

Prioritized contingencies: context-dependent regenerative effects of grazer saliva

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Abstract Naturally growing plants are able to plastically respond to myriad environmental challenges and opportunities. When confronted with multiple stresses, plants are expected to be able to prioritize their responses according to immediacy and predicted acuteness of these stresses. Here, we studied the interactive effects of competition and nutrient deprivation on growth responses of damaged *Trifolium purpureum* plants to salivary cues of a mammalian grazer. Salivary cues elicited marked growth responses in damaged but otherwise well-nourished and competition-free *T. purpureum* plants; however, this positive effect was annulled under *Stipa capensis* competition and was reversed under nutrient deficiency. The results suggest that the magnitude and direction of the effects of salivary cues on plant growth depend on an intricate prioritization of plant responses to prevailing and expected

challenges and that *T. purpureum* plants perceive competition as a more acute stress than grazing. While herbivore saliva enables plants to reliably differentiate between herbivory and physical damage, the limited correlation between prevailing and future herbivory might reduce the informative value of salivary cues, rendering their effects weaker than those of prevalent competition and nutrient deficiency, whose continued detrimental effects are usually highly predictive. The results stress the importance of further studying the interactive effects of the acuteness and reliability of prevailing and anticipated stresses, and the informational content and adaptive value of environmental cues under various environmental circumstances.

Keywords Herbivory · Grazing · Phenotypic plasticity · Prioritized responses · Salivary cues · *Trifolium purpureum*

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Introduction

Naturally grown plants are typically subjected to simultaneous stresses caused by various abiotic factors (Long et al. 1994), competition (Goldberg and Barton 1992) and herbivory (Coley and Barone 1996; Wu and Baldwin 2010). The variable severity and interactive complexity of these environmental stresses imply that plants are expected to prioritize the timing, immediacy, and extent of their plastic

responses according to their expected long-term costs and benefits, and the acuteness of the challenges (Ballare 2009; DeWitt et al. 1998; Novoplansky 2009). These theoretical considerations imply that plastic responses are invariably *context-dependent* and besides the genetic background of the plants ($G \times E$; Schlichting and Pigliucci 1998), are also contingent on a wide spectrum of factors such as plant ontogeny (Boege and Marquis 2005; Diggle 2002; Watson et al. 1995), past plastic responses (Novoplansky 1996; Weinig 2000), and various costs and limitations (DeWitt et al. 1998; Givnish 2002).

The level of stress acuteness is expected to be dictated by both its severity and probability (Halpern et al. 2010; Stewart 2001). More probable, imminent, and severe stresses are expected to elicit stronger and more immediate responses (Ballare 2009; Florig et al. 2001; Moreno et al. 2009; Stewart 2001). Information regarding future growth conditions can be perceived either directly, via prevailing resource and stress levels or through anticipatory cues, which are correlated with expected future stresses and hazards such as competition (Aphalo and Ballare 1995; Novoplansky 2009; Smith 1982), herbivory (Heil and Karban 2010; Howe and Jander 2008; Karban et al. 1999), and resource availability (Forde and Zhang 1998; Shemesh et al. 2010).

Specifically, plastic responses to herbivory can be elicited by two sources of information—(a) biomass loss and mechanical injury, which typically generate both direct damages and *resource-level* cues (sensu Aphalo and Ballare 1995) and (b) salivary cues, which are considered *pure cues* and were suggested to be used by plants to differentiate herbivory from other mechanical damages (Korth and Dixon 1997; Thivierge et al. 2010).

Previous studies found mammalian saliva had either positive (Bergman 2002; McNaughton 1985; Rooke 2003; Teng et al. 2010; Zhang et al. 2007) or no effects (Detling et al. 1980; Detling et al. 1981) on plant growth. However, these studies mostly examined the effects of herbivore saliva on plant growth outside the context of other environmental factors (but see Detling et al. 1980; and McNaughton 1985 on the interaction between salivary cues and nutrient availability).

