Title: Light Intensity-Mediated Induction of Trichome-Associated Allelochemicals Increases Resistance against Thrips in Tomato

Running head: Light-Intensity Mediated Induction of Tomato Defenses

Corresponding author: R. Escobar-Bravo; Plant Science and Natural Products, Institute of Biology of Leiden, Leiden University, Sylviusweg 72, 2333BE Leiden (The Netherlands). Tlf: +31 (0)71 527 5117, Email address: r.bravo@biology.leidenuniv.nl**.**

Subject areas:

1. Environmental and stress responses

2. Growth and development.

Number of black and white figures: 5

Number of colour figures: 2

Supplementary material: Figures S1-S3, Table S1-S2 with legends, Method S1, and Notes S1.

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Authors: Rocío Escobar-Bravo[a, *], Jasmijn Ruijgrok[a], Hye Kyong Kim[a], Katharina Grosser[b,c], Nicole M. Van Dam[b,c], Peter G.L. Klinkhamer[a], Kirsten A. Leiss[a,1]

Author's addresses:

[a] Plant Science and Natural Products, Institute of Biology Leiden (IBL), Leiden University. Sylviusweg 72, 2333BE Leiden (The Netherlands).

[b] Molecular Interaction Ecology, German Center for Integrative Biodiversity Research (iDiv), Halle-Gena-Leipzig, Deutscher Platz 5e, 04103 Leipzig (Germany).

[c] Friedrich Schiller University Jena, Institute of Biodiversity, Dornburger-Str. 159, 07743 Jena (Germany).

[1]Present address: Wageningen University & Research, Business Unit Horticulture, Violierenweg 1, 2665MV Bleiswijk (The Netherlands).

[*]**Corresponding author:** Rocío Escobar-Bravo, r.bravo@biology.leidenuniv.nl

Abbreviations: abscisic acid (ABA), analysis of variance (ANOVA), ANOVA of the cross-validated residuals (CV-ANOVA), cycle threshold (Ct), daily light integral (DLI), gamma-aminobutyric acid (GABA), gas chromatography-mass spectrometry (GC/MS) indole-3-acetic acid (IAA), jasmonic acid (JA), jasmonic acid-isoleucine (JA-Ile), *jasmonate inducible protein-21* (*JIP-21*), latent variable (LV), least significant difference (LSD), liquid chromatography-mass spectrometry (LC/MS), normalized expression (NE), nuclear magnetic resonance (NMR), *odorless-2* (*od-2*), 12-oxo-phytodienoic acid (OPDA), partial least squares discriminant analysis (PLS-DA), photosynthetically active radiation (PAR), primer efficiency (PE), *proteinase inhibitor-IIf* (*PI-IIf*), quantitative reverse transcription–PCR (qRT–PCR), relative humidity (RH), specific leaf area (SLA), *threonine deaminase* (*TD-2*), salicylic acid (SA), trimethylsilane propionic acid sodium salt (TMSP), variable importance in projection (VIP), wild-type (wt), *wound-inducible proteinase inhibitor-II* (*WIPI-II*)

Abstract

In cultivated tomato (*Solanum lycopersicum*), increases in photosynthetically active radiation (PAR) induces type VI leaf glandular trichomes, which are important defensive structures against arthropod herbivores. Yet, how PAR affects the type VI trichome-associated leaf chemistry and its biological significance with respect to other photomorphogenic responses in this agronomically important plant species is unknown. We used the type VI trichome deficient tomato mutant *odorless-2* (*od-2*) and its wild-type to investigate the influence of PAR on trichome-associated chemical defenses against thrips (*Frankliniella occidentalis*). High PAR increased thrips resistance in wild-type plants, but not in *od-2*. Furthermore, under high PAR thrips preferred *od*-2 over the wild-type. Both genotypes increased type VI trichome densities under high PAR. Wild-type plants, however, produced more trichome-associated allelochemicals, i.e. terpenes and phenolics, these being undetectable or barely altered in *od-2*. High PAR increased leaf number and thickness, and induced profound but similar metabolomic changes in wild-type and *od-2* leaves. Enhanced PAR also increased levels of abscisic acid in wild-type and *od-2* plants, and of auxin in *od-2*, while the salicylic acid and jasmonates concentrations were unaltered. However, in both genotypes, high PAR induced the expression of jasmonic acid (JA)-responsive defense-related genes. Taken together, our results demonstrate that high PAR-mediated induction of trichome-associated chemical defenses plays a prominent role in tomato-thrips interactions.

Key words: abscisic acid, *Frankliniella occidentalis*, jasmonic acid, plant defenses, tomato, type VI trichomes.

