Fig. 6). There were also significant differences (p<0.05) in root mortality rates among soil depths. Root mortality rates were lower (p<0.05) at 3 than at 6, 9, 12, 15, 21 and 27 cm soil depth (Fig. 6b).

Concentration of total non-structural carbohydrates (TNC). In 2002/03, frequency and defoliation treatments interacted significantly (p<0.05; ANOVA results not shown). In control plants, TNC concentrations showed low levels up to November (2002/03) or December (2003/04) and a significant increase (p<0.05) late in the growing period (March 2003 and January 2004 (Fig. 7a). Concentrations of TNC were reduced (p<0.05) from plants defoliated once to plants defoliated twice or three times (Fig. 7a). The first, fourth and fifth defoliation frequencies showed similar (p>0.05) TNC concentrations (Fig. 7a). Total non-structural carbohydrate concentrations were greater (p<0.05) in control plants than in plants defoliated three, four or five times (Fig. 7a).

In 2003/04, the interaction between frequencies of defoliation and defoliation treatments was significant (p<0.05; ANOVA results not shown). Control plants showed an increase (p<0.05) in TNC concentrations from the first and second to the third defoliation frequency (Fig. 7b). De-

Fig. 6. Proportion [percentage (as a fraction) per day] mortality rates of roots at the various sampling either (a) dates or (b) soil depths during the study period of 2003/04. Each histogram is the mean of n=5 for any sampling either date or soil depth. Different letters indicate significant differences (p<0.05). Vertical bars represent 1 standard error of the mean.

Fig. 6. Tasas de mortalidad de raíces en proporción [porcentaje (como fracción) por día] en las varias (a) fechas o (b) profundidades del suelo durante el período de estudio 2003/2004. Cada histograma es el promedio de n=5 para cada fecha o profundidad de muestreo del suelo. Letras diferentes indican diferencias significativas (p<0,05). Las barras verticales representan 1 error estándar de la media.

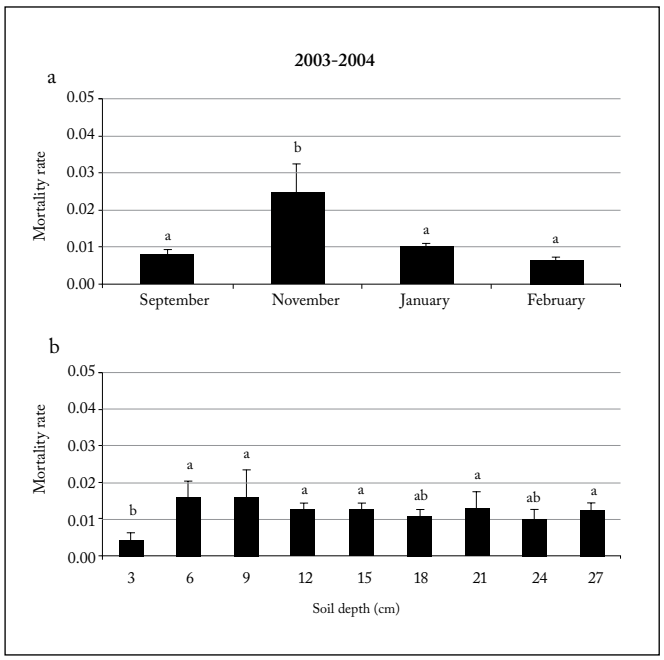
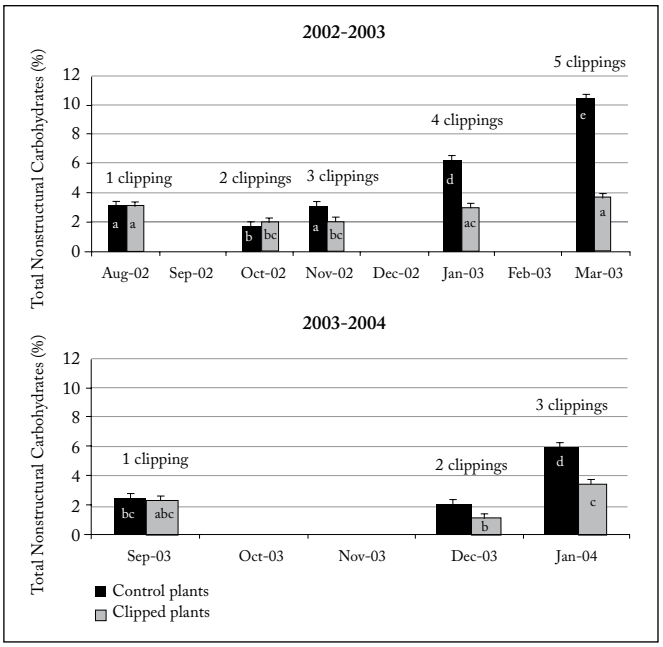


Fig. 7. TNC concentration (%) for each defoliation frequency (1 to 5 defoliations) on Control (solid histograms) and defoliated (grey histograms) during the study (2002/03 and 2003/04) growing seasons. Each histogram is the mean of n=8. Different letters indicate significant differences (p<0.05) between treatments (with or without defoliation) and defoliation frequencies. Vertical bars represent 1 standard error of the mean.

