

Implications of local-scale productivity on compensatory growth in a semi-arid shrubland[☆]

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ABSTRACT

Grazing is a dominant determinant of aboveground net primary production (ANPP) and composition of plant communities. However, ANPP can be maintained following grazing due to compensatory growth, the level of which might depend on additional environmental factors, such as precipitation and edaphic conditions. Several studies have shown that along large-scale regional gradients, community-level compensatory ability is positively correlated with ANPP and soil resource availability. However, community-level responses to grazing are also expected to be affected by local-scale heterogeneity in ANPP, particularly under low primary productivity typical to arid environments. Here, we studied the effect of local-scale variations in ANPP on the compensatory growth of an annual community in a semi-arid region. For two consecutive years, ANPP was evaluated following shoot damage in sites with different primary productivity. The results demonstrated that annual ANPP varied significantly among sites and among plots within sites; however, compensatory ability was negatively correlated with annual ANPP, with overcompensation in the least productive patches and under-compensation in the most productive patches. This pattern contradicts the positive correlation between ANPP and compensatory ability commonly found along large-scale productivity ecoclines, suggesting that the effects of ANPP on compensatory ability might be scale-dependent.

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1. Introduction

Grazing has major effects on primary productivity and composition of plant communities (Milchunas and Lauenroth, 1993; McNaughton et al., 1998; Chase et al., 2000; Cingolani et al., 2005). Although the loss of tissues and entire organs through physical damage can be detrimental to plants, both field and experimental results reveal that biomass production is commonly maintained by compensatory growth (reviewed in Belsky, 1986; Stowe et al., 2000). In some cases, grazing has even been shown to stimulate overcompensation, i.e., greater aboveground biomass production in grazed compared to control stands (e.g., Paige and Whitham, 1987; Patton et al., 2007).

The possibility of community-level compensatory growth following damage is of special importance for range management and the maximization of Aboveground Net Primary Production (ANPP) under livestock grazing (Trlica and Rittenhouse, 1993). The

effect of grazing has been shown to strongly interact with other environmental factors, such as grazing history, precipitation and edaphic conditions, in determining ANPP (Milchunas and Lauenroth, 1993; Milchunas et al., 1998; Leriche et al., 2001; Bardgett and Wardle, 2003). For example, several studies have shown that community-level compensatory ability was positively correlated with ANPP and soil resource availability (e.g., Chapin and McNaughton, 1989; Bardgett and Wardle, 2003; Leriche et al., 2003; Blanco et al., 2008), which was attributed to the facilitation of greater compensatory growth under higher availability of soil resources (but see Milchunas and Lauenroth, 1993; Oesterheld et al., 1999).

The interactive effect of productivity on community-level compensatory responses has mostly been studied at the ecosystem level along large-scale productivity ecoclines (e.g., Milchunas and Lauenroth, 1993; Chase et al., 2000; Blanco et al., 2008; Sasaki et al., 2008). At these scales, variations in community-level compensatory ability could be attributed to variations not only in precipitation and soil resource availability but also in grazing history and intensity (Milchunas and Lauenroth, 1993). However, community-level responses to grazing are also expected to be affected by local-scale heterogeneity in ANPP, which could be especially true in arid environments, whose plant communities are

[☆] This paper is dedicated to the memory of Prof. Imanuel Noy-Meir – a great scientist and teacher whose humble nature and soft-spoken demeanor could not cloak the bright man that he was.

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usually strongly affected by resource distribution in space and time (Goldberg and Novoplansky, 1997; Snyder and Tartowski, 2006). In these environments, knowledge of local-scale differences in compensatory responses to grazing could be valuable for land management; however, only a few studies have examined the effect of local-scale ANPP on community-level tolerance (Leriche et al., 2003; Patton et al., 2007; Thiel-Egenter et al., 2007), specifically in arid environments.

The goal of this study was to examine the effect of local-scale variations in ANPP on the compensatory responses of an annual plant community to grazing in a semi-arid Mediterranean region in Israel, where annual vegetation provides the main forage source for livestock grazing during winter. We hypothesized that in such a low-productivity environment, the ability of plants to recover and compensate for biomass loss depends on local ANPP, measured as total aboveground biomass (Gruner et al., 2008).

