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Geographic dialects in volatile communication between sagebrush individuals

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Abstract. Plants respond to volatile cues emitted by damaged neighbors to increase their defenses against herbivores. We examined whether plants communicated more effectively with local neighbors than distant neighbors in a reciprocal experiment at two sites. Three branches on focal plants were incubated with air from (1) a control, (2) an experimentally clipped “foreign” plant from 230 km away, or (3) an experimentally clipped “local” plant from the same population as the focal plant. Branches incubated with air from the controls experienced 50–80% more leaf damage than those receiving air from experimentally clipped plants. Of more interest, branches receiving volatiles from experimentally clipped “local” plants received 50–65% of the leaf damage as those receiving volatiles from experimentally clipped “foreign” plants. Sabinyl compounds and related terpinenes were found to differ consistently for plants from southern and northern sites. These results indicate that cues vary geographically in their effectiveness and suggest that sagebrush responds more strongly to local than foreign dialects.

Key words: *Artemisia tridentata*; communication; dialects; eavesdropping; herbivory; variation.

INTRODUCTION

Communication occurs among conspecifics, be they animals or plants, when an emitter releases a cue into the environment, which is sensed by a receiver, causing the receiver to respond (Bradbury and Vehrencamp 1998, Karban 2008). Although consensus about a definition of communication has not been reached, it is clear that many animals exhibit considerable geographic variation in their communication systems (Podos and Warren 2007).

Animals often discriminate between the signals of local, non-kin neighbors and those of distant strangers. Birdsongs, in particular, commonly vary geographically and appear to group into different local dialects (Marler and Tamura 1964, Slater 1989). Mating with a local male is thought to be advantageous for females that respond more strongly to local songs than foreign songs in playback experiments (Baker et al. 1981, Searcy et al. 2002). The ability of courting males to learn and repeat the local dialect may correlate with other advantageous

traits and these males are often preferred. Local dialects may also be well adapted to local environments (MacDougall-Shackleton et al. 2002, Luther and Baptista 2010). In territorial rather than intersexual contexts, animals also use dialects to distinguish neighbors from strangers (Temeles 1994). Individuals responded less aggressively to neighbors than to strangers (the dear enemy phenomenon), particularly when strangers posed greater potential threats.

Plants, like animals, respond to diverse environmental cues to alter behavior and morphology (Karbon 2015). Some cues are generated passively by other plants, such as the quality and quantity of reflected light, indicating competitors that receivers detect and avoid (Franklin 2008). Plants also communicate using volatile cues released when tissues on the same individual or nearby individuals have been attacked by herbivores; this phenomenon has been reported for approximately 50 plant species (Karbon 2015).

Sagebrush (*Artemisia tridentata*) individuals experienced reduced chewing damage when conspecific neighbors were experimentally clipped by scissors or herbivores (Karbon et al. 2006, Shiojiri and Karban 2008). The interplant cues responsible for induced responses to

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herbivores have not been identified definitively in this or any other system in nature. However, a green-leaf volatile, (*Z*)-3-hexenol, produced by many plants may mediate induced resistance to herbivory (Sugimoto et al. 2014). In the sagebrush system, a volatile cue is likely; plants failed to respond to damaged neighbors when air contact was blocked. Incubating receivers with air from damaged neighbors for 24 h was sufficient to elicit induced resistance (Shiojiri et al. 2012, Karban et al. 2013). As many as 100 volatile compounds have been identified from several species of *Artemisia* and many of these were found to increase more than twofold following experimental clipping (Kessler et al. 2006, Lopes-Lutz et al. 2008). The volatiles emitted by *Artemisia* species exhibit geographic variation (Abad et al. 2012, Pratt et al. 2014). Damage-induced volatiles emitted by individuals of *A. tridentata* in one meadow at our study site were found to vary and most individuals could be placed into one of two highly heritable chemotypes with profiles dominated by either camphor or thujone (Karban et al. 2014). A detailed description of these volatile profiles is provided elsewhere (Karban et al. 2016). Plants that produced mostly camphor produced no detectable thujone and those that produced mostly thujone produced only small amounts of camphor. Individuals of these two chemotypes were morphologically indistinguishable (Karban et al. 2016). These same two chemotypes were common at other field sites in California, Idaho, and Utah (Jaeger et al. 2016). Individuals of the same chemotype communicated more effectively and experienced less chewing damage than individuals receiving cues of the other chemotype, leading to the hypothesis that chemotypes may be a first step in allowing plants to distinguish kin from strangers (Karban et al. 2014).

