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Herbivore damage to sagebrush induces resistance in wild tobacco: evidence for eavesdropping between plants

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Whether plants respond to cues produced by neighbors has been a topic of much debate. Recent evidence suggests that wild tobacco plants transplanted near experimentally clipped sagebrush neighbors suffer less leaf herbivory than tobacco controls with unclipped neighbors. Here we expand these results by showing evidence for induced resistance in naturally rooted tobacco when sagebrush neighbors are clipped either with scissors or damaged with actual herbivores. Tobacco plants with sagebrush neighbors clipped in both ways had enhanced activity levels of polyphenol oxidase (PPO), a chemical marker of induced resistance in many solanaceous plants. Eavesdropping was found for plants that were naturally rooted, although only when sagebrush and tobacco grew within 10 cm of each other. Although tobacco with clipped neighbors experienced reduced herbivory, tobacco that grew close to sagebrush had lower production of capsules than plants that grew far from sagebrush. When neighboring tobacco rather than sagebrush was clipped, neither levels of PPO nor levels of leaf damage to tobacco were affected. Eavesdropping on neighboring sagebrush, but not neighboring tobacco, may result from plants using a jasmonate signaling system. These results indicate that plants eavesdrop in nature and that this behavior can increase resistance to herbivory although it does not necessarily increase plant fitness.

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Communication between plants that affects resistance to herbivores has been a very contentious notion. It was originally proposed by David Rhoades to explain his observations that caterpillars performed less well on trees with damaged neighbors compared to trees with undamaged neighbors (Rhoades 1983). However, problems of pseudoreplication, failure to consider alternative hypotheses, and lack of repeatability of this and other early demonstrations of communication led many ecologists to discount the phenomenon (see reviews in Fowler and Lawton 1985, Bruin et al. 1995, Shonle and Bergelson 1995, Karban and Baldwin 1997). Carefully controlled lab experiments indicated that communication between plants was possible under some conditions. Tomato plants that were incubated with cut branches of sagebrush in small air-tight containers increased production of proteinase inhibitors (Farmer and Ryan 1990), chemicals that were reported to affect herbivores (Broadway et al. 1986). Sagebrush was selected for these lab experiments because it was known to release large quantities of methyl jasmonate, a chemical that was suspected of acting as a volatile plant hormone. Since Farmer and Ryan's work, evidence has mounted that jasmonates are indeed highly conserved

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hormones that play an important role in regulating plant responses to herbivory as well as many other processes (Reinbothe et al. 1994, Wasternack and Parthier 1997). Although Farmer and Ryan demonstrated that communication between plants was possible in air tight containers, ecologists still felt unconvinced that similar phenomena were possible under actual conditions involving plants that co-occurred in nature.

Recent experiments have provided much more convincing evidence for eavesdropping among real plants in nature. Wild tobacco plants (*Nicotiana attenuata*) induced resistance when neighboring sagebrush plants (*Artemisia tridentata*) were experimentally clipped with scissors (Karban et al. 2000, Karban 2001). In each of five years, damage caused by grasshoppers, the primary folivores, was reduced on tobacco plants with experimentally clipped sagebrush neighbors. In one of these years cutworms (Lepidoptera: Noctuidae) were abundant and they too were less damaging to tobacco with sagebrush neighbors that had been experimentally clipped (Karban et al. 2000). In one of these years, a chemical assay was also conducted. Activity of polyphenol oxidase (PPO) was elevated in tobacco plants near clipped sagebrush neighbors (Karban et al. 2000). PPO is an oxidative enzyme that is induced by actual herbivory or by exogenous application of methyl jasmonate. It has been found to be a reliable indicator of other systemic induced responses in solanaceous plants, including tobacco (Constabel and Ryan 1998, Stout et al. 1998). PPO acts as an anti-nutritive protein to many herbivores, reacting with phenolic substrates in the herbivore gut and eventually causing alkylation of essential amino acids, making them nutritionally unavailable (Duffey and Felton 1989, Felton et al. 1992).

