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Precipitation affects plant communication and defense

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Abstract. Anti-herbivore defense shows high levels of both inter- and intraspecific variability. Defending against herbivores may be costly to the plant when it requires a tradeoff in allocation between defense and other missed opportunities, such as reproduction. Indeed, the plastic expression of defensive traits allows the plant to invest resources in defense only when the risk of being damaged actually increases, avoiding wasted resources. Plants may assess risk by responding to volatile cues emitted by neighbors that are under attack. Most plastic responses likely depend on environmental conditions. In this experiment, we investigated the effect of water availability on resistance induced by volatile cues in sagebrush. We found that plants receiving additional water over summer and/or volatile cues from neighbor donor plants showed reduced herbivore damage compared to control plants. Interestingly, we found no evidence of interactions between additional water and volatile cues. We performed an inferential analysis comparing historical records of the levels of herbivore damage during different years that had different temperature and precipitation accumulations. Results confirmed findings from the experiment, as the regression model indicated that sagebrush was better defended during wetter and hotter seasons. Reports from the literature indicated that sagebrush is extremely sensitive to water availability in the soil. We suggest that water availability may directly affect resistance of herbivory as well as sensitivity to cues of damage. Costs and benefits of allocating resources to defensive traits may vary with environmental conditions.

Key words: Artemisia tridentata; *communication; eavesdropping; herbivory; precipitation; volatiles; water availability.*

Introduction

Anti-herbivore defense plays an important role in plants due to their sessile lifestyle. Being unable to flee their enemies, plants have evolved a variety of strategies to minimize herbivore encounters or limit consequences of their damage (Agrawal 2007). Defensive strategies in plants show great variability at different scales. Theory is best developed for interspecific comparisons of strategies (Feeny 1976, Coley et al. 1985, Endara and Coley 2011). In particular, resource availability in the environment in which a species has evolved can determine the relative advantage of investing resources in growth, reproduction, or defense. In general, plants occurring in poor environments are hypothesized to gain more advantages by investing resources in defenses. According to the "Resources Availability Hypothesis" (Coley et al. 1985), plants living in poor environments are inherently slower growing and have longer leaf lifetimes, both of which enhance the risk of incurring herbivore attacks. Moreover, being damaged by herbivores means permanently losing important resources in poor environments (Coley 1987).

The expression of defensive traits may have costs for plants too (Cipollini et al. 2014), involving tradeoffs in resource allocation with other traits, such as reproduction or growth (Coley et al. 1985, Herms and Mattson 1992, Heil and Baldwin 2002). As a consequence, plants have evolved another level of variability, showing plastic expression of defensive traits to adjust their investments to match the risk of being damaged (Agrawal and Rutter 1998, Heil 2010, Karban 2011). For example, plants relax the expression of defensive traits when herbivore pressure is suppressed (Young and Bell 1998, Huntzinger et al. 2004). When damaged by herbivores, plants emit volatile organic compounds (VOCs) that can repel herbivores and attract herbivores' natural enemies (Hare 2010). VOCs can cue defensive responses in neighboring plants that perceive them (Baldwin et al. 2006, Heil 2010, Karban et al. 2014a, b). Induced resistance in plants has multiple important potential consequences (Karban 2008, Heil and Karban 2010). On the one hand plants can save resources by expressing defense only after the perception of reliable cues (Cipollini et al. 2014), but on the other hand plants take the risk of facing undefended attacks when a cue of risk is lacking or unrecognized (Karban et al. 1999).

During the last decade, several studies have shown that plant behavior is far more complex than previously thought. Error Management Theory (EMT) posits that plants employ complex decision making to adjust their

behavior depending upon their expected risk (Orrock et al. 2015). For example, plants are able to evaluate the reliability of risk signals before mounting defensive responses to airborne cues (Karban et al. 2016). Some plants responded preferably to cues from self branches or close relatives than to cues from stranger individuals. *Pisum sativum* appears able to sense risk and its likelihood of accepting risks varies with environmental conditions (Dener et al. 2016). In this study, we tested the possibility that manipulating resource availability may alter costs and benefits of investing resources in defense in sagebrush. We predict that sagebrush plants provided with supplementary water will be better able to respond to cues from damaged neighbors than plants provided with natural precipitation. Such context-dependent responses to environmental cues have not been reported for plant communication.