Like animals, plants can be considered as territorial and plants compete for space, light, nutrients, and other resources (Schenk et al. 1999, Karban 2015). We hypothesized that plants would also distinguish herbivore-induced cues based on geographic differences and bias their responses. Here we tested the hypothesis that sagebrush plants respond to cues indicating risk of herbivory more effectively from “local” conspecifics than from “foreign” individuals that grow 230 km away. We conducted reciprocal experiments involving responses of plants exposed to cues from clipped foreign individuals to those exposed to cues from clipped local individuals. We also characterized the volatile profiles of plants from two southern and two northern populations to determine which volatile chemicals consistently differed between the locations.

MATERIALS AND METHODS

Reciprocal experiments to evaluate the effectiveness of communication

We conducted two experiments, one in the north and a second, 230 km to the south. At our northern site, we

selected 32 mature focal sagebrush plants in upper Taylor meadow at the UC Sagehen Creek field station (39°26.7 N, 120°14.7 W), north of Truckee, California, USA. At our southern site, we selected 36 mature focal plants at the UC Sierra Nevada Aquatic Research Lab (SNARL, 37°36.6 N, 118°49.5 W). All plants used in the study were from the same subspecies, *Artemisia tridentata* Nutt. ssp. *vaseyana* (Rybd.) Beetle. We then selected three branches on each focal plant that were at least 20 cm away from the other two branches; each branch had approximately 100 leaves. Branches of sagebrush are highly sectored so that defenses against herbivores are localized and branches can be considered as independent (Karban et al. 2006). This lack of integration has been commonly reported for many plants, particularly those growing in arid environments (De Kroon et al. 2005, Herrera 2009).

The three branches on each focal plant were incubated with air from one of three sources: (1) the surrounding atmosphere (Control), (2) an experimentally clipped plant that was from a distant site located approximately 230 km away (Foreign), and (3) an experimentally clipped plant from the same population where it was growing (Local). The three treatments were randomly assigned to the branches on each focal plant. Emitter plants from the local and foreign sites were potted mature plants that had been grown in the greenhouse in Davis and acclimated to local field conditions. Local emitter plants came from the exact same field sites as the focal individuals. Previous experiments in this system indicated that clipped plants produce volatile profiles of two distinct chemotypes and that plants were more responsive to cues from clipped plants of the same chemotype compared to the other chemotype (Karban et al. 2014). As a result, the chemotype of the source of the cue matched the chemotype of the focal receiver plant. In other words, camphor plants received cues from other clipped camphor plants that were either foreign or local. The chemotypes of focal plants and the emitter plants that served as sources of cue were determined using GC-MS (methods described in Karban et al. 2014). Volatile profiles for individuals (genets) were consistent across seasons and conditions so that growing in Davis did not alter chemotypes (Ishizaki et al. 2011; J. D. Blande and K. Shiojiri, *unpublished data*).

We generated cues by experimentally clipping with scissors the distal half of 25% of the leaves of one branch of each emitter plant in May; headspace volatiles were collected by enclosing the clipped branch in a plastic bag for 24 h immediately following clipping. The bag was sealed around the stem of the clipped emitter branch using a wire twist-tie. Volatiles were transferred from the headspace of clipped emitter plants to the headspace of a receiver branch on focal plants using a 1-L syringe (model S-1000; Hamilton, Reno, Nevada, USA) as described in Karban et al. (2013). Different emitters were used for each receiver. The receiver branch was incubated with air from the clipped emitter for 24 h by enclosing it within a

sealed plastic bag. In addition to the two branches that were incubated with air from foreign or local emitters, one control branch was incubated with air from the ambient environment. All three receiver branches on the focal plants were covered by a plastic bag for 24 h, only the source of the headspace volatiles in the bag varied. We previously found that the cues from plants clipped with scissors produced results that were indistinguishable from those produced by cues from plants experimentally clipped by beetles and grasshoppers (Shiojiri and Karban 2008).