Recently, other workers have also found evidence of communication between plants that can affect resistance to herbivores. Alder trees growing close to conspecific neighbors that had been mechanically defoliated (20% leaf area removed) suffered less leaf damage by alder leaf beetles during the subsequent growing season than controls near neighbors that were not defoliated (Dolch and Tscharntke 2000, Tscharntke et al. 2001).

Despite growing evidence suggesting communication between plants, additional issues need to be addressed before this phenomenon can be fully embraced (Agrawal 2000, Dicke and Bruin 2001, Pickett and Poppy 2001, Preston et al. 2001). For example, experimental clipping of sagebrush and alders was done with scissors and artificial clipping can cause different plant responses than actual herbivory in many species (Baldwin 1988, Eichenseer et al. 1999). In addition, previous experiments with wild tobacco have used transplants rather than naturally rooted plants. Although tobacco grows in close proximity to sagebrush, in previous experiments there were not enough of these plants to fulfill the desired levels of replication; tobacco seedlings had to be transplanted near sagebrush. Because of these problems, reviewers have questioned whether communication between plants will be common in nature even between sagebrush and wild tobacco.

Sagebrush was selected for experiments by Farmer and Ryan (1990) because it releases relatively high levels of methyl jasmonate when wounded. Wild tobacco most often has other tobacco or sagebrush as its nearest neighbor. Damage to neighboring tobacco plants may provide more reliable information about the risk of herbivory for tobacco than damage to neighboring sagebrush (Karban et al. 1999). This reasoning suggests that selection might favor tobacco that eavesdrops on neighboring conspecifics.

In this paper, we build on previous work on communication between sagebrush and tobacco by addressing the following questions: 1) Will actual herbivores of sagebrush cause the same results as mechanical clipping? 2) Will naturally rooted tobacco plants show the same responses as transplanted tobacco plants? 3) Over what distances will eavesdropping be observed? 4) Will damage to neighboring tobacco induce resistance in conspecifics?

Methods

The tobacco and sagebrush system

Nicotiana attenuata, wild tobacco, is an annual plant native to the Great Basin that often grows in close proximity to sagebrush, *Artemisia tridentata* (Wells 1959). It is found in association with disturbances such as streambeds and roadsides and grows in dense populations following burns (Wells 1959, Baldwin 1998). Wild tobacco suffers high rates of leaf herbivory by grasshoppers (6 species in order of abundance: *Cratypedes neglectus*, *Trimerotropis fontana*, *Conozoa sulcifrons*, *Cratypedes lateritius*, *Melanoplus sanguinipes* and *Cordillacris occipitalis*) and noctuid cutworms (2 common species: *Peridroma saucia* and *Agrotis ypsilon*). These generalist herbivores also feed on *A. tridentata* although sagebrush tends to be more preferred earlier in the season when tobacco and other annual plants are seeds or small seedlings.

Experiment 1. Does natural herbivory of sagebrush induce resistance in neighboring tobacco?

