Text S1: Shade avoidance and light perception in plants

1. Shade avoidance

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, cryptochromes (CRY) and phototropins (PHOT) which absorb blue light and UV-A, LOV-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 al.* 2016; Jenkins 2017; Mawphlang & Kharshiing 2017) (**Fig. S1**).

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, changes in R:FR and other binary light ratios due to green vegetation, and increasing ethylene 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, plant volatiles other than ethylene, which can be genera- or species-specific, and are usually 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 & de Wit 2014). Cues which are detected earlier such as touch and volatiles can allow plants to predict shade and enable SAS components in order to truly avoid shading, while encroaching 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 wavelengths and other cues, and with greater spatiotemporal resolution, in order to elucidate general principles of plant neighbor perception and adaptation (Pierik & de Wit 2014; Ballaré & Pierik 2017). In addition to changes aboveground, root exudates, interactions via fungal networks, and other belowground phenomena also influence the growth environment for other plants and likely provide information about neighbor identity and traits (Pierik *et al.* 2012; Babikova *et al.* 2013). Some work has studied variation in the SAS as an indicator of plant "kin recognition", but current approaches do not separate kin recognition from phenotype matching (e.g., (Crepy & Casal 2015; Till-Bottraud & Villemereuil 2015)); and kin recognition as a concept may mislead research and confuse evolutionary inferences (Allen *et al.* 2013).

2. Photoreceptors and light signaling

Plants show pronounced growth responses to specific light wavelengths and their ratios. Charles and Francis Darwin were the first to document phototropism in plants, in response to blue light (Darwin & Darwin 1880). Still unidentified nearly 100 years later, the mysterious plant blue (UV) light receptors, thought to be flavin photoreceptors due to their putative action spectra, were dubbed "cryptochromes" (also because of their importance in cryptogamic plants) (Gressel 1979; Yang *et al.* 2017). It was the advent of molecular genetics in the model plant *Arabidopsis thaliana* (Arabidopsis) that solved the mystery. Screening mutants with constitutively elongated 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 response to light perception as this indicates penetration of soil. Interestingly, cryptochromes have since been shown to provide blue light input to the circadian clock, not only in plants, but also in cyanobacteria, as well as animals and fungi (reviewed in (Gehring 2014).

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 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 conditions, and resulting growth responses were then described in detail by Smith and colleagues (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). 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 the R:FR ratio was reliable indicator of canopy cover in field studies; that between 1.2 (full 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 calculated P_{fr}/P_{total} ratio from light sources (Smith 1982; Ballaré & Pierik 2017). Armed with 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 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 experiments, Schmitt and colleagues demonstrated that the density-dependent plasticity of the SAS in competing plants improved the performance of wild-type (WT) *N. tabacum* and *Brassica rapa* (turnip mustard) in comparison to transgenic *N. tabacum* and mutant *B. rapa* lines "stuck" with phytochrome function turned either on or off (Schmitt *et al.* 1995).

The discovery of each new photoreceptor has been facilitated by a combination of straightforward phenotypic markers, and mutant screening approaches. Molecular genetic tools, combined with knowledge of photoreceptor genes, have permitted the generation of selectively blind plants which reveal possible photoreceptor functions, and, simultaneously, indicate adaptive significance of light sensing in plants. These discoveries have broader evolutionary implications, as most plant photoreceptors have homologues in animals, fungi, and cyanobacteria; which function in phototaxis, vision, and the circadian clock (Gehring 2014). Because the majority of these molecularly "enabled" experiments have been conducted under laboratory or glasshouse conditions with cultivated plants, the functional-evolutionary loop has not been closed and our mechanistic knowledge in this field currently far exceeds our functional understanding.

As an example, it has more recently been shown that negative regulation of photoreceptor responses is critical to their function. In 2005, Sessa and colleagues identified a bHLH transcription factor already known to be a component of both CRY and PHY signaling in *A. thaliana*, HFR1, which is strongly induced by a low R/FR ratio and remains up-regulated during prolonged exposure. The protein, which they renamed HFR1/SICS1 (Slender In Canopy Shade), down-regulates the expression of several other transcription factors involved in the SAS, preventing a runaway elongation response under prolonged shade (Sessa *et al.* 2005). More 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, 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 additional protein regulator to inhibit dimerization, may be shared with LOV-domain photoreceptors and UVR8, which also require homodimerization for activity (Fankhauser & Ulm 2016). There is also evidence from attenuation of BIC expression in *cry* mutants that CRY 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 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 function of light perception. Under natural conditions, it is likely critical for plants to maintain 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 understood how plants integrate the full spectrum of light, or how this integrated information informs an adaptive SAS and other light-mediated responses, including regulation of circadian phenomena (**Fig. S1**).

