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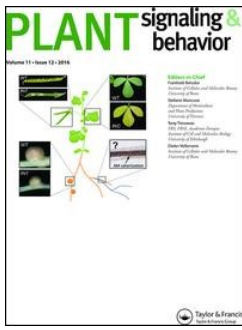
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RESEARCH PAPER



Tradeoff between resistance induced by volatile communication and over-topping vertical growth

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ABSTRACT

Plants commonly respond to reliable cues about herbivores by inducing greater defenses. Defenses are assumed to incur costs for plants when they are not needed. Sagebrush responds to volatile cues from experimentally clipped neighbors to induce resistance against chewing herbivores. Rather than experiencing costs, sagebrush seedlings that responded to dishonest cues were previously found to have increased survival and established plants that responded produced more inflorescences and new lateral branches. Here I report that young sagebrush plants that responded to cues added less vertical growth than controls that were not presented with volatile cues. This tradeoff between induced resistance and vertical, overtopping growth may allow agronomists to increase defense without sacrificing desirable traits. Overtopping growth is often beneficial for wild plants but often detrimental in agriculture.

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Introduction

Many plants sense the risk of being attacked by herbivores and adjust their defenses accordingly.¹ Plants perceive a variety of cues that predict future herbivory including insect footsteps that rupture glandular trichomes on plant surfaces,² chemicals associated with insect eggs that are glued onto plants,³ and chemicals associated with insect mouths and feeding.⁴

Perception of reliable cues allows plants to induce defenses to potential herbivores before they are actually attacked.⁵ Both common sense and theory argue that responding to cues will only be effective if those cues provide reliable information.⁶⁻⁸ Plastic inducible defenses allow plants to adjust their traits to protect against specific herbivores and pathogens and to save costs associated with defenses when those threats are unlikely.

Many plants that are attacked by herbivores have been found to emit volatile cues that neighbors perceive and respond to, becoming more resistant as a result.⁹ When sagebrush (*Artemisia tridentata*) was experimentally clipped with scissors to mimic herbivore attack, it emitted volatile cues; neighboring sagebrush plants in the field experienced reduced herbivory relative to individuals that did not receive volatile cues.¹⁰ In these cases, the experimental clipping was a dishonest signal, indicating much higher levels of herbivore pressure than was actually present. Sagebrush individuals in the field that responded to these dishonest volatile cues experienced enhanced performance; seedlings were approximately 10 x more likely to survive, and established young plants produced approximately twice as many new branches and 20% more inflorescences compared with controls that were not exposed to the volatile cues.¹¹ New branches on these young sagebrush plants were mostly lateral shoots; observations suggested that these lateral shoots may have been “bushier” and less elongated, although

these traits were not measured. Established sagebrush plants grow by increasing in area rather than height. Adult sagebrush individuals that were exposed to volatile cues from damaged neighbors tended to grow less than controls although these results were not statistically significant.¹² Wild tobacco plants (*Nicotiana attenuata*) exposed to dishonest volatile cues of experimentally clipped sagebrush neighbors produced more flowers and seed-bearing capsules than controls near unclipped sagebrush neighbors.¹³ Lima bean shoots (*Phaseolus lunatus*) that were exposed to dishonest volatile cues produced more leaves and inflorescences than untreated control shoots.¹⁴ In all of these cases, the cues indicated an exaggerated risk of attack because they were imposed by experimenters when actual risk was lower.

