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1 Text S1: Shade avoidance and light perception in plants

1. Shade avoidance 3 The shade avoidance syndrome (SAS) is a visually apparent, easy-to-measure response to neighbors which has measurable effects on plant productivity and fitness correlates (Schmitt et al. 1995; Schmitt 1997) and thus provides an excellent read-out for elucidating light, ethylene, and other signaling systems in plants. This has facilitated the discovery of specific receptor proteins, which in turn has permitted the generation of loss- and gain-of-function mutants which have advanced our understanding of neighbor responses. ETRs and EINs perceive ethylene (Hua & Meyerowitz 1998; Gallie 2015), while several receptor proteins perceive light: the chromophore-containing sensors phytochromes (PHY) which absorb red and far-red light, 10 cryptochromes (CRY) and phototropins (PHOT) which absorb blue light and UV-A, LOV-11 12 domain proteins which absorb blue light; and the UV-B receptor UVR8, which is unique in that it relies on specific tryptophan residues rather than a chromophore for light absorption (Fraser et 13 al. 2016; Jenkins 2017; Mawphlang & Kharshiing 2017) (Fig. S1). 15 Both specific and general cues can trigger components of the SAS, and the perception of these cues can be divided into early and late detection (Kegge & Pierik 2009; Pierik & de Wit 2014). At the most general end of the spectrum are physical contact between rosette leaf tips, 17 changes in R:FR and other binary light ratios due to green vegetation, and increasing ethylene 18 19 concentration in very dense canopies. Amongst these, the light ratio cues are likely most robust under field conditions of fluctuating light and wind. More specific cues include, for example, 20 21 plant volatiles other than ethylene, which can be genera- or species-specific, and are usually 22 situationally specific in their composition (Schuman et al. 2016). Together, perhaps more

importantly, relative intensity of multiple light wavelengths provides specific information about

- the nature of shade (direction, source, extent, etc.) and may allow a graduated response (Pierik &
- 25 de Wit 2014). Cues which are detected earlier such as touch and volatiles can allow plants to
- 26 predict shade and enable SAS components in order to truly avoid shading, while encroaching
- 27 changes in light quality provide information on severity at a later stage (Pierik & de Wit 2014).
- More recent work has focused on SAS-related signaling in response to specific ratios of light
- 29 wavelengths and other cues, and with greater spatiotemporal resolution, in order to elucidate
- 30 general principles of plant neighbor perception and adaptation (Pierik & de Wit 2014; Ballaré &
- 31 Pierik 2017). In addition to changes aboveground, root exudates, interactions via fungal
- 32 networks, and other belowground phenomena also influence the growth environment for other
- 33 plants and likely provide information about neighbor identity and traits (Pierik et al. 2012;
- 34 Babikova et al. 2013). Some work has studied variation in the SAS as an indicator of plant "kin
- 35 recognition", but current approaches do not separate kin recognition from phenotype matching
- 36 (e.g., (Crepy & Casal 2015; Till-Bottraud & Villemereuil 2015)); and kin recognition as a
- 37 concept may mislead research and confuse evolutionary inferences (Allen et al. 2013).
- 38 2. Photoreceptors and light signaling
- Plants show pronounced growth responses to specific light wavelengths and their ratios.
- 40 Charles and Francis Darwin were the first to document phototropism in plants, in response to
- 41 blue light (Darwin & Darwin 1880). Still unidentified nearly 100 years later, the mysterious plant
- 42 blue (UV) light receptors, thought to be flavin photoreceptors due to their putative action spectra,
- 43 were dubbed "cryptochromes" (also because of their importance in cryptogamic plants) (Gressel
- 44 1979; Yang et al. 2017). It was the advent of molecular genetics in the model plant Arabidopsis
- 45 thaliana (Arabidopsis) that solved the mystery. Screening mutants with constitutively elongated
- 46 hypocotyls (**Fig. S1**) revealed one mutant producing a long hypocotyl only under blue light, and

