

Research Note

Volume–biomass functions reveal the effect of browsing on three Moroccan dwarf shrubs

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We studied the effects of browsing on the plant architecture and volume-biomass relationships of three dominant dwarf shrubs – *Artemisia herba-alba*, *A. mesatlantica* and *Teucrium mideltense* – in a sagebrush steppe in the Central High Atlas Mountains, southern Morocco. For this purpose, we developed power-law volume-biomass functions based on nonlinear regressions for each of these species, under both browsed and unbrowsed conditions. These functions were then applied to individual-based annual monitoring data from inside and outside a browsing enclosure to calculate standing biomass for each of the years from 2004 to 2009. The biomass of the three species was well predicted by the allometric functions, and different functions for the browsed and unbrowsed conditions reflected changes in plant architecture. Browsing had a significant negative impact on biomass for *A. herba-alba* but not for *A. mesatlantica*, whereas its effects on *T. mideltense* were inconsistent between years. The fact that the latter two species hardly benefited from browsing exclusion might be because of increased competition from the more dominant *A. herba-alba*. During the study period, the standing biomass increased whether or not there was browsing, which might be because of the recovery of the shrubs after a preceding severe drought. Further studies are needed in order to investigate the generality of the findings.

Keywords: allometric function, Atlas Mountains, nonlinear regression, permanent plot, plant architecture, standing biomass

Plant biomass is the most common measure of rangeland production (Cook and Stubbendieck 1986). The assessment of the standing biomass and its fluctuations is crucial in rangeland management. Accordingly, direct and indirect methods have been developed. Direct methods based on biomass harvesting (e.g. Patton et al. 2007) are more precise, but they are laborious, costly and destructive. On the other hand, indirect methods are cheaper, less detrimental to fragile ecosystems, and allow for easy spatial extrapolation of biomass estimates. Namely, methods based on remote sensing (e.g. Kawamura et al. 2003), allometric regression models (e.g. Usó et al. 1997, Paton et al. 2002, Abdelkader et al. 2008), and combinations of these two methods are frequently used. In this context, allometric regression models generally relate dimensional plant data, i.e. measures of height and diameter, to biomass. Such methods are useful; however, as static models, they do not describe the strong fluctuations of biomass production in ecosystems with high seasonal and interannual climatic variability (Le Houérou and Hoste 1977). In consideration of this problem, several studies (Abrams et al. 1986, Xiao et al. 1996) used monitoring methods to follow vegetation changes over several years and combined this approach with some of the previously cited methods.

Southern Moroccan steppic rangelands have been the subject of research on total biomass production (Baumann 2009), but little is known about their species-specific standing biomass, or the interannual changes to this biomass with and without browsing. In this study we aimed to estimate the variability in standing biomass of three dominant dwarf shrubs in an enclosure experiment, using allometric functions.

The study was conducted in a large intramontane basin in the southern ranges of the Central High Atlas Mountains at 31° 23' N, 6° 19' W and about 1 870 m asl, near the village of Taoujgalt in the province of Ouarzazate, Morocco. The study site is located on the toeslope of a calcareous alluvial cone and is representative for the rolling plains within the basin. The mean annual precipitation from 2001 to 2006 was 238 mm and the mean annual temperature 14.2 °C (Schulz et al. 2010). The climate is characterised by two rainfall peaks in autumn and spring, separated by a short dry winter and a long dry summer. Monthly mean temperatures reach their maximum in July (26 °C) and their minimum in January (5 °C) (Schulz et al. 2010).

The vegetation is a sagebrush steppe dominated by the three dwarf shrub species *Artemisia herba-alba* Asso, *A. mesatlantica* Maire (Asteraceae), and *Teucrium*

mideltense (Batt.) Humbert (Lamiaceae). *Artemisia herba-alba* has two periods of high productivity, at the end of spring and in early autumn, with a maximum biomass in autumn, whereas *T. mideltense* has its peak biomass development between late spring and early summer (Gresens 2006). Perennial grasses play a subordinate role, whereas annual species are well represented in terms of species richness and abundance with many small individuals mainly of the families Poaceae, Brassicaceae and Asteraceae, yet are not important in terms of biomass (Baumann 2009).