If plant defenses are costly, we would expect individuals that increase defenses in response to a dishonest cue should experience a reduction in reproductive success. These observed increases in inflorescences, flowers, and seed capsules - putative correlates of fitness - demand an explanation. One possible solution to this conundrum is that plants that elevate their defenses in response to cues of herbivory experience a reduction in some other expensive feature. The original growth-differentiation model posited a zero-sum game in which resources invested in defense were removed from the pool available for growth and reproduction¹⁵ (Fig. 1A). Many studies that involve natural variation in defense, experimental elicitors, artificial selection, and genetic manipulations have examined potential costs of defense. The majority of these studies found evidence for costs of defense although these costs were often ecological or opportunity costs rather than costs in terms of diverted allocation of resources.¹⁶⁻¹⁷

This study evaluated whether sagebrush seedlings that were exposed to volatile cues from experimentally clipped neighbors

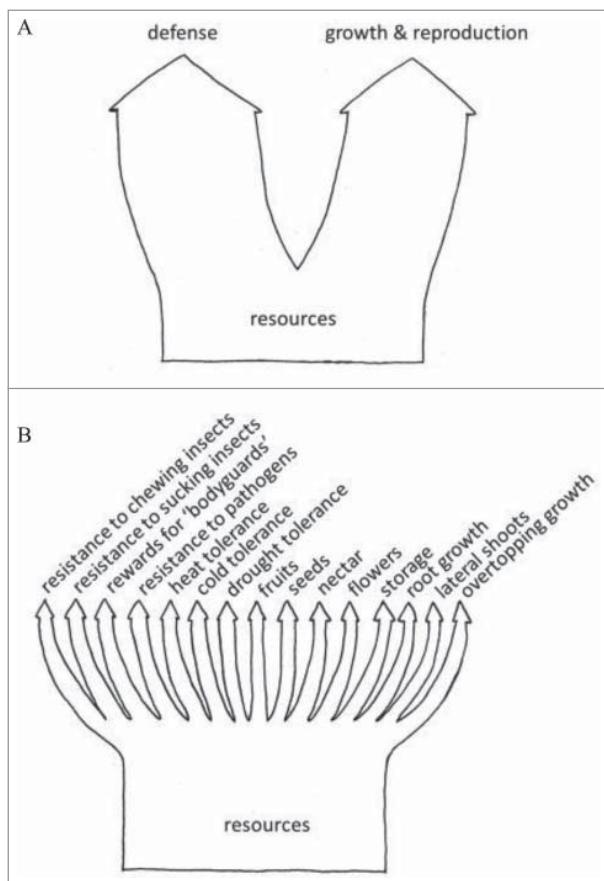


Figure 1. Models of allocation tradeoffs for plants. (A) In the classical model, a finite set of resources is available for plants to allocate either to defense or to growth and reproduction. Any resources allocated to one of these functions is unavailable to the other. (B) In a more realistic model, plants allocate resources to many different functions. Reducing allocations to any one function is not expected to result in an increase in allocations to any other specific function.

grew differently than control seedlings exposed to cues of unclipped neighbors. By examining seedlings which had not yet produced lateral branches, vertical growth could be measured unambiguously, something that would not be possible with more mature plants that often grow by adding branches to their outer edges, rather than adding vertical growth. Specifically, I asked if costs of defense would be visible as a reduction in vertical growth and as a reduction in the number of lateral branches that were produced by plants that were exposed to volatile cues of herbivory.

Methods

Sagebrush plants (*Artemisia tridentata* subsp. *vaseyana*) were started indoors in pots (10 cm x 10 cm x 25 cm) from wild-collected seeds. Plants were grown in potting soil (E.B. Stone organic potting soil, Suisun, California, USA) and were provided with light (11:13 light: dark) and watered as needed. Seedlings were thinned so that each pot contained one young focal plant. Because the timing of germination was variable, pairs of young focal plants were matched for size at the start of the experiment; both individuals of each pair were of equal height (range 2–8 cm for all pairs) and number of leaves. Initial plant height affected height at the end of the experiment

although initial plant height was equal and not biased with respect to the treatments. No plants used in the experiment had side branches.