We measured herbivory on the three treatment branches of each focal plant by counting the number of leaves with any visible damage caused by herbivores in August. We also counted the total number of leaves on each branch at this time and calculated the percentage of leaves with any visible damage. This measure of herbivory has been used in our previous work in this system and correlates with the percentage of leaf area removed. This response variable was best modeled by a Poisson distribution. Treatment effects caused by the source of volatiles (ambient air, cues from clipped foreign plant, cues from clipped local plant) were analyzed using a GLM (JMP 11.0, SAS, Cary, North Carolina, USA) with a Poisson distribution and a log link function. Assumptions regarding over-dispersion were met. Each plant was considered a block and all three treatments were represented in a randomized block design. Our a priori expectation was that cues from clipped plants of both local and foreign origin would reduce damage to the focal branches compared to the control. Of more interest, we predicted that communication would be more effective between local individuals than between individuals that originated from a different geographic location. These predictions were tested using a priori contrasts.

Chemical characterization of volatiles from northern and southern sites

We collected headspace volatiles from the experimentally clipped plants from two northern populations (Taylor meadow [39°26.7 N, 120°14.7 W], $n = 10$ plants, and Donner camp [39°22.7 N, 120°10.7 W], $n = 12$ plants) and two southern populations (UC Valentine Reserve [37°37.3 N, 118°59.3 W], $n = 16$ plants, and SNARL [37°36.6 N, 118°49.5 W], $n = 16$ plants). We clipped five leaves from one branch of each plant with scissors and collected headspace volatiles using a dynamic flow-through system described elsewhere (Karbon et al. 2014).

These volatile headspace samples were characterized using GC-MS and individual compounds were identified. We compared the peaks obtained from authentic standards that included 18 monoterpenes, eight sesquiterpenes, and 10 green leaf volatiles. Several compounds were not available and these were identified by comparing their mass spectra with those in the Wiley library (John Wiley, Hoboken, New Jersey, USA). Volatile profiles for each plant were subjected to principal component

analysis (PCA) to characterize differences between the northern and southern sites and between the two common chemotypes. We determined which compounds were consistently different between populations in the north and south using PCA and partial least squares discriminant analysis (PLS-DA) in the SIMCA-P14 software package (Umetrics, Umea, Sweden).

RESULTS

Reciprocal experiments to evaluate the effectiveness of communication

Herbivore communities were relatively similar across our sites. Chewing damage was primarily caused by grasshoppers, although the entire area experienced a drought and levels of damage were relatively low. Herbivores were more common at the northern sites. *Cratypedes neglectus* was the most common herbivore at all sites, although *Cratypedes lateritius*, *Trimerotropis fontana*, *Cammula pellicida*, and *Opeia obscura* were also present. Leaf galls made by *Rhopalomia* spp. (Cecidomiidae) were numerous at both locations. Caterpillars (*Aroga websteri* and others) and deer (*Odocoileus hemionus*) were also common, especially early in the season at the northern sites. A leaf fungus (*Cladosporium* sp.) was present at both locations but was more prevalent later in the season in the north.

Branches receiving cues from the three different sources (ambient air, clipped “foreign” plant, and clipped “local” plant) experienced different levels of leaf damage (Fig. 1; northern garden, $\chi^2 = 67.9$, $df = 2$, $P < 0.001$; southern garden, $\chi^2 = 17.1$, $df = 2$, $P < 0.001$). The control branches at the northern site that were incubated with air from the ambient atmosphere experienced 80% more chewing damage than branches incubated with air from clipped plants from either of the two geographic sources (Fig. 1A, a priori contrast $\chi^2 = 46.0$, $df = 1$, $P < 0.001$). Control branches at the southern site experienced 50% more chewing damage than branches incubated with air from clipped plants from either of the two sources (Fig. 1B, a priori contrast $\chi^2 = 11.2$, $df = 1$, $P < 0.001$). In other words, branches exposed to volatile cues from experimentally clipped plants became more resistant to chewing herbivores. Of more interest, branches incubated with cues from clipped plants from the local population experienced only 50–65% of the chewing damage as branches incubated with cues from foreign populations located 230 km away (northern site, Fig. 1A, a priori contrast $\chi^2 = 28.2$, $df = 1$, $P < 0.001$; southern site, Fig. 1B, a priori contrast $\chi^2 = 6.7$, $df = 1$, $P = 0.010$).