Introduction

Light intensity, i.e. levels of photosynthetically active radiation (PAR: 400-700 nm), is a potent regulator of plant growth and development and, consequently, has a great impact on plant-herbivore interactions (Gouinguené and Turlings, 2002; Roberts and Paul, 2006; Ballaré, 2014; Vänninen et al., 2010). PAR affects the photosynthetic capacity and CO_2 fixation, altering the concentration of primary metabolites such as carbohydrates, and the fixation of nitrogen-based metabolites, e.g. amino acids, (Nunes-Nesi et al., 2010) in plant tissues. These responses can affect the availability of nutrients for arthropod herbivores and, therefore, herbivore development and/or survival on the host plant. In addition, increased PAR induces the production of carbon-based compounds, such as phenolics and terpenes, that not only serve as 'sunscreens' and/or antioxidants (Agati *et al*., 2013), but also function as chemical defenses against biotic stressors (Roberts and Paul, 2006; Leiss et al., 2009; Holopainen and Gershenzon, 2010; Zavala et al., 2015). Similarly, leaf thickness, toughness and trichome densities all have been reported to increase under enhanced PAR conditions as part of the plant's strategy to optimize the interaction of leaves with the incident light (Kennedy et al., 1981; Pérez-Estrada et al., 2000). In particular, trichomes, which are epidermal hairy structures, can reduce the absorbance of excess solar radiation by the mesophyll and facilitate the condensation of air moisture onto the leaf surface (Ehleringer et al., 1976; Vogelmann, 1993; Bickford, 2016). Altogether, these photomorphogenic responses can negatively affect consumption of plant tissues by arthropod herbivores (Kennedy et al., 1981; Gianfagna et al., 1992; Nihoul, 1993; Martínez-Garza and Howe, 2005; Schoonhoven et al., 2005). For example, a tough leaf can be harder to chew and more energetically costly to digest for chewing insects like caterpillars (Caldwell et al., 2015). Plant trichomes also contribute to plant resistance against herbivorous arthropods by physically hindering their movement or, in the case of glandular trichomes, by producing sticky, toxic and/or volatile substances that either restrain, harm, or deter herbivores, or attract their natural enemies (van Dam and Hare, 1998; Weinhold et al., 2011; Glas et al., 2012). Thus, although trichomes are constitutively produced on leaves, plants can also modulate leaf trichome density in response to abiotic and biotic stresses (Gianfagna et al., 1992; Snyder et al., 1998; Traw and Dawson, 2002; Escobar-Bravo et al., 2016, 2017).

In cultivated tomato (*Solanum lycopersicum*) type VI glandular trichomes are the most abundant trichome-type on the leaves, contributing to important chemical and physical defenses against herbivores (Kang et al., 2010; Tian et al., 2012; Kang et al., 2014). They

consist of a short multicellular stalk and a four-celled glandular head with the capacity to produce, store and secrete diverse specialized secondary metabolites, such as terpenes, acylsugars, phenolics and defensive proteins (Kennedy, 2003; Glas et al., 2012; Balcke et al., 2017). Disruption of the type VI trichome's head by arthropod movement and/or feeding releases these compounds, thus deterring herbivory, or priming for defense-related signaling pathways (Peiffer et al., 2009). Particularly, some trichome-derived mono- and sesquiterpenes increases the antixenotic and antibiotic properties of the host plant against a wide array of herbivorous arthropods (Eigenbrode et al., 1994; Maluf et al., 2001; De Azebedo et al., 2003; Bleeker et al., 2009, 2012). Additionally, oxidation of phenolics by defensive polyphenol oxidase proteins after trichome rupture produces a rigid and sticky exudate that impedes the movement of small insects, or directly reduces herbivore performance upon ingestion (Kennedy, 2003; Constabel and Barbehenn, 2008).

Increased PAR has been reported to induce type VI leaf glandular trichome densities in cultivated tomato (*S. lycopersicum*), which was proposed to explain the enhanced physical entrapment of the spider mite *Tetranychus urticae* onto the leaf surface (Nihoul, 1993). However, to the best of our knowledge, the effect of light intensity on the trichome-associated leaf chemistry of cultivated tomatoes has not been studied before. Induction of tomato leaf trichome-associated allelochemicals by abiotic conditions has only been described for the wild species *S. habrochaites* f. *glabratum* and *S. habrochaites* f. *hirsutum*, respectively (Kennedy et al., 1981; Gianfagna et al., 1992). The first one reported on the effect of light intensity on trichome density and production of methylketones by type VI trichomes, and the latter on the effect of temperature and photoperiod on the production of a sesquiterpene that is not produced by the glandular trichomes of cultivated tomatoes. Hence, the trichome chemistry of cultivated and wild tomatoes is very different, in terms of which compounds are produced and in terms of quantities (McDowel et al., 2011). Furthermore, although the above-mentioned studies addressed the effect of light intensity on some of the trichome-associated features, the role of other plant photomorphogenic responses in tomato defenses against herbivores was mostly overlooked. Hence, it is unknown whether light intensity-mediated induction of type VI trichome density and associated chemistry might be responsible for an increased resistance against arthropod pests in cultivated tomatoes. Additionally, and most importantly, knowledge on the responses of these biochemical factories to increasing light intensities will be useful for improving tomato defenses against pests and pathogens in agriculture systems under changing climatic conditions.

Here we investigated the effect of changes in light intensity (i.e. PAR levels) on trichome-associated chemical defenses of cultivated tomato against the generalist Western flower thrips *Frankliniella occidentalis* [Pergande], a key agricultural pest that affects both crop and ornamental plant production (Mouden et al., 2017). To do so, we used the tomato mutant *odorless-2* (*od-2*), which is deficient in type VI glandular trichome development and production of diverse trichome-associated metabolites, specially terpenes and flavonoids (Kang et al., 2010). We analyzed how two contrasting PAR levels, low and high, affected type VI trichome density and their associated volatile and non-volatile allelochemicals, as well as tomato resistance against thrips, by performing non-choice and choice bioassays. In addition, we characterized tomato physiological responses to PAR by analyzing the leaf metabolome and concentrations of growth- and defense-related hormones, as well as the expression of jasmonic acid-related defense genes, a defense signaling pathway involved in tomato resistance against thrips (Li et al., 2002; Escobar-Bravo et al., 2017). Together, our study reveals how light intensity not only influences trichome densities in cultivated tomato, but also modulates the glandular trichome-associated leaf chemistry and other leaf tissue-associated defenses against an insect pest.