One young focal plant from each pair was assigned to receive volatile cues from experimentally clipped neighbors. This young plant was surrounded on 2 sides by larger plants (18–26 cm tall) and the distal end of leaves of the branch of the larger neighbors closest to focal plant were clipped with scissors. Focal plants that were assigned to receive volatile cues remained next to clipped neighbors for 24 hrs. The other young focal plant from each pair served as a control that was surrounded for 24 hrs by larger plants that were not clipped. All focal plants used in these experiments were within 10 cm of their clipped or unclipped surrounding neighbors. Following the clipping treatment, all focal plants were kept > 1 m from clipped plants for at least one week to prevent contamination of controls with volatiles from clipped plants. Previous experiments established that sagebrush emits cues for up the 3 d that neighbors respond to.¹⁸ This artificial clipping treatment has been found consistently to provide volatile cues that induce resistance in undamaged receiver plants that is similar to that caused by herbivory under field and artificial conditions.^{10,19,20} Aside from the clipping exposure, focal plants in the 2 treatments were treated identically. There were 48 focal plants included in this study, 24 matched pairs.

I measured growth in height and number of side branches for each focal plant 14 d after treatments were applied. At this time, plants were rapidly growing and had not exhausted the soil resources in their pots. I calculated growth rate for each focal plant as (height at day 14 post-treatment – height at day 0 post-treatment) / (height at day 0). I compared the growth rate and number of side branches of focal plants exposed to cues of damage versus control plants using paired t-tests (JMP Pro 12.1).

Results

Young focal plants that were exposed to volatile cues emitted by experimentally clipped neighbors grew less in height than controls that had not been exposed to these cues. This effect was revealed in 2 comparisons. The mean height increase of control plants was 35% greater than matched plants that had been exposed to damage-induced volatile cues (Fig. 2A; paired t-test, $t = 3.31$, $df = 23$, $P = 0.003$). For 18 of 24 pairs of matched plants, the control individual grew more than the individual exposed to volatile cues from a clipped neighbor (Fig. 2B).

Young focal plants that were exposed to volatile cues emitted by experimentally clipped neighbors did not produce significantly more branches than controls that had not been exposed to these cues (paired t-test, $t = 0.98$, $df = 23$, $P = 0.34$). For 9 of 24 pairs controls produced more branches than matched plants exposed to volatile cues of damage; for 10 of 24 pairs controls and exposed plants produced the same number of branches; and for 5 of 24 pairs controls produced fewer branches (Fig. 3).

Discussion

Young sagebrush plants that have been shown to induce resistance to herbivory when they are exposed to volatile cues from neighboring sagebrush plants that have been chewed by insects

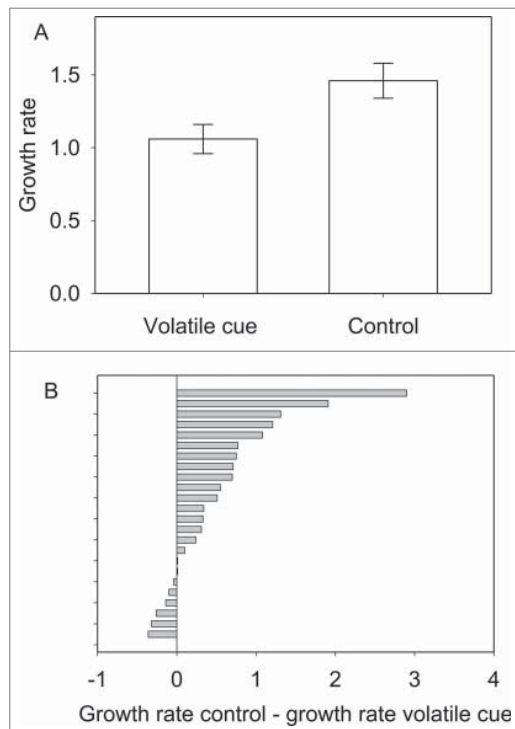


Figure 2. (A) Mean vertical growth in cm (± 1 se) of sagebrush plants that were exposed to volatile cues from experimentally clipped neighbors or cues from unclipped control neighbors. (B) The difference in vertical growth rate for matched pairs of young plants that were exposed to volatile cues from experimentally clipped neighbors vs. cues from unclipped control neighbors. Each horizontal bar represents one pair of sagebrush plants. The value along the x-axis is growth rate for each control plant minus growth rate for the plant exposed to cues of damage. Values to the right of the vertical line indicate pairs for which the control plant grew more than the exposed plant.

or, as an experimental proxy, clipped with scissors.^{10,19,20} As noted above, this experimental protocol caused plant responses that we could not distinguish from actual herbivory. However, responding to these volatile cues was costly, being associated with a reduction in vertical growth (Fig. 2).

