

F. Van der Heyden · W.D. Stock

Nonstructural carbohydrate allocation following different frequencies of simulated browsing in three semi-arid shrubs

Received: 14 May 1994 / Accepted: 11 December 1994

Abstract Nonstructural carbohydrate allocation patterns in response to different frequencies of simulated browsing (leaf and twig removal) were studied in the following semi-arid shrubs: *Osteospermum sinuatum*, a dwarf deciduous shrub, *Pteronia pallens*, a dwarf evergreen shrub, and *Ruschia spinosa*, a dwarf leaf-succulent shrub. Simulated browsing at all frequencies resulted in the elevation, or had no effect, on total nonstructural carbohydrate (TNC) concentrations of *O. sinuatum* plant parts, and resulted in the decrease in TNC concentrations of *R. spinosa* plant parts. The responses of *P. pallens* were intermediate with elevations as well as declines in TNC concentrations of plant parts measured in response to various clipping frequencies. At the low frequency of simulated browsing (every 26 weeks) elevations in plant TNC content were measured in the two non-succulent shrubs *O. sinuatum* and *P. pallens*. It was concluded that the overcompensation with respect to TNC accumulation observed in the two non-succulent species represents one of the ways in which excess photosynthate is utilized by browsed shrubs with a limited regrowth potential. Simulated browsing was the least detrimental with respect to biomass production to the non-succulent *O. sinuatum* and *P. pallens*, and most injurious to the leaf-succulent shrub, *R. spinosa*. The observed TNC allocation patterns could not adequately explain the variation among species in the production of new growth and it was concluded that some factor(s) other than the carbon resource was limiting regrowth.

Key words Browsing responses · Semi-arid shrubs
Nonstructural carbohydrate accumulation · Regrowth

F. Van der Heyden (✉)¹ · W.D. Stock
Department of Botany, University of Cape Town, Private Bag,
Rondebosch 7700, South Africa,

Present address:

¹Roodeplaat Grassland Institute, c/o Department of Botany,
University of the Western Cape, Private Bag X17, 7535 Bellville,
South Africa, EMAIL: FRANCOIS@BOTANY.UWC.AC.ZA

Introduction

Regrowth of rangeland and pasture plant species is often studied in relation to some aspect of plant carbon balance, since grazing or browsing reduces absolute photosynthetic carbon gain. Aspects such as changes in reserve carbohydrate status (White 1973; Buwai and Trlica 1977; Danckwerts 1993), translocation of stored nonstructural carbohydrates (Danckwerts and Gordon 1987), net photosynthesis (Painter and Detling 1981) and partitioning of recently fixed photosynthates (Ryle and Powell 1975) have all been examined. Many of the earlier studies of plant regrowth and carbon balance have focused on the quantification of nonstructural carbohydrates since this group of compounds is considered to function as a readily available source of energy which can be used for plant regrowth (Smith 1973). Studies on grasses (Davidson and Milthorpe 1966), lucerne (Hodgkinson 1969), clover (Culvenor et al. 1989) and shrubs (Buwai and Trlica 1977), for example, have shown that regrowth following defoliation often depends on mobilization of stored nonstructural carbohydrates. The importance of stored carbohydrates as a resource for regrowth following defoliation has, however, been questioned and it has been suggested that the contribution of photosynthates, produced by the remaining leaf biomass, to subsequent regrowth can exceed that of reserve carbohydrates (Davidson and Milthorpe 1966; Richards 1986; Richards and Caldwell 1985). Although the carbon allocation patterns observed in these studies do not provide a model which is generalizable for all plant species, there is general consensus that reserve carbon plays a potentially important role in regrowth.

Present knowledge of the carbon relations of woody plants is based on studies undertaken on trees (Kozlowski 1992). Almost no research has been undertaken on the carbon relations of semi-arid woody shrubs, or the effects of browsing on the carbon economy of shrubs with different leaf morphologies. The responses of the leaf-succulent species, in particular, have not been addressed, since this leaf form is rare in most rangelands,

although of significance in the karoo region of southern Africa. The semi-arid karoo region of South Africa is an extensive livestock production area of approximately 652 339 km² (Rutherford and Westfall 1986). This region has a low annual rainfall (100–400 mm), hot dry summers and cold winters. The over-utilization of the natural plant cover (grasses, woody and succulent shrubs) by domestic livestock has been recognized as a major cause for degradation of karoo rangelands (Acocks 1955; Roux and Vorster 1983) as well as rangelands in other parts of the world (Noy-Meir 1974). Solving the problem of rangeland deterioration necessitates a knowledge of the utilization limits of individual species, which in turn requires an understanding of functional responses to browsing. This study addresses these questions by examining to what extent regrowth of semi-arid shrubs is governed by the availability of reserve carbon.

The objectives of this study were to determine (i) whether different frequencies of simulated browsing have similar effects on nonstructural carbohydrate accumulation of semi-arid shrubs with different leaf morphologies and (ii) whether these allocation responses can explain variation in ability to regrow following browsing. Responses with respect to nonstructural carbohydrate accumulation, in particular, were examined since sufficient carbohydrate reserves is often considered as an important determinant of regrowth of grazed grasses, browsed shrubs and pruned trees (Jameson 1963; Buwai and Trlica 1977; Loescher et al. 1990).