This experiment builds on results that clipping sagebrush with scissors induced resistance in neighboring tobacco (Karban et al. 2000). Here we asked if actual herbivory would do the same. In this experiment tobacco seedlings were grown within 15 cm, downwind of a sagebrush neighbor. Each sagebrush plant had two tobacco neighbors: one to be used as a chemical assay and the other as a biological assay of induced resistance. We chose 85 individuals of sagebrush, established their neighboring tobacco plants, and assigned them to three treatments: 25 sagebrush assigned to be clipped with scissors, 28 sagebrush assigned to be damaged by herbivores, and 32 controls. For all three treatments, only sagebrush plants were manipulated and great care was taken not to disturb the tobacco foliage. For sagebrush that were assigned to be clipped experimentally, we cut with scissors and removed 4.6 ± 0.5 (se) g of leaves and stems from each plant once on 23 June 1999. The cut leaves and stems were the closest foliage to the tobacco neighbors (7.2 ± 0.7 (se) cm distant); sagebrush foliage greater than 15 cm from the assay tobacco plants was not disturbed. For pairs assigned to experimental herbivory we caged 1 grasshopper nymph (assorted species, see above) and 2 beetle larvae (Chrysomelidae: *Trirhabda pilosa*) on the sagebrush shoot nearest to the neighboring tobacco. The grasshoppers and beetles used to damage sagebrush were the most common folivores encountered on sagebrush at the time. Sleeve cages were constructed of white polyester organdy (wedding veil material, 24 cm long $\times$ 24 cm in circumference). These herbivores fed from 22–27 June 1999 after which time they and the cages were removed. All sagebrush plants in this treatment were damaged successfully by these herbivores (9.7 ± 1.3 (se) sagebrush leaves damaged within 15 cm of the tobacco neighbor).

All of our experiments were conducted on the flood plain of Convict Creek at the Sierra Nevada Aquatic Research Lab near Mammoth Lakes, California (SNARL, 37° 36′57″ N, 118° 49′47″ W) at an elevation on 2160 m, unless otherwise noted. Although wild tobacco grows at this site, it was not naturally abundant enough to fulfil the desired levels of replication, so tobacco plants were transplanted as small seedlings from local sites. Treatments were applied only after tobacco plants had completely recovered from transplanting (9–14 days) as evidenced by their ability to grow new leaves and to withstand sun without wilting. All sagebrush plants used in these experiments were already established.

For chemical assays, one leaf was excised at the petiole with a razor blade from the basal rosette of 18 tobacco plants with manually clipped sagebrush neighbors, 20 tobacco plants with neighbors damaged by herbivores, and 21 tobacco plants with undamaged control neighbors. We collected a leaf from only those tobacco plants that had lost no leaf tissue to other herbivores prior to our assay on 28 June. Leaves for chemical assays were excised on 28 June and placed immediately on dry ice. Methods of chemical extraction and analysis of polyphenol oxidase (PPO) activity were described by Felton et al. (1989). Activity levels of PPO were log transformed in the analysis to satisfy assumptions of normality. Wet weight of the excised tobacco leaf was included as a covariate in the statistical model since activity levels are total amounts rather than concentrations (analysis of covariance using MGLH in Systat 5.0).

Biological assays of induced resistance were conducted by monitoring the proportion of wild tobacco leaves that were naturally damaged by herbivores every fifth day throughout the entire season. The maximum proportion of leaves with damage by herbivores was used as a nondestructive measure of damage for each plant and was arcsine square root transformed for analyses. A destructive sample of other plants that were not used in these experiments indicated that this measure of herbivory was correlated with percent leaf area removed ($R^2 = 0.46$, $n = 50$, $P < 0.001$).

Experiment 2. Does clipping sagebrush induce resistance in naturally rooted tobacco and over what distance?

In this experiment we clipped sagebrush with scissors and recorded levels of leaf damage caused by grasshoppers, numbers of seed-feeding bugs, and numbers of seed-bearing capsules on neighboring tobacco plants. These tobacco plants were naturally rooted at various distances ranging from 0 cm (touching) to 100 cm downwind from their closest sagebrush neighbor. This experiment was conducted near Moran Springs in the Benton Range of eastern California (N 37° 39.35′ W 118° 35.31′) at an elevation of 2124 m.