Fig. 7. Concentración de CNET (%) para cada frecuencia de defoliación (1 a 5 defoliaciones) en plantas Control (histogramas sólidos) y defoliadas (histogramas grises) durante las estaciones de crecimiento estudiadas (2002/03 y 2003/04). Cada histograma es el promedio de n=8. Letras diferentes indican diferencias significativas (p<0,05) entre tratamientos (con o sin defoliación) y frecuencias de defoliación. Las barras verticales representan 1 error estándar de la media.



foliated plants also showed an increase (p<0.05) in TNC concentrations from the second to the third defoliation frequency. These values, however, were similar (p>0.05) to those shown in the first frequency of defoliation (Fig. 7b). Control plants had greater (p<0.05) concentration of TNC only when compared to plants defoliated three times (Fig. 7b).

Content of total non-structural carbohydrates. The interaction between frequencies of defoliation and defoliation treatments was significant (p<0.05; ANOVA results not shown) in 2002/03. Control plants showed a TNC content increase (p<0.05) from the first and second to the third and fourth frequencies of defoliation (Fig. 8a). The maximum (p<0.05) TNC content in control plants occurred in the fifth defoliation frequency. Defoliated plants from all defoliation frequencies had similar (p>0.05) contents of TNC (Fig. 8a). Plants defoliated three or more times had lower (p<0.05) TNC contents than control plants (Fig. 8a). Contents of TNC were on average 34%, 57% or 68% lower (p<0.05) in plants defoliated three, four or five times, respectively, than on controls.

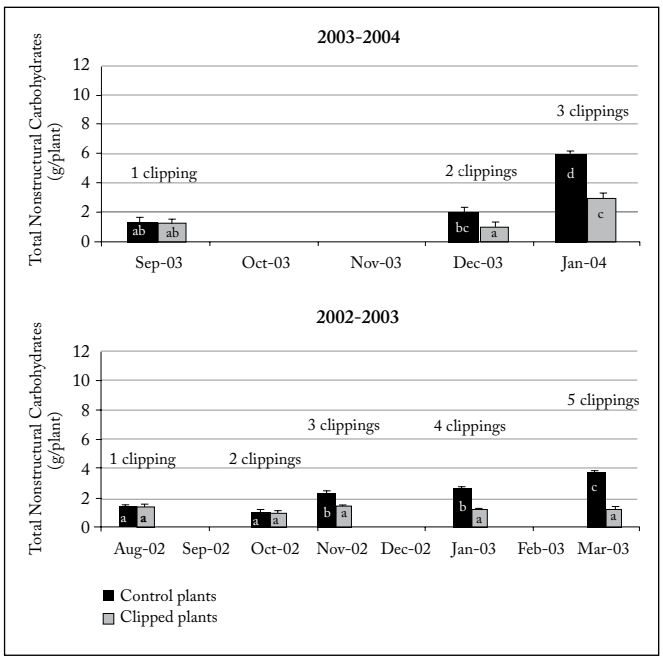
In 2003/04, the interaction between frequencies of defoliation and defoliation treatments was also significant (p<0.05; ANOVA results not shown). Control and defoliated plants showed an increase (p<0.05) from the second to the third frequency of defoliation (Fig. 8b). Total nonstructural carbohydrate contents were greater in control plants than in plants defoliated two or more times (Fig. 8b). Reduction (p<0.05) in TNC content on defoliated plants was approximately 50% with respect to control plants.

DISCUSSION

Soil moisture content. Soil moisture content variation during the growing season agrees with that demonstrated by Peláez et al. (2001) for rangelands in central Argentina. Increases of soil moisture content with increasing depth are also similar to those reported by Brown (1995).