the mutation was localized to a gene first named HY4, and then CRY1: the first cryptochrome (Ahmad & Cashmore 1993; Yang et al. 2017). In wild-type seedlings, hypocotyls shorten in 48 response to light perception as this indicates penetration of soil. Interestingly, cryptochromes 49 have since been shown to provide blue light input to the circadian clock, not only in plants, but 50 51 also in cyanobacteria, as well as animals and fungi (reviewed in (Gehring 2014). 52 Around the time that cryptochromes were maligned as a mystery, however, progress was being made on identifying a different conserved family of photoreceptors: the phytochromes (PHY). Kasperbauer showed that the ratio between red and far-red light (R:FR) was lower 54 beneath Nicotiana tabacum (cultivated tobacco) canopies and that subjecting N. tabacum plants to FR promoted stem elongation (Kasperbauer 1971). The perception of shade, natural shade 56 conditions, and resulting growth responses were then described in detail by Smith and colleagues 57 58 (Holmes & Smith 1975; Smith 2000) and attributed to phytochrome, a protein described from plants in the 1950's as R:FR-reversible (Hendricks & Borthwick 1959; Ballaré & Pierik 2017). 59 60 Phytochromes have also been identified in some bacteria, fungi, heterokont and glycauphyte algae (Duanmu et al. 2014). Over the following years, Smith and colleagues demonstrated that 61 the R:FR ratio was reliable indicator of canopy cover in field studies; that between 1.2 (full 62 63 sunlight) and 0.1 (deep shade), changes in R:FR correlate linearly to estimated phytochrome photoequilibrium in seedling extracts; and that the rate of internode elongation is inverse to the 64 calculated P_{fr}/P_{total} ratio from light sources (Smith 1982; Ballaré & Pierik 2017). Armed with 65 66 these precise phenotyping and physiological tools, biologists in the 1980's and 1990's began to conduct field experiments to determine the relationship among phytochrome, the SAS, and plant 67 68 performance in nature (reviewed in (Ballaré & Pierik 2017)), but these studies lacked tools for precise genetic manipulation of plants' capacity for the SAS. In the 1990's, in glasshouse

- 70 experiments, Schmitt and colleagues demonstrated that the density-dependent plasticity of the
- 71 SAS in competing plants improved the performance of wild-type (WT) N. tabacum and Brassica
- 72 rapa (turnip mustard) in comparison to transgenic N. tabacum and mutant B. rapa lines "stuck"
- 73 with phytochrome function turned either on or off (Schmitt *et al.* 1995).
- 74 The discovery of each new photoreceptor has been facilitated by a combination of
- 75 straightforward phenotypic markers, and mutant screening approaches. Molecular genetic tools,
- 76 combined with knowledge of photoreceptor genes, have permitted the generation of selectively
- 77 blind plants which reveal possible photoreceptor functions, and, simultaneously, indicate
- 78 adaptive significance of light sensing in plants. These discoveries have broader evolutionary
- 79 implications, as most plant photoreceptors have homologues in animals, fungi, and
- 80 cyanobacteria; which function in phototaxis, vision, and the circadian clock (Gehring 2014).
- 81 Because the majority of these molecularly "enabled" experiments have been conducted under
- 82 laboratory or glasshouse conditions with cultivated plants, the functional-evolutionary loop has
- 83 not been closed and our mechanistic knowledge in this field currently far exceeds our functional
- 84 understanding.
- As an example, it has more recently been shown that negative regulation of photoreceptor
- 86 responses is critical to their function. In 2005, Sessa and colleagues identified a bHLH
- 87 transcription factor already known to be a component of both CRY and PHY signaling in
- 88 A. thaliana, HFR1, which is strongly induced by a low R/FR ratio and remains up-regulated
- 89 during prolonged exposure. The protein, which they renamed HFR1/SICS1 (Slender In Canopy
- 90 Shade), down-regulates the expression of several other transcription factors involved in the SAS,
- 91 preventing a runaway elongation response under prolonged shade (Sessa et al. 2005). More
- 92 recently, Wang and colleagues showed that CRY2 in A. thaliana undergoes light-mediated