For tobacco plants assigned to be near clipped neighbors, we clipped with scissors the shoots of the closest, upwind sagebrush individual on 14 June 2000. Tobacco plants were at the vegetative, rosette stage and had not begun to elongate. Biological assays of induced resistance were conducted by monitoring the proportion of tobacco leaves that were damaged by herbivores every seventh day throughout the entire season. The maximum proportion of leaves with damage by herbivores was used as a nondestructive measure of herbivory for each plant and was arcsine square root transformed for analyses. We also counted the number of corimelaenid bugs (Hemiptera: Corimelaenidae: *Corimelaena virilis*) on the flowers and capsules of each tobacco plant at weekly intervals. These bugs are locally abundant seed feeders that can reduce the weight and viability of tobacco seeds (Wells 1959, Baldwin 1998, Maron and Karban unpublished data). Finally, we recorded the number of seed-bearing capsules produced by each tobacco plant. We conducted analyses of covariance of three response variables: the maximum proportion of leaves damaged, total number of corimelaenid bugs observed during the season, and number of filled seed capsules for naturally rooted tobacco at various distances from sagebrush with clipping treatments as a fixed effect and distance as a covariate using the GLM Procedure in Systat version 5.05.

Experiment 3. Does clipping tobacco induce resistance in neighboring tobacco?

We established a garden of 60 pairs of tobacco seedlings in 1999; plants of each pair were grown within 5 cm of each other and were 50 cm from other pairs. Half of the pairs were randomly assigned to have the upwind plant clipped with scissors on 12 July ('clipped') and the other pairs were controls. The distal quarter of each leaf was clipped through the mid-vein and removed for plants assigned to the clipped treatment. The downwind plant of each pair was not clipped and was used for chemical and biological assays of induced resistance. For chemical assays, one leaf was excised as described above from 19 tobacco plants whose neighbor had been clipped and from 12 plants whose neighbor was an unclipped control. Assay leaves were handled and analyzed as described for the chemical assay in experiment 1. Biological assays on the downwind plant of each pair were conducted by observing the damage caused by herbivores every fifth day throughout the season. Several plants were destroyed which left 24 'clipped' pairs and 29 'control' pairs.

We repeated this experiment using 58 pairs of naturally rooted tobacco in 2000 near Moran Springs in the Benton Range; as in 1999, plants of each pair were within 5 cm of each other. The upwind plant of 28 pairs was clipped experimentally on 10 June and damage by herbivores to the downwind plant was recorded every five days thereafter as described above. One leaf from 25 downwind plants with clipped tobacco neighbors and from 25 downwind plants with unclipped tobacco neighbors was sampled on 22 June and analyzed for PPO as described above. Maximum levels of damage (arcsine square root transformed) caused by grasshoppers and levels of PPO were analyzed from both years using two-way analysis of variance with treatment (clipped or unclipped tobacco neighbor), year, and treatment × year as effects.

Results

Experiment 1. Does natural herbivory of sagebrush induce resistance in neighboring tobacco?

Tobacco plants near sagebrush neighbors that had been clipped or fed upon by herbivores had increased activity of the oxidative enzyme, PPO, compared to tobacco plants with unclipped neighbors (Fig. 1; $F_{2,55} = 3.56$, $P = 0.035$ for effect of damage treatments on PPO with wet weight of the tobacco leaf used in the chemical assay as a covariate). Tobacco plants with artificially clipped neighbors did not differ from those with neighbors damaged by real herbivores (a priori contrast: $F_{1,55} = 0.14$, $P = 0.71$). Tobacco plants with sagebrush neighbors that were clipped either artificially or with herbivores both differed from the controls with unclipped neighbors (a priori contrast: $F_{1,55} = 6.93$, $P = 0.01$).

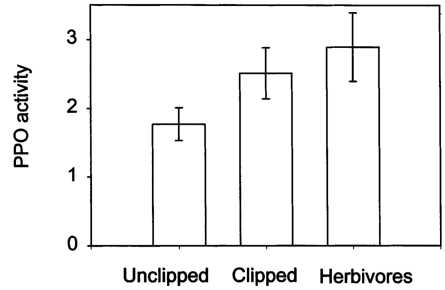

Fig. 1. Levels of polyphenol oxidase (PPO) activity (change in OD/min/g) for tobacco plants near unclipped sagebrush neighbors and near sagebrush clipped manually or with real herbivores. Bars are unadjusted means ± 1 se.