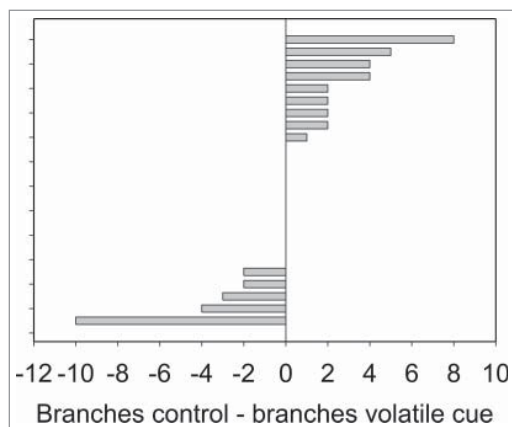


Figure 3. The difference in the number of lateral branches produced for matched pairs of young plants that were exposed to volatile cues from experimentally clipped neighbors vs. cues from unclipped control neighbors. Each horizontal bar represents one pair of sagebrush plants. The value along the x-axis is the number of lateral branches for each control plant minus the number of lateral branches for the plant exposed to cues of damage. Values to the right of the vertical line indicate pairs for which the control plant added more lateral branches than the exposed plant.

This cost of defense is consistent with current models of tradeoffs involving defense and the many other roles that plants must fulfill to survive, reproduce, and ultimately to be represented in subsequent generations.^{17,21} The early zero-sum model that posited a tradeoff between investments in defense vs. growth and reproduction (Fig. 1A) was overly simplistic; empiricists who expected that experimental treatments which elevated some specific defensive trait would necessarily reduce specific traits associated with growth or reproduction often got negative results (reviewed by 16, 17). Once the models acknowledge that plants must invest in many different functions to be successful, then manipulating any single investment is not expected to affect any other single investment (Fig. 1B).

This study examined the consequences for sagebrush plants of responding to volatile cues that induced resistance. Previous observations suggested that sagebrush may reduce growth after receiving cues from damaged neighbors.¹² Sagebrush has been a model for the study of communication although many other plant species, including several crops, have recently been found to increase levels of resistance when exposed to volatile cues associated with herbivore damage.⁹ For example, volatile cues increased resistance against aphids for some cultivars of barley.²² These induced responses were associated with morphological changes and a reallocation that favored roots at the expense of leaves and stems.²³ In general, stem length is more plastic than many other traits and morphological traits tend to be more plastic than allocation patterns.²⁴

Increased investment in defense against herbivores is not necessarily associated with a reduction in traits of value in agricultural crop systems. In most natural (non-agricultural) situations, plants prioritize vertical growth that allows them to overtop their neighbors and compete successfully for light.^{25,26} Overtopping growth is favored when light is a limiting resource and taller individuals are able to capture more light while shading their neighbors. As a result many plants in nature invest heavily in growing taller. Overtopping growth is of little value in agriculture where humans plant monocultures with the goal of maximizing yield of the entire crop field. Overtopping growth maximizes individual plant fitness at the expense of community-level characteristics such as yield; an individual that grows taller than its neighbors will be more successful even if investment in vertical growth reduces other traits that humans view as desirable such as the collective yield of the field.²⁶⁻²⁸ Wild relatives of current crops were often vigorous growers and subsequent domestication has selected more even more overtopping growth in some cases.²⁹⁻³¹ Crop breeding during the green revolution favored reduced overtopping growth but agronomists estimate that there are still substantial increases to be had by breeding for beneficial agronomic traits at the expense of overtopping growth.^{26,32}