Here, we studied the effects of goat saliva on plant growth in *Trifolium purpureum* plants, which were grown under two levels of nutrient availability and

competition. We hypothesized that the direction and intensity of plant responses to goat saliva depend on the severity of prevailing and anticipated stresses. Specifically, we predicted that plants would be responsive to salivary cues under otherwise benign conditions but less responsive to salivary cues when subjected to severe stresses, which are likely to sustain once started, such as competition or nutrient limitation.

Materials and methods

Plant material

The experiment was conducted with *T. purpureum* (Papilionaceae) as the target species and *Stipa capensis* (Gramineae) as a competitor. Both species are obligatory annuals which often co-occur in close proximity in Mediterranean and semi-arid grassland communities in the Middle-East, a region subjected to millennia of intense grazing by goats and sheep (Landau et al. 1995; Luikart et al. 2001), which is evident from both current grazing practices and archeological findings (e.g., Bruins 1990). Seeds of both species were collected in September 2007 from a natural shrubland 15 km north of Beer-Sheva, Israel, (31°14' N, 34°48' E; average annual rainfall of 300 mm) regularly grazed by mixed herds of goats and sheep.

Experimental design and growth conditions

The experiment was conducted in a greenhouse at the Ecological Growth Facility, Sede Boker Campus (30°51' N, 34°46' E), under nearly ambient temperatures and light levels but protected from frost, rain, and wind gusts. We compared *T. purpureum* plants that were grown under high or low nutrient availability, with or without *S. capensis* competition, clipping and goat saliva. Clipping was included to test whether biomass removal was required to facilitate saliva effects. Accordingly, the full factorial design included 16 treatments, 15 replications per treatment, and a total of 240 pots. Plants were randomly assigned to blocks so that each block included one replication of all treatments, controlling for possible positioning effects within the greenhouse.

Plants were grown in 1.5 l, 25 cm deep, and 8.5 cm in diameter opaque polyethylene sleeves. The

sleeves were filled with washed sandy Rhodoxeralf soil (Goldshleger et al. 2009). One and a half grams of Osmocote controlled-release fertilizer (15% N, 9% P₂O₅, 10% K₂O; Scotts, Geldermalsen, The Netherlands) was thoroughly mixed into the top 10 cm of the soil in the high-nutrient pots, and no fertilizer was supplemented to the low-nutrient pots. Four seeds of *T. purpureum* and *S. capensis* (in the competition treatment) were sown in each pot on November 14, 2007, which is within the natural germination season of the experimental plants. Fifteen days after sowing, the seedlings were thinned down to the desired densities of similarly sized seedlings. Throughout, the plants were irrigated to field capacity (≤ 300 ml per pot) once every few days, according to weather conditions, using an automated drip irrigation system.

Competition

Individual *T. purpureum* target plants were grown either alone (no neighbors) or with two *S. capensis* plants (competition), at a distance of 2–3 cm from either sides of the target plants.

Clipping

Clipping was carried out on March 20, 2008, which is within the typical grazing season of these plants in the field, yet allowing the plants sufficient time for regeneration before the termination of the growing season. The seminal shoot and the lateral basal branches of the target plants were individually clipped with scissors so each shoot was left with five nodes, allowing for later regeneration from axial primordia. Clipping imposed the loss of approximately 60–70% of the total aboveground biomass at the time of clipping (data not shown). In the competition treatments, the *S. capensis* neighbors were clipped to the same height of the seminal shoot of the *T. purpureum* targets, which mimicked even-level grazing, approximately 10 cm above the ground. Clipped biomass was used as a co-factor in the statistical analysis.