Clipping of sagebrush neighbors with scissors or by actual herbivores reduced the maximum proportion of tobacco leaves that were damaged throughout the season by naturally occurring herbivores (Fig. 2; one-way ANOVA $F_{2,81} = 4.48$, $P = 0.014$). Both of the clipping treatments were different from the control (a priori contrast: $F_{1,81} = 7.43$, $P = 0.008$) and clipping by natural herbivores did not differ from clipping with scissors (a priori contrast: $F_{1,81} = 1.38$, $P = 0.244$).

Experiment 2. Does clipping sagebrush induce resistance in naturally rooted tobacco and over what distance?

Tobacco plants that were closer to sagebrush experienced less leaf herbivory than those farther from sagebrush (distance was significant in Table 1A). However, clipping the sagebrush did not affect herbivory and clipping did not accentuate the negative effect that neighboring sagebrush had on herbivory (neither clipping treatment nor the interaction between clipping treatment and distance were significant in Table 1A). Larger sagebrush individuals were not more likely to release cues that affected herbivory; the volume of the sagebrush plant had no effect on the level of herbivory

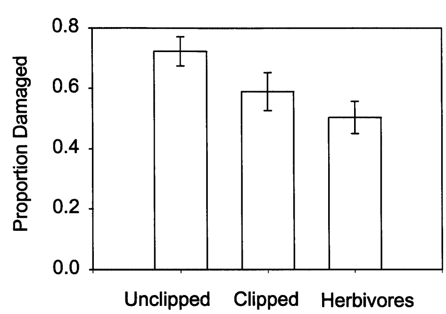

Fig. 2. Maximum proportion of leaves that were damaged by herbivores on tobacco plants with sagebrush neighbors that were unclipped, clipped artificially, or clipped by real herbivores (means ± 1 se).

Table 1. Analysis of the maximum proportion of leaves that were damaged by herbivores for naturally rooted tobacco plants at varying distances from clipped or unclipped sagebrush.

Source	SS	DF	MS	F	P
A. Analysis of variance with distances (0–100 cm) as a continuous variable					
Clipping	129	1	129	0.55	.458
Distance	3001	1	3001	12.87	.001
Clipping × Distance	366	1	365	1.57	.212
Sagebrush Volume	1	1	1	0.00	.960
Error	43 610	187	233		
B. Analysis of variance with 2 categories of distance between sagebrush and tobacco, less than 10 cm and more than 10 cm					
Clipping	44	1	44	0.19	.664
Distance	1633	1	1633	6.94	.009
Clipping × Distance	1011	1	1011	4.30	.040
Error	44 250	188	235		

experienced by its neighboring tobacco (Table 1A). Examination of the data indicated that tobacco plants within 10 cm of sagebrush responded to the clipping treatment differently than those at greater distances (Fig. 3). A re-analysis of the data that included two categories for the distance between sagebrush and tobacco, under 10 cm and over 10 cm, confirmed this impression (Table 1B). Tobacco plants less than 10 cm from clipped sagebrush were affected by whether the sagebrush had been clipped; those close to clipped sagebrush experienced lower levels of leaf herbivory than those close to unclipped sagebrush (Fig. 3). Tobacco plants that were more than 10 cm from sagebrush were unaffected by whether that sagebrush had been clipped or not. Including other distances in the model failed to improve its explanatory power (data not shown).

Corimelaenid bugs were more abundant on tobacco plants that produced more capsules although clipping the neighboring sagebrush did not affect this relationship (Table 2A, model $R^2 = 0.080$). Tobacco plants produced more seed-bearing capsules as the distance between sagebrush and tobacco increased (Fig. 4). This depression in tobacco reproduction caused by sagebrush was not influenced by whether the sagebrush had been clipped or not (no significant interaction between clipping × distance in Table 2B). Larger sagebrush depressed capsule production in neighboring tobacco more than smaller sagebrush (sagebrush volume was significant in Table 2B).