dimerization in order to be active, and that the protein BIC1 inhibits this dimerization process, 94 maintaining a pool of monomers even under blue light and thus maintaining blue light sensitivity (Fankhauser & Ulm 2016; Wang et al. 2016). Such a regulatory mechanism, relying on an 95 additional protein regulator to inhibit dimerization, may be shared with LOV-domain 96 photoreceptors and UVR8, which also require homodimerization for activity (Fankhauser & Ulm 97 98 2016). There is also evidence from attenuation of BIC expression in cry mutants that CRY 99 signaling may up-regulate the BIC negative regulators (Fankhauser & Ulm 2016) as in the case of PHY signaling up-regulating HFR1/SICS1 (Sessa et al. 2005). The apparent wide 100 101 conservation across photoreceptors of negative regulation and the maintenance of an active pool even under prolonged stability of light conditions indicate that these features are important to the 103 function of light perception. Under natural conditions, it is likely critical for plants to maintain 104 sensitivity to all "plant-visible" wavelengths of light. Although plant photoreceptors have been identified for UV-A, UV-B, PAR wavelengths, green, and far-red (Fraser et al. 2016), it is not 105 understood how plants integrate the full spectrum of light, or how this integrated information 106 107 informs an adaptive SAS and other light-mediated responses, including regulation of circadian phenomena (Fig. S1). 108

110 Figure S1

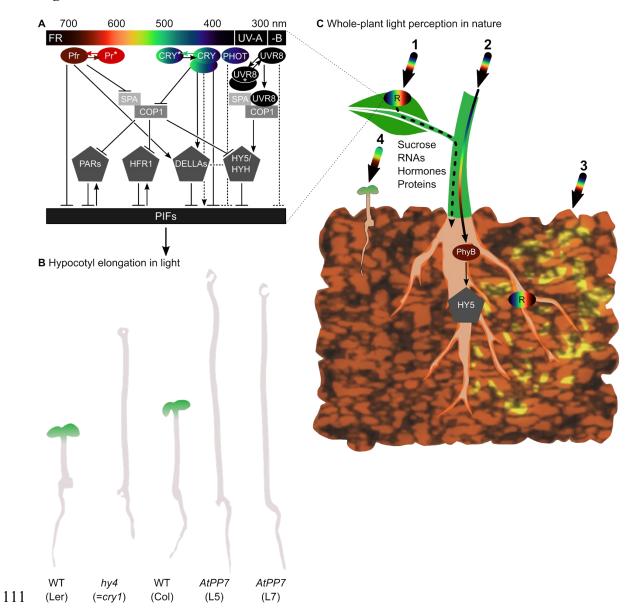


Figure S1. Light signaling: An example where mechanistic understanding surpasses ecological understanding. (A) Photoreceptors which are sensitive to all colors of light in the visible spectrum as well as UV-B, UV-A, and far-red, have now been identified in plants, and these light receptors interact in complex signaling cascades channeled through so-called phytochrome interacting factors (PIF) and other protein intermediaries, as indicated here in a simplified

scheme (based on (Fraser et al. 2016)). *Asterisks indicate inactive forms, and solid lines represent mechanisms shown to regulate at least one of the key PIFs controlling shade avoidance 118 and seedling hypocotyl elongation (PIF4, PIF5 or PIF7) while dotted lines represent 119 hypothesized regulatory mechanisms. See (Fraser et al. 2016) for a detailed discussion of 120 121 photoreceptor interactions. Monomerization and dimerization provide an additional regulatory 122 layer: in A. thaliana, the cryptochrome CRY2 is active as a homodimer; in contrast, UVR8 123 homodimers are inactive, and in both cases regulatory proteins (not shown) facilitate either 124 monomer- or dimerization (Fankhauser & Ulm 2016). (B) Laboratory screens for mutant 125 seedlings with elongated hypocotyls under specific light conditions are traditionally used to 126 identify photoreceptor genes and their interaction partners: image drawn from a study identifying 127 AtPP7, a protein interactor of CRY1 (the A. thaliana mutant is named hy4) (Eckardt 2003; Moller et al. 2003). Ler and Col are the wild-type (WT) accessions used to produce the hy4 mutant and two lines (L5 and L7) of the AtPP7 mutant, respectively. (C) Seedling screens can 129 130 identify mutants with extreme phenotypes which may not be viable in nature. Photoreceptors are 131 expressed with tissue-specific patterns, including in roots, and information from different light wavelengths is integrated to inform plastic and adaptive responses in a complex natural light 132 133 environment. Three paths of whole-plant light perception are illustrated. 1: Light is perceived by 134 photoreceptors (R) in shoots, resulting in changes to sugar signaling, RNA and hormone 135 production, and protein accumulation involved in root-shoot signaling and other responses; 2: 136 light piped through stems, likely by the vasculature, is perceived by root-expressed phytochrome B (PhyB); 3: light penetrating the soil is directly perceived by photoreceptors (R) expressed in 137 138 roots (based on (Lee et al. 2017)). Arrow 4 shows green- and far red-enriched light filtered 139 through a canopy towards a recently emerged seedling.