Saliva collection and application

Goat saliva was collected on March 19 and was stored at -20° C until use (after Bergman 2002). Saliva was collected from five individual goats

(*Capra aegagrus hircus*) belonging to the Azazme Bedouin tribe while grazing on natural vegetation 15 km south-east of the location of the seed collection, where the vegetation is dominated by *Noaea mucronata*, *Thymelaea hirsute*, *Helianthemum kahiricum*, *Asphodelus ramosus*, and *S. capensis*. *T. purpureum* was not present at this site, therefore eliminating the possibility of morphogenetic induction by macerated tissues of *T. purpureum*. Saliva was collected in the early afternoon, after the goats had spent a few hours grazing in the field. Five milliliters of saliva was extracted from the mouth of each goat, using a small hand-pump connected to a rubber tube. The saliva collected from all goats was pooled and thoroughly mixed before application. In treatments which included saliva application, saliva was brushed over the leaves of both the target *T. purpureum* and the *S. capensis* competitor plants using a fine brush, 0.1 ml per plant. In clipped plants, the saliva was applied over the entire surface of the shoot stumps. In order to increase the exposure of undamaged plants to salivary cues, saliva was applied to longitudinal lacerations made along the main veins of the leaflets of the fifth leaf of the lowest branch, using a razor blade. Plants that were not treated with saliva were treated with distilled water according to the same protocol.

Data collection

Harvest was carried out at the natural end of the growing season on May 1, 2008 (168 days after sowing, when the target *T. purpureum* plants had ripened their fruits). The roots of the *T. purpureum* target and its *S. capensis* neighbors could not be separated and thus were weighed together. The biomasses of the roots and the shoots of plants growing without neighbors were highly correlated (Pearson's $R = 0.73$, $P < 0.001$). Dry biomass of plant parts was estimated after plants were dried in a ventilated oven at 60° C for 72 h. Measurements included the number of basal branches (branches that emerge from the lowest two cm of the seminal shoot) and the dry biomasses of the inflorescences and the rest of the vegetative shoot system. Vegetative shoot biomass was highly correlated with total aboveground biomass ($R = 0.988$, $P < 0.001$; Bonferroni corrected probability), and thus, the presented data include total aboveground biomass, number of basal

branches and reproductive biomass as indicators of plant size, architecture, and fitness, respectively. Additional data regarding the vegetative biomasses as well as the root allocation of *T. purpureum* and the aboveground biomass of the *S. capensis* plants are appended in the supplementary material (Tables S1–S7; Figs. S1, S2).

Statistical analysis

The results were analyzed using a full factorial design and a general linear model (GLM). The effects of saliva on aboveground biomass at the end of the season were analyzed, as it best reflected the plant's ecological performance. Treatment effects on total aboveground biomass (including clipped biomass) displayed similar trends to those of aboveground biomass (Table S7). In order to control for differences in the biomass that was clipped from each plant, "total clipped mass" was added to the model as a covariate. Similar trends were attained when analyzing the data with or without the incorporation of the total clipped biomass as a covariate in the statistical model (data not shown). Block was found to be significant for some of the parameters and was included in the analysis. No significant interactions were found between block and any of the main factors; therefore, the presented results do not include block by treatment interactions. All analyses were conducted using SYSTAT 11 (Systat software, Inc. CA, USA).

Results

As expected, both competition and nutrient deficiency had significant negative effects on the size of the target plants (Figs. 1, 2). In order to quantify the effect of each factor separately, we compared unstressed plants (no competition, clipping or nutrient deficiency) to plants that experienced only one of these stresses. Competition was found to be the most influential stress, with an 85% reduction in plant size, followed by nutrient deficiency and clipping, with 55 and 48% size reductions compared with controls, respectively. Saliva, on the other hand, did not have a significant effect on plant growth (Tables 1, 2).

The statistical analysis revealed a significant interaction between all experimental factors for the

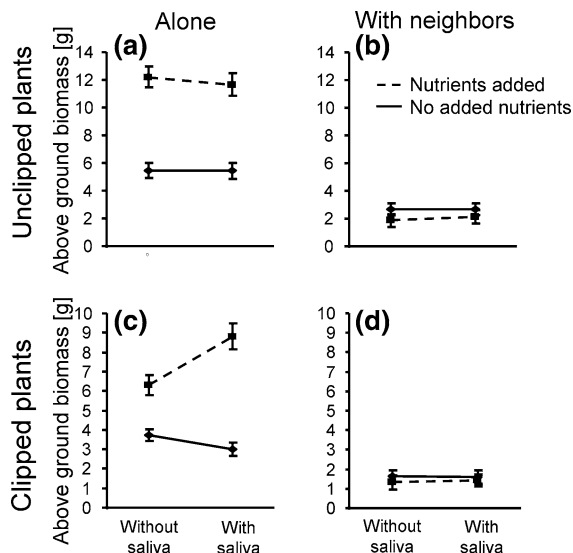


Fig. 1 The effects of *S. capensis* competition, nutrient availability, and saliva cues on the aboveground biomass of *T. purpureum*. Error bars represent one standard error