Results

High PAR increases tomato resistance to thrips in the wild-type but not in od-2

Under low PAR (~56-65 μmol m^{-2} s^{-1}) conditions both wild-type and *od-2* plants showed similar levels of susceptibility to thrips, displaying equivalent amounts of silver damage (Fig. 1). However, under high PAR (~200-300 μmol m^{-2} s^{-1}), a significant reduction in silver damage was observed in wild-type plants when compared to low PAR-treated wild-type plants (ANOVA: PAR, $P = 0.024$; plant genotype, $P = 0.103$; interaction, $P = 0.007$). Conversely, no reduction in silver damage symptoms was observed for *od-2*.

High PAR increases antixenosis properties in wild-type and od-2 plants, but thrips preferred od-2 over the wild-type

To further investigate whether PAR altered host plant suitability for thrips in *od-2* and wild-type plants differently, thrips feeding preference for low versus high PAR-treated wild-type or *od-2* plants, and for wild-type versus *od-2* plants when both genotypes were subjected to low or high PAR conditions, were determined in leaf-disc dual-choice assays. Thrips caused more silver damage in leaf-discs taken from low PAR-treated wild-type plants over those taken

from high PAR-treated wild-type plants (Z = -4.706, P < 0.001) (Fig. 2a). The same pattern was observed for *od-2*, thrips caused more silver damage in leaf-discs taken from low PAR-treated plants than in those subjected to high PAR (Z = -2.83, P = 0.005) (Fig. 2b). Yet, when exposed to wild-type and *od-2* leaf-discs taken from plants subjected to high PAR, thrips showed preferential feeding for the *od-2* (Z = -2.962, P = 0.003) (Fig. 2c). Conversely, thrips did not discriminate between leaf-discs taken from wild-type and *od-2* plants both grown under low PAR (Z = -0.959, P = 0.338) (Fig. 2d).

High PAR increases type VI trichome densities in wild-type and od-2 plants, but trichome-associated volatiles are induced only in the wild-type

Light intensity had a significant effect on type VI trichome densities in wild-type and *od-2* plants (Fig. 3a, b). High PAR increased type-VI trichome densities on adaxial leaf sides (ANOVA: PAR, P = 0.002; genotype, P = 0.278; interaction, P = 0.988) (Figure 3a), as well as on abaxial leaf sides (ANOVA: PAR, P = 0.001; genotype, P = 0.234; interaction, P = 0.628) (Fig. 3b) in both tomato genotypes. Despite the induction of type-VI trichomes in *od-2*, the size of type VI glands was visibly smaller than those of the wild-type (Supplementary Fig. S2). This agrees with prior observations by Kang *et al*. (2010).

To determine whether higher type VI trichome densities positively correlated with increased production of trichome-derived allelochemicals, levels of phenolic and terpene compounds reported to be produced by type VI glands (Kang et al., 2010) were measured in leaf exudates of low and high PAR-treated wild-type and *od-2* plants (Fig. 3c,e). Significantly higher levels of the flavonoid rutin were detected in the leaf exudates of wild-type and *od-2* plants grown under high PAR (ANOVA: PAR, P = 0.043; genotype, P = 0.015; interaction, P = 0.025) (Fig. 3c). Yet, rutin content in leaf exudates of low and high PAR-treated *od-2* plants was significantly lower than in the wild-type. The flavonoid kaempferol 3-*O*-β-rutinoside was also slightly induced in the wild-type under high PAR, however the effect of PAR was not significant (ANOVA: PAR, P = 0.372; genotype, P = 0.411; interaction, P = 0.244). High PAR increased the total terpene content in leaf exudates of wild-type plants (*t-test*: P = 0.005) (Fig. 3d). Terpene compounds were not detected in the leaf exudates of *od-2* under any of the light conditions. Similar results were observed in a second repetition of the experiment (Supplementary Fig S3, Notes S1). Among the terpenes significantly induced by high PAR in wild-type plants, increased levels of α-pinene, δ-carene, α-phellandrene, α-terpinene, β-phellandrene and β-caryophyllene were observed (*t-test's*: P < 0.05) (Fig. 3e).

High PAR increases the number and thickness of tomato leaves

PAR conditions did not affect the length of the stems of wild-type and *od-2* plants, and no differences between the two genotypes were observed either (ANOVA: PAR, P = 0.751; genotype, P = 0.848; interaction, P = 0.170) (Fig. 4a). Conversely, high PAR significantly increased the number of leaves in wild-type and *od-2* plants (ANOVA: PAR, P = 0.018; genotype, P = 0.215; interaction, P = 0.081) (Fig. 4b). SLA was significantly reduced in wild-type and *od-2* plants grown under high PAR conditions (ANOVA: PAR, P = 0.023; genotype, P = 0.012; interaction, P = 0.261) (Fig. 4c). Notably, when compared to the wild-type, *od-2* plants displayed lower SLA values (i.e. thicker leaves) under both low and high PAR.