Materials and methods

Field studies were carried out at the Tierberg Karoo Research Site (33°10'S, 22°17'E) near the southern boundary of the Great Karoo, South Africa. Average annual rainfall for the site is 167 ± 7 mm ($n = 92$ years). Heavy rains often occur between February and May and dry periods are most likely between September and January (Milton et al. 1992). Total monthly rainfall and temperature minima and maxima for the period June 1988 to December 1989, which includes the period of study, are illustrated in Fig. 1. Details of the study site have been described by Milton et al. (1992). Livestock had been excluded from the study site for 2 years prior to the commencement of field studies.

The three study species were selected on the basis of their dominance in the study area and to represent various leaf morphological types. *Osteospermum sinuatum* (DC.) T. Norl., is a dwarf (<0.25 m in height) asteraceous deciduous shrub with orthophyllous and fleshy leaves, and is one of the most palatable shrubs in the karoo. *Pteronia pallens* L.f., a dwarf (<0.40 m in height) asteraceous evergreen shrub with ericoid sclerophyllous leaves, is recognized as a poisonous plant causing livestock losses (Vahrmeijer 1981). *Ruschia spinosa* (L.) H.E.K. Hartm. and Stuber (Mesembryanthemaceae) is a dwarf (<0.25 m in height) evergreen shrub with succulent leaves and spinescent stems. Although palatable, it is grazed less extensively than *O. sinuatum*. The tap root of *O. sinuatum* penetrates to a depth of 400 mm and is supported by lateral roots. *P. pallens* has a large ramified system of roots extending to a depth of 400 mm while *R. spinosa* has a branched lateral root system which is confined to the upper 80 mm of the soil.

Clipping treatments were carried out to simulate browsing by sheep, i.e. only twigs of 1 mm diameter or less, and leaves were clipped. This mode of leaf and twig removal was representative of a typical browsing pattern as effected by sheep. Similar percentages of apical meristems were removed with each treatment (except control plants) to avoid the danger of imposing different meristematic

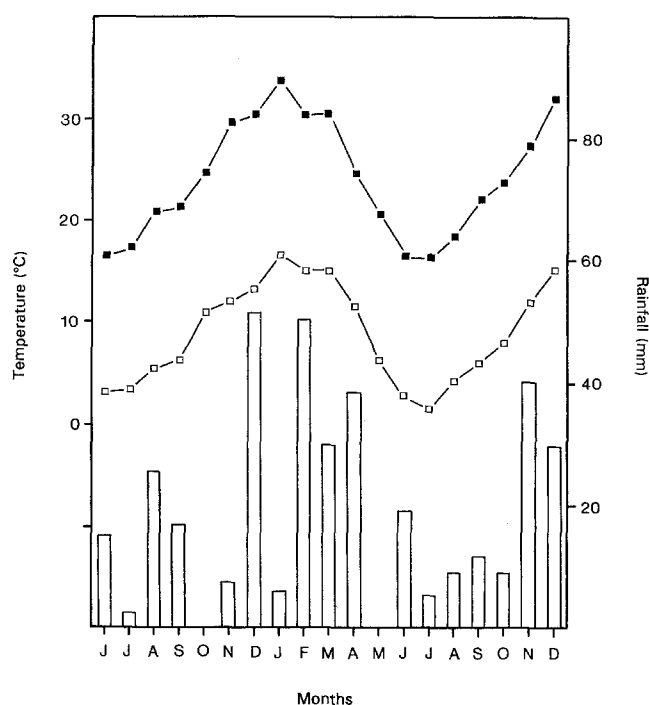


Fig. 1 Monthly rainfall (histograms) and monthly maximum (closed squares) and minimum temperatures (open squares) recorded at Tierberg Karoo Research Centre, South Africa, from June 1988 to December 1989 (adapted from Milton et al. 1992)

limitations as illustrated by Richards (1986). Fifteen individuals of each species were defoliated on 8 January 1989. A simulated browsing intensity of 80% was applied by removal (clipping) of leaf and twig (<1 mm) material starting at the periphery of the plant crown, moving systematically towards the centre until the desired percentage of the volume of the canopy had been removed. Following this initial clipping treatment, plants were repeatedly treated over a 1-year period at either 6-, 13- or 26-week intervals (five replicates) by removing all regrowth that had occurred since the previous leaf and twig removal treatment. Control plants were left uncut throughout the experiment. Plants were harvested on 3 January 1990 and divided into the following plant part categories: leaves, twigs, stems, root-crown and roots. Sections of the stem which extend just below the soil surface were considered as the root-crown. The shallow soil of the study site limited root growth of *O. sinuatum* and *P. pallens* to a depth of 400 mm and the entire root system could be harvested by removal of the soil containing the roots followed by sieving. The branched lateral roots of *R. spinosa*, confined to the upper 80 mm of the soil, were harvested in a similar way. Plant material was frozen in liquid nitrogen to retard enzyme activity and then transported to the laboratory in insulated freezer boxes packed with dry ice (-78°C). Plant material was oven-dried to constant weight at 70°C and dry weights were determined prior to chemical analyses.

