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PLANT-MICROBE-ANIMAL INTERACTIONS – ORIGINAL RESEARCH

Consistent individual variation in plant communication: do plants have personalities?

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Abstract

Animal biologists have recently focused on individual variation in behavioral traits and have found that individuals of many species have personalities. These are defined as consistent intraspecific differences in behaviors that are repeatable across different situations and stable over time. When animals sense danger, some individuals will alert neighbors with alarm calls and both calling and responding vary consistently among individuals. Plants, including sagebrush, emit volatile cues when they are attacked by herbivores and neighbors perceive these cues and reduce their own damage. We experimentally transferred volatiles between pairs of sagebrush plants to evaluate whether individuals showed consistent variation in their effectiveness as emitters and as receivers of cues, measured in terms of reduced herbivore damage. We found that 64% of the variance in chewing damage to branches over the growing season was attributable to the identity of the individual receiving the cues. This variation could have been caused by inherent differences in the plants as well as by differences in the environments where they grew and their histories. We found that 5% of the variance in chewing damage was attributable to the identity of the emitter that provided the cue. This fraction of variation was statistically significant and could not be attributed to the environmental conditions of the receiver. Effective receivers were also relatively effective emitters, indicating consistency across different situations. Pairs of receivers and emitters that were effective communicators in 2018 were again relatively effective in 2019, indicating consistency over time. These results suggest that plants have repeatable individual personalities with respect to alarm calls.

Keywords Alarm call · Behavior · Plant communication · Personality · Repeatability · Volatiles

Introduction

Many animals emit cues when they perceive danger or are actually attacked by consumers. Often neighbors sense these alarm cues and respond to defend themselves (Caro 2005). Individuals that emit alarm cues may experience costs if they become more conspicuous to predators, or if they provide useful information to neighbors with whom they compete (Sherman 1977; Hoogland 1996). Conversely, alarm calls may be beneficial to the emitter if they startle or dissuade the predator (Sherman 1985), signal that they are aware of the predator making successful predation unlikely (Hasson 1991), or provide useful information to kin, with whom the emitter shares genes (Maynard Smith 1965). As such, emission rates of animal alarm calls have been found to vary based on the social composition and relatedness of the potential audience (Townsend et al. 2002, Coppinger et al. 2018; Woods et al. 2018). Some animal alarm calls are probably epiphenomena in the sense that animals scream or

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release chemicals when attacked and the main evolutionary response has been to perceive the calls of neighbors (Caro 2005).

When plants are attacked by herbivores, they emit volatile organic compounds (Holopainen and Blande 2013). Some of these volatiles act as alarm cues; neighboring unattacked branches on the attacked plant and neighboring unattacked plants perceive these emissions and increase their own defenses against herbivory (Karban et al. 2006; Frost et al. 2007; Heil and Adame-Alvarez 2010). This phenomenon has now been reported for many plant systems (Karban et al. 2014a, b). Many of these volatile chemicals dissipate rapidly so that they are present in biologically active concentrations over relatively short distances (often less than 1 m). In many instances, cues may be emitted unintentionally, and this process is probably best described as eavesdropping by the receiving plant (Heil and Karban 2010). These same plant volatile cues have been found to serve other functions in some instances such as repelling herbivores (e.g., De Moraes et al. 2001; Kessler and Baldwin 2001), and attracting the predators and parasites of the herbivores (Dicke and Sabelis 1988; Turlings et al. 1990).

Animal behaviorists have recently become aware that individuals exhibit consistent variation in behavioral tendencies, giving rise to the idea of individual animal personalities (Dall et al. 2004; Sih et al. 2004; Reale et al. 2007; Bell et al. 2009; Wolf and Weissing 2012; Kaiser and Muller 2021). We use the term 'personality' to refer to intraspecific expression of behaviors that are stable over time and consistent across different situations (Reale et al. 2007; Kaiser and Muller 2021). Animal personalities have been found for a wide range of species throughout the animal kingdom and include a diversity of behavioral traits (see refs above). This intraspecific variation can strongly affect ecological processes (e.g., survival, fecundity, dispersal) and provide plasticity and genetic variability that serve as the basis of natural selection (Sih et al. 2004, Stamps 2007, Sih et al. 2012, Wolf and Weissing 2012, but see Moiron et al. 2020 for a cautionary note).