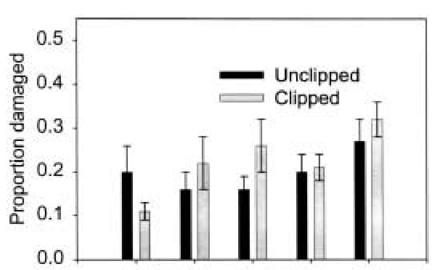

Fig. 3. Maximum proportion of leaves that were damaged by herbivores on naturally rooted tobacco plants with sagebrush neighbors at various distances that were clipped or unclipped (means ± 1 se).

Experiment 3. Does clipping tobacco induce resistance in neighboring tobacco?

We conducted chemical and biological assays of tobacco plants with clipped and unclipped tobacco neighbors. We detected no differences in levels of activity of the oxidative enzyme, PPO, for tobacco plants near tobacco neighbors that had been clipped compared to tobacco plants with unclipped tobacco neighbors (Fig. 5; $F_{1,75} = 0.43$, $P = 0.45$ for effect of clipping treatments on PPO with wet weight of the tobacco assay leaf as a covariate). The effect of clipping did not vary significantly among the two years (clipping × year interaction $F_{1,75} = 1.50$, $P = 0.16$). In addition, tobacco plants near clipped tobacco neighbors experienced relatively similar amounts of leaf damage as those near unclipped neighbors (Fig. 6; $F_{1,105} = 0.80$, $P = 0.37$).

Discussion

Eavesdropping and induced resistance

Tobacco near clipped sagebrush exhibited elevated levels of PPO activity and reduced levels of leaf loss by herbivores (Fig. 1,2, Table 1); these results were consistent over five years (Karban 2001). Actual herbivory to the sagebrush caused reduced leaf damage to neighboring tobacco (Fig. 2), much as artificial clipping had in previous experiments. In all cases, less than 5% of the above ground biomass of the sagebrush was removed. Tobacco apparently increases its resistance in response to an airborne cue that is released by clipped sagebrush (Karban et al. 2000).

Increased resistance near clipped sagebrush neighbors was found for tobacco plants that were naturally rooted (Fig. 3, Table 1B), extending previous results for transplanted tobacco. These results indicate that communication is not an artefact of clipping with scissors or transplanted tobacco. Evidence for eavesdropping by

Table 2. Analysis of the total number of corimelaenid bugs and seed-bearing capsules observed for naturally rooted tobacco plants at varying distances from clipped or unclipped sagebrush.

Source	SS	DF	MS	F	P
A. Corimelaenid bugs					
Clipping	3	1	3	0.06	.809
Distance	110	1	110	1.89	.171
Clipping × Distance	1	1	1	0.03	.874
Capsules	38 498	1	38 498	661.47	.001
Error	10 942	188	58		
B. Filled Capsules					
Clipping	14	1	14	0.01	.923
Distance	20 345	1	20 345	13.48	.001
Clipping × Distance	954	1	954	0.63	.428
Sagebrush Volume	9280	1	9280	6.15	.014
Error	28 3661	188	1509		

naturally rooted plants was found only when sagebrush and tobacco were within 10 cm of each other. This critical effective distance is smaller than that found in previous work (15 cm reported in Karban et al. 2000). Two factors likely contribute to this discrepancy in critical effective distances. First, the wind direction at SNARL, where eavesdropping was found to occur over at least 15 cm, is far more predictable than at Moran Springs, where eavesdropping was limited to 10 cm. Second, winds were calm during, and for at least 8 h following, clipping at SNARL whereas winds consistently exceeded 0.2 m/sec during clipping at Moran Springs and frequently gusted much higher. Experiments in both places suggest that the volatile cues released by sagebrush dissipate over relatively short distances. This is likely to set a limit on the importance and generality of eavesdropping between plants in nature.