Since the three karoo shrubs accumulate nonstructural carbohydrates in varying mixtures of starch, sucrose and fructans (Van der Heyden 1992), a modified Shaeffer-Somogyi copper-idiometric titration technique (Smith 1981) was used because it includes all glucose and fructose units in the quantification of total nonstructural carbohydrates (TNC). Nonstructural carbohydrates were extracted from 100–500 mg tissue samples by boiling in 25 ml distilled water for 5 min followed by cooling to room temperature and the addition of 400 units amyloglucosidase enzyme extracted from *Asperilligis niger* (Sigma Chemical Co.). The mixture was buffered to pH 4.5 by addition of 10 ml of an acetic acid/sodium acetate solution and incubated at 55°C for 24 h. Samples were filtered through Whatman No. 1 filter paper, treated with 10% neutral lead acetate to precipitate proteins, made up to 100 ml with distilled H₂O and centrifuged at 8000 rpm to remove the precipi-

tate. A 1–10 ml aliquot was acid hydrolysed (0.5 M H₂SO₄, 100°C water bath, 15 min), neutralized with 1 M NaOH and tested for reducing power to obtain a total nonstructural carbohydrate (TNC) value which includes mono- and disaccharides, starch and fructans. Results are expressed as glucose equivalents on a dry weight basis. All data were analysed using a one-way analysis of variance technique (Zar 1974) followed by Tukey's multiple range test to identify significant differences among treatments.

Gross annual aboveground production could not be compared among species or treatments because (i) foliage removed was not added to plant biomass, and (ii) because plants in the low-frequency treatment had a longer period to produce vegetative material than plants in the high-frequency treatment at the time of harvest. The standing biomass (not above-ground production) of plants subjected to the different frequencies of foliage removal was measured after 1 year. Because of the variation in plant age and biomass among replicates, a proportional increment in biomass, called regrowth ratio, was used to indicate growth. Regrowth ratio

(GR) was calculated as the ratio of the dry mass of potentially browsed material (leaves and twigs) to the dry mass of the unbrowsed material (stems, root-crown and roots) for each plant. Regrowth ratio values were arcsine transformed prior to statistical analysis. One-way analysis of variance was used to compare the effects of frequency of simulated browsing on regrowth ratio within each species. This was followed by Tukey's multiple range test to determine significant between-treatment differences (Zar 1974).

Results

Nonstructural carbohydrate concentrations

Leaf TNC concentrations of *O. sinuatum* plants subjected to different frequencies of simulated browsing were

Fig. 2 Total nonstructural carbohydrate (TNC) concentrations in five organs of *Osteospermum sinuatum*, *Pteronia pallens* and *Ruschia spinosa* plants subjected to the following frequencies of simulated browsing (clipping) over a 1-year study period: every 6 weeks (6w), every 13 weeks (13w), every 26 weeks (26w) and no clipping (co). Each point represents the mean of five measurements, and the bars represent ± 1 SEM. Where there are no bars, the SEMs are too small to show on the scale. Different letters for organ TNC concentrations (within species) show significant differences at *P* < 0.01