Traditionally, the steppes within the basin were managed as summer pastures with restricted access. Currently, the steppe is used throughout the year for browsing by sheep and for firewood extraction, and in some localities for crop farming practised by sedentary people. The sagebrush steppe is in good condition in terms of biomass production and ecological integrity (SENS 2005). The stocking rates vary considerably between seasons. Mahler (2010) found 0.25 small stock units (SSU) ha⁻¹ in 2009, whereas Freier et al. (2011) found 0.5 SSU ha⁻¹ in early summer of 2009 for the area of the study site. In addition, two short stocking rate peaks occur in early May when many transhumant pastoralists gather in the area with their herds waiting for the opening of the high mountain pasture and in autumn when the herders migrate back to the lowlands.

In early spring 2001, an enclosure experiment of about 1 250 m² was installed within the rangelands of the study site. Two plots of 10 m × 10 m each placed inside and outside the enclosure in sites with similar and representative vegetation and soil conditions. Each plot was divided into a grid of 400 quadratic subplots of 0.25 m². Length, width, and height of all individuals of the three dominant species *A. herba-alba*, *A. mesatlantica* and *T. mideltense* were monitored once per year from 2004 to 2009. As precipitation and productivity in the study area show a bimodal distribution with spring and autumn peaks (Schulz et al. 2010), we shifted the measurements in dry years to autumn in order to capture always the main part of the annual biomass increase. However, in autumn 2006 measurements could not be obtained because of strong thunderstorms that destroyed roads and blocked access to the study area. For this reason, measurements were taken prior to the beginning of the growing period in early spring 2007 and used as a surrogate for the 2006 data.

To establish volume–biomass relationships, we harvested 10 individuals of each species both inside and outside the enclosure in 2008, representing the full size ranges occurring in the respective treatment. Length, width, and height of the harvested individuals were measured in order to calculate the plant volume. After measurement, the aboveground biomass of the individuals was cut, oven-dried at 80 °C for 24 h, and weighed.

For the individual plants, volumes were calculated assuming the shape of a half ellipsoid for all three species with the following formula:

$$V = 1/6 LWH\pi,$$

where V = volume, L = length, W = width and H = height.

We developed power-law regressions for each species, both inside and outside the enclosure in order to describe

the volume–biomass relationships for the measured species. These calculations were based on the spring biomass harvested in 2008. The formula was:

$$B = aV^b,$$

where B = biomass, V = volume, and a and b are fitted parameters.

We chose to model this power law directly with a nonlinear regression approach (Motulsky and Christopoulos 2004) instead of applying log-transformations to both axes and then using a linear regression ($\log B = \log a + b \log V$) as it is frequently done. Our approach with B instead of $\log B$ as the dependent variable gives relatively more weight to the larger individuals, which are more relevant in terms of biomass per area. The regression equations were calculated with the nonlinear regression module of STATISTICA 8.0 (StatSoft 2007). We used the default setting of the program (loss function = $[\text{OBS} - \text{PRED}]^2$; estimation method = quasi-Newton; convergence criterion = 0.0001; step width for all parameters = 0.5; starting values for all parameters = 0.1).

In order to apply the equations established for 2008 to all years between 2004 and 2009, we assumed that outside the enclosure, overall browsing pressure remained constant at 0.25–0.5 SSU ha⁻¹. Therefore, plant architecture, i.e. canopy shape, should hardly have changed over the years, and thus the same function was assumed valid over the whole period. For the subplots inside the enclosure, two different approaches were applied. The first approach (further referred to as the static method) used the formula established in 2008 for all the years. In the second approach we applied a linear transition (transitional method) between the starting point in 2001, when the enclosure was installed, using the function for the browsed subplots and the function established for the enclosure in 2008, assuming that plant architecture only gradually adapted to the relaxation from browsing pressure (Figure 1). According to this idea, we adopted different equations for the growing biomass in