Aerial yield responses to defoliation. Aerial biomass of *Poa ligularis* showed a seasonal pattern, with maximum production occurring in late spring and early summer. This pattern

Fig. 8. TNC content (g/plant) for each defoliation frequency (1 to 5 defoliations) on Control (solid histograms) and defoliated (grey histograms) plants during the study (2002/03 and 2003/04) growing seasons. Each histogram is the mean of n=8. Different letters indicate significant differences (p<0.05) between treatments (with or without defoliation) and defoliation frequencies. Vertical bars represent 1 standard error of the mean.
Fig. 8. Contenido de CNET (g/planta) para cada frecuencia de defoliación (1 a 5 defoliaciones) en plantas Control (histogramas sólidos) y defoliadas (histogramas grises) durante las estaciones de crecimiento estudiadas (2002/03 y 2003/04). Cada histograma es el promedio de n=8. Letras diferentes indican diferencias significativas (p<0,05) entre tratamientos (con o sin defoliación) y frecuencias de defoliación. Las barras verticales representan 1 error estándar de la media.



has been observed by other authors in the Occidental District (Fernández & Busso, 1999). Biomass values on control plants were similar to those reported in other works conducted in Patagonia (Fernandez & Busso, 1999).

The absence of significant differences in aerial biomass values between control and defoliated plants in 2002-03, demonstrated that defoliated plants exactly compensated for the forage removals of controls. This can be partly explained as a result of greater growth rates on defoliated plants than control plants. During the second growing season, the accumulated effect of one year of defoliations produced a 50% reduction in dry matter production in the treatment with three defoliations (T3). More frequent defoliations (four and five defoliations) produced 80% less aerial biomass than control plants. Additionally, these defoliated plants did not reach the appropriate height (10 cm) for making the subsequent defoliation treatments after the third defoliation. In the second year, none of the defoliation treatments was able to reach growth rates as large as those of control plants; lowest values were reached on plants defoliated four or five times. Reduction in biomass production as a result of increased defoliation frequency has been reported in several perennial grass species (Briske & Richards, 1995).

Plants defoliated at least three times in 2002-03 had a greater dry matter production than those defoliated once or twice during the growing season. We recognize that this is partially due to the fact that frequencies 1 and 2 had shorter growing periods. Plants in frequency 1 were defoliated and accumulated biomass since the start of the experiment until August, while those of frequency 2 did so until September. However, it was not the case for plants defoliated from 3 to 5 times during the growing season of 2002-2003, despite it increased from November 2, 2002 to March 3, 2003. Even more, accumulated defoliation pressure on aerial dry matter production was even greater in 2003-04, when plants defoliated more than 4 times showed a lower dry matter production than those defoliated either three or less times or remained undefoliated, even though the growing season increased from January 4 (up to 3 defoliations) to February 4 (four or more defoliations), respectively. These results clearly indicate the effects of defoliation pressure (increased defoliation frequency) on dry matter production during two consecutive growing seasons. Reductions in plant biomass on perennial range grasses have also been reported elsewhere as a result of defoliation treatments in previous years (Zhang & Romo, 1994).

Poa ligularis presented a compensatory response in aerial biomass production when defoliation frequency was light. During the second year, three or more defoliations produced an undercompensatory response in the study species; this could eventually affect persistence of *P. ligularis* in Patagonian rangelands on a long-term basis. Similar results related to compensatory responses in dry matter production after light to moderate defoliations have been reported on forage grasses of semiarid environments (Zhao et al., 2008). Increases in time for recuperation after defoliation helps occurrence of compensatory responses (Briske & Richards, 1995).

Biomass growth rates, given by the slopes of the relationships between dry matter production versus time, declined from the first to the second study growing season on control and defoliated plants (Table 2). In 03/04 control plants accumulated, by the end of the season, more aerial biomass than control plants in 02/03; however, their estimated growth rate (gr dry matter/day) was less than half in 03/04 than in 2002/03 (Table 2; 0.035 vs 0.081, respectively). This was because during 2002/2003, the maximum dry matter production per plant was reached much earlier (November 02) than in 2003/04 (February 04). Days from the first sampling date to reaching the maximum aerial dry matter production (X axis for the simple linear regression) were about 90 in 2002/03 (Y=12 gr/plant), and a 150 in 2003/04 (Y=15 gr/plant). Differences between years might also be related to differences in environmental (climatic) conditions between growing seasons.