140 Table S1

- 141 A functional overview of (mostly non-hormonal) plant volatiles in plant-plant-arthropod interactions: 34 years of literature on 33
- 142 neighbor plant species and 35 emitter species (all 33 "neighbor" species plus Solanum lycopersicum and Rhododendron tomentosum)
- 143 from 14 families, presented chronologically. Key: ▲, increase; ▼, decrease; —, no change.

Effect on neighb	oring plants		Emitters			P (* 1	
Dependent variables	Plants	Treatment	Control	Plants	Setting	Functional inference	Reference
Caterpillar growth ▼	3- to 4-year- old <i>Alnus</i> rubra, <i>Salix</i> sitchensis	Experimental infestation with Malacosoma californicum pluviale, Hyphantria cunea	Paired uninfested plants	Same as neighbors, different plants	Field study: Natural stands/ Lab study: Cut leaves from wild plants. No root contact observed.	Increased direct resistance in damaged and nearby trees due to aerial factors	(Rhoades 1983)
Resistance-related metabolites ▲	1.5- to 4- month-old Populus x euroameric- ana and Acer saccharum	Experimental mechanical damage (tearing of leaves)	Leaves not damaged	Same as neighbors, different plants	Lab study: Plexiglass enclosure	Increase in resistance-related leaf metabolites due to volatile factors	(Baldwin & Schultz 1983)
Caterpillar growth	Alnus rubra, Rosa nutkana, Malus diversifolia	Naturally occurring herbivory by Malacosoma californicum pluviale	None: correl- ational	Same as neighbors, different plants	Field study: Natural stands/ Lab study: Cut leaves from wild plants	No correlation of resistance with proximity to naturally damaged neighbors	(Myers & Williams 1984)

Effect on neighbor	oring plants		Emitters			Functional	
variables	Plants	Treatment	Control	Plants	Setting	inference	Reference
Herbivorous mite oviposition ▼/ Predatory mite attraction ▲	Gossypium hirsutum seedlings	Experimental Tetranychus urticae infestation	Not infested	Same as neighbors, different plants	Lab study: Wind tunnel	Increased direct and indirect resistance due to volatile factors	(Bruin <i>et al.</i> 1992)
Aphid fecundity ▼	Nicotiana tabacum leaf discs	Experimental mechanical damage to cut leaves (crushing)/ Synthetic compound dilutions	Leaves not damaged/ Solvent	Solanum lycopersi- cum and Nicotiana tabacum leaf discs	Lab study: Closed glass Petri dishes	Increased direct resistance with exposure to GLV alcohols and aldehydes, and direct effect of aldehydes on aphids	(Hildebrand et al. 1993)
Leaf damage and oviposition by <i>Agelastica alni</i> beetles ▼	Alnus glutinosa	Experimental mechanical damage (crunching and tearing leaves)	Leaves not damaged	Same as neighbors, different plants	Field study: Natural stands/ Lab study: Cut leaves from wild plants	Increased direct resistance in damaged and nearby trees	(Dolch & Tscharntke 2000)
Damage by generalist herbivores ▼/ Polyphenol oxidase activity ▲	Nicotiana attenuata	Experimental mechanical damage (clipping branches)	Branches not clipped	Artemisia tridentata	Field study: Natural A. tridentata populations, transplanted N. attenuata, experimental air or soil barriers	Increased resistance due to aerial contact with emitter, hypothesized to be mediated by methyl jasmonate	(Karban <i>et al</i> . 2000)
Emission of herbivory-induced volatiles ▲/ Stored	Gossypium hirsutum	Diluted methyl jasmonate	Methanol (solvent)	None	Lab study: Exposure in ventilated	Exposure to methyl jasmonate induces release of	(Rodriguez- Saona <i>et al</i> . 2001)