Figure S1

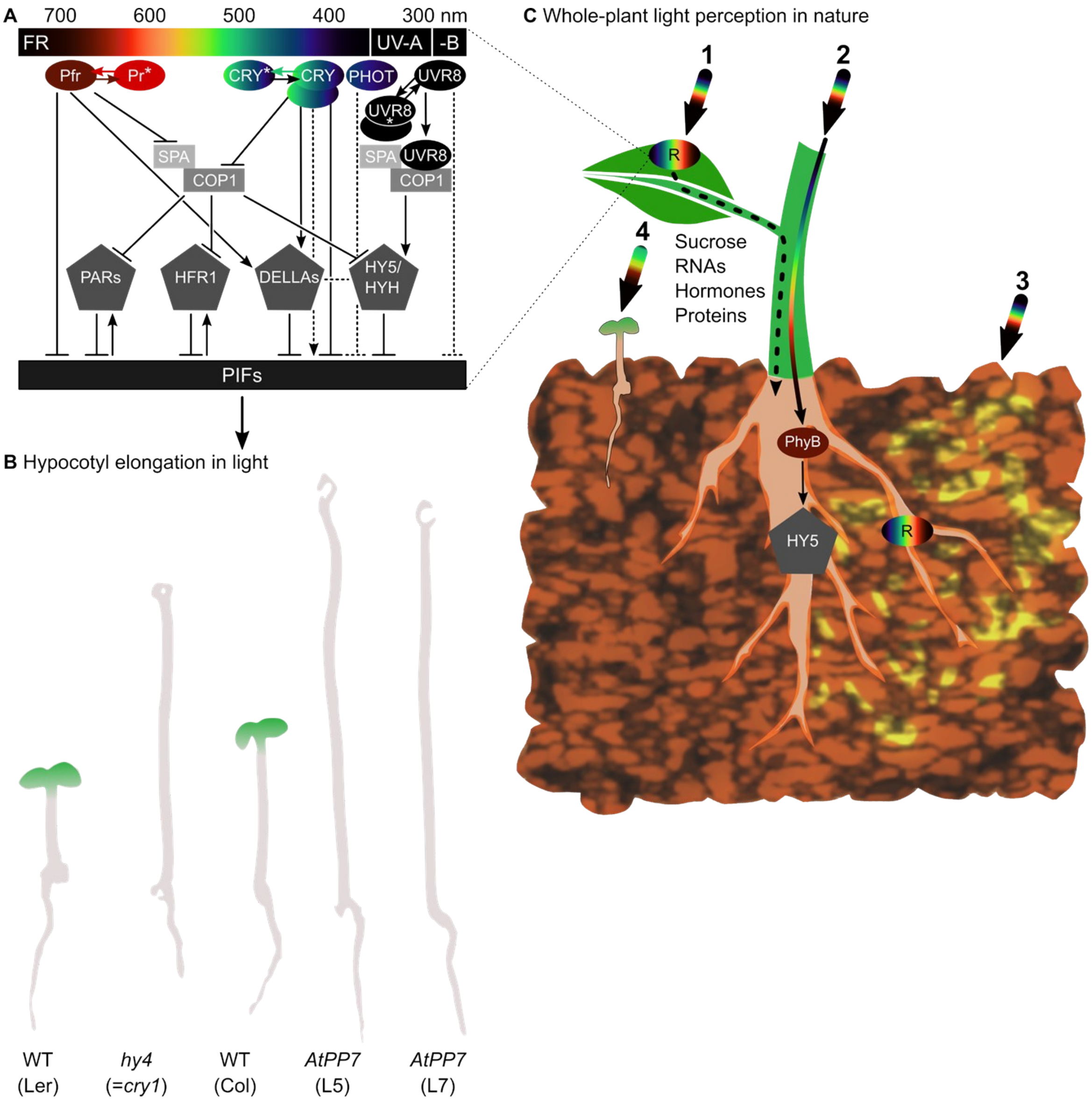

Figure S1. Light signaling: An example where mechanistic understanding surpasses ecological understanding. (A) Photoreceptors which are sensitive to all colors of light in the visible spectrum as well as UV-B, UV-A, and far-red, have now been identified in plants, and these light receptors interact in 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 and seedling hypocotyl elongation (PIF4, PIF5 or PIF7) while dotted lines represent hypothesized regulatory mechanisms. See (Fraser *et al.* 2016) for a detailed discussion of photoreceptor interactions. Monomerization and dimerization provide an additional regulatory layer: in *A. thaliana*, the cryptochrome CRY2 is active as a homodimer; in contrast, UVR8 homodimers are inactive, and in both cases regulatory proteins (not shown) facilitate either monomer- or dimerization (Fankhauser & Ulm 2016). (B) Laboratory screens for mutant seedlings with elongated hypocotyls under specific light conditions are traditionally used to identify photoreceptor genes and their interaction partners: image drawn from a study identifying 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 identify mutants with extreme phenotypes which may not be viable in nature. Photoreceptors are 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 environment. Three paths of whole-plant light perception are illustrated. **1**: Light is perceived by photoreceptors (R) in shoots, resulting in changes to sugar signaling, RNA and hormone production, and protein accumulation involved in root-shoot signaling and other responses; **2**: 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 roots (based on (Lee *et al.* 2017)). Arrow **4** shows green- and far red-enriched light filtered through a canopy towards a recently emerged seedling.

Table S1

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

Effect on neighboring plants		**Emitters**					
Dependent variables	*Plants*	*Treatment*	*Control*	*Plants*	**Setting**	**Functional inference**	**Reference**
Caterpillar growth ▼	3- to 4-year-old *Alnus rubra*, *Salix 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 *euroamericana* 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: correlational	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 neighboring plants		**Emitters**					
Dependent variables	*Plants*	*Treatment*	*Control*	*Plants*	**Setting**	**Functional 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 *et al.* 1992)
Aphid fecundity ▼	*Nicotiana tabacum* leaf discs	Experimental mechanical damage to cut leaves (crushing)/ Synthetic compound dilutions	Leaves not damaged/ Solvent	*Solanum lycopersicum* 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 *Agelastica alni* 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 *et al.* 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 *et al.* 2001)