Chemical characterization of volatiles from northern and southern sites

Profiles characterizing the damage-induced volatile emissions of plants from two northern sites and two southern sites were analyzed using PCA. Six principal components were found, explaining 58.8% of the overall

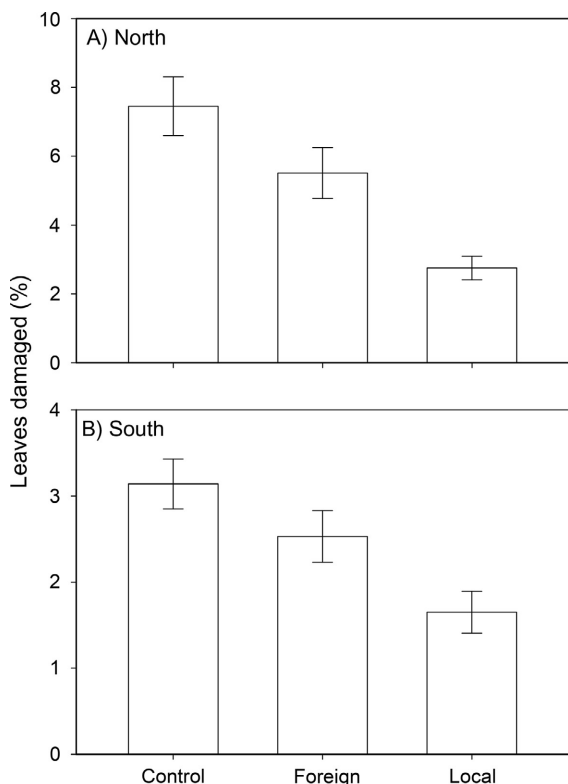


FIG. 1. The percentage of leaves with damage caused by chewing herbivores on branches of focal plants that were incubated with headspace volatiles from (1) the ambient-atmosphere "control," (2) a clipped "foreign" plant from 230 km away, and (3) a clipped "local" plant from the same meadow. Focal plants were located in two gardens, either in the north (A) or south (B). Values are mean \pm 1 S.E.

chemical variation. The first principal component explained 15.1% of the variation and mainly separated plants of the two common chemotypes, thujone and camphor (Fig. 2). The second principal component explained 12.4% of the chemical variation and separated plants from the northern sites from those of the southern sites (Fig. 2).

Further PLS-D analyses attempted to identify the specific compounds that differed between northern and southern plants. For plants of the thujone chemotype, the first principal component in PLS-D separated plants from the northern and southern locations and explained 14.4% of the variation (Fig. 3A). For plants of the camphor chemotype, the first principal component in PLS-D separated those originating from the northern and southern sites and explained 31.7% of the variation (Fig. 3B).

Many compounds were emitted by plants from both populations and these are not described further. In general, emissions from southern populations tended to have several peaks that were absent or low in northern plants (Fig. 4). Four compounds were found in emissions of thujone plants from the southern sites but not from the northern ones (santolina triene, santolina epoxide, *a*-santolina alcohol, and artemiseole; Fig. 4A). Several sabinyl compounds were differently represented from the two locations with sabinene, (*E*)-sabinene hydrate, and (*Z*)-sabinene hydrate common in the south and sabinyl acetate and (*Z*)-sabinol predominating in the north. Some of these same sabinyl compounds were also found in greater abundance in plants of the camphor chemotype from southern sites compared to northern ones (Fig. 4B). In addition, several terpinene compounds (α -terpinene, γ -terpinene, terpinen-4-ol, and α -terpineol) were more

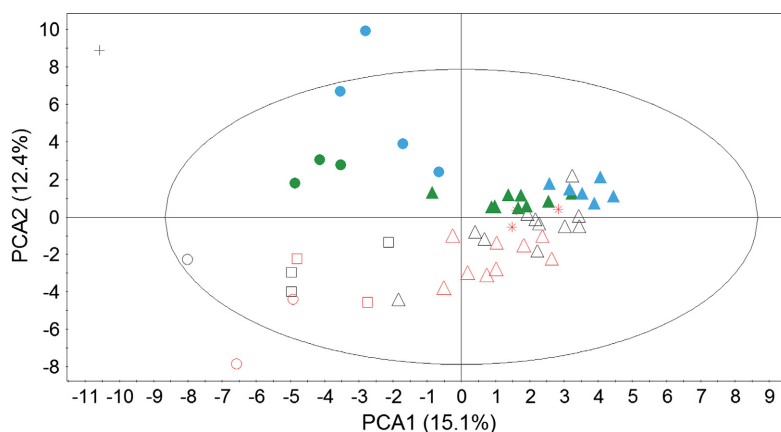


FIG. 2. Principal component scores for plants from the four field sites. The shape of the symbol represents the volatile chemotype of each individual plant: camphor, circle; thujone, triangle; additional chemotypes, square, star, cross. Sites in the north are shown as solid symbols (Sagehen, blue; Donner, green) and sites in the south are open symbols (SNARL, red; Valentine, black). The first principal component (horizontal axis) separates plants based mainly on chemotype and the second principal component (vertical axis) separates plants based on geographic location. Ellipse indicates 95% confidence based on Hotelling's T^2 statistic.