Effect on neighb Dependent	oring plants		Emitters			Functional	
variables	Plants	Treatment	Control	Plants	Setting	inference	Reference
terpene volatiles					plexiglass containers	many herbivory- induced volatiles, but not stored compounds: tissue disruption required	
Leaf damage by specialist herbivores ▼/ Resistance-related metabolites and proteins ▲	Alnus glutinosa	Experimental mechanical damage/ Experimental infestation by Agelastica alni	Leaves not damaged	Same as neighbors, different plants	Field study: Natural stands/ Lab study: Potted plants	Increased direct resistance in damaged and nearby trees	(Tscharntke et al. 2001)
Leaf damage ▼/ Polyphenol oxidase activity ▲/ Filled seed capsules ▼	Nicotiana attenuata	Experimental mechanical damage (clipping branches)/ Experimental herbivory	Branches not clipped/ No infestation	N. atten- uata, A. tridentata	Field study: Natural A. tridentata populations, planted or co-occurring N. attenuata	N. attenuata plants with damaged A. tridentata neighbors have increased resistance but not increased fitness; clipping conspecific neighbors has no effect on resistance	(Karban <i>et al.</i> 2003)
Biomass allocated to roots vs. shoots	Hordeum vulgare cv. Kara	No treatment	No plant	H. vulgare cv. Alva or Kara	Lab study: Open-flow chambers with large rooting	Exposure to volatiles from the Alva cultivar increased root:shoot	(Ninkovic 2003)

Effect on neighbor Dependent	oring plants		Emitters			Functional	
variables	Plants	Treatment	Control	Plants	Setting	inference	Reference
					volume	biomass ratio, likely altering competitive ability	
Induced stress hormone (jasmonic acid, JA) and sesquiterpenes ▲	Zea mays seedlings	Experimental infestation with Spodoptera exigua larvae/GLV dilutions	No infestation/ Solvent	Same as neighbors, different plants	Lab study: Flow- through (longer exposure) or closed (<3 h exposure) glass chambers	GLV exposure primes induction of resistance- related hormones and volatiles	(Engelberth et al. 2004)
Leaf damage by generalist and specialist herbivores ▼/ —	Lomatium dissectum, Lupinus polyphyllus, Valeriana californicum, and Artemisia tridentata	Experimental mechanical damage (clipping branches)	Branches not clipped	A. tridentata	Field study: Natural populations	Exposure to damaged A. tridentata volatiles, which are abundant, induces resistance in conspecifics and a highly inducible tobacco (previous studies), but not in all plants.	(Karban <i>et al.</i> 2004)
Resistance-related gene transcripts, metabolites and proteins A /Specialist	Nicotiana attenuata	Clipped foliage placed around receiver/ Dilutions of pure	No clipped foliage/ Solvent	Artemisia tridentata	Field study: Natural populations/ Lab study: Exposure in	Exposure to volatiles from <i>A. tridentata</i> clippings, specifically (<i>E</i>)-2-	(Kessler et al. 2006)

Effect on neighb Dependent	oring plants		<u>Emitters</u>			Functional	
variables	Plants	Treatment	Control	Plants	Setting	inference	Reference
herbivore mortality ▲/ Herbivore damage ▼		compounds.			chimney- ventilated chambers	hexenal and methacrolein, primes resistance in <i>N. attenuata</i>	
Herbivory-induced gene transcripts ▼/ Induced hormones, metabolites, and proteins —	Nicotiana attenuata rosette-stage plants	Experimental mechanical damage (holes punched in leaves) with or without added <i>Manduca sexta</i> regurgitant (R)	Leaves not damaged	Same as neighbors, different plants	Glasshouse study: Exposure in flow-through boxes	Some transcriptional responses to wounded or R-treated neighbor leaf volatiles are suppressed by GLV and terpenoid components	(Paschold et al. 2006)
Extrafloral nectar (EFN) secretion with or without mechanical damage \(\Lambda \)	Phaseolus lunatus	Aerial exposure to synthetic volatile blend in lanolin paste on plastic strips	Lanolin	None	Field study: Aerial exposure of plants in natural populations	A synthetic blend representative of herbivore-induced volatiles primes EFN secretion	(Heil & Kost 2006)
Extrafloral nectar secretion ▲/ Leaf, inflorescence production ▲/ Predator population ▲/ Herbivore damage ▼	Phaseolus lunatus	48 h of damage by naturally occurring herbivores/ Synthetic blend or single compounds in lanolin paste	No damage/ Lanolin	Same as neighbors, different plants/ None	Field study: Aerial exposure of plants in natural populations to emitting tendrils or synthetic blend	Exposure to herbivore-induced volatiles, specifically (<i>Z</i>)-3-hexenyl acetate, increases EFN secretion and indirect defense in naturally occurring plants	(Kost & Heil 2006)