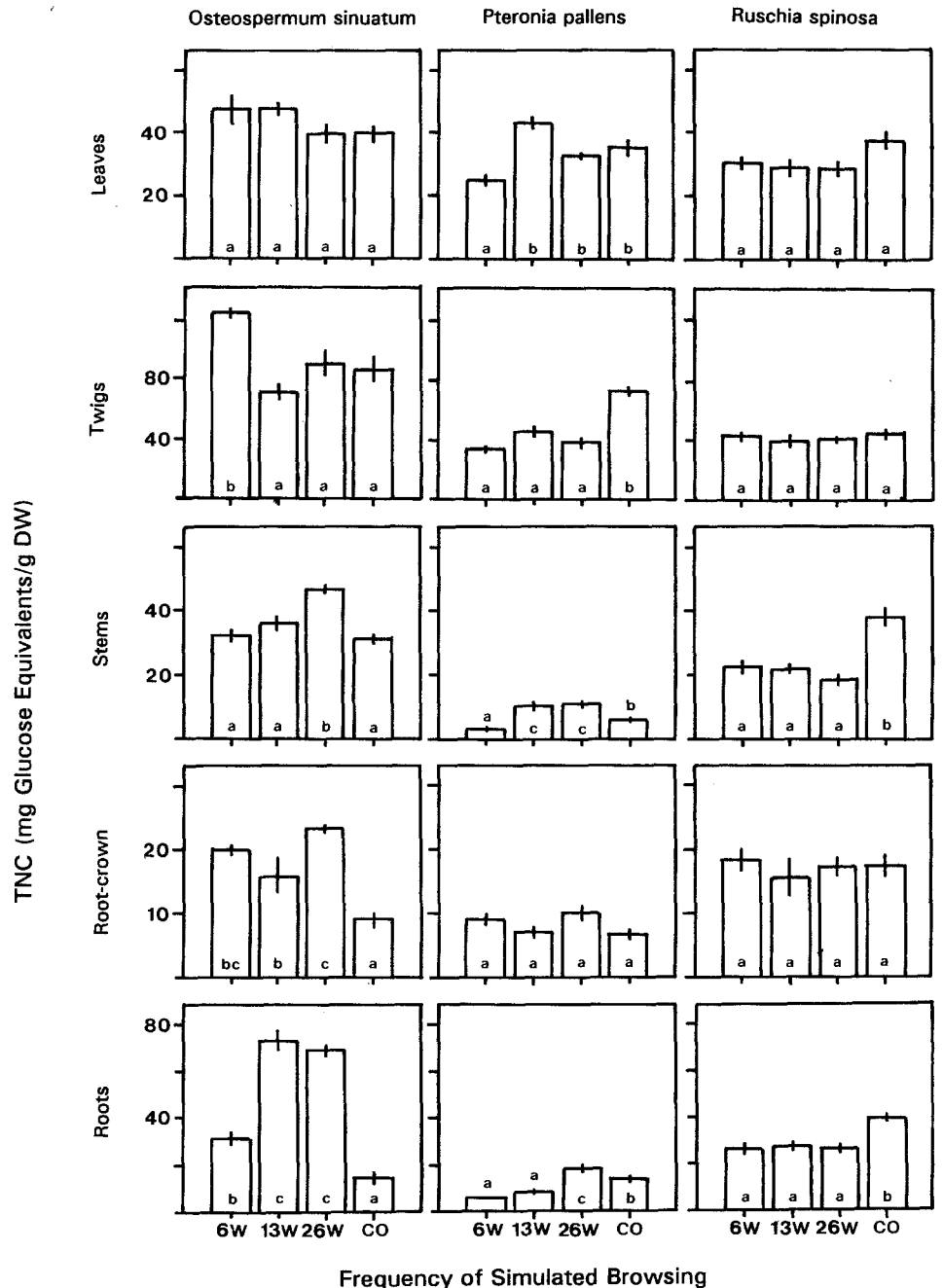
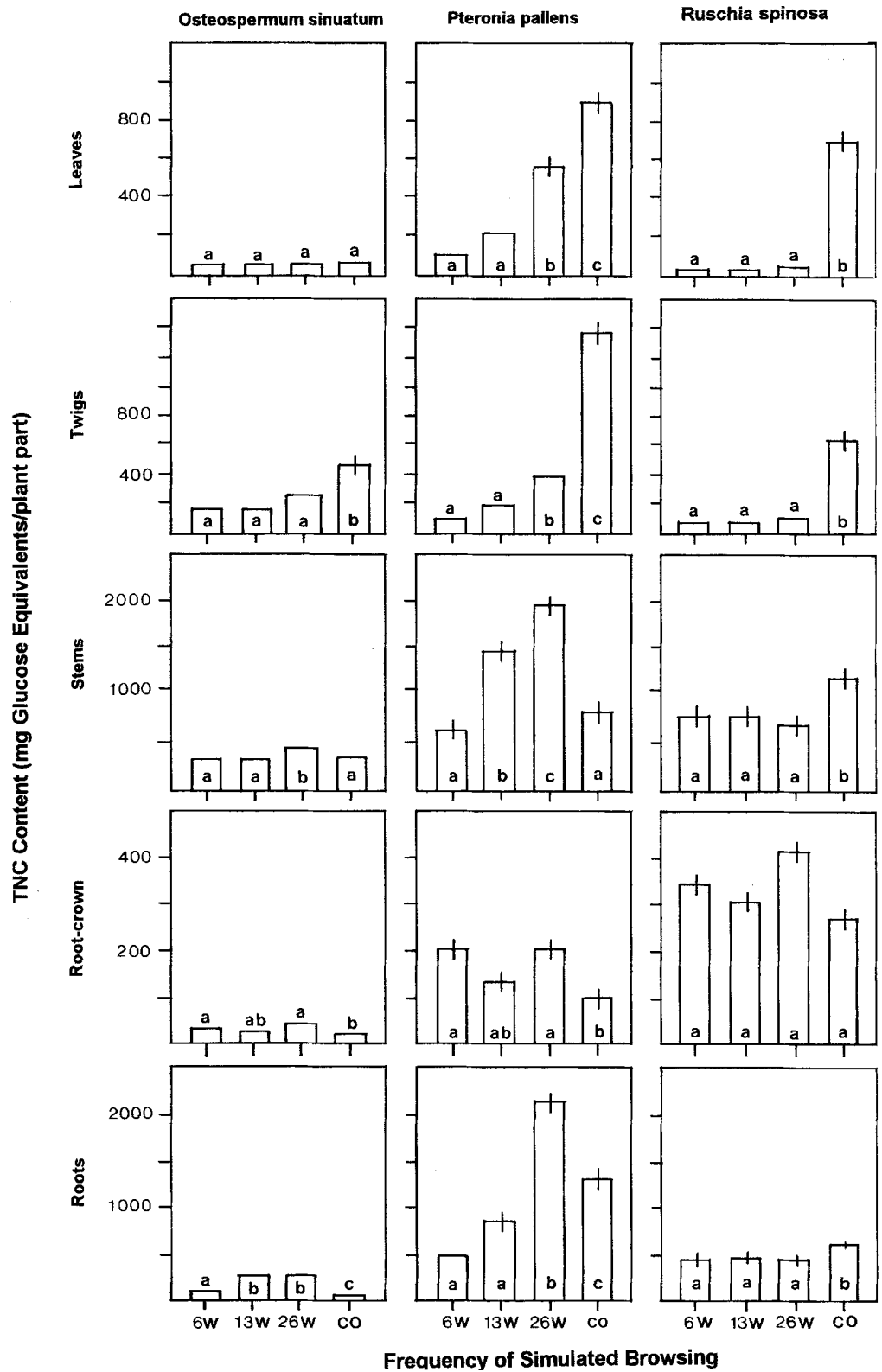
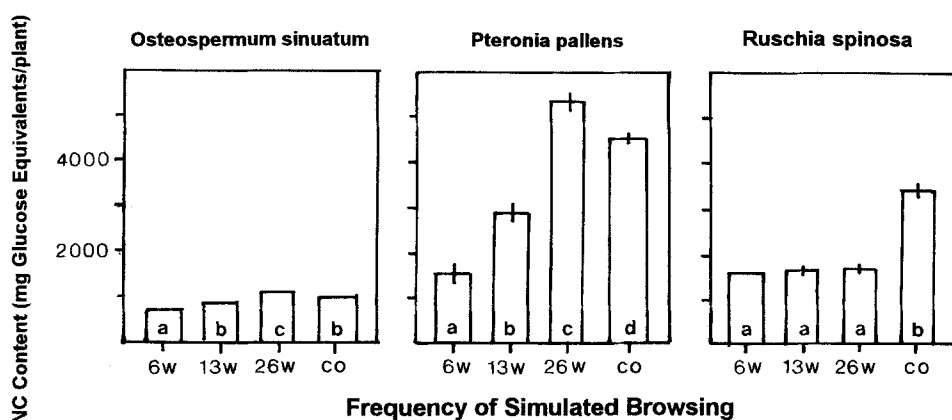