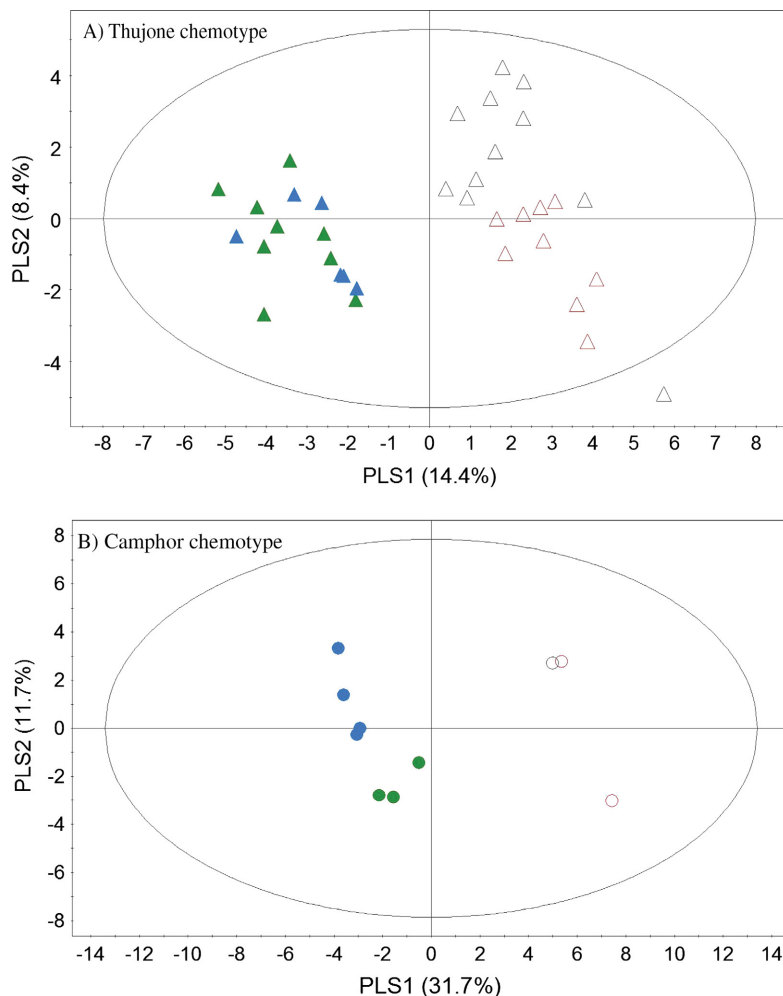


FIG. 3. Partial least squares discriminant analysis of the volatile emissions of plants of the (A) thujone chemotype and (B) camphor chemotype. Plants from the north are indicated by solid symbols and those from the south as open symbols. For both chemotypes, the horizontal axis separates plants based on their geographic location. Ellipses indicate 95% confidence based on Hotelling's T^2 statistic.

abundant in camphor chemotype individuals from the southern sites.