Effect on neighb Dependent	oring plants		Emitters			Functional	
variables	Plants	Treatment	Control	Plants	Setting	inference	Reference
Leaf number ▲/ Leaf tip number ▲/ Induced EFN secretion ▲/ Herbivore damage ▼	Phaseolus lunatus	Detatched tendrils or same plant: Herbivory by bagged beetles/ Mechanical damage (holes punched in leaf) plus JA	No infestation/ No damage	Phaseo- lus lunatus	Field study: Natural population/ Glasshouse study: Potted plants; bags used to constrain volatile diffusion	Herbivore- induced volatiles primes secretion of EFN, reduces herbivory and increases leaf production in nature	(Heil & Silva Bueno 2007)
JA production ▲/ Transcripts of JA biosynthetic genes ▲	Zea mays seedlings	Dilutions of pure compounds	Solvent	None	Lab study: Exposure of plants in closed plexiglass chambers	GLVs, particularly (<i>Z</i>)-3-hexenyl acetate, induce JA biosynthesis in <i>Z. mays</i>	(Engelberth et al. 2007)
JA ▲/ Linolenic acid ▲/ JA biosynthetic genes ▲/ Defense-related gene transcripts ▲	12- to 15- week-old Populus deltoides × nigra cuttings	Dilution of pure compound used	Solvent; non- orthosti- chous, similarly aged leaf on same plant	None	Lab study: Exposure of two single leaves on- plant in leaf plexiglass chambers	The GLV (Z)-3-hexenyl acetate primes the herbivore induction of JA biosynthesis and defense metabolites	(Frost <i>et al.</i> 2008)
Seedling germination ▼	Seeds of Artemisia tridentata, Eriogonum umbellatum, and Leymus	Experimental mechanical damage (clipping branches)	No damage to branches	A. tridentata	Field study: Natural population/ Lab study: Potted plants with or	Volatiles released from clipped branches inhibit germination of seeds of other species	(Karban 2007)

Effect on neighbored Dependent	oring plants		Emitters			Functional	
variables	Plants	Treatment	Control	Plants	Setting	inference	Reference
	cinereus				without different barriers		
Defense-related gene transcripts ▲/ Induced volatile emission ▲/ Induced parasitoid attraction ▲/ Herbivore growth ▼/ Damage from herbivore ▼	Zea mays seedlings (10-14 days old)	Infestation by Spodoptera littoralis	Not infested	Same as neighbors, different plants	Lab study: Potted plants in controlled flow-through glass chambers	Herbivory- induced volatiles prime direct and indirect defense responses in neighbors.	(Ton et al. 2007)
Attractiveness to the following: generalist aphid ▼/ specialist aphid ▲/ generalist parasitoid ▲/ specialist parasitoid —/ Transcriptome regulation (subset) ▲/ Phenotype of upregulated CYP450 ▲	Arabidopsis thaliana	Pure compounds: cis-jasmone, methyl jasmonate	No compound addition	None	Lab study: Plants exposed in closed glass chambers; olfacto- meters used for choice assays	cis-Jasmone increases non- glucosinolate- based resistance against generalist herbivores	(Bruce et al. 2008)
Leaf damage from herbivores ▼	Artemisia tridentata	Experimental mechanical damage (leaf clipping)/	Not clipped/ Not infested	Same as neighbors, different plants	Field study: Natural populations	Exposure to a damaged emitter induces resistance if exposure occurs	(Shiojiri & Karban 2008a)