Wild-type and od-2 leaves experience similar metabolomic changes under high PAR conditions

A total of 244 signals were detected in leaf extracts of low and high PAR-treated wild-type and *od-2* plants by ^{1}H NMR. A multivariate PLS-DA analysis of the detected signal profiles resulted in a model with three latent variables (LV) explaining 82% of the total metabolomic variation and 84.6% of the light treatment response, with a 76.3% total model predictability (model statistics: R^2X=0.82, R^2Y=0.846 and Q^2=0.763; CV-ANOVA, $P < 0.001$) (Fig. 5). The first LV explained 47.73% of the variance and separated low PAR-treated from high PAR-treated wild-type and *od-2* plants (Fig. 5a). The second LV explained 23.4% and did not show a clear pattern of separation, suggesting a component related to the variability among samples. Differences between low and high PAR-treated wild-type and *od-2* plants were mainly explained by 90 signals with variable importance for projection [VIP] scores higher than 1 (Fig. 5b). Among these, twenty signals were identified, which corresponded to glutamate (δ 2.04), aspartic acid (δ 2.68, 2.80), fumaric acid (δ 6.56), malic acid (δ 2.48), gamma-aminobutyric acid (GABA) (δ 2.32, 3.0), glucose (δ 4.56, 5.20), rutin (δ 5.04, 6.32, 7.0) and chlorogenic acid (δ 5.12, 6.40, 6.44, 6.48, 6.88, 7.08, 7.16, and 7.68). Effect of PAR and plant genotype were tested on the relative abundance (i.e. scaled to the internal standard) of these compounds (Fig. 5c). High PAR increased leaf content of the amino acids glutamate, aspartic acid and the non-protein amino acid GABA in wild-type and *od-2* plants. Significant induction of aspartic acid, however, was only observed in the wild-type. High PAR also increased levels of the organic acids fumaric and malic acid, though induction of malic acid was statistically significant only in the wild-type. In both genotypes higher levels of glucose, the flavonoid rutin and the phenylpropanoid chlorogenic acid were detected under high PAR.

High PAR increases the leaf levels of ABA in both genotypes, and of auxin in od-2, but it does not affect the concentrations of SA, OPDA, JA and JA-Ile

To get more insight into the physiological responses of tomato leaves to high PAR that might explain the differences in susceptibility to thrips, we determined the levels of growth- and defense- related hormones (Fig. 6). PAR did not affect the levels of IAA (auxin), but under low PAR the *od-2* mutant contained significant lower concentrations than the wild-type, while under high PAR both wild-type and *od-2* had similar levels (ANOVA: PAR, $P = 0.180$; genotype, $P = 0.012$; interaction, $P = 0.042$) (Fig. 6a). In both genotypes, high PAR significantly increased the levels of ABA, being these levels higher in the wild-type than in *od-2* (ANOVA: PAR, $P < 0.001$; genotype, $P < 0.001$; interaction, $P = 0.536$) (Fig. 6b). High PAR did not affect the levels of SA (ANOVA: PAR, $P = 0.301$; genotype, $P = 0.259$; interaction, $P = 0.092$) nor the JA precursor OPDA (ANOVA: PAR, $P = 0.475$; genotype, $P = 0.821$; interaction, $P = 0.701$) (Fig. 6c,d). JA levels were also not affected by PAR conditions (ANOVA: PAR, $P = 0.414$; genotype, $P = 0.462$; interaction, $P = 0.150$) (Fig. 6e). Similarly, PAR did not affect JA-Ile levels, but these were significantly higher in *od-2* plants than in the wild-type irrespective of the treatment (ANOVA: PAR, $P = 0.930$; genotype, $P < 0.001$; interaction, $P = 0.708$) (Fig. 6f).

High PAR induces the expression of JA-associated defense genes in both wild-type and od-2 plants

To investigate whether increased PAR altered basal levels of JA-associated defenses, which are important for tomato defenses against thrips (Li et al., 2002; Escobar-Bravo et al., 2017), expression of the JA responsive genes *PI-IIf, TD-2* and *JIP-21* was analyzed in low and high PAR-treated wild-type and *od-2* plants (Fig. 7). High PAR significantly induced the expression of *PI-IIf* in wild-type and *od-2* plants (ANOVA: PAR, $P < 0.001$; genotype, $P = 0.985$; interaction, $P = 0.608$) (Fig. 7a). Likewise, expression of *TD-2* (ANOVA: PAR, $P < 0.001$; genotype, $P = 0.117$; interaction, $P = 0.612$) (Fig. 7b) and *JIP-21* (ANOVA: PAR, $P < 0.001$; genotype, $P = 0.234$; interaction, $P = 0.592$) (Fig. 7c) were significantly induced under high PAR in both genotypes.

Discussion

Here we have demonstrated that increased PAR does not only affect trichome densities, but also the accumulation of trichome-derived allelochemicals in the leaf, JA-associated defenses,

ABA concentrations, as well as leaf number and thickness in cultivated tomato. Moreover, the use of two tomato genotypes differing in the presence of functional trichomes, but displaying similar physiological responses when exposed to two contrasting PAR levels, allowed us to demonstrate that PAR-mediated induction of type VI trichome-associated allelochemicals significantly increases resistance of cultivated tomatoes to Western flower thrips.