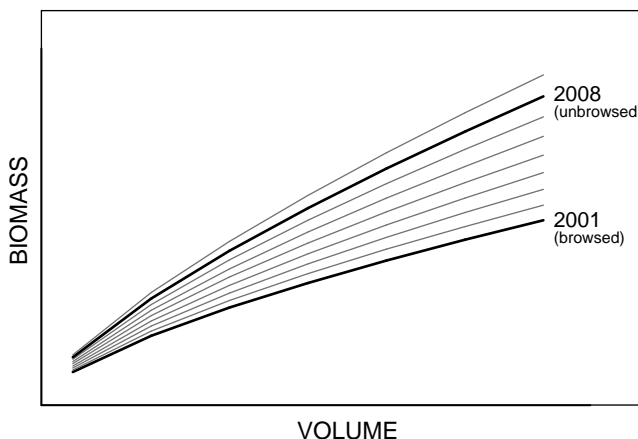


Figure 1: Schematic representation of transitional method for biomass calculation inside of the enclosure. The lower thick curve represents the volume–biomass function outside the enclosure; the upper thick curve shows that inside the enclosure. The curves between these are calculated assuming a linear transition between the two functions

each year. To achieve this, we calculated the difference of the fitted parameters a and b between the outside formula and the static inside formula. Then we let both parameters change over the years with a constant increment between these endpoints (Figure 1).

We used the specific regression functions for species, treatments, and years to estimate the biomass of each of the measured individuals. In the case of the dominant *A. herba-alba*, we used these values to calculate the standing biomass for each of the 0.25 m² subplots. For the two other species, which were only present in a small subset of subplots, we followed the development of the plant individuals separately. For *A. mesatlantica*, we had 25 plants inside and 29 outside, whereas *T. mideltense* was represented by 33 plants inside and 36 plants outside. We displayed the plots and the individual plants in a grid using a GIS to follow the time series in a spatially explicit manner and to correct for position errors. Missing records, i.e. individuals that were overlooked in a certain year, were entered by using the averaged biomass between the previous year and the subsequent year.

In order to test for differences in mean biomass between the browsed and unbrowsed plots and for changes between pairs of subsequent years within each 0.25 m² subplot, we used the permutation-based analogue to a two-sample t -test as implemented in the software PAST 1.95 (Hammer et al. 2001) with 10 000 permutations. A permutation-based comparison of means does not require any distributional assumption, as both parametric and non-parametric tests do (Quinn and Keough 2002, Manly 2007). Accordingly, such an approach is well suitable for extremely skewed distributions as in our case. The effect of browsing on biomass changes was evaluated by comparing the plots or individuals of the treatments between all pairs of subsequent years and for the cumulative changes over the five-year study period. As the replication was done only on the level of subplots or individuals, but not at the level of treatments, the case study can mainly address the question of whether and how plant architecture differs between species and treatments, but does not allow for formal inferences about browsing effects in the rangelands of the study region in general (see e.g. Quinn and Keough 2002, pp 158 et seq.).

The biomass of the three study species was well predicted with power-law functions of their volume in both management variants (Figure 2). The regressions explained 67–89% of the variance. The proportions of variance explained within species were similar inside and outside of the enclosure, with the exception of *T. mideltense*, which had a considerably higher R^2 value inside.

Our analyses returned different volume–biomass functions for the species with and without browsing. In the case of *A. herba-alba* (Figure 2a), biomass was higher inside than outside for the same plant volume, which means that the individuals grew more densely without browsing. By contrast, the biomass of *A. mesatlantica* was higher outside of the enclosure (Figure 2b). Finally, for small plants (volume < 5 dm³) of *T. mideltense* (Figure 2c) there was no difference, whereas the biomass per volume of large individuals was higher with browsing.

The static and transitional methods of biomass calculation yielded very similar results for *A. herba-alba* and *T. mideltense*, whereas the patterns found in *A. mesatlantica* strongly differed between these two methods (Table 1, Figure 3). The static method for *A. mesatlantica* indicated no significant differences between the treatments, whereas the transitional method found a negative impact of browsing exclusion on cumulative biomass development of this species over the five years (Table 1).

For *A. herba-alba*, the cumulative biomass from 2004 to 2009 increased strongly both inside and outside the enclosure, but the absolute biomass increase was three-fold higher without browsing (Table 1). Considering the interannual changes, browsing was strongly negative for biomass development in three cases (2005–2006, 2007–2008 and 2008–2009), negative in 2004–2005, whereas it showed inconsistent effects among the two calculation methods for 2006–2007 (Figure 3a).