Effect on neighboring plants		**Emitters**					
Dependent variables	*Plants*	*Treatment*	*Control*	*Plants*	**Setting**	**Functional 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. attenuata*, *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 *et al.* 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 neighboring plants		**Emitters**					
Dependent variables	*Plants*	*Treatment*	*Control*	*Plants*	**Setting**	**Functional 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 *et al.* 2004)
Resistance-related gene transcripts, metabolites and proteins ▲/ 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 *A. tridentata* clippings, specifically (*E*)-2-	(Kessler *et al.* 2006)

Effect on neighboring plants		**Emitters**					
Dependent variables	*Plants*	*Treatment*	*Control*	*Plants*	**Setting**	**Functional inference**	**Reference**
herbivore mortality ▲/ Herbivore damage ▼		compounds.			chimney-ventilated chambers	hexenal and methacrolein, primes resistance in *N. attenuata*	
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 *Manduca sexta* 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 ▲	*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 (*Z*)-3-hexenyl acetate, increases EFN secretion and indirect defense in naturally occurring plants	(Kost & Heil 2006)

Effect on neighboring plants		**Emitters**					
Dependent variables	*Plants*	*Treatment*	*Control*	*Plants*	**Setting**	**Functional 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	*Phaseolus 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 (*Z*)-3-hexenyl acetate, induce JA biosynthesis in *Z. mays*	(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-orthostichous, 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 *et al.* 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 neighboring plants		**Emitters**					
Dependent variables	*Plants*	*Treatment*	*Control*	*Plants*	**Setting**	**Functional 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; olfactometers 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 neighboring plants		**Emitters**					
Dependent variables	*Plants*	*Treatment*	*Control*	*Plants*	**Setting**	**Functional inference**	**Reference**
		Experimental infestation with *Trirhabda 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 *A. cana*	(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 *L. dispar* larvae	Mock treatment (polyester bags used to contain larvae)	Neighboring 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 *et al.* 2009)
Volatile emission	*Betula*	None: Vicinity	Mono-	*Rhodo-*	Field study:	*B. pendula*	(Himanen *et*