First, we found that wild-type tomato plants grown under high PAR suffered less thrips damage than those grown under low PAR in whole plant no-choice bioassays. This difference, however, was not observed in the tomato mutant *od-2*, deficient in type VI trichome-associated compounds (Kang et al., 2010) (Fig. 1). Consistent with these results, thrips caused more damage to leaf-discs taken from wild-type plants grown under low PAR conditions in dual-choice assays (Fig. 2a). Surprisingly, thrips showed a similar preference in *od-2*, i.e. they caused less damage on leaf-discs from plants grown under high PAR than on those from the low PAR treatment (Fig. 2b). However, when compared to the wild-type, a 4-fold reduction in silver damage was observed in leaf-discs of high- versus low-PAR-treated wild-type plants, while only a 2-fold reduction in silver damage was detected in leaf-discs taken from high- versus low- PAR-treated *od-2* plants (Fig. 2a,b). To further investigate the level of susceptibility of *od-2* with respect to the wild-type under high PAR, we determined thrips feeding preference between high PAR-treated wild-type and *od-2* plants. Our results showed that thrips preferred leaf-discs of high PAR-treated *od*-2 plants over those taken from high PAR-treated wild-type plants (Fig. 2c). Thus, we concluded that *od-2* plants grown under high PAR were more susceptible to thrips than the wild-type.

Our results also showed that although type VI trichome densities were increased in wild-type and *od-2* under high PAR, only wild-type plants produced significantly more trichome-associated allelochemicals. Both terpenes and flavonoids were strongly induced under high PAR in the wild-type, but not detected or hardly altered in *od-2* trichome-derived extracts. This agrees with results previously reported by Kang et al., (2010), where lower levels of trichome-derived monoterpenes, sesquiterpenes and flavonoids were described for *od-2* and associated with higher susceptibility to diverse arthropod herbivores. The lack of induction of these trichome-associated allelochemicals might explain the differences in thrips susceptibility between the wild-type and *od-2* under high PAR conditions, as well as the higher vulnerability to thrips in wild-type plants subjected to low PAR conditions (Fig. 1). Terpenes are well known for their significant role in direct and indirect plant defenses against herbivorous arthropods (Kant et al., 2009). Multiple trichome-derived mono- and sesqui-

terpenes have been identified as potent repellent compounds against arthropod pests in wild tomato species (De Azevedo et al., 2003; Gonçalves et al., 2006; Bleeker et al., 2009, 2012). For instance, the monoterpenes *p*-cymene, *α*-terpinene and *α*-phellandrene have repellent properties against whiteflies in tomato (Bleeker et al., 2009). Notably, higher levels of *α*-phellandrene and α-terpinene were detected in leaf exudates of high PAR-treated wild-type plants. Additionally, the amount of β-phellandrene was strongly increased in the trichome-derived exudates of wild-type plants grown under high PAR. However, β-phellandrene has not been associated with repellent properties against insects. Finally, a 4.2-fold induction of the flavonoid rutin (quercetine 3-O-rutinoside) was observed in the trichome-derived exudates of wild-type plants under high PAR. Interestingly, the magnitude of this induction was higher when compared to the 2.5-fold increase in terpene levels. This might be explained by the fact that flavonoids can function as photo-protective "sunscreens" and antioxidants by inhibiting and/or reducing high light stress-induced reactive oxygen species levels (Agati et al., 2012). Accordingly, quercetine glycosides have been reported to increase in various plant species (Agati et al., 2009; Løvdal et al., 2010), as well as in the secretory products of *Phillyrea latifolia* leaf glandular trichomes, upon high irradiance (Tattini et al., 2000). Furthermore, the enhanced content of flavonoids in the leaf exudates of high PAR-treated wild-type plants was higher than the increase in type VI trichome densities (i.e. 2.2 fold-increase), suggesting a higher production of these compounds per trichome. To our knowledge the induction of flavonoids in type VI glandular trichomes by environmental cues has not been previously reported. In addition to their photo-protective and antioxidant properties, flavonoids and other phenolics might play an important role in plant defenses against insects. Enzymatic oxidation and browning reaction of phenolics has been proposed to increase entrapment of small arthropods, impede their feeding or act as anti-nutritive defenses (Duffey, 1986). This might explain the increased physical entrapment of *T. urticae* mites in tomato plants exposed to higher light intensities described by Nihoul (1993).

Plant physiology and metabolome of wild-type and *od-2* plants were profoundly affected by PAR. In greenhouse conditions, PAR fluctuates along the day. For instance, Gómez and Mitchell (2015) described that this can result in daily light integrals (DLI) of 2-10 mol m^{-2} d^{-1} during the winter and of 25-35 mol m^{-2} d^{-1} during the summer in a humid continental climate (data collected in Indiana, USA). It should be noticed that DLI measured inside greenhouses is generally lower than outside levels (i.e. DLI values in June and July of the northern hemisphere are close to 46 mol m^{-2} d^{-1}), as the greenhouse infrastructure might