Materials and Methods

We conducted a crossed two-factor field experiment during summer 2015. We compared the proportion of leaves damaged by herbivores when plants were provided with volatile cues from mechanically damaged conspecifics and/or with irrigation water during summer. Cues were transferred at the beginning of the growing season from experimentally clipped branches on different donor plants in a manner described herein that has been shown to induce resistance to herbivory (Karban et al. 2013).

The fieldwork was conducted at Taylor Meadow, UC Sagehen Creek Field Station, north of Truckee, California. We selected 60 assay plants and 18 volatile cue donors among a group of 99 plants whose levels of relatedness were known (Ishizaki et al. 2010). Assay plants were divided into four different treatments (Fig. 1). Group "C" received volatile cues from donor plants at the start of the season; group "W" was watered through the summer; group "C+W" received both volatile cues at the start of the season and water through the summer; the group "/" consisted of the control group, receiving neither volatile cues nor water. Fifteen assay plants were haphazardly assigned to each of the four treatment groups, and one assay branch on each plant was flagged. All experimental plants were separated by at least 5 m.

Since closely related plants communicate more effectively than distantly related plants (Karban et al. 2013), we matched donors and receivers considering their relatedness in order to exclude biases due to kinship. Relatedness of these plants was determined previously using seven microsatellites that varied among assay and donor plants as described in Ishizaki et al. (Ishizaki et al. 2010). Relatedness (r) was estimated using the method described by Queller and Goodnight (1989) with values ranging from −1 to 1. Indeed, only plants whose r were ranging ±0.25 from the population average ($r = -0.012$) were matched as donors and receivers. Donors and receivers were selected taking their chemotypes into account as well (Karban et al. 2014a, b). The chemotypes of these plants were determined previously by collecting
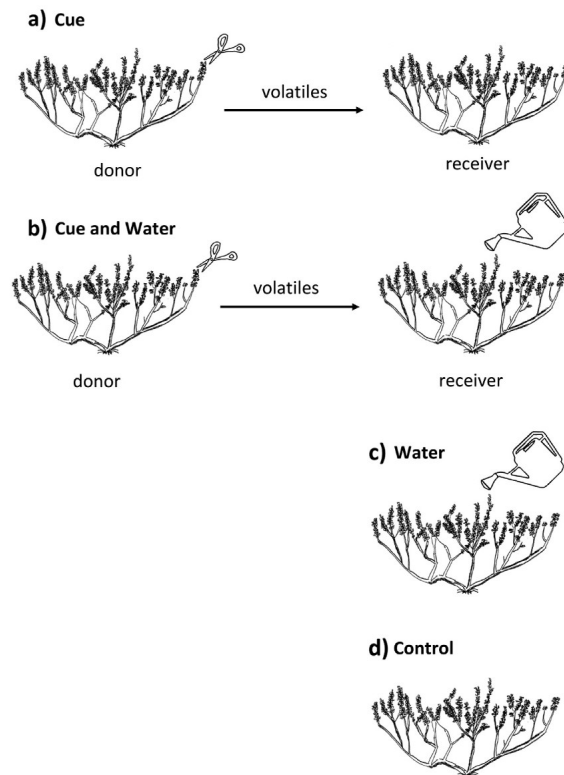

Fig. 1. Design of the field experiment showing the four treatments: (a) Cue; (b) Water and Cue; (c) Water; (d) Control. The scissors indicate mechanically clipped donor plants, which VOCs were transferred to assay branches on receiver plants. The watering cans indicate plants receiving supplementary water over summer 2015.

volatiles and analyzing them using GC-MS (Kessler et al. 2006, Shiojiri et al. 2015). Volatiles used to characterize the chemotypes were collected prior to any watering treatments. Only pairs of plants having similar chemotypes were matched as donors and receivers.

Plants assigned to be clipped had the distal half of 25% of leaves of one branch removed with scissors. Volatile cues were collected from each experimentally clipped donor plant and transferred to the assay branch of the corresponding receiver plants using a 1 l syringe (model S-1000, Hamilton Co., Reno, NV, USA) between June 3rd and June 5th 2015 as described in Karban et al. (2013). Assay branches of all four treatments were covered in a plastic bag for 24 h. Assay branches differed in whether cues came from experimentally clipped neighbors (Fig. 1a, b) or from the ambient environment dominated by unclipped sagebrush (Fig. 1c, d).