It is plausible that larger individuals of sagebrush may emit more cue than smaller ones (Preston et al. 2001). However, we found no evidence that the volume of the clipped sagebrush individual influenced the level of resistance achieved by tobacco plants (Table 1A). Similarly, the amount of sagebrush clipped did not affect the level of resistance in any of the other experiments that we have conducted (data not shown).

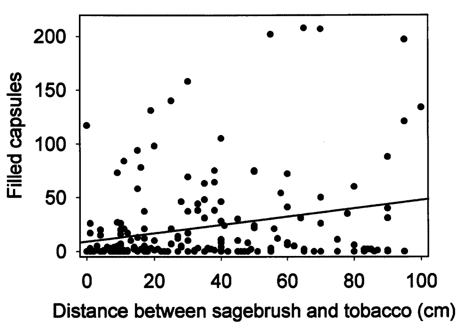

Fig. 4. Naturally rooted tobacco plants produced more filled capsules farther from a sagebrush neighbor (capsules = 0.387 [distance in cm] + 9.20, n = 193, $R^2 = 0.065$).

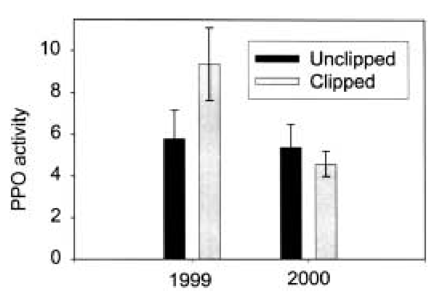

Fig. 5. Levels of polyphenol oxidase (PPO) activity (change in OD/min/g) for tobacco plants near unclipped or clipped tobacco neighbors in 1999 and 2000. Bars are unadjusted means ± 1 se.

Eavesdropping and plant fitness

Induction caused by clipping sagebrush decreased leaf damage and increased flowering and capsule production of neighboring transplanted tobacco in some years but not in others (Karban and Maron 2002). When considered together, transplanted tobacco with clipped sagebrush neighbors had greater or equal fitness than plants with unclipped neighbors. However, the current

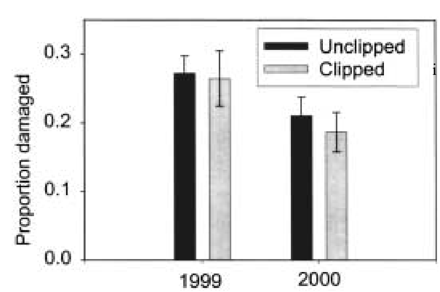

Fig. 6. Maximum proportion of leaves that were damaged by herbivores for tobacco plants with unclipped or clipped tobacco neighbors in 1999 and 2000 (mean ± + 1 se).

study demonstrated that the overall effect of growing near a sagebrush neighbor was negative for tobacco plants. Tobacco that were closer to sagebrush produced fewer filled capsules than those farther from sagebrush (Fig. 4). This result was unaffected by whether the sagebrush had been clipped or not (Table 2B). Larger sagebrush plants depressed seed production in neighboring tobacco more than smaller sagebrush (Table 2B). The negative competitive effects of growing near a sagebrush exceeded any benefits that tobacco might receive in terms of directly reduced herbivory (Table 1A) or eavesdropping (Table 1B). This comparison helps to put eavesdropping in perspective. Even in a situation where eavesdropping was strong and repeatable, the positive effects to tobacco of eavesdropping were less than the negative effects of competition with sagebrush.

Eavesdropping, information and induced resistance

Clipping neighboring tobacco, rather than sagebrush, did not affect damage to tobacco caused by herbivores (Fig. 6) nor levels of PPO activity (Fig. 5). These and previous results indicate that clipped sagebrush, but not clipped tobacco, releases an airborne cue that tobacco responds to.