The study was conducted in shrubland areas of the Yatir forest, where current management practices include grazing of the native vegetation by local herds of sheep and goats through the winter and early summer (February–June). We predicted that due to over-compensatory regeneration the administration of a single clipping event earlier in the growth season (January) would enhance compensatory ability and result in greater forage production later in the season (Ramula, 2008). Moreover, we predicted that compensatory responses would be greater in sites with greater annual productivity due to greater amount of resources that could be available for regeneration, as was previously found at the ecosystem scale (Chase et al., 2000; Bardgett and Wardle, 2003; Blanco et al., 2008).

2. Methods

2.1. Study site

The study was conducted in the Yatir forest, located in the semi-arid region of the southern Judean Hills (31°21' N, 35° 02' E, 620 m a.s.l.). Yatir is Israel's largest planted forest, covering an area of ca 30 km², most of which is dominated by 40- to 50-yr-old *Pinus halepensis* Mill trees. The climate is dry Mediterranean with a single rainy season between October and April, mean annual rainfall of 270 mm, and average daily air temperatures of 13 °C and 31 °C in winter and summer, respectively (Israeli Meteorological Service). The surface is typically covered by a 30–50 cm deep Rendzina soil on limestone and chalk bedrocks (Singer, 2007). As most, if not all, of the Eastern Mediterranean region, the landscape and vegetation of the Yatir region have been highly disturbed over the last 7–8 millennia by various anthropogenic effects, mainly related to livestock grazing and agriculture (Perevolotsky and Seligman, 1998). However, due to livestock management practiced during the last 50 years, the landscape of the Yatir region is less degraded than the surrounding areas.

The experiment was conducted in large open sites within the forest (Safriel et al., 2002), which are covered by a sparse shrubland (Batha), dominated by sub-shrubs such as *Sarcopoterium spinosum* L. and *Noaea mucronata* Aschers. & Schweinf., hemicryptophytes such as *Asphodelus ramosus* L. and *Gundelia tournefortii* L. During the winter the natural vegetation is dominated by annual grasses such as *Hordeum spontaneum* K. Koch and forbs such as *Calendula arvensis* L. and *Hymenocarpus circinnatus* (L.) Savi.

2.2. Experimental design

The study was conducted over two consecutive growing seasons. In September 2005, five open 15 × 15 m sites were chosen within the forest and fenced to prevent livestock grazing. The sites

were located 300–900 m apart, 590–620 m a.s.l. and were chosen so that they differed in inclination and aspect to represent the range of common habitats and levels of annual plant productivity in the region (Safriel et al., 2002): site A was inclined by 13° toward east; site B was inclined by <1° toward southwest; site C was inclined by 5° toward northwest, and both sites D and E were inclined by 6° toward southeast.

2.2.1. The 2005–6 season

The experiment was designed as part of a larger remote-sensing project, which necessitated large experimental plots so each site included two 10 × 5 m plots, which were assigned to either a control (no-clipping) treatment, or an artificial clipping treatment. Livestock grazing has been shown to remove 50% and 75% of plant biomass in sites with low and high ANPP, respectively (Osem et al., 2002). Accordingly, we removed 50% of the biomass of each shoot of all the annual plants. Clipping was conducted at the end of January following the initial establishment of the seedlings but sufficiently early to allow the plants adequate time for regeneration. At the natural end of the growing season (May) all annual aboveground biomass was clipped and collected from the experimental plots, oven dried at 60 °C for 48 h and weighed using an analytic balance.

2.2.2. The 2006–7 season

The second experiment was conducted at the same sites. Because large plots were no longer required in the second year and to increase statistical power, the plot design was altered to increase the sample number at the expense of sample size. Accordingly each site included five pairs of clipped and control 0.6 × 0.6 m plots that had similar micro-scale levels of ANPP. As the plots were assigned prior to the emergence of annual plants, differences in ANPP were estimated according to the densities of standing dry biomass and micro-topography such as stoniness and proximity to mounds, swales and shrubs (Boeken and Shachak, 1994). Clipping was conducted at the beginning of February following seedling establishment. In April 2007, all aboveground biomass was collected, dried and weighed as per the 2005–6 season.