Effect on neighboring plants		**Emitters**					
Dependent variables	*Plants*	*Treatment*	*Control*	*Plants*	**Setting**	**Functional inference**	**Reference**
▲/ Herbivore attraction ▼/ Aphid incidence ▬	*pendula*	in mixed species stands	cultures of *B. pendula*	*dendron tomentosum*	Experimental plantation, natural population	growing within 5 m of *R. tomentosum* accrue semi-volatiles (C15) from *R. tomentosum*, likely by surface adherence, rendering *B. 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 *et al.* 2010)
Attraction of *Cotesia glomerata* parasitoids to induced plants ▲/ LIPOXYGENASE transcript abundance ▲/ Growth of *Pieris brassicae* and *Mimestris*	*Brassica oleracea*	Experimental infestation with *P. brassicae* 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 *B. oleracea*	(Peng *et al.* 2011)

Effect on neighboring plants		**Emitters**					
Dependent variables	*Plants*	*Treatment*	*Control*	*Plants*	**Setting**	**Functional inference**	**Reference**
brassicae larvae ▼							
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 (*E*)-β-ocimene synthase	Wild-type	*Nicotiana tabacum*	Lab study: Exposure in open-flow tunnel/ Glasshouse study: Proximity of potted plants	Exposure to (*E*)-β-ocimene in a plant volatile background increases direct and indirect resistance to herbivores in distantly related crop species	(Muroi *et al.* 2011)
Growth of *Mythimna separata* larvae ▼	*Zea mays* seedlings (7 d old)	Experimental infestation by *M. separata*	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 *et al.* 2011)
Proportional leaf damage in the field/ Lifetime seed production/ Developmental phenology/ Leaf	*Achyrachaena 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 *et al.* 2012)

Effect on neighboring plants		**Emitters**					
Dependent variables	*Plants*	*Treatment*	*Control*	*Plants*	**Setting**	**Functional 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 *Salix* spp. to herbivores; unclear role of relatedness	(Pearse *et al.* 2013)

Effect on neighboring plants		**Emitters**					
Dependent variables	*Plants*	*Treatment*	*Control*	*Plants*	**Setting**	**Functional inference**	**Reference**
Leaf area consumed by experimentally added *Pieris rapae* 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 *P. rapae* larvae	(Savchenko *et al.* 2013)
Biomass allocated to roots vs. shoots	*Hordeum vulgare* cv. Kara	Far-red light supplementation (reduced R:FR)	No supplementation 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**					
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 *T. virgate*	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 *T. virgate* via induced volatiles, increasing herbivore movement	(Morrell & Kessler 2017)

References

1.Ahmad, M. & Cashmore, A.R. (1993). HY4 gene of *A. thaliana* encodes a protein with characteristics of a blue-light photoreceptor. *Nature*, 366, 162–166

2. Allen, B., Nowak, M.A. & Wilson, E.O. (2013). Limitations of inclusive fitness. *Proc. Natl. Acad. Sci.*, 110, 20135–20139

3.Babikova, Z., Gilbert, L., Bruce, T.J.A., Birkett, M., Caulfield, J.C., Woodcock, C., *et al.* (2013). Underground signals carried through common mycelial networks warn neighbouring plants of aphid attack. *Ecol. Lett.*, 16, 835–843

4.Baldwin, I.T. & Schultz, J.C. (1983). Rapid changes in tree leaf chemistry induced by damage: evidence for communication between plants. *Science*, 221, 277–279

5.Ballaré, C.L. & Pierik, R. (2017). The shade-avoidance syndrome: Multiple signals and ecological consequences. *Plant Cell Environ.*, 40, 2530–2543

6.Bruce, T.J., Matthes, M.C., Chamberlain, K., Woodcock, C.M., Mohib, A., Webster, B., *et al.* (2008). cis-Jasmone induces Arabidopsis genes that affect the chemical ecology of multitrophic interactions with aphids and their parasitoids. *Proc. Natl. Acad. Sci. U. S. A.*, 105, 4553–4558

7.Bruin, J., Dicke, M. & Sabelis, M.W. (1992). Plants are better protected against spider-mites after exposure to volatiles from infested conspecifics. *Experientia*, 48, 525–529

8.Crepy, M.A. & Casal, J.J. (2015). Kin recognition by self-referent phenotype matching in plants. *New Phytol.*, 209, 15–16

9.Darwin, C. & Darwin, F. (1880). *The power of movement in plants*. John Murray, London, England, UK