reduce the DLI (Bugbee, 1994; Hanan, 1998). In our study, plants were exposed to 65 or 300 μmol m^{-2} s^{-1} for 16 h per day, resulting in DLI of ca. 2.8 and 17 mol m^{-2} d^{-1}, respectively. Notably, DLIs of 13 to 16 mol m^{-2} d^{-1} are reported to increase the net photosynthesis rate and considered the most optimal growth conditions for young tomato plants (Fan *et al*., 2013). Thus, we expected that increases in light intensity from 50 to 300 μmol m^{-2} s^{-1} would induce strong photomorphogenetic responses in young tomato plants (de Groot et al., 2001; Fan et al., 2013). Accordingly, plants grown under high PAR had significantly more and thicker leaves, which can result from both increased tissue density and cell wall thickness as described in Fan et al. (2013) for tomato leaves. These responses were similar to those described for tomato (Fan et al., 2013) and other plant species (Kitaya et al., 1998; Oguchi et al., 2003; Chang et al., 2008) under high PAR. Yet, leaf thickness was markedly higher in *od-2* than in the wild-type under both PAR conditions. This might be explained by a larger investment of resources in plant growth in the tomato mutant, but also by the reduced levels of auxin in comparison with the wild-type under low PAR (Fig. 6a) (Deng et al., 2012). Hence, the lack of PAR-mediated induction of trichome-associated metabolites in *od-2* might have conferred certain growth-related advantages (i.e. more and thicker leaves) over the wild-type (Neilson et al., 2013; Zust and Agrawal, 2017). Thicker leaves can affect the leaf mechanical properties and, therefore, defenses against insect herbivores (Hanley et al., 2007; Caldwell et al., 2015). Increased leaf thickness might have reinforced the mechanical resistance of *od-2* leaves against thrips feeding. However, although this might explain the preferential feeding of thrips for low PAR-treated *od-2* leaf-discs over those from high PAR-treated plants in the dual-choice assays, the level of susceptibility in the tomato mutant was still higher than in the wild-type under high PAR (Fig. 1).

Untargeted NMR metabolomic analysis of wild-type and *od-2* leaves further revealed that both genotypes experienced similar responses when grown under increased PAR conditions. High PAR increased the content of amino acids, organic acids, glucose and phenolics in wild-type and *od-2* young leaves. These results are in line with previous studies reporting the increased production of soluble sugars, and organic acids such as fumaric acid, under enhanced light irradiance (Chia et al., 2000; Couée et al., 2006). Light also controls the nitrate assimilation, providing the reducing power for the incorporation of nitrate into amino groups in plants (Foyer et al., 2006). This higher photosynthetic capacity might explain the increase in glutamate, a C- and N-source for the biosynthesis of most other amino acids, as well as the non-protein amino acid GABA (Forde and Lea, 2007). Accumulation of GABA is

a common plant response to biotic and abiotic stresses (Ramesh et al., 2015), and its induction might be involved in plant defenses against herbivores (Ramputh and Bown, 1996; McLean et al., 2003; Scholz et al., 2015; Bown and Shelp, 2016). However, the detected variations in GABA, amino acid and glucose levels cannot explain the differences in tomato susceptibility because they experienced the same variations in both genotypes. On the contrary, an increased production of some of these photo-assimilates was expected to increase the nutritional quality of tomato plants for thrips. This reinforces the hypothesis that food requirements of generalist insects might not be a limiting factor for host plant selection, but that the latter mostly relies on differences in secondary metabolites and other chemical plant defenses (Fraenkel, 1959; Chen et al., 2005; Köhler et al., 2015), such as the reinforcement of trichome-associated defenses described here. Yet, under high PAR, the increases in phenolic compounds levels observed in both genotypes, such as rutin and chlorogenic acid, might have contributed to the increased repellency against thrips observed in the two-choice leaf-disc bioassays. Enhanced rutin levels can deter insect feeding (reviewed by Simmonds, 2001), and chlorogenic acid has been positively associated to thrips resistance in Chrysanthemum (Leiss et al., 2009).

Plant hormones are central regulators of light acclimation (Kazan and Manners, 2011; Dietz et al., 2015) and defenses against herbivorous arthropods (Pieterse et al., 2012). Particularly, ABA plays a fundamental role in the regulation of plants' water status (Christmann et al., 2006), and its production is required for an effective physiological response of leaves to a fluctuating light environment (Gálvez-Valdivieso et al., 2009). Leaf trichomes can affect the plant water use efficiency when exposed to high light irradiances (Bickford, 2016). The lack of functional trichomes in *od*-2 was expected to increase the water- and high light-associated stress and, accordingly, ABA levels in comparison with the wild-type. However, our results showed that high PAR similarly affected the levels of ABA in wild-type and *od-2* plants. Yet, these levels were significantly higher in the wild-type irrespective of the light treatment (Fig. 6b), which might be associated to a stronger response to high irradiances and water stress. Notably, ABA is also required to fully activate JA-dependent defense responses against herbivores in systemic tissues, and this synergistic interaction is suggested to occur upstream and downstream of JA signaling (see review by Nguyen et al., 2016). To which extent the higher levels of ABA detected in wild-type tomato plants are involved in resistance against thrips is unknown. Future experiments using ABA and JA deficient tomato genotypes might extend our knowledge on the molecular mechanisms of high PAR-mediated induction of plant resistance to arthropod herbivores.