One of the behavioral traits in animals that has been most thoroughly investigated in terms of individual variation is the continuum from boldness to shyness (Wilson et al. 1994; Reale et al. 2000; Smith and Blumstein 2008; Kaiser and Muller 2021). Bold individuals are more risk prone while shy individuals are more risk averse. Shy individuals of both guppies and chipmunks responded to alarm cues by responding more strongly than bold individuals (Brown et al. 2014; Couchoux et al. 2018). Shy individuals may also have a lower threshold that elicits emission of an alarm cue than bold individuals. Bold individuals may be less likely to emit alarm cues, but their cues may provide more reliable information. Receiver individuals that sensed alarm calls modulated their responses based on the learned reliability of the caller in the case of vervet monkeys (Cheney and Seyfarth 1988), ground squirrels (Hare and Atkins 2001), marmots (Blumstein et al. 2004), and chipmunks (Couchoux et al. 2018).

Volatile cues of sagebrush (*Artemisia tridentata* spp. vaseyana) and the induced resistance that they elicit have been studied intensively under field conditions (Karban et al. 2006). Individual plants are highly sectored with very limited communication among branches occurring through the vascular system (Cook and Stoddart 1960). When damaged, sagebrush emits many volatile compounds; as many as 100 have been detected although it is not known which of these are biologically active (Lopes-Lutz et al. 2008; Karban et al. 2014a, b). Plants that receive volatile cues from neighboring branches or individuals produce higher concentrations of secondary compounds; these are thought to provide resistance against herbivores and plants receiving cues experience less damage over the growing season (Karban et al. 2006). Sagebrush seedlings that were induced by exposure to volatiles survived at a higher rate than unexposed controls and established plants exposed to volatiles produced more branches and inflorescences than unexposed controls (Karban et al. 2012). Individual plants within a population vary in the chemical makeup of their volatile emissions and the composition of these damage-induced cues is highly heritable (Karban et al. 2014a, b). Plants responded most effectively to other individuals that produced emissions that were more similar to their own (chemotypes).

In this study, we asked whether sagebrush plants exhibited the characteristics that animal behaviorists have established for animal personalities. (1) Do individual plants within a population consistently vary in their responses to cues emitted by different experimentally clipped conspecifics? (2) Do individual plants consistently vary in their effectiveness as sources of volatile cues to different receivers? (3) Are these differences stable over time such that pairs of individuals that communicate relatively well in one season will also communicate well in the next season? 4) Are effective emitters also effective receivers of volatile cues?

Methods

This experiment was conducted in Taylor meadow at the UC Sagehen Natural Reserve in Tahoe National Forest, north of Truckee, California (39°26.7 120°14.7). We have previously determined the chemotype of each plant based on volatiles analyzed by GC–MS (methods in Karban et al. 2014a, b). We observed plants of four chemotypes in this meadow although more than 95% of individuals belonged to either the α-thujone or camphor chemotypes (Karban et al. 2014a, b). We determined the relatedness of pairs of individuals in this population based on an analysis of eight microsatellites

(Ishizaki et al. 2010). Relatedness was estimated on a scale of -1 to 1 following the methods described in Queller and Goodnight (1989).