Fig. 3 TNC pool size (content) of five organs of *O. sinuatum*, *P. pallens* and *R. spinosa* plants subjected to the following frequencies of simulated browsing (clipping) over a 1-year study period: every 6 weeks (6w), every 13 weeks (13w), every 26 weeks (26w) and no clipping (co). Each point represents the mean of five measurements, and the bars represent ± 1 SEM. Where there are no bars, the SEMs are too small to show on the scale. Different letters for organ TNC pool sizes (within species) show significant differences at $P < 0.01$



of the same order of magnitude (Fig. 2) with no significant differences ($F = 1.64$, $P > 0.05$) between treatments. A significant increase ($F = 11.34$, $P < 0.05$) in TNC concentration was, however, observed in the twigs of the 6-week treatment with no significant differences between

the twigs of control plants, 13-week and 26-week interval clipped plants. In the stems of *O. sinuatum* a significant increase ($F = 20.65$, $P < 0.05$) in TNC concentration was found only in the 26-week treatment (Fig. 2) while in the roots and root-crown, significant increases



($F = 17.15$ and 88.91 respectively, $P < 0.05$) were observed in all treatments, relative to the values of the controls. Particularly marked increases in TNC concentrations in the roots of the 13-week and 26-week treatments were evident (Fig. 2).

Leaves of the 13-week and 26-week interval clipped *P. pallens* plants showed the same TNC concentrations as the leaves of the control plants while in the 6-week treatment, leaf TNC concentrations were significantly lower ($F = 7.13$, $P < 0.05$) than those of the control plants (Fig. 2). Significantly lower TNC concentrations ($F = 32.01$, $P < 0.05$) were observed in the twigs of all defoliated plants (relative to controls) with no significant differences among treatments. In the stems of *P. pallens*, a significant decrease ($F = 26.09$, $P < 0.05$) in TNC concentration was observed in the 6-week treatment while the opposite trend was found in the lower frequency (13- and 26-week) clipping treatments. No significant differences were found among TNC concentrations in the root-crowns of all treatments of *P. pallens* ($F = 2.93$, $P > 0.05$). In the roots, however, decreases in the 6-week and 13-week treatments were observed with significant increases ($F = 66.06$, $P < 0.05$) being observed in the roots of *P. pallens* individuals clipped every 26 weeks.

TNC concentrations in the leaves, twigs and root-crowns of clipped plants and the controls of *R. spinosa* (Fig. 2) did not differ significantly ($F = 2.75$, 0.71 and 0.29 respectively, $P > 0.05$). TNC concentrations of the stems and roots did not differ among clipping treatments, but they were all considerably lower than the concentrations measured in the same organs of the control plants ($F = 17.07$ and 15.77 respectively, $P < 0.05$).

Nonstructural carbohydrate pool sizes

There was no difference ($F = 0.022$, $P > 0.05$) in leaf TNC pool sizes of *O. sinuatum* plants subjected to different frequencies of simulated browsing (Fig. 3). Twig TNC content of control plants, however, were significantly higher ($F = 27.448$; $P < 0.05$) than the TNC contents of the 6-week, 13-week and 26-week clipping treatments, with no significant differences among the

Fig. 4 Total nonstructural carbohydrate content (plant total pool size) of *O. sinuatum*, *P. pallens* and *R. spinosa* plants subjected to the following frequencies of simulated browsing (clipping) over a 1-year study period: every 6 weeks (6w), every 13 weeks (13w), every 26 weeks (26w) and no clipping (co). Each point represents the mean of five values, and the bars represent ± 1 SEM. Where there are no bars, the SEMs are too small to show on the scale. Different letters for TNC pool sizes (within species) show significant differences at $P < 0.01$.

TNC contents of these clipping treatments (Fig. 3). There was no significant difference in TNC pool sizes of the leaves of *P. pallens* plants subjected to 6-week and 13-week simulated browsing frequencies (Fig. 3). However, TNC pool size of leaves of the 26-week treatment was significantly higher than the values for the 6-week and 13-week frequency treatments, and lower than the values for control plants ($F = 43.74$, $P < 0.05$). The relative differences in twig TNC pool sizes of the various frequency treatments were similar to the pattern found for leaves ($F = 205.25$; $P < 0.05$). TNC contents of the leaves and twigs of *R. spinosa* did not differ among clipping treatments, but they were all considerably lower than the TNC contents of the same organs of the control plants ($F = 105.73$ and 149.3 respectively, $P < 0.05$). Relative differences among clipping treatments with respect to TNC contents of stems, root-crown and roots of all three species (Fig. 3) were generally similar to the patterns found for TNC concentrations (Fig. 2).