For *A. mesatlantica*, the cumulative biomass from 2004 to 2009 showed generally a slightly more positive trend with browsing than without (Table 1). For this species, we found the largest differences between our two methods of biomass calculation. We observed a positive trend with and without browsing for the static method. By contrast, a slight negative trend was observed with the transitional method. Furthermore, the difference between the browsed

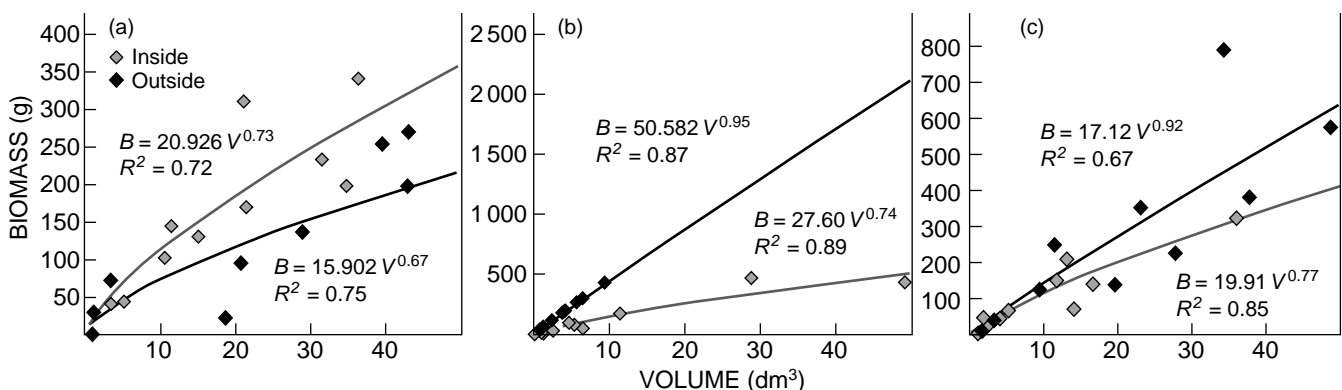


Figure 2: The power-law functions determined with nonlinear regression inside and outside the enclosure for (a) *Artemisia herba-alba*, (b) *Artemisia mesatlantica* and (c) *Teucrium mideltense*. B = aboveground biomass (g), V = volume (dm³)

Table 1: Mean cumulative annual biomass change from 2004 to 2009 in comparison between grazed and ungrazed plots. The mean biomass changes for *Artemisia herba-alba* are given in g m^{-2} , and those for *A. mesatlantica* and *T. mideltense* in g individual^{-1}

Species	Grazed	Ungrazed (static method)	<i>P</i>	Ungrazed (transitional method)	<i>P</i>
<i>Artemisia herba-alba</i>	+92	+230	<0.001	+279	<0.001
<i>Artemisia mesatlantica</i>	+61	+56	0.798	-1	0.009
<i>Teucrium mideltense</i>	+11	+17	0.847	+13	0.855