10.Dolch, R. & Tscharntke, T. (2000). Defoliation of alders (*Alnus glutinosa*) affects herbivory by leaf beetles on undamaged neighbours. *Oecologia*, 125, 504–511

11.Duanmu, D., Bachy, C., Sudek, S., Wong, C.-H., Jimenez, V., Rockwell, N.C., *et al.* (2014). Marine algae and land plants share conserved phytochrome signaling systems. *Proc. Natl. Acad. Sci.*, 111, 15827–15832

12.Eckardt, N.A. (2003). A component of the cryptochrome blue light signaling pathway. *Plant Cell*, 15, 1051–1052

13.Engelberth, J., Alborn, H.T., Schmelz, E.A. & Tumlinson, J.H. (2004). Airborne signals prime plants against insect herbivore attack. *Proc. Natl. Acad. Sci. U. S. A.*, 101, 1781–1785

14.Engelberth, J., Seidl-Adams, I., Schultz, J.C. & Tumlinson, J.H. (2007). Insect elicitors and exposure to green leafy volatiles differentially upregulate major octadecanoids and transcripts of 12-oxo phytodienoic acid reductases in *Zea mays*. *Mol. Plant-Microbe Interact.*, 20, 707–716

15.Erb, M., Veyrat, N., Robert, C. a. M., Xu, H., Frey, M., Ton, J., *et al.* (2015). Indole is an essential herbivore-induced volatile priming signal in maize. *Nat. Commun.*, 6, 6273

16.Fankhauser, C. & Ulm, R. (2016). A photoreceptor's on-off switch. *Science*, 354, 282–283

17.Fraser, D.P., Hayes, S. & Franklin, K.A. (2016). Photoreceptor crosstalk in shade avoidance. *Curr. Opin. Plant Biol.*, 33, 1–7

18.Frost, C.J., Mescher, M.C., Dervinis, C., Davis, J.M., Carlson, J.E., De Moraes, C.M., *et al.* (2008). Priming defense genes and metabolites in hybrid poplar by the green leaf volatile *cis*-3-hexenyl acetate. *New Phytol.*, 180, 722–734

19.Gallie, D.R. (2015). Ethylene receptors in plants - why so much complexity? *F1000 Prime Reports*, 7, 39

20.Gehring, W.J. (2014). The evolution of vision. *Wiley Interdiscip. Rev. Dev. Biol.*, 3, 1–40

21.Gressel, J. (1979). Blue light photoreception. *Photochem. Photobiol.*, 30, 749–754

22.Heil, M. & Silva Bueno, J.C. (2007). Within-plant signaling by volatiles leads to induction and priming of an indirect plant defense in nature. *Proc. Natl. Acad. Sci. U. S. A.*, 104, 5467–5472

23.Hendricks, S.B. & Borthwick, H.A. (1959). Photocontrol of plant development by the simultaneous excitations of two interconvertible pigments. *Proc. Natl. Acad. Sci. USA*, 45, 344–349

24.Hildebrand, D.F., Brown, G.C., Jackson, D.M. & Hamilton-Kemp, T.R. (1993). Effects of some leaf-emitted volatile compounds on aphid population increase. *J. Chem. Ecol.*, 19, 1875–1887

25.Himanen, S.J., Blande, J.D., Klemola, T., Pulkkinen, J., Heijari, J. & Holopainen, J.K. (2010). Birch (Betula spp.) leaves adsorb and re-release volatiles specific to neighbouring plants--a mechanism for associational herbivore resistance? *New Phytol.*, 186, 722–732

26.Holmes, M.G. & Smith, H. (1975). The function of phytochrome in plants growing in the natural environment. *Nature*, 254, 512–514

27.Hua, J. & Meyerowitz, E.M. (1998). Ethylene responses are negatively regulated by a receptor gene family in *Arabidopsis thaliana*. *Cell*, 94, 261–271

28.Jenkins, G.I. (2017). Photomorphogenic responses to ultraviolet-B light. *Plant. Cell Environ.*, 40, 2544–2557

29.Karban, R. (2007). Experimental clipping of sagebrush inhibits seed germination of neighbours. *Ecol. Lett.*, 10, 791–797

30.Karban, R., Baldwin, I.T., Baxter, K.J., Laue, G. & Felton, G.W. (2000). Communication between plants: induced resistance in wild tobacco plants following clipping of neighboring sagebrush. *Oecologia*, 125, 66–71