Consistency across contexts

We selected 40 large sagebrush plants from this population to be used in an air transfer experiment with a reciprocal crossed design (Fig. 1). Ten branches from each plant were experimentally clipped and the volatiles from these clipped branches were transferred to branches of ten receiver plants. Each individual served as both a volatile donor to ten receiver plants and each individual also received volatiles from the clipped branches of those same ten donor plants. Each branch on an individual experimental plant served as either a donor or a receiver, but not both. A total of 400 air transfers were conducted (40 plants × 10 transfers) over a five-day period. The identification tags on 9 branches were lost and the fates of these branches were not recorded. Volatile transfers were only conducted between individuals of the same chemotype (α-thujone or camphor) since this was shown in a previous study to increase the effectiveness of communication (Karban et al. 2014a, b). Since chemotype is highly heritable, plants of the same chemotype are more closely related than plants of different chemotypes, on average. As mentioned above, the branches of individual plants fail to communicate effectively through the vasculature and are largely independent of one another when volatile cues are blocked (Karban et al. 2006). This lack of integration among branches has been reported commonly, particularly for species that grow in arid environments (De Kroon et al. 2005; Herrera 2009). Individual plants served as both donors and receivers of cues; on each day, each plant donated volatiles to two other plants and received volatiles from two plants. This procedure was repeated for five consecutive days. When day of the trial was included as a factor in analyses, it was never significant and was removed. In other words, we detected no indication that experimental clipping or exposure of cues to one branch increased the responsiveness of subsequently clipped or exposed branches over the five days during which treatments were applied.