Watered plants were irrigated 5 times, once every 2 weeks from June 27th to August 12th, by pouring 5 L of water at the base of each plant. We didn't measure irrigation efficiency or distribution uniformity (Burt et al. 1997). However, we can reasonably hypothesize that the irrigation efficiency was equal to the system efficiency of a surface irrigation system, i.e., 60%. Furthermore,

assuming that water was applied on a surface of 0.2 m², we estimate that a water depth of 125 mm was applied to watered plants and that 75 mm actually reached plant roots (Reinders et al. 2010).

During the growing season (from June 3rd to September 23rd) six precipitation events >3 mm occurred naturally for a total accumulation of 65.6 mm; average air temperature was 13.7°C, while average minimum and maximum daily temperatures were 2.7° and 24.6°C, respectively. Weather data recorded by the Sagehen Creek weather station are available on the Western Regional Climate Center web site (wrcc@dri.edu).

We measured herbivory by calculating the ratio of the number of leaves showing any visible sign of herbivore damage to the total number of leaves on assay branches on September 23rd 2015. Treatment effects were analyzed using two-way ANOVA (standard least squares model, JMP 11.2). Specific a priori hypotheses that volatile cues and water would reduce herbivory to the receivers were tested using planned contrasts in JMP.

We hypothesized that anti-herbivore defense would be most effective in sagebrush during wetter seasons. We performed an inferential analysis comparing historical records of the levels of herbivore damage during different years that had different temperature and precipitation accumulations. We retrieved estimates of annual risk of herbivore damage for control plants from previous published and unpublished works conducted at Sagehen Creek Field Station and Sierra Nevada Aquatic Research Lab (SNARL) (Table 1). Risk of herbivory was estimated as number of leaves with herbivore damage/total number of leaves. Monthly temperature and precipitation data recorded by the Sagehen Creek weather station and SNARL weather station are available on the Western Regional Climate Center web site (wrcc@dri.edu).

We designed a multiple beta regression model in which risk of herbivory for controls for each year (H) was predicted by the annual July-August cumulative precipitation (P) and the annual July-August average max temperature (T) (H~P+T). Mean values for risk of herbivory for each year (H) were used in the regression. Furthermore, since the predicted variable H is a rate ranging from 0 to 1 we used a beta regression model to evaluate the relationship between risk of herbivory and the climatic variables (R, v. 3.2.5, package "betareg", function betareg (Cribari-Neto and Zeileis 2010)). Strength of predictors was further examined using Wald tests (package "aod", function wald.test).

To test if summer rain was associated with temperature at our field sites, we conducted a correlation between July-August average temperature and July-August cumulative rain over the period 1979–2015 (R, v. 3.2.5, package "hmisc", function rcorr, type "pearson").

Results

Generalist grasshoppers (*Cratypedes neglectus* Thomas, *Camnula pellucida* Scudder, *Trimerotropis fontana* Thomas and *Leprus intermedius* Saussure) caused most of the herbivory damage that plants experienced during the season. Damage by herbivores to plants of the four treatments differed in the two way ANOVA ($F_{3,51} = 3.39$, $P = 0.02$). Plants in the control treatment (no cue, no additional water) experienced more herbivore damage than the other three treatments (Fig. 2) ($F_{1,51} = 9.86$, $P = 0.003$), consistent with expectations. Of more interest, there was not a significant difference in herbivore damage for assay plants receiving cue or water ($F_{1,51} = 0.38$, $P = 0.54$). Plants receiving both volatile cue and water did not differ from those receiving either of

TABLE 1. Natural level of herbivore damage occurred to sagebrush assay branches (±1 SE) recorded from 2001 to 2015 at Sagehen Creek and SNARL field stations and corresponding July-August Air temperature and Precipitation.