Interannual variations in precipitation within a given semiarid rangeland region may determine different annual biomass

productions (Giorgetti et al., 1997). In the study area, annual precipitation in 2002 (338 mm) was greater than that of 2003 (240 mm) and the 30-year average of 264 mm. Fall and winter were unusually wet during 2002: precipitation during fall and winter were 162 mm and 103 mm, respectively. Long-term average precipitation (last 30 years) for fall and winter are 109 mm and 85 mm, respectively. In addition, precipitation during spring 2002 was 18 mm, whereas the 30-year-average is 50 mm. During 2003, fall and winter precipitation were 85 mm and 70 mm, respectively; these values are below the 30-year-average. During spring 2003, precipitation was 50 mm similar to the long-term average. A relationship between temporal precipitation variation and rangeland production has been reported in semiarid environments (Giorgetti et al., 1997). Observed changes in growth rates in this study might be attributed, at least in part, to variations in the distribution of precipitations during 2002/03 and 2003/04.

Precipitation quantity has been shown to influence grassland aboveground net primary productivity (ANPP) positively, whereas experimental increases of temporal variability in water availability, however, have commonly exhibited a negative relationship with ANPP (Nippert et al., 2006). It is interesting to note that Oesterheld et al. (2001) reported that one third of the unexplained variation in ANPP is related to previous-year ANPP: ANPP per mm of precipitation was higher in years preceded by wet, more productive years (i.e, 2002/03 in our study) than in years preceded by average years; similarly, ANPP per mm of precipitation was reported to be lower in years preceded by dry, less productive years than in years preceded by average years (Oesterheld et al., 2001). Since previous-year ANPP was, in turn, associated with precipitation of a year before (Oesterheld et al., 2001), current-year ANPP was also explained by precipitation of two previous years. Their findings not only increase our predictive ability, but they also change our understanding of how ANPP responds to fluctuations in precipitation. If ANPP is thought to vary according to current-year precipitation only, it will simply track annual precipitation in time. According to Oesterheld et al. (2001), however, ANPP fluctuations are buffered if wet, more productive years alternate with dry, less productive years. Anyhow, the increase in the decline from one year to the next of 60% on controls to 90% on plants defoliated 4 or 5 times during the growing season is a clear indication of the detrimental effects of increased defoliation frequency on dry matter production.

Belowground yield responses to defoliation. Biomass of crown + roots also showed a seasonal production pattern. During the first growing season, a biomass increase was observed in November (mid-spring), for defoliated and undefoliated plants. This seasonality in root biomasses during the year has also been observed in other grass species of temperate grasslands (Liu & Huang, 2001). Increases in root biomass were corresponded with greater values in the rates of increase, survival and recruitment.

Root biomass of defoliated and undefoliated plants appeared to increase from the first to the second studied year. These results could partially be attributed to more favorable conditions during 2003/04 than in 2002/03, related to a wetter spring in 2003 (Fig. 1a). A novel approach in the root dynamics study was the way of determining the survival and recruitment rates (to determine the increase rates), and the rates of mortality. Root growth rates in *P. ligularis* were similar between undefoliated and defoliated plants during 2002/03 and 2003/04. This indicates that photoassimilates continue to be partitioned to root growth even under severe defoliation frequencies. This is similar to that reported by Richards (1984) in the grazing-sensitive *Pseudoroegneria spicata.* In this species, root growth continues after a severe defoliation to the expense of mobilizing less photoassimilates for photosynthetic canopy re-establishment. This highlights an important factor which most likely contributes to the persistence of this species in rangelands of Central and Southern Argentina. *Poa ligularis* was able to sustain root growth maintaining high shoot growth rates during the first study growing season (2002/03), when plants were moderately defoliated (up to three defoliations). Defoliated plants had similar root+crown biomass, root increase rates, recruitment rates and survival rates than control plants; thus, it was observed a seasonal variation in the magnitude of these parameters irrespectively of defoliation frequency. Holding survival and recruitment rates during both study growing seasons secured maintenance of root exploration for soil water and nutrients. The results from this study differ from those of Becker et al. (1997b). These authors reported lower rates of root appearance and disappearance after plants of the perennial grasses *Stipa tenuis* and *Piptochaetium napostaense* were severely defoliated, late in the growing season under rainfed conditions. Their results differ from ours because they defoliated plants of those perennial grasses only once at each of various phenological stages during each of two growing cycles.

Root dynamic responses to defoliation. Control and defoliated plants showed similar root mortality rates during both study growing seasons. These results differ from other studies on root dynamics which reported increased root mortality in perennial grass plants after defoliation (Briske & Richards, 1995). These authors attributed this response to a reduced canopy photosynthesis immediately following defoliation, and emphasized that these experiments clearly demonstrate the importance of current photosynthesis for the maintenance of root growth and function.