Development and chemical content of type VI trichomes has been described to be controlled by JA (Li et al., 2004; Boughton et al., 2005; Van Schie et al., 2007; Escobar-Bravo et al., 2017). Notably, levels of the jasmonates OPDA, JA and JA-Ile were not altered in plants exposed to 35 days of low or high PAR. Increases in these plant hormones have been described during light acclimation of *Arabidopsis thaliana* plants transferred from low to high light conditions (Alsharafa et al., 2014). Yet, those changes were reported to occur within hours, and JA and JA-Ile returned to basal levels at 6 h after the transfer to high light conditions. Possibly, fluctuations in jasmonate levels prior to our sampling moment might explain the induction of type VI trichomes in wild-type and *od-2* plants. Interestingly, although no differences in jasmonates concentrations were detected, JA-responsive genes were significantly induced in wild-type and *od-2* plants under high PAR. The similar levels of induction of JA-associated responses in *od-2* and the wild-type confirmed previous results described by Kang et al. (2010), where responses to mechanical wounding were comparable in both genotypes. Activation of JA defenses is important for tomato resistance against thrips (Li et al., 2002; Escobar-Bravo et al., 2017). Thus, reinforcement of these defenses in wild-type and *od-2* plants would be expected to increase tomato resistance to thrips in both genotypes. In whole plant bioassays, however, high PAR increased resistance against thrips in the wild-type but in not in *od-2*. Moreover, under high PAR *od-2* showed higher susceptibility than the wild-type in dual-choice assays. We hypothesize that PAR-mediated enhancement of JA signaling might have indeed increased *od-2* defenses, but they were insufficient to reach the resistant levels observed in the wild-type. Taken together, these results suggest that high PAR-mediated induction of type VI trichome-associated chemical defenses in the wild-type, but absent in *od-2*, indeed play an important role in tomato resistance against thrips.

Until recently, research on type VI trichomes of cultivated tomatoes has focused on unraveling their development and the genetic control of their associated metabolites (McDowell et al., 2011; Balcke et al., 2014; Bergau et al., 2015; Balcke et al., 2017). We have previously described that trichome density and overall production of their volatiles per leaf are affected by herbivory in cultivated tomato (Escobar-Bravo et al., 2017). Here we provide novel insights into the modulation and the biological significance of trichome-associated leaf chemistry under variable abiotic conditions, thus bringing a new perspective for future studies on chemistry and genetic engineering of these biochemical epidermal factories. These novel insights have important implications for agriculture under changing climate conditions.

Materials and methods

Plant material and light treatments

Seeds of *Solanum lycopersicum* Mill. cv. 'Castlemart' (wild-type) and the trichome-deficient mutant *odorless-2* (*od-2*) (kindly provided by prof. Gregg Howe from Michigan State University, USA) were sown in plastic trays filled with potting soil and placed in one of the two climate cabinets provided either with low or high PAR conditions. Fifteen days after germination plantlets were transplanted to 11-cm diameter plastic pots. Wild-type and *od-2* plants were kept under low or high PAR conditions for a total period of 35 days from sowing. To generate low and high PAR levels, the number of incandescent light tubes (Sylvania T8, F30W/830) and distance to the light source were adjusted in each chamber at the beginning of the experiment. Light intensity at the level of the apical tomato leaves increased progressively along with plant height during the experiment, ranging from ~56 (at day 1) to ~65 µmol m^{-2} s^{-1} (at day 35) under low PAR, and from ~200 (at day 1) to ~300 µmol m^{-2} s^{-1} (at day 35) under high PAR. PAR was measured by a light meter sensor (Eijkelkamp, The Netherlands), and the spectral composition by a spectrometer equipped with a cosine corrector (Flame-S, Ocean Optics) (Supplementary Fig. S1). Both cabinets were provided with a photoperiod of 16L:8D, 20°C, and 70% RH. At day 35, plants were used for non-choice whole plant and two-choice thrips preference bioassays, trichome density determination, assessment of plant growth parameters, chemical and gene expression analyses.

Thrips

Western flower thrips (*Frankliniella occidentalis*) were obtained from a colony reared on chrysanthemum flowers maintained in a climate room at 16L:8D, 25°C and 70% RH.

Whole plant no-choice thrips bioassay

Low and high PAR-treated wild-type and *od-2* plants were individually placed into thrips-proof cages consisting of a clear plastic cylinder (80 cm height, 20 cm diameter) closed at the top end with a lid made of thrips-proof gauze (Leiss et al., 2009). Cages with plants were randomly placed in a climate room provided with 113.6 µmol m^{-2} s^{-1} of PAR, a photoperiod of 16L:8D, 25°C and 70% RH. Each plant was infested with twenty adult thrips (18 females and 2 males). After 12 days, thrips feeding damage, hereafter referred as 'silver damage', was evaluated for the whole plant and expressed as mm^2 of total damaged leaf area. This bioassay was replicated three times with 6-10 plant replicates per treatment.

Two-choice leaf-disc thrips bioassay

A dual-choice assay (Leiss et al., 2009) was used to test thrips preference for leaf-discs taken from low versus high PAR-treated wild-type or *od-2* plants, and for wild-type versus *od-2* plants subjected to low or high PAR conditions. Leaf-discs (diameter of 10 mm), each corresponding to an individual plant, were punched from the third/fourth youngest leaf and placed on a thin layer of 1% agar in a 90-mm diameter Petri dish. Ten starved female *F. occidentalis* adults were shortly anesthetized with CO_2 and placed on a filter paper positioned between the discs. The Petri dishes were then sealed with parafilm and placed in a climate room provided with 110 µmol m^{-2} s^{-1} of PAR, 25°C and 16L:8D light regime. Silver damage was determined at 72 h after thrips release. This bioassay was performed three times with 6-10 replicates (i.e. petri dishes) per pair-wise comparisons.

Trichome density determination

Type VI glandular trichome density was measured on the adaxial and abaxial surfaces of leaflets taken from the third/fourth youngest as described in Escobar-Bravo et al., (2017). A Leica MZ16 stereomicroscope (Leica Microsystems, Wetzlar, Germany) equipped with a Leica DFC420 digital camera was used to take two pictures of an area of 12 mm^2 at both leaf sides of the main vein. Type VI trichomes were counted using the ImageJ software (http://imagej.nih.gov/ij/) and density was expressed as number of type VI trichomes per mm². Trichome density measurements were taken over three independent experiments with 9-10 plant replicates per treatment.