		Meteorological data		Herbivory measurement		
Year	Field station	Jul-Aug cumulative rain, mm	Jul-Aug avg max Temp, °C	Damaged leaf ratio	1SE	Reference
2001a	SNARL	17.2	27.3	0.030	0.0072	Karban et al. (2004)
2001b	SNARL	17.2	27.3	0.046	0.0116	Karban et al. (2004)
2002a	SNARL	1.3	27.8	0.055	0.0183	Karban et al. (2004)
2002b	SNARL	1.3	27.8	0.028	0.0042	Karban et al. (2004)
2004	Sagehen	2.5	25.8	0.144	0.0096	Shiojiri and Karban (2008)
2004	SNARL	10.1	27.2	0.056	0.0063	Karban et al. (2006)
2005	Sagehen	1.8	27.0	0.120	NA	Shiojiri and Karban (2008)
2005	SNARL	25.6	27.3	0.054	0.0063	Karban et al. (2006)
2007	Sagehen	14.7	26.7	0.032	NA	Karban and Shiojiri (2009)
2007	SNARL	38.4	26.3	0.064	0.0084	Shiojiri and Karban (2008)
2008	Sagehen	1.5	27.0	0.043	NA	Karban and Shiojiri (2009)
2009	Sagehen	7.6	26.5	0.093	NA	Shiojiri et al. (2012)
2010	Sagehen	17.8	25.7	0.063	NA	Shiojiri et al. (2012)
2011	Sagehen	1.3	25.1	0.299	0.0434	Ishizaki et al. (2016)
2014	Sagehen	66.8	26.3	0.038	0.0042	R. Karban, *unpublished data*
2015	Sagehen	53.3	25.3	0.050	0.0090	Experimenta l results

Herbivore damage to assay branches

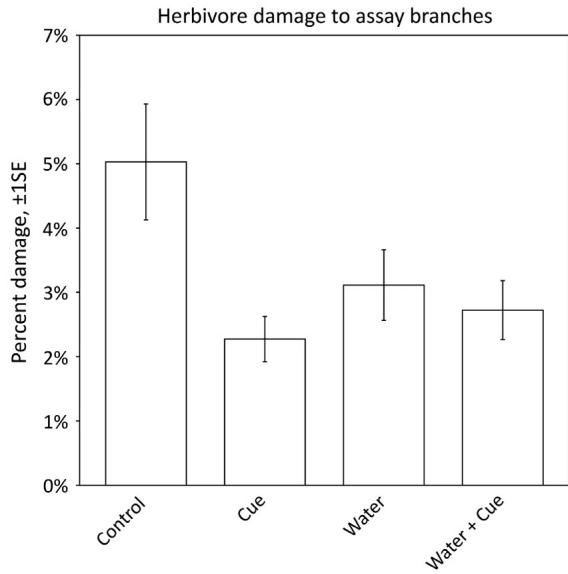Fɪɢ. 2. Mean (±1 SE) levels of natural herbivore damage standardized for assay branches of 100 leaves on plants of the four treatments.

those two treatments ($F_{1,51}$ = 0.005, P = 0.95), showing no interaction between cue and water. This means that plants responded to both volatile cues and water by increasing resistance to herbivory. Relatedness of the pair of plants was not significant in a more complicated model (data not presented) as the pairs were chosen to minimize the variance in this factor.

The historical data indicated that both July-August cumulative precipitation (β = −0.026034, P = <0.001) and July-August max average temperature (β = −0.703148, P = <0.001) were significant predictors of leaf damage during the growing season (Fig. 3). The model precision parameter was φ = 96.01 (P = 0.005), while the overall model fit was pseudo-R^2 = 0.64. Wald tests confirmed the strength of July-August cumulative precipitation and July-August max average temperature as predictors of the risk of herbivory. In fact, the regression model showed a high overall significance (χ^2 = 54.3, P = <0.001). Of more interest, both climatic predictors showed a negative correlation with the risk of herbivory, supporting results obtained during the shorter-term field experiment. July-August average temperature and July-August cumulative rain over the period 1979–2015 didn't show any significant correlation (correlation coefficient r = −0.06, n = 35, P = 0.73).