Effect on neighbo	oring plants		Emitters				
Dependent variables	Plants	Treatment	Control	Plants	Setting	Functional inference	Reference
		Experimental infestation with <i>Trirhabda</i> pilosa larvae				during peak herbivory season	
Percent of leaves damaged by herbivores ▼	Artemisia cana, A. douglasiana	Experimental mechanical damage (leaf clipping)	Clipped and bagged to block aerial contact	Same as neighbors; same plants or different plants	Field study: Natural population	Aerial contact with emitter induces resistance regardless of whether the receiver is a branch of the same plant or a neighbor, but only in <i>A. cana</i>	(Shiojiri & Karban 2008b)
Leaf area consumed by Lymatria dispar ▼/ Volatile emission per leaf area consumed ▲/ leaf JA concentration ▲/ SA concentration —/ Linolenic acid concentration —/ evidence of defensive metabolites in FT-IR spectra ▲	Vaccinium corymbosum	Experimental infestation by <i>L. dispar</i> larvae	Mock treatment (polyester bags used to contain larvae)	Neighbor- ing branch on same plant	Lab study: Plexiglass containers and polyester or plastic bags to control exposure and assay volatiles	Exposure to HIPVs from neighboring branches elicits direct and indirect defense within a plant	(Rodriguez-Saona <i>et al.</i> 2009)
Volatile emission	Betula	None: Vicinity	Mono-	Rhodo-	Field study:	B. pendula	(Himanen et

Effect on neighb Dependent	oring plants		Emitters			Functional	
variables	Plants	Treatment	Control	Plants	Setting	inference	Reference
▲/ Herbivore attraction ▼/ Aphid incidence	pendula	in mixed species stands	cultures of B. pendula	dendron tomen- tosum	Experimental plantation, natural population	growing within 5 m of <i>R</i> . tomentosum accrue semi- volatiles (C15) from <i>R</i> . tomentosum, likely by surface adherence, rendering <i>B</i> . pendula less attractive to some herbivores.	al. 2010)
Number of leaves damaged by herbivores of 100 assay leaves ▼	Artemisia tridentata	Air transfer from plants with experimental mechanical damage (leaf clipping)	Air transfer from unclipped plants	Same as neighbors, different plants	Field study: Natural population	Exposure to headspace transferred from clipped neighbors increases resistance	(Karban <i>et al.</i> 2010)
Attraction of Cotesia glomerata parasitoids to induced plants / LIPOXYGENASE transcript abundance / Growth of Pieris brassicae and Mimestris	Brassica oleracea	Experimental infestation with <i>P. brassicae</i> larvae	Not infested	Same as neighbors, different plants	Lab study: Controlled flow design	Exposure to herbivory-induced volatiles from neighbors primes direct and indirect resistance in <i>B. oleracea</i>	(Peng et al. 2011)

Effect on neighb Dependent	oring plants		Emitters			Functional	
variables	Plants	Treatment	Control	Plants	Setting	inference	Reference
<i>brassicae</i> larvae ▼					<u> </u>		
Herbivore performance ▼/ Attractiveness to predators or parasitoids of herbivores ▲/ Herbivory-induced volatile emission ▲/ Attractiveness of exposed, herbivore-infested conspecifics to predators or parasitoids ▲	Phaseolus lunatus, Zea mays	Transgenic plants overexpressing (<i>E</i>)-β-ocimene synthase	Wild-type	Nicotiana tabacum	Lab study: Exposure in open-flow tunnel/ Glasshouse study: Proximity of potted plants	Exposure to (<i>E</i>)- β-ocimene in a plant volatile background increases direct and indirect resistance to herbivores in distantly related crop species	(Muroi <i>et al</i> . 2011)
Growth of <i>Mythimna separata</i> larvae ▼	Zea mays seedlings (7 d old)	Experimental infestation by <i>M. separata</i>	Not infested	Zea mays seedlings (14 d old)	Lab study: Exposure in flow-through box	Aerial exposure to herbivory- induced volatiles from conspecifics increases resistance to a specialist herbivore in maize	(Ramadan <i>et al.</i> 2011)
Proportional leaf damage in the field/ Lifetime seed production/ Developmental phenology/ Leaf	Achyra- chaena mollis, Lupinus nanus, Sinapis	Experimental mechanical damage (pins or pliers)	Not damaged	Conspecifics, either more related (same	Field study: Experimental plantation including transplanted and potted	The outcome of exposure to damaged neighbor volatiles depends on species and	(Pearse <i>et al.</i> 2012)