31.Karban, R., Huntzinger, M. & McCall, A.C. (2004). The specificity of eavesdropping on sagebrush by other plants. *Ecology*, 85, 1846–1852

32.Karban, R., Maron, J., Felton, G.W., Ervin, G. & Eichenseer, H. (2003). Herbivore damage to sagebrush induces resistance in wild tobacco: evidence for eavesdropping between plants. *Oikos*, 2, 325–332

33.Karban, R., Shiojiri, K. & Ishizaki, S. (2010). An air transfer experiment confirms the role of volatile cues in communication between plants. *Am. Nat.*, 176, 381–384

34.Kasperbauer, M. (1971). Spectral distribution of light in a tobacco canopy and effects of end-of-day light quality on growth and development. *Plant Physiol.*, 47, 775–778

35.Kegge, W., Ninkovic, V., Glinwood, R., Welschen, R.A.M., Voesenek, L.A.C.J. & Pierik, R. (2015). Red:far-red light conditions affect the emission of volatile organic compounds from barley (*Hordeum vulgare*), leading to altered biomass allocation in neighbouring plants. *Ann. Bot.*, 115, 961–970

36.Kegge, W. & Pierik, R. (2009). Biogenic volatile organic compounds and plant competition. *Trends Plant Sci.*, 15, 126–132

37.Kessler, A., Halitschke, R., Diezel, C. & Baldwin, I.T. (2006). Priming of plant defense responses in nature by airborne signaling between *Artemisia tridentata* and *Nicotiana attenuata*. *Oecologia*, 148, 280–292

38.Lee, H.-J., Park, Y.-J., Ha, J.-H., Baldwin, I.T. & Park, C.-M. (2017). Multiple routes of light signaling during root photomorphogenesis. *Trends Plant Sci.*, 22, 803–812

39.Mawphlang, O.I.L. & Kharshiing, E. V. (2017). Photoreceptor-mediated plant growth responses: implications for photoreceptor engineering toward improved performance in crops. *Front. Plant Sci.*, 8, 1181

40.Moller, S.G., Kim, Y.S., Kunkel, T. & Chua, N.H. (2003). PP7 is a positive regulator of blue light signaling in Arabidopsis. *Plant Cell*, 15, 1111–1119

41.Morrell, K. & Kessler, A. (2017). Plant communication in a widespread goldenrod: keeping herbivores on the move. *Funct. Ecol.*, 31, 1049–1061

42.Muroi, A., Ramadan, A., Nishihara, M., Yamamoto, M., Ozawa, R., Takabayashi, J., *et al.* (2011). The composite effect of transgenic plant volatiles for acquired immunity to herbivory caused by inter-plant communications. *PLoS One*, 6, e24594

43.Myers, J.H. & Williams, K.S. (1984). Does tent caterpillar attack reduce the food quality of red alder foliage? *Oecologia*, 62, 74–79

44.Ninkovic, V. (2003). Volatile communication between barley plants affects biomass allocation. *J. Exp. Bot.*, 54, 1931–1939

45.Oluwafemi, S., Dewhirst, S.Y., Veyrat, N., Powers, S., Bruce, T.J.A., Caulfield, J.C., *et al.* (2013). Priming of defence volatile organic compound production in maize by the natural plant activator cis-jasmone. *PLoS One*, 8, e62299

46.Paschold, A., Halitschke, R. & Baldwin, I.T. (2006). Using " mute " plants to translate volatile signals. *Plant J.*, 45, 275–291

47.Pearse, I.S., Hughes, K., Shiojiri, K., Ishizaki, S. & Karban, R. (2013). Interplant volatile signaling in willows: revisiting the original talking trees. *Oecologia*, 172, 869–75

48.Pearse, I.S., Porensky, L.M., Yang, L.H., Stanton, M.L., Karban, R., Bhattacharyya, L., *et al.* (2012). Complex consequences of herbivory and interplant cues in three annual plants. *PLoS One*, 7, e38105

49.Peng, J., van Loon, J.J. a, Zheng, S. & Dicke, M. (2011). Herbivore-induced volatiles of cabbage (*Brassica oleracea*) prime defence responses in neighbouring intact plants. *Plant Biol.*, 13, 276–84

50.Pierik, R., Mommer, L. & Voesenek, L.A. (2012). Molecular mechanisms of plant competition: neighbour detection and response strategies. *Funct. Ecol.*, 27, 841-853