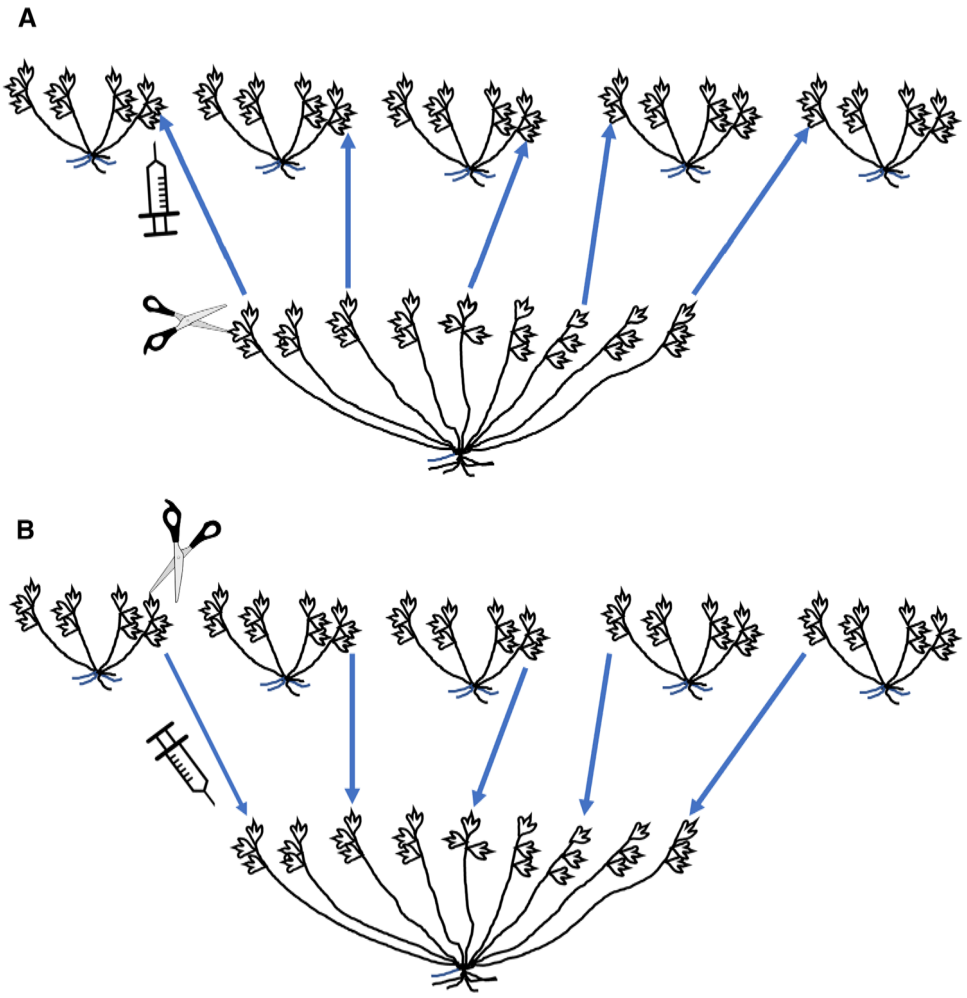

Fig. 1 A schematic diagram showing the design of the volatile transfer experiment. **A** This experiment examines the effects that receiving damage cues from the same individual has on different receiver plants. The diagram shows 5 receiver individuals but the actual design included 10 different receivers. The scissors indicate that leaves of the branches of the emitter were experimentally clipped. The syringe indicates that volatiles were transferred from the emitter to receiver plants. **B** This experiment examines the effects of different emitter plants as sources of volatile cues. The diagram shows 5 receiver individuals but the actual design included 10 receivers. The scissors indicate that leaves of the emitter branches were experimentally clipped. The syringe indicates that volatiles were transferred from emitter to receiver plants. In summary, each plant had 10 branches that served as emitters and 10 branches that served as receivers. Branches were enclosed in plastic bags (not shown in the diagram) during the experiment to reduce air flow among branches

Branches were experimentally damaged by clipping the distal half of five leaves with scissors in early May 2018. The procedure has been used previously and produces changes that we were unable to distinguish from those caused by actual insect herbivory (Shiojiri and Karban 2008). The clipped branch was immediately enclosed in a plastic bag which was sealed at the stem of the branch with a wire twist-tie. Volatiles were allowed to collect in the plastic bag for 24 h. The following day, volatiles were transferred from the headspace of the clipped donor branch to the headspace of the receiver branch using a 1-L syringe (Hamilton, Model S-1000, Reno, Nevada). The receiver branch was enclosed in a sealed plastic bag and incubated with air from the receiver for 24 h. Effective cues dissipate rapidly over space and time in this system and the plastic bags reduced contamination of cues between damaged emitter branches and other branches on the same plant (Karban et al. 2006; Kessler et al. 2006; Shiojiri et al. 2009).

Our response variable was the percentage of leaves on each receiver branch that received chewing damage by herbivores at the end of the growing season (August). This estimate of damage correlates with the percent of leaf area removed by herbivores (Karban and Yang 2020). Chewing damage was done by chrysomelid leaf beetles (*Trirhabda pilosa* and *Monoxia grisea*), grasshoppers (primarily *Craty-pedes neglectus, Trimerotropis fontana*, and *Conozoa sulci-frons*), caterpillars, and mule deer (*Odocoileus hemionus*).

We analyzed these data using a mixed model structure (rptR, package CRAN in R; Stoffel et al. 2017). Leaf damage from chewing herbivores was log transformed to meet model assumptions; this transformation provided a better fit than a glmer with a binomial distribution. Relatedness (−1 to 1) and chemotype ($n = 2$) were included as fixed effects and emitter identity ($n = 40$) and receiver identity ($n = 40$) were included as random effects. In this analysis, we were most interested in estimating the portion of the variance that was attributable to the individual receiver and the portion that was attributable to the individual emitter once the fixed effects had been controlled, what geneticists and animal behaviorists term repeatability (Reale et al. 2007). Repeatability is the portion of consistent individual variation (Repeatability = Phenotypic var among individuals / [var within individuals + var among individuals]). Uncertainty around estimates of repeatability were calculated by bootstrapping 1000 times and likelihood ratio tests were used to estimate p values (Stoffel et al. 2017).

Are good emitters also good receivers?

We evaluated whether those individuals that were good emitters were also good receivers. We calculated the mean level of chewing damage associated with each individual as both an emitter and as a receiver and conducted a Pearson's correlation analysis of these means.