Plant TNC pool sizes increased with decreasing clipping frequency in *O. sinuatum* and *P. pallens* (Fig. 4). TNC pools of plants with the lowest clipping frequency (26-week interval) of both species were significantly greater than the TNC pools of their respective control treatments. In *O. sinuatum*, the 13-week treatment values were not significantly different ($P > 0.05$) from the TNC values of the control plants. The 13-week interval *P. pallens* plants, however, had significantly lower ($P < 0.05$) plant TNC levels than the control plants. No differences were observed among the clipping treatments of *R. spinosa* in terms of TNC levels per plant (Fig. 4), but the values of the control plants were considerably greater than the values for the plant individuals subjected to simulated browsing treatments.

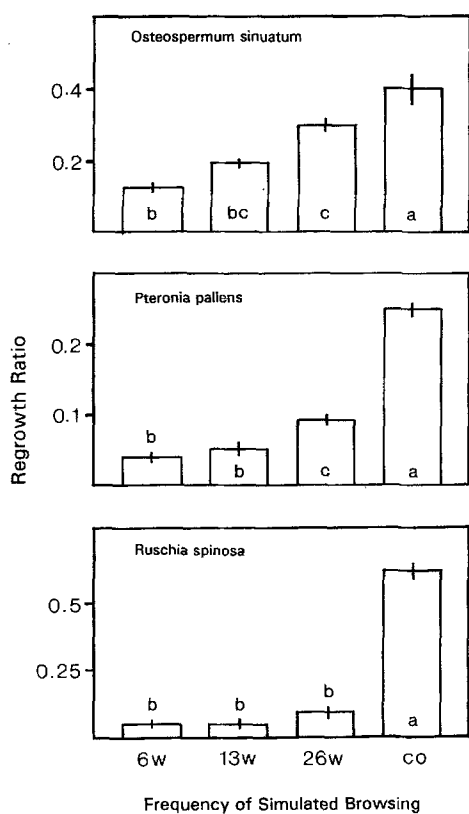


Fig. 5 Regrowth ratios of three karoo shrubs subjected to the following frequencies of simulated browsing (clipping) over a 1-year study period; every 6 weeks (6w), 13 weeks (13w), 26 weeks (26w) and no clipping (co). Each point represents the mean of five observations, and the bars represent ± 1 SEM

Regrowth ratio

Control plants had the highest regrowth ratio values (GR) in all three species (Fig. 5). GR values of *O. sinuatum* and *P. pallens* increased with decreasing clipping frequency (Fig. 5). Between-treatment differences were smaller in *P. pallens* and a more pronounced difference between the controls and the other simulated browsing treatments was evident, with no significant difference ($P > 0.05$) between the 6-week and 13-week treatments. The greatest difference between the controls and the clipping treatments was observed in *R. spinosa* (Fig. 5). No significant between-treatment differences were observed for the clipped individuals of this species.

Discussion

The effects of simulated browsing on nonstructural carbohydrate accumulation of shrubs from the semi-arid rangelands of the karoo differed among species and with clipping frequency. *O. sinuatum* was the only species where repeated clipping rarely resulted in a decrease in TNC concentrations or pools of plant tissues. Clipping resulted in the elevation or had no effect on TNC con-

centrations and pools of *O. sinuatum* tissues. The only exception was the twigs where clipping resulted in a decrease in twig TNC pools because of a lower twig biomass (lower GR values) in the clipping treatments. The leaves were expected to show a similar trend but all clipping treatments (including control) of the summer-deciduous *O. sinuatum* had few leaves at the time of harvest (summer; January 1990), and there was consequently no difference among treatments with respect to leaf biomass or leaf TNC pools. The leaf-succulent *R. spinosa* represents the other extreme where simulated browsing at low and at high frequencies mostly caused a decrease in TNC pools or had no effect (root-crown). The responses of *P. pallens* were intermediate in that decreases (high clipping frequency) as well as increases (low clipping frequency) in TNC concentrations and pools were observed. The generally higher net photosynthetic rates of deciduous plants (Oechel et al. 1981) as shown for *O. sinuatum* by Van der Heyden (1992), coupled with the greater availability of photosynthetic material per plant (generally higher GR; Van der Heyden 1992), probably contributed towards more carbon being assimilated by *O. sinuatum* plants than by the evergreen *P. pallens* and *R. spinosa*, resulting in more carbon being accumulated as nonstructural carbohydrates.

All the clipped *O. sinuatum* plants, irrespective of frequency of clipping, as well as the most leniently defoliated *P. pallens* plants, positively readjusted nonstructural carbohydrate allocation patterns after 1 year. It was expected therefore that the total TNC pool sizes of these plants would be greater than the levels of their respective control plants. However, only the 26-week interval plants of these species had higher TNC pool sizes than the control plants. This phenomenon can be explained by the low leaf and twig biomass values of severely clipped plants which, although having elevated or similar TNC concentrations, contributed minimally to plant TNC pools, thereby reducing TNC pool sizes to well below the values of control plants.

Regrowth capacity also varied greatly among species and with frequency of simulated browsing within each species. The greatest capacity to regrow following simulated browsing was shown by *O. sinuatum*, the dwarf deciduous shrub, followed by *P. pallens*, the dwarf evergreen shrub and lastly *R. spinosa*, the dwarf leaf succulent shrub. None of the clipped plants attained the biomass levels of the controls, even at the lowest frequency (26 weeks) of simulated browsing, suggesting relatively slow regrowth rates compared to North American evergreen and deciduous shrubs (Wandera et al. 1992).