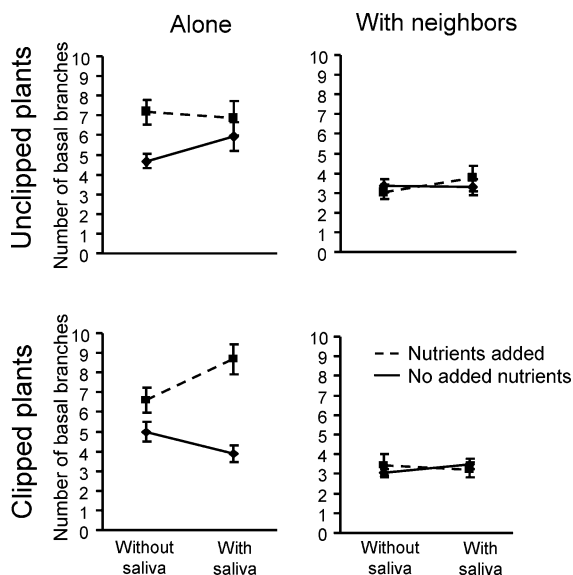


Fig. 2 The effects of *S. capensis* competition, nutrient availability, and saliva cues on the number of basal branches of *T. purpureum*. Error bars represent one standard error

aboveground biomass of the target plants (four-way interaction; $F_{1,200} = 5.594$, $P = 0.019$) and number of basal branches (four-way interaction; $F_{1,196} = 36.330$, $P = 0.001$). In order to decipher this high-order interaction, we separately examined the results of the *clipped* and *unclipped* treatments. We chose to divide the data according to clipping, as

Table 1 The effect of the experimental manipulations on the aboveground biomass, number of basal branches and reproductive biomass of unclipped *T. purpureum* plants

	Aboveground biomass			Number of basal branches			Reproductive biomass		
	df	F-ratio	P	df	F-ratio	P	df	F-ratio	P
Nutrients	1	76.334	***	1	5.871	*	1	58.217	***
Competition	1	332.739	***	1	61.907	***	1	285.181	***
Saliva	1	0.218	0.64	1	1.112	0.29	1	0.104	0.74
Block	14	2.573	**	14	2.250	*	14	1.669	0.07
Competition × Nutrients	1	103.424	***	1	4.858	*	1	99.963	***
Saliva × Nutrients	1	0.218	0.64	1	0.383	0.54	1	0.205	0.65
Saliva × Competition	1	1.093	0.30	1	0.080	0.78	1	0.133	0.71
Saliva × Competition × Nutrients	1	0.952	0.33	1	2.203	0.14	1	0.569	0.45
Error	90			91			91		

The results presented are for a randomized block ANOVA. (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$)

Table 2 The effect of the experimental manipulations on the aboveground biomass, number of basal branches and reproductive biomass of clipped *T. purpureum* plants

	Aboveground biomass			Number of basal branches			Reproductive biomass		
	df	F-ratio	P	df	F-ratio	P	df	F-ratio	P
Nutrients	1	13.809	***	1	3.041	0.08	1	13.769	**
Competition	1	12.652	***	1	0.650	0.42	1	31.399	***
Saliva	1	0.276	0.60	1	0.146	0.70	1	0.201	0.65
Block	14	0.897	0.56	14	1.628	0.09	14	1.617	0.09
Clipped biomass	1	84.774	***	1	19.518	***	1	27.911	***
Competition × Nutrients	1	2.774	0.10	1	0.150	0.70	1	7.911	*
Saliva × Nutrients	1	5.235	*	1	1.588	0.21	1	2.476	0.12
Saliva × Competition	1	0.251	0.62	1	0.118	0.73	1	0.077	0.78
Saliva × Competition × Nutrients	1	10.068	**	1	7.942	**	1	4.246	*
Error	92			89			92		