Dɪsᴄᴜssɪᴏɴ

In the field experiment, assay branches on treated plants receiving cues and/or additional water showed reduced herbivore damage compared to controls. However, we detected no interaction between these two factors in both the two-way ANOVA and subsequent contrasts. Sagebrush may invest more in defense when water is more abundant than under constrained water conditions. Well-watered plants may have possessed higher levels of constitutive resistance to herbivores although this was not measured. Previous work at the same location showed that under natural precipitation conditions receiver assay branches of sagebrush responded to volatile cues from
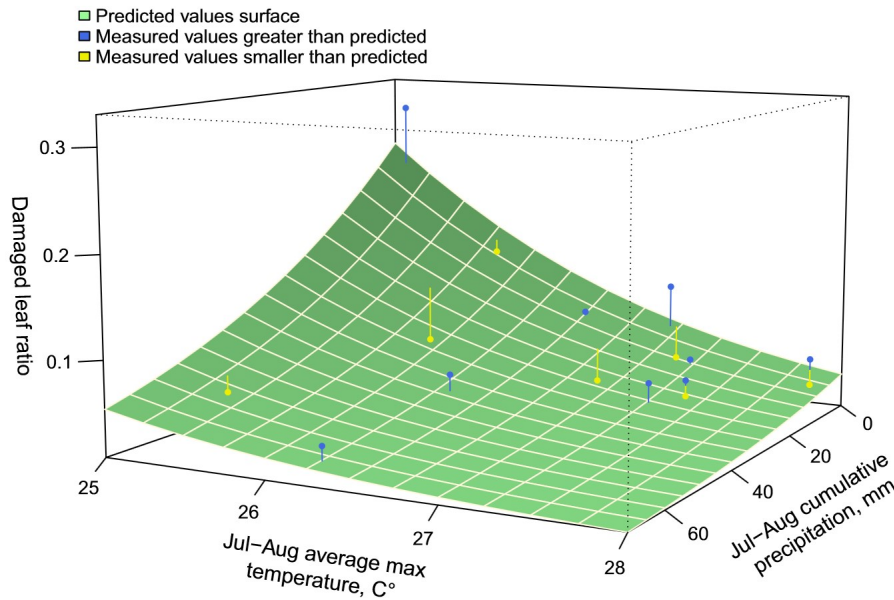

Fɪɢ. 3. The graph represents the prediction surface of the beta regression Herbivore damage ~ Precipitation + Temperature for records reported in Table 1. Measured leaf damage values are represented as either blue or yellow for values that were greater or smaller than predicted, respectively. [Color figure can be viewed at wileyonlinelibrary.com]

damaged neighbors by increasing local resistance to herbivory (Karban et al. 2006). When water is limited, sagebrush may rely on herbivory-related airborne cues from neighbors to trigger defensive responses only when perceiving increased risk of attack. In any case, we can't evaluate whether the increase in resistance with additional water was constitutive, induced or some combination.

These results are generally consistent with Carbon/Nutrient Balance theory (CNB), which suggests that plants may invest more resources in defense when available resources exceed growth requirements (Bryant et al. 1983). However, other models may also produce this same pattern. Variation in water availability may affect tolerance to herbivory as well as resistance. As predicted by the Limited Resource Model (LRM) (Wise and Abrahamson 2005), tolerance to herbivory may be higher, equal, or lower in high resource environments than in low resource environments. Since effects of herbivory on plant fitness are expected to vary depending on environmental conditions (Wise and Abrahamson 2007), plants may perceive and/or respond differently to cues of increased risk of herbivore attack depending on resource availability.

Increased defense under well-watered conditions may be mechanistically linked to sagebrush physiological adaptations to drought. Sagebrush evolved in arid environments; it is extremely sensitive to soil water availability and has the capability to limit water loss during dry periods by reducing stomatal conductance and net photosynthesis (DePuit and Caldwell 1973, Kolb and Sperry 1999). Sagebrush has also been reported to respond to water availability by modifying many physiological processes. For example, photosynthetic rates and stomata conductance follow a seasonal pattern reaching their highest levels in spring, when soil water depth is high after snowmelt (DePuit and Caldwell 1973, Downs and Black 1998). In a recent work, Reed and Loik (2016) reported increasing stem water potential, stomatal conductance and photosynthetic rate along an elevation gradient in response to higher annual precipitation. In addition, plants at the lower and drier elevation responded to summer water applications by increasing photosynthesis. Furthermore, Loik (2006) reported a stronger increase in certain photosynthetic parameters as a response to multiple water pulses than to an equivalent single water application. Previous studies on sagebrush reported variation in stomatal conductance and CO_2 assimilation depending on snow depth during the previous winter (Loik et al. 2015) and even to antecedent soil water conditions (Ogle et al. 2015). It is likely that the reduced CO_2 assimilation due to drought may negatively affect the expression of defensive traits. In this regard, it is worth noting that VOCs emission is not directly controlled by stomatal opening. Monoterpene synthase activity is directly correlated to plant photosynthetic rates (Niinemets et al. 2004). Similarly, airborne cues from neighbors are more effective at spring budburst after snowmelt when water is more abundant