The question has often been debated whether grazing (or browsing) benefits the production of new growth (McNaughton 1979; Belsky 1986). As evidence for these arguments, vegetative and reproductive growth parameters have almost exclusively been used. Our results indicate that clipping of karoo shrubs, even at a lenient frequency of every 26 weeks, does not benefit the plants in terms of vegetative compensatory growth. However, in

the two non-succulent species, restoration of storage TNC levels to values in excess to those of unclipped plants was observed, and this readjustment occurred prior to compensatory vegetative regrowth. Clipped non-succulent karoo shrubs therefore overcompensated with respect to TNC accumulation, and not in terms of vegetative regrowth as was noted for some grass species (McNaughton 1979) and shrubs in nutrient rich environments (Wandera et al. 1992) which compensated exactly for lost tissues in a matter of a few weeks. Therefore some factor other than the carbon resource was possibly limiting regrowth in these karoo shrubs. Low decomposition and leaching rates which curtail nutrient availability in arid ecosystems (Hadley and Szarek 1981), or the removal of the apical meristems during simulated browsing, coupled with a poor ability to activate axillary buds to produce new shoots, could account for the limited production of new photosynthetic tissue. It was recently illustrated that the removal of active meristems may severely limit the capacity of some shrubs to regrow, and consequently lower the ability to tolerate mammalian herbivory (Bilbrough and Richards 1993).

Plants adapted to low-resource environments such as arid rangelands do not show compensatory regrowth following browsing but are suggested to have evolved carbon-based chemical defences (Bryant et al. 1983; Coley et al. 1985). In contrast, high-resource plants regrow rapidly following browsing and N-based defences appear to be more important than carbon based chemical defences (Bryant et al. 1983). This carbon/nutrient balance hypothesis developed by Bryant and co-authors was developed further by Baas (1989) to include biological interactions (carbon/nitrogen cycle theory). The theory of Baas (1989) proposed that under suboptimal conditions such as drought or low-nutrient conditions, vegetative growth is inhibited due to limitations of nutrient supply. The author hypothesized that the continuation of photosynthetic processes, despite the lack of vegetative growth, would result in the formation of carbon based compounds from the excess photosynthates. We propose that in addition to life history and soil conditions, as suggested by Baas (1989), browsing of shrubs by mammalian herbivores also imposes suboptimal conditions for primary regrowth since active meristems are removed during this process. We further suggest that excess photosynthates are produced following browsing because of the resulting lack of primary growth (meristem deficiency), and that the three karoo shrubs studied represent alternatives of how the excess carbon is utilized. These alternatives are (i) accumulation of storage carbohydrates and (ii) production of secondary carbon defence compounds. In *O. sinuatum* and *P. pallens*, the surplus photosynthates are stored as nonstructural carbohydrates as shown by our study, and are not allocated to secondary carbon defence compounds (Stock et al. 1994). *R. spinosa* represents the second alternative where excess carbon is used for the production of secondary carbon compounds (Stock et al. 1994), and is not allocated to storage nonstructural carbohydrates.

Our results suggest that the observed differences in regrowth capacity among species is not a function of stored carbon. Carbon was found to be in abundance, and was allocated either towards storage as nonstructural carbohydrates or to secondary carbon defence compounds. It is more likely that variation in regrowth among these semi-arid shrubs is determined by (i) differences with respect to developmental growth processes as shown by Bilbrough and Richards (1993) for North American shrubs, (ii) the presence or ability to activate axillary buds meristems or (iii) the ability to activate epicormic buds (Zimmermann and Brown 1971). Variation with respect to nutrient turnover (mineralization and decay), which is considered to be species specific and strongly localized (i.e. concentric plant specific nutrient cycling, Garzia-Moya and McKell 1970), may also contribute towards the variation in regrowth capacities among species.

The findings from this study suggest that browsing management systems involving high intensity utilization (in semi-arid regions) should accommodate resting periods of much longer than 26 weeks, since not one of the 80%-clipped plants attained the biomass levels of the controls, even at the most lenient frequencies of simulated browsing i.e. 26-week intervals. Extremes of temperatures, generally low water availability, the resultant limitation on nutrient availability (Hadley and Szarek 1981), as well as browsing induced shortage of active meristems, possibly did not favour compensatory vegetative regrowth over the 1-year study period.

This study provides a new insight into nonstructural carbohydrate allocation patterns of semi-arid shrubs in response to browsing where it appears that regrowth of these shrubs is not limited by carbon reserves. Furthermore, differences in carbon allocation patterns do not readily explain variation in regrowth capacities. Variation among species with respect to localized nutrient return as well as developmental growth processes (including meristematic considerations) should be examined since these factors may explain the variation in regrowth capacities among semi-arid shrubs.

Acknowledgements The financial support of the Karoo Biome Project, Foundation for Research Development, CSIR is gratefully acknowledged.