2.3. Data analysis

The effect of clipping on plant performance was evaluated by the aboveground biomass produced by the plants throughout the season. For the 2005–6 experiment, the effects of clipping and site were analyzed separately using Kruskal–Wallis tests, due to the low sample size ($n = 5$). For the 2006–7 experiment, the effects of treatment, site and plot were analyzed using a split-plot ANOVA design, where plots were nested within sites (whole plot) and the clipping treatment served as a subplot. Post-hoc Tukey comparisons were used to compare sites. The assumptions of normality and homogeneity of variances were met for the 2007 results. The difference in ANPP between the two growing seasons was evaluated using Kruskal–Wallis test, after averaging biomass per plot within each site in the 2006–7 experiment to produce single values for the control and clipped plots per site, to match the sample size in 2005–6.

To analyze the relationship between compensatory ability and ANPP, a correlation analysis was performed between the Relative Change in Biomass (RCB) of clipped (B_{clipped}) compared to control (B_{control}) plots [$\text{RCB} = (B_{\text{clipped}} - B_{\text{control}})/B_{\text{control}}$] and biomass of the control plots (Ferraro and Oesterheld, 2002). Accordingly, negative, zero and positive values of RCB indicated under- full- and over-compensation in biomass production, respectively. This correlation was analyzed for the 2005–6 results and for average biomass per plot in 2006–7. Due to the small sample sizes, all correlations were

analyzed using non-parametric Spearman's correlation test. The difference in compensatory ability between the two years of the study was analyzed using the Wilcoxon Signed Ranks test, where average RCB per year was the dependent variable. All statistical analyses were performed using SPSS ver. 15 (SPSS Inc., Chicago).

3. Results

ANPP significantly varied between the two years of the study, with four times greater biomass in 2006–7 compared to 2005–6 (Fig. 1; Kruskal–Wallis test, $\chi^2 = 2.012$, $p = 0.001$, $n = 10$), corresponding to 48% greater annual precipitation in 2006–7 compared to 2005–6 (Israeli Meteorological Service). Though marginally significant, overall community-level compensation differed between the years with a 40% increase in biomass following clipping in 2005–6 compared to a 4% decrease in 2006–7 (Fig. 2; Wilcoxon Signed Ranks test, $Z = -1.753$, $p = 0.08$, $n = 5$). In 2005–6, neither site nor clipping had significant effects on productivity (Fig. 1a, b; Kruskal–Wallis test for site and clipping: $\chi^2 = 1$, $p > 0.05$, $n = 2$; $\chi^2 = 0.632$, $p > 0.05$, $n = 5$, respectively). However, in 2006–7, productivity varied among both sites and plots (Fig. 1a, b; Table 1), and clipping had a marginally significant negative effect on productivity (Fig. 1; $p = 0.079$). Moreover, the effect of clipping varied among sites, as different sites demonstrated either under- full- or overcompensation (significant site by clipping interaction, Fig. 1a, b; Table 1).

The weak overall negative effect of clipping in 2006–7 was mainly due to a significant reduction in biomass following clipping in site A compared to the other sites (Fig. 1b; $F_{1,10} = 8.415$, $p < 0.05$). When plot A was excluded from the analysis, neither clipping nor site effect were significant, but the effects of plot or clipping by site interaction remained significant (Fig. 1b; $F_{20,20} = 2.098$, $p < 0.05$; $F_{3,20} = 4.828$, $p < 0.05$, respectively).

Primary productivity reflected in the biomass of the control plots negatively affected the relative change in biomass due to clipping between sites in both years (Fig. 3; 2005–6: Spearman's $\rho = -0.9$, $p < 0.05$, $n = 5$, $r^2 = 0.658$; and 2006–7: Spearman's $\rho = -0.9$, $p < 0.05$, $n = 5$, $r^2 = 0.399$), with overcompensation in the least productive plots and the greatest under-compensation in the most productive plots (Fig. 3).