Rates of root increase (recruitment + survival) and mortality during 2002/03 and 2003/04 showed variation with soil depth. Lowest values were in general registered in the first 3 cm soil depth; intermediate values in intermediate soil depths (about 20 cm from the soil surface), and low values at the greatest study soil depths (24 - 27 cm). Rates of recruitment and survival fol-

lowed in general the same pattern of variation. This pattern of new root production rates in relation to soil depth was reported by Liu and Huang (2001) in *Agrostis palustres*, and Steinke et al. (1996) in *Agropyretum repentis*. Various authors have observed a low root density in the most superficial soil layers, followed by an increase toward the more subsuperficial soil depths, and back to low root density values at the deepest soil layers (Steinke et al., 1996). Finally, root increase rates were greater than root mortality rates at each depth during both study growing seasons, but January 2003-04, which contribute to explain the root biomass increases until November and February during the first and second study growing seasons, respectively.

The lowest root survival and mortality rates were found at 3 cm depth. A negative relationship between both rates was most likely expected. However, other studies found a great variation when studying such relationship (http://mercury.bio.uaf.edu/~roger_ruess/Errata.htm). These authors pointed out that their relationship was expected to have poor predictive power: it was attributed to the fact that low longevity could translate to either high or low mortality depending on the number of roots that die, and vice versa (http://mercury.bio.uaf.edu/~roger_ruess/Errata.htm). In their study, for example, browsed and unbrowsed plots had extremely low, nearly identical survival rates in winter on a two-year-study, yet mortality of unbrowsed plots averaged 2.5 times that of browsed plots over the same time interval.

The results of this study suggest that the immediate effect of defoliating *P. ligularis* up to three times per year do not affect either root biomass or root dynamics. This is because root growth was not affected by defoliation frequency, since defoliated plants had similar value as undefoliated ones. This root response to the study defoliation frequencies has been shown in other grass species of temperate climate (Wallace, 1981). It is interesting to note that root and crown biomass was almost one order of magnitude larger than the aerial biomass, a fact that has been extensively reported on perennial grasses in arid regions (Distel & Fernández 1986).

Total non-structural carbohydrate yield responses to defoliation. Concentration and content of TNC showed a seasonal pattern in control plants, exhibiting an increase with the time from mid-winter (August) to early fall (March) in 2003-04, and from late winter (September) to early summer (January) in the next growing season. This TNC pattern has been shown in other species like *Bromus inermis* (Brueland et al., 2003) and *Agrostis stolonifera* (Narra et al., 2004). However, some authors have proposed that TNC availability is reduced as a result of temperature increases and reductions of water availability during summer (Liu & Huang, 2001). This has been attributed to an unbalance in carbon production via photosynthesis and its consumption throughout respiration (Liu & Huang, 2001). In *Agrostis palustris*, however, the decline in carbohydrate content in roots was related to the cessation of shoot growth at supraoptimal temperatures (Xu & Huang, 2000).

At the end of spring (November)-early summer (December) of both study years, time of high physiological activity in shoots and roots, concentration of TNC was lower on defoliated than on undefoliated plants. This result may have been due to use of carbohydrates as an energy source for re-establishing a photosynthetic surface removed by defoliation. Reichman & Smith (1991) emphasized that a great energy inversion is needed to compensate the loss of aerial biomass immediately after defoliation. Total non-structural carbohydrate concentration (2002-2003) and content (2002-2003 and 2003-2004) were reduced when defoliation frequency increased. These results agree with those reported in other studies on perennial grass species (Sosebee et al., 2004).

Carbohydrate reserves contribute to regrowth initiation for a few days when there are no photosynthetic structures or these are insufficient to sustain plant respiration and growth demands (Richards & Caldwell, 1985). These TNC reserves are most likely very important for survival of *Poa ligularis* in the study region. This is because these reserves might contribute to respiration of the dormant, but alive, meristems which retains its growth potential in the range plants during the winter period (low temperature stress). Cyr & Bewley (1989) reported that an enough TNC amount needs to be accumulated in roots for winter survival, and the initial spring regrowth if no photosynthetic surface areas are available in perennial grasses.

MANAGEMENT IMPLICATIONS

Our results indicate that TNC availability in crown and roots, and plant vigor on *P. ligularis* in dry Patagonia are favored by light to moderate defoliation frequencies immediately before internode elongation: no more than two or three defoliations annually to 5 cm stubble height each. Becker et al. (1997a,b) demonstrated that defoliation previous to differentiation of the growth apex from vegetative to reproductive was conducive to overcompensation of dry matter production and a much greater root dynamics compared to later defoliations during the growing season in two perennial grasses of Central Argentina. Resting periods immediately prior to apex differentiation from vegetative to reproductive are thus critical (i.e., Becker et al. 1997a). Our results on plant aerial biomass production agree with those of Becker et al. (1997a).

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