One such advantage may be greater investment in defense if it comes at the expense of vertical growth, as was the case for sagebrush seedlings. This observation is consistent with recent physiologic findings as well. Many studies have found that natural selection will favor plants that acquire resources at the expense of defense (e.g., 33-36). However, when they receive cues that initiate defensive responses involving the jasmonic acid pathway, genes related to growth are actively suppressed and the overall pattern of metabolism appears to

be reprogrammed in some cases.³⁷⁻³⁹ In other words, plants are sufficiently plastic so that we can encourage them to invest in traits that are desirable for agriculture instead of traits that were favored in competitive environments but no longer match our needs for crop species. This study suggests that, for sagebrush at least, receiving cues that induce defenses against herbivores restricts vertical growth, a result that could be tested in agricultural species as well.

In summary, sagebrush plants that were exposed in previous studies to dishonest cues of damage to neighbors increased their resistance to herbivory and had greater seedling survival and production of new branches and inflorescences. This result was puzzling since it suggested no costs of defense, which should create selection for greater levels of defenses, expressed all the time. Instead, costs of defense caused by these dishonest cues were expressed as reduced overtopping vertical growth for young sagebrush plants. Volatile communication has now been observed in many plant species, including crops, where overtopping growth is an undesirable trait. If this tradeoff is general, it may allow development of crops that are both better defended and have other desirable agronomic traits.

Disclosure of potential conflicts of interest

No potential conflicts of interest were disclosed.