The results presented are for a randomized block ANCOVA with clipped mass as a covariate. (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$)

it was the only treatment where biomass was removed, thus complicating direct comparisons of plant biomasses between the two treatment levels. As expected, in both treatment groups, competition had a negative effect and nutrient supplementation had a positive effect on aboveground biomass (Fig. 1; Tables 1, 2). The clipped biomass equaled $40\% \pm 0.08$ (1SD) and $52\% \pm 0.1$ (1SD) of the plants' total aboveground biomass at the end of the experiment, in the *T. purpureum* targets and *S. capensis* neighbors, respectively.

As expected, the growth of unclipped plants was positively affected by supplementary nutrients and

decreased under competition, with a greater effect of competition under high nutrients (significant Nutrients × Competition interaction; Fig. 1; Table 1). By contrast, saliva had no significant effect on aboveground biomass of the unclipped plants, regardless of contingent factors (Fig. 1a, b; Table 1). However, in the clipped plants, saliva increased the aboveground biomass of plants which grew without competition and under high nutrients. This positive effect was 96% lower and completely annulled in plants experiencing competition, and competition and low nutrients, respectively. Surprisingly, saliva decreased biomass by 19% in plants experiencing only nutrient

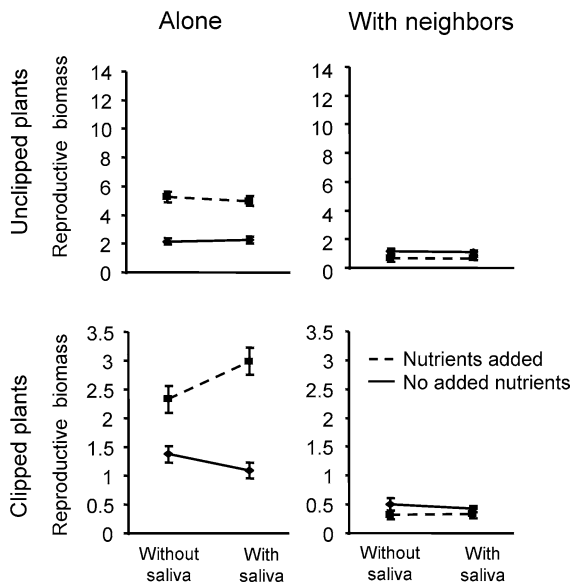


Fig. 3 The effects of *S. capensis* competition, nutrient availability, and saliva cues on the reproductive biomass of *T. purpureum*. Error bars represent one standard error

deficiency without competition (significant Saliva \times Nutrients \times Competition interaction; Fig. 1c, d; Table 2). Number of basal branches and reproductive biomass demonstrated similar trends to those of aboveground biomass (Tables 1, 2; Figs. 2, 3).

Discussion

Plants are known to be highly responsive to environmental cues, which are tightly correlated with anticipated stresses (Ballare 2009), perils (Heil and Karban 2010), and opportunities (Forde and Zhang 1998; Shemesh et al. 2010), even at the expense of reduced short-term performance (Aphalo and Ballare 1995; Ballare et al. 1990; Novoplansky 1991, 2009). Previous studies have shown that mammalian saliva may enhance growth in a variety of plants (Bergman 2002; Rooke 2003; Teng et al. 2010; Zhang et al. 2007); however, most studies have not considered the effects of competition or nutrient availability with the exception of McNaughton (1985), who demonstrated that when subjected to severe damage, nutrient addition was more affective in enhancing plant regenerative growth than thiamine, a plant growth factor commonly found in bovine saliva. However, no interaction between nutrient availability and

thiamine was reported. Our findings demonstrate that the level and direction of such responses might depend on additional ecological contingencies. Similar to previous studies, the results show positive effects of salivary cues on the size, branching, and reproductive output of clipped *T. purpureum* plants, but only when well-nourished and competition-free.