Theory predicts that plants will respond to information released by damaged neighbors only if the information is reliable and allows them to respond appropriately to increase fitness (Levins 1968, Lloyd 1984, Lively 1986, 1999, Adler and Karban 1994, Getty 1996, Jaremo et al. 1999, Karban et al. 1999). There is evidence that induced resistance in this system can increase plant fitness in environments with an intermediate or high risk of herbivory (Baldwin 1998). It seemed reasonable to assume that a tobacco plant's risk of herbivory is more closely correlated with damage to neighboring tobacco plants than to neighboring sagebrush plants since herbivores feeding on one tobacco plant are likely to find other conspecifics also attractive. This line of thinking led to the prediction that tobacco should be more responsive to clipping neighboring tobacco than to clipping neighboring sagebrush. However, the data did not support this prediction.

Several additional details of the natural history seem relevant to this conundrum. First, sagebrush and tobacco share grasshoppers as important herbivores. Grasshoppers feed on sagebrush early in the season while tobacco is either a seed or a small seedling. Once tobacco and other annuals become available, grasshoppers feed little on sagebrush (personal observation). Presumably tobacco responds early in the season and early in its development to airborne cues released by sagebrush. When neighboring sagebrush experiences damage early in the season, tobacco in the vicinity may be more likely to be damaged later. The difference in the timing of damage may make sagebrush a particularly good source of information about risk of herbivory for neighboring tobacco. In summary, a tobacco plant induces resistance when herbivores damage its own tissues but not when herbivores damage neighboring tobacco. It also increases resistance when herbivores damage neighboring sagebrush which may presage a high risk of future herbivory to tobacco.

Second, phylogenetic constraints or selection involving other, unknown factors may have predisposed sagebrush to be much easier to eavesdrop on than tobacco. Jasmonates are highly conserved as signals mediating induced responses in tobacco and most other plants examined to date (Staswick 1992, Reinbothe et al. 1994, Baldwin 1996, Baldwin et al. 1997, Karban and Baldwin 1997). For reasons that are unknown, sagebrush is unusual in producing very high concentrations of methyl jasmonates relative to other plants (Ueda and Kato 1980, Farmer and Ryan 1990). In addition, emissions of methyl jasmonate increase locally and in sufficient quantities when sagebrush foliage is clipped for methyl jasmonate to function as a signal (Karban et al. 2000, Preston et al. 2001). Tobacco has the machinery to respond to jasmonates. Initially, selection may have favored plants that use methyl jasmonate signaling to regulate their own internal defenses (and other traits as well). Since sagebrush emits relatively large quantities of methyl jasmonate following leaf clipping, tobacco may be pre-adapted to respond to this cue. The fact that tobacco increases its resistance in response to cues from damaged sagebrush, may simply represent a side effect of using a jasmonate signaling system. Alternately, this response may be the result of selection for tobacco to eavesdrop on signals involuntarily released by sagebrush.

Either explanation suggests that many other plants that use jasmonate signaling and grow in association with sagebrush might induce resistance when a neighboring sagebrush is damaged. By determining whether these induced responses increase the expected fitness of the plants that respond, we are likely to gain insight into the evolutionary forces that have produced eavesdropping.

In conclusion, eavesdropping between plants is a real phenomenon in nature. In replicated experiments over five seasons involving randomly assigned clipping treatments, we found that tobacco near clipped sagebrush neighbors became more resistant to herbivory than tobacco near unclipped neighbors (Karban et al. 2000, Karban 2001). These results were found when actual herbivores were used to do the clipping and for tobacco and sagebrush plants that were naturally rooted. Eavesdropping may increase the fitness of tobacco relative to tobacco near sagebrush that do not eavesdrop (Karban and Maron 2002). However, the overall effects of growing near sagebrush were negative because the costs of competition were stronger than the benefits of eavesdropping.

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