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References

- Karban R. Plant sensing and communication. Chicago, USA: University of Chicago Press; 2015; <https://doi.org/10.7208/chicago/9780226264844.001.0001>
- Peiffer M, Tooker JF, Luthe DS, Felton GW. Plants on early alert: Glandular trichomes as sensors for insect herbivores. *New Phytol* 2009; 184:644-56; PMID:19703113; <https://doi.org/10.1111/j.1469-8137.2009.03002.x>
- Hilker M, Meiners T. How do plant “notice” attack by herbivorous arthropods? *Biol Rev* 2010; 85:267-80; PMID:19961475; <https://doi.org/10.1111/j.1469-185X.2009.00100.x>
- Felton GW, Tumlinson JH. Plant-insect dialogs: Complex interactions at the plant-insect interface. *Curr Opin Plant Biol* 2008; 11:457-63; PMID:18657469; <https://doi.org/10.1016/j.pbi.2008.07.001>
- Kim J, Felton GW. Priming of antiherbivore defensive responses in plants. *Insect Sci* 2013; 20:273-85; PMID:23955880; <https://doi.org/10.1111/j.1744-7917.2012.01584.x>
- Zahavi A, Zahavi A. The handicap principle: A missing piece of Darwin’s puzzle. New York: Oxford University Press; 1997.
- Karban R, Agrawal AA, Thaler JS, Adler LS. Induced plant responses and information content about risk of herbivory. *Trends Ecol Evol* 1999; 14:443-7; PMID:10511721; [https://doi.org/10.1016/S0169-5347\(99\)01678-X](https://doi.org/10.1016/S0169-5347(99)01678-X)
- Kessler A, Heil M. The multiple faces of indirect defences and their agents of natural selection. *Funct Ecol* 2011; 25:348-57; <https://doi.org/10.1111/j.1365-2435.2010.01818.x>
- Karban R, Yang LH, Edwards KF. Volatile communication between plants that affects herbivory: A meta-analysis. *Ecol Lett* 2014; 17:44-52; PMID:24165497; <https://doi.org/10.1111/ele.12205>
- Karban R, Shiojiri K, Huntzinger M, McCall AC. Damage-induced resistance in sagebrush: Volatiles are key to intra- and interplant communication. *Ecology* 2006; 87:922-30; PMID:16676536; [https://doi.org/10.1890/0012-9658\(2006\)87\[922:DRISVA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[922:DRISVA]2.0.CO;2)
- Karban R, Ishizaki S, Shiojiri K. Long-term demographic consequences of eavesdropping for sagebrush. *J Ecol* 2012; 100:932-8; <https://doi.org/10.1111/j.1365-2745.2012.01974.x>
- Ishizaki S, Shiojiri K, Karban R, Ohara M. Seasonal variation of responses to herbivory and volatile communication in sagebrush (*Artemisia tridentata*) (Asteraceae). *J Plant Res* 2016; 129:659-66; PMID:27056097; <https://doi.org/10.1007/s10265-016-0818-z>
- Karban R, Maron J. The fitness consequences of interspecific eavesdropping between plants. *Ecology* 2002; 83:1209-13; [https://doi.org/10.1890/0012-9658\(2002\)083\[1209:TFCOIE\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[1209:TFCOIE]2.0.CO;2)
- Kost C, Heil M. Herbivore-induced plant volatiles induce an indirect defence in neighboring plants. *J Ecol* 2006; 94:619-28; <https://doi.org/10.1111/j.1365-2745.2006.01120.x>
- Hermes DA, Mattson WJ. The dilemma of plants: To grow or defend. *Q Rev Biol* 1992; 67:283-335; <https://doi.org/10.1086/417659>
- Strauss SY, Rudgers JA, Lau JA, Irwin RE. Direct and ecological costs of resistance to herbivory. *Trends Ecol Evol* 2002; 17:278-85; [https://doi.org/10.1016/S0169-5347\(02\)02483-7](https://doi.org/10.1016/S0169-5347(02)02483-7)
- Cipollini D, Walters D, Voelckel C. Costs of resistance in plants: From theory to evidence. *Annu Plant Rev. Insect-Plant Interact* 2014; 47:263-307; <https://doi.org/10.1192/10.1002/9781118829783.ch8>
- Shiojiri K, Karban R, Ishizaki S. Volatile communication among sagebrush branches affects herbivory: Timing of active cues. *Arthropod-Plant Interact* 2009; 3:99-104; <https://doi.org/10.1007/s11829-009-9060-0>
- Shiojiri K, Karban R. Seasonality of herbivory and communication between individuals of sagebrush. *Arthropod-Plant Interact* 2008; 2:87-92; <https://doi.org/10.1007/s11829-008-9037-4>
- Karban R, Shiojiri K, Ishizaki S. An air transfer experiment confirms the role of volatile cues in communication between plants. *Am Nat* 2010; 176:381-4; PMID:20635861; <https://doi.org/10.1086/655222>
- Lind EM, Borer E, Seabloom E, Adler P, Bakker JD, Blumenthal DM, Crawley M, Davies K, Firn J, Gruner DS, et al. Life-history constraints in grassland plant species: A growth-defence trade-off is the norm. *Ecol Lett* 2013; 16:513-21; PMID:23347060; <https://doi.org/10.1111/ele.12078>
- Ninkovic V, Olsson U, Pettersson J. Mixed barley cultivars affects aphid host plant acceptance in field experiments. *Entomol Exp Appl* 2002; 102:177-82; <https://doi.org/10.1046/j.1570-7458.2002.00937.x>
- Ninkovic V. Volatile communication between barley plants affects biomass allocation. *J Exp Bot* 2003; 54:1931-9; PMID:12815028; <https://doi.org/10.1093/jxb/erg192>
- Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L. Biomass allocation to leaves, stems and roots: Meta-analyses of interspecific variation and environmental control. *New Phytol* 2012; 193:30-50; PMID:22085245; <https://doi.org/10.1111/j.1469-8137.2011.03952.x>
- Falster DA, Westoby M. Plant height and evolutionary games. *Trends Ecol Evol* 2003; 18:337-43; [https://doi.org/10.1016/S0169-5347\(03\)00061-2](https://doi.org/10.1016/S0169-5347(03)00061-2)
- Denison RF. Darwinian agriculture. Princeton, NJ: Princeton University Press; 2012.
- Donald CM. Breeding of crop ideotypes. *Euphytica* 1968; 17:385-403; <https://doi.org/10.1007/BF00056241>
- Anten NPR, Vermeulen PJ. Tragedies and crops: Understanding natural selection to improve cropping systems. *Trends Ecol Evol* 2016; 31:429-39; PMID:27012675; <https://doi.org/10.1016/j.tree.2016.02.010>
- Cunniff J, Wilkinson S, Charles M, Jones G, Rees M, Osborne CP. Functional traits differ between cereal crop progenitors and other wild grasses gathered in the Neolithic fertile crescent. *PLoS One* 2014; 9:e87586; PMID:24489941; <https://doi.org/10.1371/journal.pone.0087586>
- Milla R, Morente-Lopez J, Alonso-Rodrigo JM, Martin-Robles N, Chapin FS. Shifts and disruptions in resource-use trait syndromes during the evolution of herbaceous crops. *Proc Roy Soc B - Biol Sci* 2014; 281:20141429; PMID:25185998; <https://doi.org/10.1098/rspb.2014.1429>