References

- Acocks JPH (1955) Agriculture in relation to a changing vegetation. *S Afr J Sci* 52:101–108
- Baas WJ (1989) Secondary plant compounds, their ecological significance and consequences for the carbon budget. In: Lambers H, Cambridge ML, Konings H, Pons TL (eds) Causes and consequences of variation in growth rate and productivity of higher plants. SPB Academic, The Hague, pp 313–340
- Belsky AJ (1986) Does herbivory benefit plants? A review of the evidence. *Am Nat* 127:870–892
- Bilbrough CJ, Richards JH (1993) Growth of sagebrush and bitterbrush following simulated winter browsing: mechanisms of tolerance. *Ecology* 74:481–492

- Bryant JP, Chapin FS III, Klein DR (1983) Carbon/nutrient balance of boreal plants in relation to herbivory. *Oikos* 40:357–368
- Buwai M, Trlica MJ (1977) Multiple defoliation effects on herbage yield, vigor and total nonstructural carbohydrates of five range species. *J Range Manage* 30:164–172
- Coley PD, Bryant JP, Chapin FS III (1985) Resource availability and plant antiherbivore defense. *Science* 230:895–899
- Culvenor RA, Davidson IA, Simpson RJ (1989) Regrowth by swards of subterranean clover after defoliation. 1. Growth, non-structural carbohydrate and nitrogen content. *Ann Bot* 64: 545–556
- Danckwerts JE (1993) Reserve carbon and photosynthesis: their role in regrowth of *Themeda triandra*, a widely distributed subtropical graminaceous species. *Funct Ecol* 7:634–641
- Danckwerts JE, Gordon AJ (1987) Long-term partitioning, storage and remobilization of ^{14}C assimilated by *Lolium perenne* (cv. Melle). *Ann Bot* 59:55–66
- Davidson JL, Milthorpe FL (1966) The effect of defoliation on the carbon balance in *Dactylis glomerata*. *Ann Bot* 30:185–198
- Garzia-Moya E, McKell CM (1970) Contributions of shrubs to the nitrogen economy of a desert-wash plant community. *Ecology* 51:81–88
- Hadley NF, Szarek SR (1981) Productivity of desert ecosystems. *Bioscience* 31:747–753
- Hodgkinson KC (1969) The utilization of root organic compounds during the regeneration of lucerne. *Aust J Biol Sci* 22: 1113–1123
- Jameson DA (1963) Responses of individual plants to harvesting. *Bot Rev* 29:532–594
- Kozłowski TT (1992) Carbohydrate sources and sinks in woody plants. *Bot Rev* 58:107–222
- Loescher WH, McCamant T, Keller JD (1990) Carbohydrate reserves, translocation, and storage in woody plant roots. *Hort-Science* 25:274–281
- McNaughton SJ (1979) Grazing as an optimization process: grass-ungulate relationships in the Serengeti. *Am Nat* 113:691–703
- Milton SJ, Dean WRJ, Kerley GIJ (1992) Tierberg karoo research centre: history, physical environment, fauna and flora. *Trans R Soc South Africa* 48:15–46
- Noy-Meir I (1974) Desert ecosystems: higher trophic levels. *Annu Rev Ecol Syst* 5:195–214
- Oechel WC, Lawrence W, Mustapha J, Martinez J (1981) Energy and carbon acquisition. In: Miller PC (ed) *Resource use by chaparral and matorral*. Springer, Berlin Heidelberg New York, pp 151–183
- Painter EL, Detling JK (1981) Effects of defoliation on net photosynthesis and regrowth of western wheatgrass. *J Range Manage* 34:68–71
- Richards JH (1986) Plant response to grazing: the role of photosynthetic capacity and stored carbon reserves. In: Ross PJ, Lynch PW, Williams OB (eds) *Rangelands: a resource under siege*. Proceedings of the Second International Rangeland Congress 1984. Cambridge University Press, Cambridge, pp 428–430
- Richards JH, Caldwell MM (1985) Soluble carbohydrates, concurrent photosynthesis and efficiency in regrowth following defoliation: a field study with *Agropyron* species. *J Appl Ecol* 22: 907–920
- Roux PW, Vorster M (1983) Vegetation change in the karoo. *Proc Grassland Soc S Afr* 18:25–29
- Rutherford MC, Westfall RH (1986) The biomes of southern Africa – an objective categorization. *Mem Bot Surv S Afr* 54:1–98
- Ryle GJA, Powell CE (1975) Defoliation and regrowth in the graminaceous plant: the role of current assimilate. *Ann Bot* 39: 297–310
- Smith D (1973) The nonstructural carbohydrates. In: Butler GW, Bailey RW (eds) *Chemistry and biochemistry of herbage*. Academic Press, London, pp 105–155
- Smith D (1981) Removing and analyzing total nonstructural carbohydrates from plant tissues (University of Wisconsin, College of Agriculture and Life Sciences Publication No. R-2107). University of Wisconsin, Madison
- Stock WD, Le Roux D, Van der Heyden F (1993) Regrowth and tannin production in woody and succulent karoo shrubs in response to simulated browsing. *Oecologia* 96:562–568
- Vahrmeijer J (1981) Poisonous plants of South Africa that cause stock losses. Tafelberg, Cape Town
- Van der Heyden F (1992) Effects of defoliation on regrowth and carbon budgets of three semi-arid karoo shrubs. PhD thesis, University of Cape Town, South Africa
- Wandera JL, Richards JH, Mueller RJ (1992) The relationships between relative growth rate, meristematic potential and compensatory growth of semiarid-land shrubs. *Oecologia* 90:391–398
- White LM (1973) Carbohydrate reserves of grasses: a review. *J Range Manage* 26:13–18
- Zar JH (1974) *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs
- Zimmermann MH, Brown CL (1971) *Trees; structure and function*. Springer, Berlin Heidelberg New York