(Shiojiri and Karban 2008). Sagebrush photosynthetic rates and stomatal conductance are at their highest seasonal level in spring as well (DePuit and Caldwell 1973, Downs and Black 1998). These findings suggest that communication and expression of resistance traits may be favored in well-watered conditions due to the increased carbon assimilation. In this context, our results are particularly relevant because, to our knowledge, they provide the first possible links between environmental conditions and defense triggered by plant communication tested in the field. These results should stimulate additional experiments addressing how plants evaluate risk and its relation with photosynthetic activity and carbon assimilation. Previous work showed that the strength of responses to airborne cues of attack depended on the reliability of the signal perceived. Sagebrush showed stronger responses to cues emitted by genetically closer plants (Karban et al. 2016). In this study, it's possible that additional water may have lowered that reliability threshold resulting in an increased sensitivity to airborne cues. Indeed, cues from naturally damaged neighboring plants may have been effective in triggering defensive responses in watered plants. It is worth noting that sagebrush has previously been shown to be more responsive to airborne cues in spring after snowmelt, when water is more abundant (Shiojiri and Karban 2008).

Looking at the historical record, levels of herbivory were negatively correlated with both July-August cumulative rain and July-August max average temperature. This correlative result, linking precipitation with reduced damage supports the conclusion of our field experiment. The result that herbivory is reduced at higher summer temperatures should not necessarily be interpreted as an increase in plant defense. It may be caused by reduced activity and feeding of the herbivores as they meet their thermal requirements (Willott 1997, Karban and Baxter 2001). For example, during the hottest summer days, grasshoppers flee the sunlight, seeking shaded areas to avoid overheating. Even a slight heating over optimal thermal conditions can cause torpor or even death for many grasshoppers (Chappell and Whitman 1990). Interestingly, sagebrush has been shown to be highly sensitive to temperature variations as well. At warmer temperatures sagebrush shows evidence of stress and growth reductions (Smith et al. 2002). Effects of drought and heat on plant photosynthetic activity are similar, both causing a reduction of photosythates available for growth, reproduction, or defense. Although heat and drought generally occur at the same time over the year, this may not be the case at our study site. We failed to find a significant correlation between July-August average temperatures and July-August cumulative precipitation at our field location over the period 1979–2015. This lack of correlation suggests that the response of sagebrush to drought and heat may be independent as they do not necessarily occour at the same times over the summer.

The presence and abundance of herbivores may be difficult for plants to predict (Heil 2010). Indeed the expression of defense in plants is the result of the perception of cues of attack (Karban et al. 1999, 2016) and the evaluation of cost and benefits of defensive responses (Cipollini et al. 2014). Error Management Theory (EMT) has been recently introduced to explain plastic expression of resistance in plants (Orrock et al. 2015). According to EMT, the expression of defense is the result of the evaluation of benefits of defending and corresponding costs of different types of error due to the uncertainness of herbivore attacks. That is, false positive errors (i.e., defense expression not actually followed by an attack) and false negative errors (i.e., undefended attack) may have different consequences for plants depending on their physiological state, ontogenetic stage, phenology, and external cues like water availability. As a result, plants may be able to tailor defensive trait expression to err toward the less costly mistake based on risk evaluation (Orrock et al. 2015). In this study, we recorded variation in defense expression as a consequence of the manipulation of water availability which is consistent with EMT predictions. Future work incorporating relations between plant physiology and defense expression as well as evaluation of risk sensitivity (Dener et al. 2016) might reveal how plant defense is shaped by complex decision rules. Past and present events may affect prediction and management of future allocation in plants (Novoplansky 2016).

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