31. Milla R, Osborne CP, Turcotte MM, Violle C. Plant domestication through an ecological lens. *Trends Ecol Evol* 2015; 30:463-9; PMID:26138385; <https://doi.org/10.1016/j.tree.2015.06.006>
32. Denison RF. Past evolutionary tradeoffs represent opportunities for crop genetic improvement and increased human lifespan. *Evol Appl* 2011; 4:216-24; PMID:25567969; <https://doi.org/10.1111/j.1752-4571.2010.00158.x>
33. Kurashige NS, Agrawal AA. Phenotypic plasticity to light competition and herbivory in *Chenopodium album* (Chenopodiaceae). *Am J Bot* 2005; 92:21-26; PMID:21652380; <https://doi.org/10.3732/ajb.92.1.21>
34. Izaguirre MM, Mazza CA, Biondini M, Baldwin IT, Ballare CL. Remote sensing of future competitors: Impacts on plant defenses. *Proc Natl Acad Sci U S A* 2006; 103:7170-4; PMID:16632610; <https://doi.org/10.1073/pnas.0509805103>
35. Moreno JE, Tao Y, Chory J, Ballare CL. Ecological modulation of plant defense via phytochrome control of jasmonate sensitivity. *Proc Natl Acad Sci U S A* 2009; 106:4935-40; PMID:19251652; <https://doi.org/10.1073/pnas.09007011106>
36. de Wit M, Kegge W, Evers JB, Vergeer-van Eijk M, Gankema P, Voeseek LACJ, Pierik . Plant neighbor detection through touching leaf tips precedes phytochrome signals. *Proc Natl Acad Sci U S A* 2013; 109:14705-10; <https://doi.org/10.1073/pnas.1205437109>
37. Yan Y, Stolz S, Chetelat A, Reymond P, Pagni M, Dubugnon L, Farmer EE. A downstream mediator in the growth repression limb of the jasmonate pathway. *Plant Cell* 2007; 19:2470-83; PMID:17675405; <https://doi.org/10.1105/tpc.107.050708>
38. Bilgin DD, Zavala JA, Zhu J, Clough SJ, Ort DR, DeLucia EH. Biotic stress globally downregulates photosynthesis genes. *Plant Cell Environ* 2010; 33:1597-613; PMID:20444224; <https://doi.org/10.1111/j.1365-3040.2010.02167.x>
39. Yang DH, Hettenhausen C, Baldwin IT, Wu J. Silencing *Nicotiana attenuata* calcium-dependent protein kinases, CDPK4 and CDPK5, strongly up-regulates wound- and herbivory-induced jasmonic acid accumulations. *Plant Physiol* 2012; 159:1591-607; PMID:22715110; <https://doi.org/10.1104/pp.112.199018>