Consistency across years

We conducted another transfer experiment in May 2019 using those pairs of emitters and receivers that had been most effective communicators and reduced levels of chewing damage in 2018 and those pairs that had been least effective in 2018 and had the highest level of damage. To do this, we selected 18 receiver individuals that had large variation among branches due to different emitters in the amount of damage that they experienced in our experiment the previous year. We randomly selected four branches on each receiver individual and assigned the following four treatments to those branches so that each receiver had one branch with each treatment: (1) We clipped the distal half of five leaves on one branch and enclosed that branch in a plastic bag for 24 h (clipped treatment). (2) We incubated one branch for 24 h with the headspace volatiles (collected for 24 h) from an experimentally clipped branch of another individual emitter that had resulted in reduced damage to that receiver in the previous season (good communication treatment). (3) We incubated one branch with the headspace volatiles from an experimentally clipped branch of another individual emitter that had not resulted in reduced damage to that receiver in the previous season (poor communication treatment). (4) We enclosed one branch with a plastic bag for 24 h but neither clipped it nor exposed it to the volatiles of another clipped branch (control treatment). The specific branches on the receiver individuals that were selected in 2019 had not been used in our experiments in 2018. We recorded the percentage of leaves on each branch that received chewing damage by herbivores at the end of the growing season (September).

We analyzed the percentage of leaves with chewing damage for the four treatments using a linear mixed model with treatment as a fixed effect and plant identity as a random effect (glmmTMB package in R [Brooks et al. 2017]). As with our previous analysis, we used a log transformation of our response variable, damage over the season, to meet the assumptions of the model. Our a priori expectation was that those pairs of emitters and receivers that were effective in 2018 would be more effective in 2019 than those pairs that were not effective in 2018. We used a contrast to evaluate this hypothesis.

Results

Consistency across contexts

Branches on individual receiver plants were incubated with volatiles from ten different donor individuals. The

mean level of chewing damage that different individual receivers experienced varied from less than 5% to greater than 80% (Fig. 2). The amount of chewing damage that a branch received over the season was strongly influenced by the identity of receiver plant which explained 64% of the overall variance in damage (Fig. 2, Repeatability = 0.645, CI = 0.480–0.736, LRT $P < 0.001$).

Cues from some clipped individuals were associated with reductions in damage that also varied depending on the identity of the emitter. Different emitters were associated with levels of damage that ranged from less than 5% to approximately 40% (Fig. 3). The identity of the emitter explained approximately 5% of the variance in the amount of chewing damage that a branch received (Repeatability = 0.054, CI = 0.018–0.100, LRT $P = 0.003$). The fixed effects due to relatedness of the emitter and receiver and the chemotype of the pair explained less than 2% of the observed variance in damage and the confidence intervals for both overlapped with zero (Effect of relatedness = 0.006, CI = 0 – 0.018; Effect of chemotype = 0.010, CI = 0–0.131).

Are good emitters also good receivers?

There was a significant positive relationship between the mean level of damage experienced by branches receiving cues from a given individual and the mean level of damage to that individual when it received cues from others (Fig. 4, correlation coefficient = 0.316, $t = 2.056$, df = 38, $P = 0.047$). In other words, those individuals that were on average more effective communicators as emitters were also more effective as receivers at reducing damage.

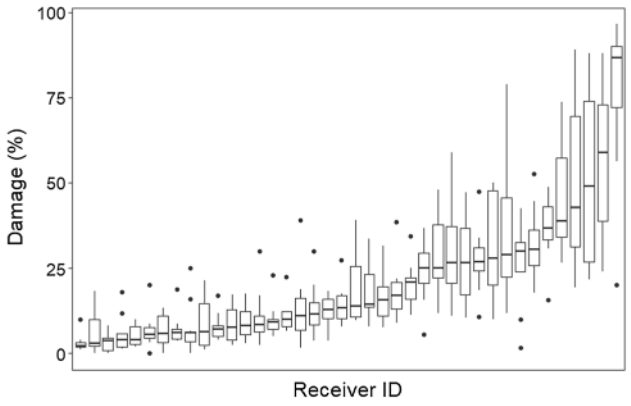

Fig. 2 Consistency of damage for branches of receiver plants. Boxplots show median and the first and third quartiles of the percentage of leaves that were damaged by chewing herbivores on 10 branches over the growing season for each of the 40 receiver plants. Circles represent values outside 1.5 × the interquartile ranges. Each of the 40 plants served as a receiver of volatile cues from 10 different plants that had been experimentally clipped