4. Discussion

In this study we evaluated the effect of local-scale differences in ANPP on community-level compensatory ability. Annual ANPP in the Yatir forest varied remarkably in both time and space, between years, sites and plots. Additionally, while clipping had no net effect

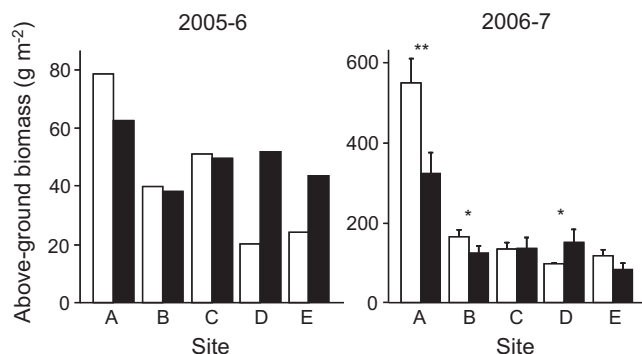


Fig. 1. Above-ground biomass per 1 m² in control (white bars) and clipped (black bars) plots in the 2005–6 (means) and 2006–7 (means ± SE) field experiments. Mean comparisons between control and clipped plots per site in the 2006–7 experiment are indicated according to level of significance: * $P < 0.05$, ** $P < 0.01$.

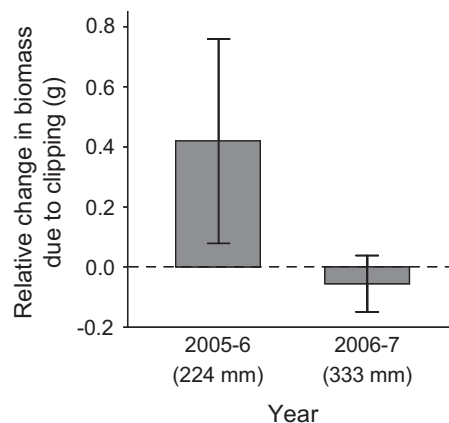


Fig. 2. The effect of growing season (annual precipitation indicated in brackets) on annual community compensatory ability (relative change in aboveground biomass due to clipping) (means ± SE).

on aboveground biomass in the entire range, a significant interaction between clipping and site suggests that community-level tolerance was affected by site properties. Interestingly, and in contrast to our prediction, we found a significant negative correlation between the relative change in biomass following clipping and biomass of the controls, suggesting that community-level compensatory ability decreased with ANPP, a pattern that was consistent over the two years of the study despite the four-fold difference in overall productivity between them. This general pattern is further supported by the greater overall compensation in the drier year (2005–6).

The strong effects of water availability at the large (seasonal) and local (site/plot) scales and the lack of effect of clipping on annual ANPP in Yatir are consistent with several studies in arid and semi-arid regions (Milchunas and Lauenroth, 1993; Proulx and Mazumder, 1998; Vetter, 2005; Sasaki et al., 2008). These results reflect the high temporal and spatial heterogeneity in soil fertility and plant productivity characterizing dryland environments (Noy-Meir, 1985; Snyder and Tartowski, 2006). The greater productivity of site A compared to the other sites, particularly in 2006–7, could be attributed to anthropomorphic influences, such as higher nutrient content in the soil due to the close proximity of site A to caves which in historical times were used for human habitation and animal enclosure (Goldberg and Sherwood, 2006).

The negative relationship between post-damage regeneration and ANPP contradicts the common pattern found in most studies, where community-level compensation is positively correlated with precipitation and ANPP (Chapin and McNaughton, 1989; Bardgett and Wardle, 2003; Leriche et al., 2003; Blanco et al., 2008). Studies at the individual-plant level lead to the formulation of two alternative models for the contrasting patterns of the effect of resource levels on plant tolerance to damage (Wise and

Table 1

Results of a split-plot ANOVA for the effects of site, clipping treatments and plot nested within site on total biomass production (including early clipped and harvested biomass at the end of the season) for the 2006–7 field experiment.

Source of variation	df	MS	F
Site	4	35573.821	36.218***
Clipping	1	1145.756	3.385 ns
Plot (site)	25	981.886	2.901**
Site × Clipping	4	1767.807	5.223**
Error	23	338.444	

ns - $p > 0.05$, ** - $p < 0.01$, *** - $p < 0.001$.

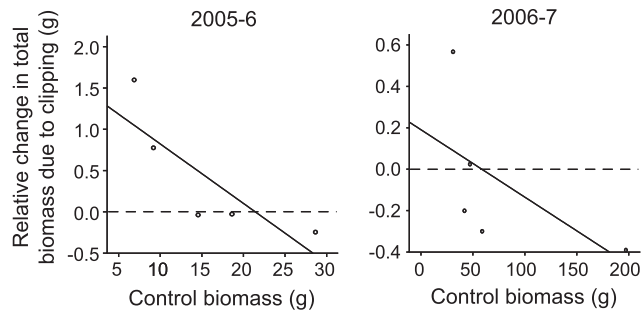


Fig. 3. The effect of ANPP (biomass in control plots) on annual community compensatory ability (relative change in aboveground biomass due to clipping) in the 2005–6 and the 2006–7 field experiments. The dashed lines represent no difference between biomass production of CONTROL and CLIPPING, and thus represent full-compensation. Accordingly, data points above and below the dashed lines represent over- and under-compensation, respectively.