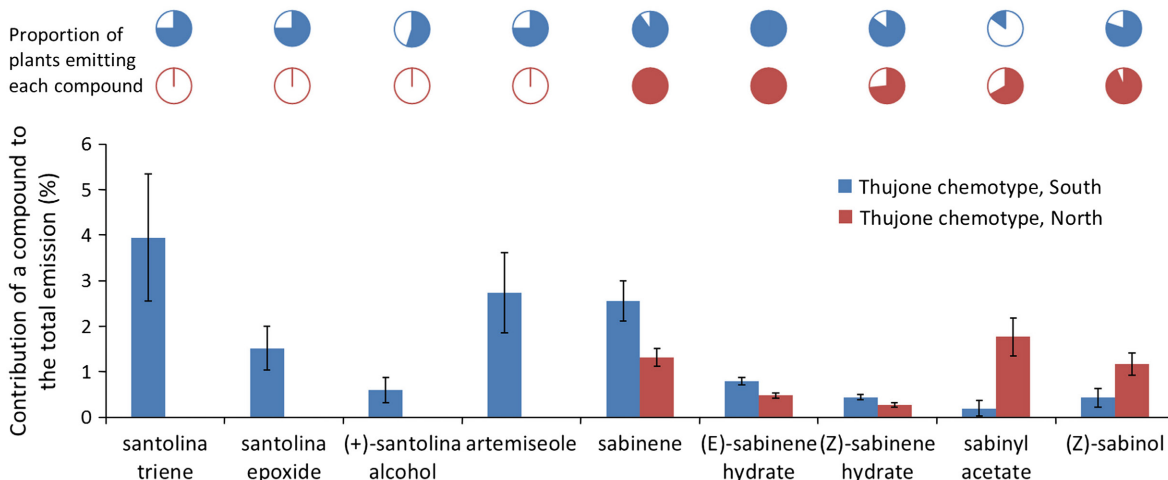
DISCUSSION

Sagebrush tissues respond to the volatile cues emitted by experimentally damaged neighboring plants to increase their levels of resistance to herbivory (Karban et al. 2006, Shiojiri and Karban 2008). Branches that were incubated with the volatile cues of clipped neighbors experienced reduced levels of chewing damage compared to branches incubated with ambient air (Fig. 1). This result was consistent with previous findings (e.g., Karban et al. 2013). Experimentally clipped plants emit many volatile compounds although we know little about which of these chemicals serve as informative cues to plants under natural conditions (Shiojiri et al. 2015).

Branches responded to cues from local plants from the same population more effectively than they did to cues from plants that originally grew 230 km away (Fig. 1). This population-specific effect was found for focal plants from both localities. This suggests that the result was caused by more effective communication and was not the result of one population consistently emitting a stronger cue or having stronger constitutive defenses.

Once a plant emits volatile cues into the environment, that information becomes available to potential competitors of the same or different species (e.g., Heil 2014) and also to herbivores searching for hosts (e.g., Horiuchi et al. 2003). It has been unclear whether emission of herbivore-induced volatile cues benefits or harms individuals that emit them and whether certain characteristics of the cues or the communication system might influence these outcomes. Cues that are more specific are predicted to make the information more private and

A) Thujone chemotype



B) Camphor chemotype

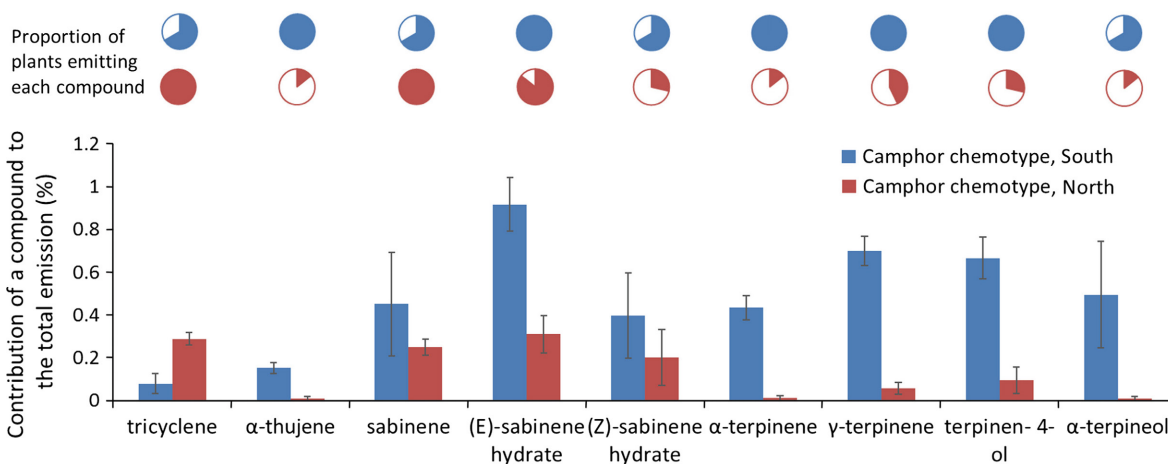


FIG. 4. Volatile compounds that differentiate emissions from plants from the north (red) and south (blue). The pie charts at the top of each panel indicate the proportion of plants that emitted each compound. The bars show the mean percentage that each compound contributed to the total emission (\pm SE). (A) Plants of the thujone chemotype from the north ($n = 15$) and from the south ($n = 20$). (B) Plants of the camphor chemotype from the north ($n = 7$) and from the south ($n = 3$).

hence more beneficial to the emitter (Schaefer et al. 2004, Raguso 2008).