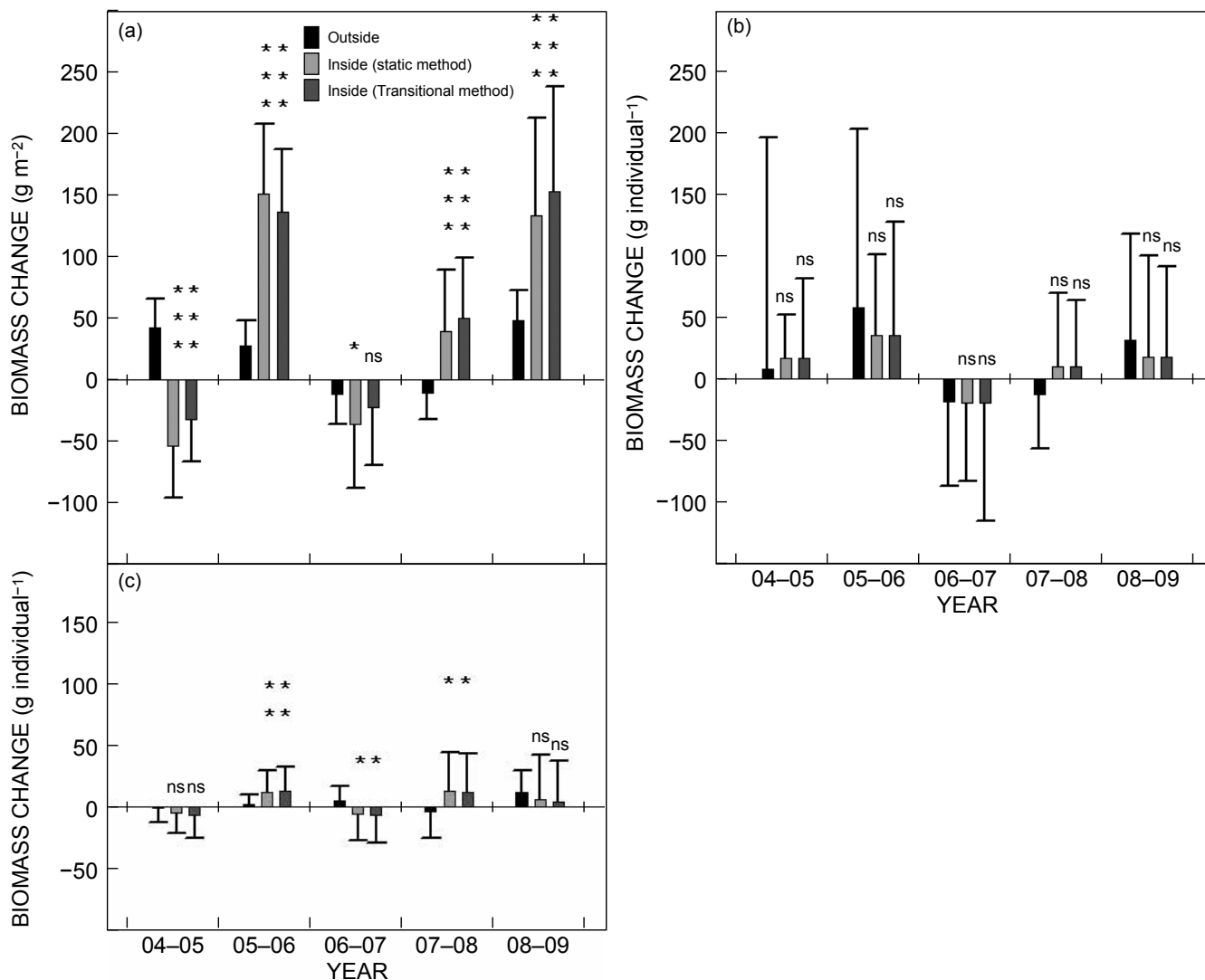


Figure 3: Mean interannual biomass changes for (a) *Artemisia herba-alba*, (b) *Artemisia mesatlantica* and (c) *Teucrium mideltense* inside (static and transitional methods) and outside the enclosure. The symbols above the bars indicate the significance of different biomass development compared to plots outside the enclosure. Error bars represent the SD. ns = $P \geq 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

and unbrowsed treatments was significant only with the transitional method (Table 1). The same was observed for biomass changes between subsequent years (Figure 3b).

For *T. mideltense*, the cumulative biomass change from 2004 to 2009 did not differ significantly between the browsed and unbrowsed plots (Table 1). Mean biomass hardly varied between the browsed and unbrowsed plots. Mean biomass per individual fluctuated from year to year

(Figure 3c). Biomass development was significantly higher within the enclosure during only two observation periods, whereas for 2006–2007 it was significantly lower.

The results show that the volume–biomass relations of the three species behaved differently on browsed and unbrowsed plots. *Artemisia herba-alba*, which is the dominant species in the study site, was found within both treatments in all sizes from juvenile to mature. We further

observed that individuals of *A. herba-alba* grew less dense with browsing. This could be because of their growth habit: individuals tended to respond to browsing pressure by developing long and sparse perpendicular twigs and shoots. With browsing exclusion, we observed that individuals developed more short and dense perpendicular shoots. Accordingly, if the same volume–biomass function would have been applied to both treatments, it would have returned biased biomass estimations.