Abrahamson, 2005). According to the ‘compensatory continuum model’, greater resource availability is expected to support greater compensatory growth (Maschinski and Whitham, 1989). Alternatively, the ‘growth rate model’ (Hilbert et al., 1981), which is consistent with our results, predicts greater compensation in plants that grow under low resource availability. According to this model, when growth is resource-limited, even relatively small increases in growth rates following damage may enable significant increases in regenerative compensation. In contrast, plants that grow under high resource availability have relatively higher background growth rates that are harder to augment by post-damage regeneration. Similar predictions were presented more recently by the ‘limiting resource model’, according to which plants growing under high levels of soil resources become increasingly limited by carbon due to light competition and thus are expected to demonstrate lower compensatory ability to shoot grazing, which further exacerbates carbon limitation (Wise and Abrahamson, 2005).

The apparent contrasting patterns between local scales and larger productivity clines suggest that the effects of productivity on compensatory ability might be scale-dependent (Leriche et al., 2001; Chase and Leibold, 2002). Accordingly, studies on individual taxa or communities such as the present work might depict plastic traits that reflect adaptations to local-scale temporal and spatial heterogeneities. Conversely, comparative data from different locations on large-scale ecoclines are expected to reflect differential responses that are based on greater genotypic specialization to a wider spectrum of resource levels and dynamics (Milchunas and Lauenroth, 1993), consumption rates (Frank et al., 1998) and competitive regimes (Becker et al., 2006; Gruntman and Novoplansky, unpublished data).

In arid environments greater biomass is usually associated with increased plant height rather than greater plant density (Shilo-Volin et al., 2005). Therefore, the negative association between annual ANPP and compensatory growth suggests that following damage, large and tall plants, whose dominance increases with productivity, incur greater biomass loss than smaller plants. Such differential tolerance to damage is expected to promote coexistence and greater species diversity in moderately-grazed stands via an indirect augmentation of the well-documented effects of dominance-suppression by various disturbances (Connell, 1978; Niedrist et al., 2009). Poorer tolerance of the dominant species to damage could partially explain the often-observed negative impact of grazing on the abundance of larger species in semi-arid and Mediterranean rangelands, which is commonly attributed to their greater apparency to grazers (Noy-Meir et al., 1989; Sternberg et al., 2000; Osem et al., 2004).

4.1. Concluding remarks

Our results agree with several studies demonstrating the ability of plants to fully compensate for simulated grazing in grazing-dominated systems (e.g., Biondini et al., 1998; Blatt et al., 2008). As in most drylands of the Middle-East region, the Yatir forest, and especially its annual plant communities, has a long history of intensive livestock grazing (Perevolotsky and Seligman, 1998), which might have selected for differential responses of plants to grazing under different productivity levels (Osem et al., 2002).

While our results demonstrate the ability of plants to regrow following damage, plants have also been shown to respond to salivary chemicals, soil trampling and root pulling associated with grazing (reviewed in Baldwin, 1990; Tiffin and Inouye, 2000). Grazing can also have additional effects on biomass production that are not mimicked by tissue removal such as changes in soil fertility (Augustine et al., 2003) and regulation of resources (Tongway et al., 2003), and thus the above conclusions may only partially represent the long-term effect of grazing on biomass production. Further experiments are therefore required, where the effects of grazing by local livestock on the compensatory ability of the Yatir plant community could be compared to that of artificial clipping.

The negative correlation between compensatory ability and ANPP suggests that early grazing might not incur a significant cost in overall forage production, particularly in sites of low productivity and even in drought years. Accordingly, prescribed early (winter) grazing might induce overcompensation in low productivity patches with little or no negative effects on biomass productivity in more productive patches although detailed studying of this possibility and its calibration for different ecosystems are required before specific management protocols are recommended.

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