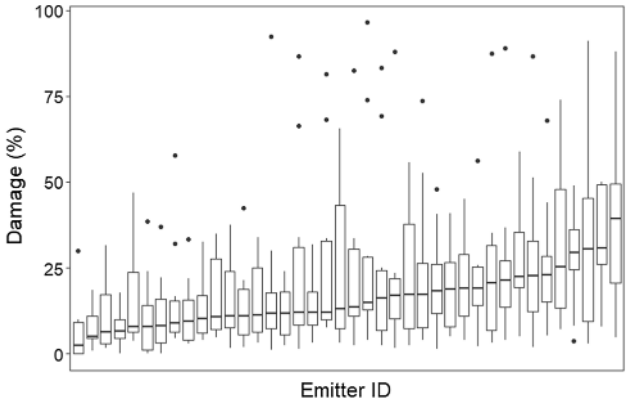

Fig. 3 Consistency of damage for plants serving as emitters of cues. Boxplots show the median, and the first and third quartiles of the percentage of leaves that were damaged by chewing herbivores over the growing season for branches on plants that received cues from each emitter. Each emitter served as a source of volatile cues for 10 different receiver plants. Cues from emitter plants were collected after experimentally clipping the branch

Consistency across years

Our treatments affected the chewing damage that branches received in 2019 (Fig. 5; treatment $X^2 = 25.2$, df = 3, $P = 0.001$). As expected, the control branches experienced the most damage and those that had been clipped experienced the least damage. We were most interested in the comparison between those pairs of branches that were effective communicators in 2018 (experienced less damage at the end of that season) and those pairs that were not effective communicators in 2018 (experienced high levels of damage). We found that good communicators in 2018 experienced less damage again in 2019 compared to poor communicators ($t = 4.16$, df = 34, $P = 0.001$).

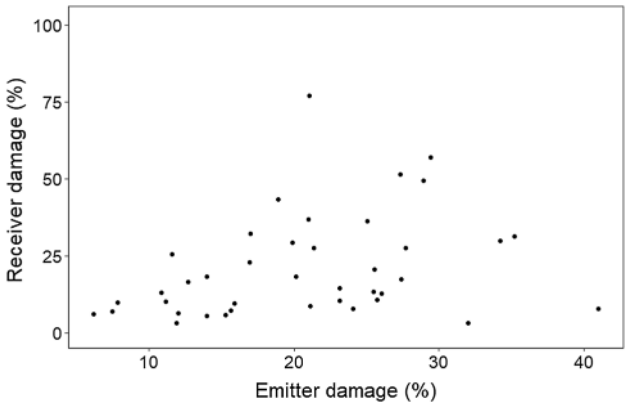

Fig. 4 The correlation between the chewing damage associated with each plant as a receiver and as an emitter of cues. The positive correlation indicates that plants that were relatively effective communicators as emitters were also relatively effective as receivers

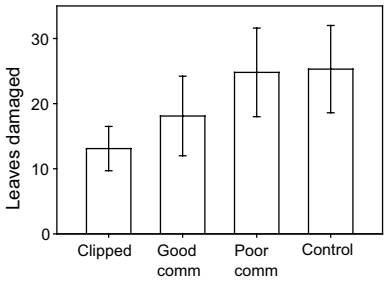

Fig. 5 The mean ± 1 se of the percentage of leaves damaged by chewing herbivores in 2019 on four branches of each plant. Each plant had one branch that was either experimentally clipped, one that received volatiles from an emitter plant which had served as an effective emitter for that receiver in 2018 (good comm), one branch that received volatiles from an emitter plant which had served as an ineffective emitter for that receiver in 2018 (poor comm), and one branch that was a bagged control which did not receive volatile cues