For *A. mesatlantica*, individuals under the browsing treatment grew denser than without browsing. This result again can be explained by plant architecture with a woody base and parallel, ascending shoots. Browsing animals preferentially consume the less dense upper shoots of the plants (MF pers. obs.). Another reason for the denser plants in the browsing treatment might be the dominance of small individuals with browsing, whereas we found larger individuals in the enclosure. Tausch (1989) attributed similar results to the presence of more abundant smaller plants, which generally had denser crowns with more biomass per unit of crown volume than the fewer, larger plants.

For *T. mideltense*, the absence of differences between browsed and unbrowsed small individuals (<5 dm³) could be explained by the selective browsing of sheep. Selectivity of sheep was also documented for other North African shrubs, including *A. herba-alba* in Tunisia (Ben Salem et al. 1994). Large individuals of *T. mideltense* have a growth habit similar to *A. mesatlantica* and hence the same reasoning may apply here.

The two different approaches for biomass estimation (the transitional and static methods) yielded qualitatively similar results in *A. herba-alba* and *T. mideltense*. This congruence lends support to our estimation, and theoretically the true development must be within the boundaries defined by these two estimation approaches. The relatively greatest difference between the two methods was found for *A. mesatlantica*, which might be only because of the relatively small sample size, especially in the larger volume classes. Tausch (1989) found that the nonlinear regression method, which we chose for the present study, is the most appropriate for sagebrush species, whereas Abdelkader et al. (2008) found reasonable linear correlations for volume–biomass relationships for *A. herba-alba* in Tunisia. However, he argued that using the mean diameter of individuals resulted in a better fit than using volume estimates. We feel that further studies are necessary to gain a clearer understanding of how the two estimation approaches might affect biomass estimations in monitoring studies and which allometric parameter is most useful.

Browsing had a significant negative effect on cumulative biomass development of *A. herba-alba* over the five years. This is not surprising given the high density and palatability of this shrub (Ben Salem et al. 1994), and thus its importance to the animals' diet in comparison with the other two species. The fact that browsing had only minor effects on the two other studied species perhaps indicates that they are more resistant to browsing (Le Houérou 1980). Our findings indicate that they might even benefit indirectly from browsing through the reduction of the most competitive species in this ecosystem. According to the transitional method, *A. mesatlantica* benefited significantly from

browsing over the five-year period as a whole, but not between individual years. *Teucrium mideltense*, meanwhile, did not show a cumulative difference, being affected by browsing positively in some years and negatively in others. We cannot infer too much from these inconsistent results, however, and confirmation of the potentially positive effect of browsing must await further studies.

The main merit of our study is the characterisation of volume–biomass functions for three ecologically and agronomically important dwarf shrubs in Moroccan steppe ecosystems. We have been able to show that these species change their architecture when subjected to browsing. Furthermore, we introduced two alternative approaches for the estimation of annual biomass changes based on allometric functions gained by nonlinear regression. These two approaches, i.e. the static and transitional methods, represent the two extremes of plant individual response to relaxation from herbivore pressure. The truth must lie between the values obtained by the two approaches and when both yield consistent results one can be sure about the outcome. Our study has also clearly demonstrated how plant response to browsing exclusion can differ strongly not only between species but also between years. Data from a single year is clearly not sufficient to describe plant behaviour. This was demonstrated by *A. herba-alba*, which showed a positive browsing effect for two of the five interannual transitions, but a negative cumulative effect over the study period.

Our case study was not designed to make inferences about browsing effects at the ecosystem level, as we did not replicate the treatments. However, it gives valuable insights into the processes that need taking into account in any future attempts at the ecosystem-wide quantification of browsing impact. One result meriting further investigation was the varying effect of browsing on the dominant versus two subdominant species found in our plots. Another interesting finding was how the standing biomass for all three species increased over the five years. This was strongest without browsing, but nevertheless apparent with browsing. It might be attributable to a recovery of the whole ecosystem after a long period of drought ending in the year 2000 (Born et al. 2008). This relatively quick biomass rehabilitation is a common feature of such non-equilibrium ecosystems (Finckh and Goldbach 2010). Relatively short time periods, i.e. up to 5–10 years, can apparently result in the restoration of biomass resources of the major dwarf shrub species, depending on the type of ecosystem.

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