The population-specificity demonstrated in this study may make cues emitted by sagebrush more useful to both the emitter and receiver. Previous work demonstrated that plants communicated more effectively with kin than strangers (Karban et al. 2013) and plants that were geographically closer were more likely to share genes (McArthur et al. 1998, Ishizaki et al. 2011; D. McArthur, *personal communication*). As such, this experiment does not allow us to disentangle effects caused by geographic distance and genetic distance although these two are often correlated in nature. The effect size due to geographic distance (Fig. 1A,B) was approximately 50–100% larger than that reported for differences in relatedness in the same receiver population at our northern site, Taylor

meadow (Karban et al. 2013; Fig. 3). This suggests that geographic variation in cues is likely to play a role in the overall effectiveness of this communication system. Other studies have found that plants proliferate roots differentially in response to neighbors and that both kin recognition and population specificity are involved in perception and response to root exudates (Dudley and File 2007, Semchenko et al. 2014).

Population-specific communication has also been found for communication between geographically distinct populations of wild lima beans (Moreira et al. 2016). Receivers from the same populations as emitters experienced less leaf damage but this effect was not seen when receivers and emitters were from different populations. This situation is similar to the geographic specificity observed in many animal communication systems (Podos

and Warren 2007). Geographic variation in bird songs has probably been facilitated by the tendency of many birds to imitate and learn vocalizations. Learning of this nature has not been reported for plants (Karban 2015), although other processes could lead to geographic variation in communication. For example, if plants recognize or respond more readily to local cues, then geographic structure in those cues can arise as long as mating populations are viscous. This structure can arise even in the absence of selection for cues that match the local environmental conditions.

Geographic variation in birdsong was only recognized as an important phenomenon once ornithologists were able to characterize and quantify the cues (songs) using spectrograms (Podos and Warren 2007). For example, spectrograms of individual White-crowned Sparrows from one population showed consistent patterns that differed from neighboring populations (Marler and Tamura 1964). Similarly, in this study we attempted to identify those compounds that differed geographically and could produce population-specific communication.

We found that plants at our two northern populations produced cues that were consistently different from cues produced by plants at our two southern populations. In particular, the santoliny compounds (sanolina triene, α -santolina alcohol, santolina epoxide, and artemiseole) were only emitted by thujone plants from the southern sites. The sabinyl compounds and related terpenoids also differed for plants from northern and southern sites. Thujone plants from the two northern sites had greater emissions of sabinyl acetate and (*Z*)-sabinol (Fig. 4A). Thujone plants from the southern sites produced greater concentrations of sabinene, (*E*)-sabinene hydrate, and (*Z*)-sabinene hydrate. These same three compounds were also more commonly emitted by plants of the camphor chemotype from the southern sites, although neither southern nor northern camphor plants emitted sabinyl acetate or (*Z*)-sabinol (Fig. 4B). Camphor plants from the southern sites also had greater emissions of terpinyl compounds including α - and γ -terpinene, terpinen-4-ol and α -terpineol. Both sabinyl and terpinene compounds are known to have biological activity and to co-occur in many plants (e.g., Espinosa-Garcia and Langenheim 1991). Sabinene can be readily pyrolyzed to produce the terpinenes (Mitzner and Theimer 1962). We do not yet know whether any of these compounds are actually perceived by sagebrush plants or important in the communication process.

CONCLUSIONS

The language that sagebrush plants use to communicate about risk of herbivory has been found to vary at several different scales. Plants communicate more effectively over short distances (60 cm; Karban et al. 2006), with other tissues that are genetically identical (Karban and Shiojiri 2009), or at least related (Karban et al. 2013). Individuals within a single population emit different

chemicals when damaged and those of the same heritable chemotypes communicate more effectively with similar individuals than with individuals of different chemotypes (Karban et al. 2014). The results of this study indicate that plants also communicate more effectively with individuals from the same population than with individuals from other populations located 230 km away. Wild bean individuals showed even stronger population specificity, only responding to cues from conspecifics from the same population (Moreira et al. 2016). These two studies suggest that plant individuals may be thought of as communicating with local dialects, similar to those observed in the songs of birds and other animals.

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