51.Pierik, R. & de Wit, M. (2014). Shade avoidance: phytochrome signalling and other aboveground neighbour detection cues. *J. Exp. Bot.*, 65, 2815–24

52.Ramadan, A., Muroi, A. & Arimura, G.-I. (2011). Herbivore-induced maize volatiles serve as priming cues for resistance against post-attack by the specialist armyworm *Mythimna separata*. *J. Plant Interact.*, 6, 1550158

53.Rhoades, D.F. (1983). Responses of alder and willow to attack by tent caterpillars and webworms: evidence for pheromonal sensitivity of willows. In: *Plant Resistance to Insects* (ed. Hedin, P.). American Chemical Society, Washington, D.C., USA, pp. 55–68

54.Rodriguez-Saona, C., Crafts-Brandner, S.J., Paré, P.W. & Henneberry, T.J. (2001). Exogenous methyl jasmonate induces volatile emissions in cotton plants. *J. Chem. Ecol.*, 27, 679–695

55.Rodriguez-Saona, C.R., Rodriguez-Saona, L.E. & Frost, C.J. (2009). Herbivore-induced volatiles in the perennial shrub, *Vaccinium corymbosum*, and their role in inter-branch signaling. *J. Chem. Ecol.*, 35, 163–175

56.Savchenko, T., Pearse, I.S., Ignatia, L., Karban, R. & Dehesh, K. (2013). Insect herbi qvores selectively suppress the HPL branch of the oxylipin pathway in host plants. *Plant J.*, 73, 653–662

57.Schmitt, J. (1997). Is photomorphogenic shade avoidance adaptive ? Perspectives from population biology. *Plant Cell Environ.*, 20, 826–830

58.Schmitt, J., Mccormac, A.C. & Harry, S. (1995). A test of the adaptive plasticity hypothesis using transgenc and mutatnt plant s Disabled in Phytochrome-Mediated Elongation Responses to Neighbors Author (s): Johanna Schmitt , Alex C . McCormac and Harry Smith Published by : The University of Chicago P. *Am. Nat.*, 146, 937–953

59.Schuman, M.C., Valim, H.A. & Joo, Y. (2016). Temporal dynamics of plant volatiles: mechanistic bases and functional consequences. In: *Deciphering Chemical Language of Plant Communication* (eds. Blande, J.D. & Glinwood, R.). Springer, Switzerland, pp. 3–34

60.Sessa, G., Carabelli, M., Sassi, M., Ciolfi, A., Possenti, M., Mittempergher, F., *et al.* (2005). A dynamic balance between gene activation and repression regulates the shade avoidance response in Arabidopsis. *Genes*, 19, 2811–2815

61.Shiojiri, K. & Karban, R. (2008a). Seasonality of herbivory and communication between individuals of sagebrush. *Arthropod. Plant. Interact.*, 2, 87–92

62.Shiojiri, K. & Karban, R. (2008b). Vascular Systemic Induced Resistance For Artemisia cana and Volatile Communication for Artemisia douglasiana. *Am. Midl. Nat.*, 159, 468–477

63.Smith, H. (1982). Light quality, photoperception, and plant strategy. *Annu. Rev. Plant Physiol.*, 33, 481–518

64.Smith, H. (2000). Phytochromes and light signal perception by plants--an emerging synthesis. *Nature*, 407, 585–591

65.Till-Bottraud, I. & Villemereuil, P. de. (2015). Kin recognition or phenotype matching? *New Phytol.*, 2019, 13–14

66.Ton, J., D'Alessandro, M., Jourdie, V., Jakab, G., Karlen, D., Held, M., *et al.* (2007). Priming by airborne signals boosts direct and indirect resistance in maize. *Plant J.*, 49, 16–26

67.Tscharntke, T., Thiessen, S., Dolch, R. & Boland, W. (2001). Herbivory, induced resistance, and interplant signal transfer in Alnus glutinosa. *Biochem. Syst. Ecol.*, 29, 1025–1047

68.Wang, Q., Zuo, Z., Wang, X., Gu, L. & Yoshizumi, T. (2016). Photoactivation and inactivation mechanisms of Arabidopsis cryptochrome 2, 354, 1–13

69.Yang, Z., Liu, B., Su, J., Liao, J., Lin, C. & Oka, Y. (2017). Cryptochromes orchestrate transcription regulation of diverse blue light responses in plants. *Photochem. Photobiol.*, 93, 112–127