Discussion

Sagebrush displayed all of the criteria that animal behaviorists require to conclude that individual plants possess personalities—consistent behaviors that are repeatable over different contexts (cues) and over time (Kaiser and Muller 2021). Levels of damage from herbivores differed among individuals in the population. The various branches on individual receivers exhibited characteristic levels of damage that were consistent after receiving volatile cues from different experimentally clipped emitters (Fig. 2). Indeed, the identity of the receiver explained a majority (64%) of the variance in the level of damage that it experienced over the season.

The biological inferences that can be drawn from this result are limited for several reasons. First, our response variable, chewing damage at the end of the growing season is a composite operational trait (sensu Reale et al. 2007), meaning that it was affected by many different factors in addition to the responsiveness of each branch to volatile cues. This limitation applies to all of the results from this study since this response variable was considered throughout. Second, consistent levels of damage among the branches of an individual receiver indicate repeatable among-individual variation caused by factors that are characteristic of the individuals. Even though branches had limited opportunities to communicate in our experiment, the machinery that underlies volatile communication may be shared among the branches of each individual. Consistent levels of damage do not necessarily represent genetically based characteristics; damage levels are also influenced by environmental factors that are specific to each individual (where the plant is growing, how many resources it has access to, its past history, and so on). Environmental factors experienced by branches on an individual are likely to be relatively similar. Since only heritable variation can serve as the raw material of evolution by natural selection, determining the repeatability of a phenotypic trait such as a plant behavior should be viewed as only a first step (Falconer and Mackay 1996). This same limitation also applies in studies of animal personalities (Reale et al. 2007), although repeatability often underlies heritability in studies of animals (Dochtermann et al. 2015). In addition, since branches on an individual plant remain in place, consistency attributable to environmental causes may be biologically more relevant for plants than for animals.

The identity of the emitter that produced the alarm cue explained less of the variance in the damage that receivers experienced (5%) (Fig. 3). Cues from some individuals were consistently more effective at reducing damage than those emitted by other individuals. This pattern was apparent over all of the emitters that were considered. This result was statistically significant and was more surprising than the higher repeatability estimated for receivers because it could not be attributed to variation in the conditions of the receivers. This effect of emitter identity was also larger than effects attributable to the relatedness of the emitter and receiver and to the chemotype being tested.

Those individuals that were effective as emitters were also effective as receivers (Fig. 4). This is analogous to a behavioral syndrome in which competence in one behavior is correlated to competence in another (Sih et al. 2004). In this case, the underlying cause of the positive correlation between receiver and emitter function is not known. Those individuals that are more sensitive to risk of herbivory may both emit alarm cues and respond to alarm cues of their neighbors more strongly or at a lower threshold. It is possible that the correlation is driven by some genetic, developmental, or environmental characteristic of individuals. For example, young sagebrush plants were found to be better as both emitters and receivers than older individuals (Shiojiri and Karban 2006). All of the plants in this study were large although their precise ages were not known. Physical characteristics involving the cuticle or stomata may make some individuals more effective as both emitters and receivers. In addition, those individuals that have a history of chewing damage may be more risk averse to subsequent damage. The results of our study provided evidence that some combinations of emitters and receivers were consistently more effective at reducing damage to the receivers than were other combinations. This does not mean that receivers recognize individual emitters nor discriminate among emitters as some animals do.

Finally, communication was consistent over time. Pairs of individuals that were more effective communicators in one year were also more effective communicators in the following year (Fig. 5). All of the common herbivores in this system are mobile as adults so there is no reason to suspect that carryover of herbivores from one year to the next caused

this correlation. Receivers paired with poor communicators were damaged as heavily as receivers that were incubated with air containing no cues. Branches that were experimentally clipped themselves experienced less additional damage than receivers that were paired with relatively effective communicators. One possible explanation for the stability of the effectiveness of communication over time is that the factors that determine effectiveness (the environment, past history of damage, genes) or the traits associated with resistance have limited plasticity.