We suggest that these findings reflect an intricate prioritization of plant responses to *prevailing* and *anticipated* challenges, according to their expected harshness and cumulative long-term costs. Herbivore saliva was suggested to enable plants to differentiate between herbivory and physical damage (Korth and Dixon 1997; Thivierge et al. 2010); however, the correlation between present and future herbivory might be rather limited (Karban and Adler 1996), reducing the predictive value of salivary cues. On the other hand, prevailing competition and nutrient deficiency often present severe stresses, which are *highly autocorrelated with continued stress*. The fact that nutrient deficiency altered the direction of the response to saliva, while competition eliminated it, suggests that plants perceive competition as a more acute stress than grazing. Accordingly, under nutrient limitation, at least some plants prioritize their responses to competition over tissue loss, presumably due to their better ability and lower costs of regenerating lost tissues compared with the expected costs of being out-competed by their neighbors (Ballare 2009).

Our results are consistent with those of a recent study which demonstrated that mere cues of prospective future light competition, in contrast to prevailing shade, are prioritized over responses to herbivory (Moreno et al. 2009). Accordingly, prioritization of shade avoidance over defense responses would be expected in plants from competitive communities, where *average* fitness costs of light competition are greater than those of grazing. In the present study, the target *T. purpureum* plants were subjected to both spectral cues and root competition by their *S. capensis* neighbors, and thus, further work is required to assess the relative role of various environmental cues in down-regulating plant's responses to the salivary cues under competition.

The surprising reversal in the effects of saliva on plants experiencing low nutrient availability (Figs. 1c, 2c) might imply alternative grazing tolerance behaviors. While the commonly observed

regeneration via decreased apical dominance and increased lateral growth is possible under nutrient abundance, despite the prospects for continued grazing, plants might prefer to “lay low”, reduce their growth rates, and perhaps allocate more resources to alternative functions, such as the production of defensive metabolites (Heil et al. 2000; Heil and Walters 2009).

A seemingly more parsimonious interpretation of the differential response under variable levels of nutrient availability and competition might be based on the plant’s limited ability to respond to salivary cues under stress; however, this alternative interpretation is not consistent with the saliva effects under and regardless of nutrient limitation (Fig. 1c).

Similar to previous studies (Bergman 2002; Teng et al. 2010), in response to saliva, plants not only increased the size of existing branches but also actively added large infrastructural branches (Fig. 2). Decreased apical dominance might be a form of diversified bet-hedging, whereby damaged plants not only regenerate more rapidly by synchronously developing more primordia (Stowe et al. 2000; Tiffin 2000), but also reduce the risk of a catastrophic loss of the entire shoot system in case of further herbivory (Nilsson et al. 1996).

Although the physiology underlying salivary induction is still largely obscure, previous studies have suggested that it might relate to the absorption of various minerals from the grazer saliva (Detling et al. 1981), or to inductive effects of plant growth factors found in bovine saliva, such as thiamine (McNaughton 1985). In a recent study, Fan et al. (2011) showed that in response to ovine saliva, rice plants modified the production of a large number of proteins related to photosynthesis, stress, chemical defense, and carbohydrate metabolism. The demonstration of contingent prioritization of plant response to herbivory and competition (Moreno et al. 2009) stresses the need for further investigation of the metabolomic and genomic aspects of higher-level regulation of plant responses to multiple challenges (Hinman and Davidson 2007; Keurentjes et al. 2011).

In conclusion, besides supporting the notion that plants are able to utilize salivary cues to differentiate between biotic damage and mechanical injury, our results suggest that the magnitude and direction of the effects of salivary cues on plant growth might depend on intricate prioritization of plant responses to

competition and nutrient availability. The results stress the importance of further studying the interactive effects of the *acuteness* and *reliability* of present and anticipated stresses, and the informational content and adaptive value of environmental cues when faced with various opportunities and challenges.

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