Effect on neighbored Dependent	oring plants		Emitters			Functional	
variables	Plants	Treatment	Control	Plants	Setting	inference	Reference
damage in a laboratory assay	arvensis			maternal family) or less related (different maternal families)	plants/ Lab study: Assays using potted plants from field	relatedness; more related emitters result in lower fitness for neighbors, perhaps because related neighbors are worse competitors	
Volatile emission —/ Cicadulina storeyi-induced volatile emission ▲/ Attraction of C. storeyi —/ Attraction of C. storeyi to induced plants ▲	Zea mays	None	Solvent spray (aqueous)	cis- Jasmone spray	Lab study: Y-tube olfactometer assays	cis-Jasmone application primes volatile-mediated defense, making plants less attractive to aphids.	(Oluwafemi et al. 2013)
Percent of leaves damaged by naturally occurring herbivores ▼	Salix exigua, S. lemmonii	Experimental mechanical damage (cutting leaves)	No cutting	Con- specific, clone or non-clone	Field study: Potted cuttings from plants in the local population, or naturally occurring plants	Exposure to wounded neighbor volatiles increases resistance of <i>Salix</i> spp. to herbivores; unclear role of relatedness	(Pearse <i>et al.</i> 2013)

Effect on neighbore Dependent	oring plants		<u>Emitters</u>			Functional	
variables	Plants	Treatment	Control	Plants	Setting	inference	Reference
Leaf area consumed by experimentally added <i>Pieris rapae</i> larvae ▼	Arabidopsis thaliana (WT Col-0)	Experimental mechanical damage (crushing leaves with forceps)	Not damaged	OsHPL3- over- expressing (OE) transgenic A. thaliana	Glasshouse study: Neighbors placed between 2 emitters, 1 m between sets of potted plants	Volatile HPL pathway products released after damage (GLVs) increase resistance to <i>P. rapae</i> larvae	(Savchenko et al. 2013)
Biomass allocated to roots vs. shoots	Hordeum vulgare cv. Kara	Far-red light supplement- ation (reduced R:FR)	No supplement -ation or no plant	H. vulgare cv. Alva	Lab study: Open-flow chambers with large rooting volume	Volatiles indicate whether emitter is shaded (exposed to FR-enriched light), in which case root:shoot biomass allocation in receiver is reduced, while exposure to volatiles from the unshaded Alva cultivar increases the root:shoot biomass ratio, indicative of the receiver tuning a competitive growth response	(Kegge et al. 2015)
Herbivore-induced	Zea mays	Synthetic	Empty	Z. mays	Lab study:	Indole exposure	(Erb et al.

Effect on neighboring plants		Emitters				T	
Dependent variables	Plants	Treatment	Control	Plants	Setting	Functional inference	Reference
mono- and homoterpenes ▲/ Herbivore-induced jasmonoyl- isoleucine (JA-Ile) ▲/ Herbivore- induced abscisic acid (ABA) ▲		indole, or experimental infestation with Spodoptera littoralis	dispenser, or indole- deficient mutant	with same genetic back- ground as neighbor	Controlled- flow system	primes emission of mono- and homoterpene volatiles and is required for their systemic induction; and primes induced JA-Ile and ABA.	2015)
Movement of Trirhabda virgate ▲/ Leaf area consumed by T. virgate ▼/ Relative growth rate of T. virgate ▼	Solidago altissima	Experimental infestation by <i>T. virgate</i>	No infestation	Same as neighbors, different plants	Field study: Natural stands/ Glasshouse study: Potted clones at different distances	Proximity to an emitter elicits resistance to <i>T. virgate</i> via induced volatiles, increasing herbivore movement	(Morrell & Kessler 2017)

145 References

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