Repeatability occurs when individuals perform similar behaviors in similar contexts and situations and its significance has been well accepted by animal behaviorists for some time (Boake 1994). Several studies have examined the repeatability of plant behaviors. *Mimosa pudica* individuals in a lab setting failed to show repeatability in closing their leaflets in response to repeated experimental stimulation although this 'hiding' behavior was affected by the individual's nutritional state and environment (Simon et al. 2016). A field experiment with the same species provided stronger evidence that hiding behaviors of individual plants were indeed repeatable (Reed-Guy et al. 2017). We are not aware of other examples of repeatability of plant behaviors or of other examples of repeatability of emission or response to alarm cues in plants.

Conclusion: why plant personalities may matter

There have been several recent attempts to use the progress made in animal behavior and even psychology to understand plant behavior. Those are better developed fields and only recently have ideas about plant behavior gained some acceptance. There has also been considerable pushback among some plant biologists who rightly point out that plants lack central nervous systems and have evolved very different systems to sense their environments and to respond appropriately (Alpi et al. 2007; Chamovitz 2018). Our goal in discussing plant personalities is not to insinuate that plants are people or are intelligent in a similar way that we are, but to highlight that animal behavior has much to offer the development of plant biology.

Recognizing that plants exhibit consistent behaviors that are repeatable in different situations and stable over time (i.e., personalities) has several important consequences. Recent reviews have made convincing arguments for links between animal personalities and ecological and evolutionary effects (e.g., Reale et al. 2007; Sih et al. 2012; Wolf and Weissing 2012). First, most plant biologists have historically focused on mean differences among groups of individuals experimentally placed in different treatments and individual variation has been considered to be uninteresting noise (Bolnick et al. 2003; Kaiser and Muller 2021). The idea that individual plants may show consistent tendencies that can be quantified, independent of other treatments, leads to a different research focus. Indeed, there has been recent evidence that genetic diversity among individual plants within a population has important consequences (Crutsinger et al. 2006; Johnson et al. 2006; Schuman et al. 2015; Wetzel et al. 2016). In addition, the existence of plant personalities means that knowledge of an individual's past provides information that can predict its behavior in the future. In Bayesian jargon, the existence of personalities means that informed priors can be used to improve predictive power.

Second, recognition of correlations among different plant behaviors suggests that there may be tradeoffs among important traits that are not independent of one another (Sih et al. 2004). For example, a negative correlation between growth of roots and shoots suggests an allocation tradeoff between above and below ground tissues while a positive correlation between growth of roots and shoots suggests that differential access to resources is more important than such an allocation tradeoff. Life-history tradeoffs of this nature are familiar to evolutionary plant biologists and this framework can be applied to other plant behaviors.

Third, alarm calls that affect herbivory influence plant growth, survival, and reproduction in the few systems where they have been studied (Karban and Maron 2002; Kost and Heil 2006; Karban et al. 2012; Schuman et al. 2012). These demographic effects have the potential to shape plant adaptations, population sizes and distributions, ability to respond to natural and human induced changes, and interactions with other species, although potential effects of variation in plant communication have been largely neglected. Just as animal biologists have come to consider consistent individual personalities to be an important factor in shaping animal phenotypes, behaviors, and interactions, so too should plant biologists include individual variation in plant communication as a significant individual attribute that influences their evolution and ecology.

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Author contribution statement RK and CC designed the study, RK and PGT conducted the experiments, PGT and RK analyzed the data, and RK wrote the manuscript with input from PGT.

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Data availability Data will be archived at Dryad Data (https://doi.org/10.5061/dryad.cfxpnvx6g).

Declarations

Conflict of interest Not available.

Ethics approval Not available.

Consent for publication Not available.

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