LC/MS analysis of phenolics

Production of the most abundant phenolic compounds produced by type VI glandular trichomes were analyzed in trichome-derived leaf exudates collected from the third/fourth youngest leaf following the protocol described by Kang et al. (2010, 2014) with some modifications. Fresh weight was measured before extraction. Leaflets were placed in 1 mL of 80% methanol aqueous solution and gently shaken for 2 min. The extracts were filtered through a 45-mm syringe filter and 5 µL was used for liquid chromatography-mass spectrometry (LC/MS) analysis. LC/MS was performed using a micrOTOF- QII (Bruker Daltonics GmbH, Germany) coupled to an Ultimate 3000 RS (ThermoScientific, USA) UHPLC quaternary pump with a diode array detector. Detection was carried out using electrospray ionization in negative mode over the mass range of m/z 120–1200. Reverse-

phase liquid chromatographic separation was performed using a Kinetex C_{18} column (100 x 2.10 mm, 2.6 μm particles) (Phenomenex, USA) maintained at 30°C. An elution gradient with a solvent system consisting of 0.1% formic acid (Optima, Fisher Scientific) in MilliQ water (solvent A) and methanol (Merck Millipore, Germany) + 0.1% formic acid (solvent B) was used. The gradient profile used an initial condition of 10% solvent B, a 12 min linear gradient to 65% solvent B, a 4 min ramp to achieve 90% solvent B, a 1 min hold at 90% solvent B, and return to 10% solvent B over 1.1 min, resulting in a run time of 18.1 min per sample. The flow rate was set at 0.35 ml min^{-1}. Quantification of the main flavonoids detected in leaf exudates was performed in the UV light (280-340 nm) using calibration curves derived from the external standards rutin and kaempferol 3-*O*-β -rutinoside (Sigma-Aldrich). Phenolic content was expressed as μg g^{-1} of fresh weight. This analysis was performed in two independent experiments with 4-5 plant replicates per treatment.

GC/MS analysis of terpenes

Terpene production by type VI glandular trichomes was analyzed in leaf exudates collected from two leaflets, belonging to the same leaf used for trichome density measurement, by using the leaf dip method (Kang et al., 2010, 2014; Sallaud et al., 2012). This protocol was chosen because the terpenoid profile detected in individually collected type VI glands has been shown to be nearly identical to that observed with the leaf dip procedure (Kang et al., 2010b, 2014). Leaf fresh weight was measured before extraction. Leaf exudates were obtained by dipping the leaf tissue in 2 mL pentane (Sigma-Aldrich) containing 10 μg of tetradecane (Sigma-Aldrich) as internal standard. Following an incubation period of 2 min with gentle shaking the leaflets were removed. One microliter of the resulting pentane leaf extract was injected into an Agilent model 7890 gas chromatograph fitted with a 5975C inert XL MSD Triple Axis Detector using a split ratio of 20:1. The initial column (30m x 0.25mm, 0.25μm film thickness, DB-5MS, Agilent Technologies) temperature was set at 40°C, then ramped to 150°C at 15°C/min and finally to 220°C at 6°C min^{-1}. The helium carrier gas flow was 1.6 mL min^{-1}. Terpenes were identified by comparison with authentic standards when possible, or by comparison with retention times and spectral information available in Agilent GC/MSD ChemStation. Compounds were quantified on the basis of the internal standard procedure described in Escobar-Bravo et al. (2017). For this, α-pinene and β-caryophyllene (Sigma-Aldrich) were used as external standards. Terpene content was expressed as μg g^{-1} of fresh weight. This analysis was performed in two independent experiments with 4-5 plant replicates per treatment.

Plant growth parameters

Number of leaves and stem length were measured in all the plants that were also used for trichome density and specific leaf area (SLA) determination, chemical analysis and thrips bioassays. Stem length was assessed above the cotyledons. SLA, a parameter used to estimate leaf thickness (Vile et al., 2005), was determined in one leaflet taken from the third/fourth youngest leaf from the apex. This leaflet was also used for trichome density measurement prior to SLA determination. For SLA calculation, the leaflet was scanned and the leaf area was determined by using ImageJ software. Then, the leaflet was dried in an oven at 60°C for two days, and dry leaf material was weighed. SLA was expressed as $cm^2\ g^{-1}$ of dry mass. Plant growth parameters were determined in three independent experiments with 12-27 plant replicates per treatment.

Nuclear magnetic resonance (NMR) analysis

NMR metabolic analysis was performed on leaflets taken from the third/fourth youngest leaf from the apex. For this, ten milligrams of freeze-dried plant material were extracted with 1 mL of KH_2PO_4 buffer in D_2O (pH 6) containing 0.05% trimethylsilane propionic acid sodium salt (TMSP) and CH_3OH-d_4 (1:1). Plant extracts were vortexed, sonicated for 20 min and centrifuged at 13,000 rpm for 10 min at room temperature. Three hundred microliters of the supernatant were transferred to NMR-tubes for the spectral analysis. ^{1}H NMR spectra were recorded at 25 °C on a 600 MHz Bruker AV 600 spectrometer equipped with cryo-probe operating at a proton NMR frequency of 600 MHz, following the procedure described in López-Gresa *et al*. (2012). The resulting spectra were manually phased, baseline corrected, and calibrated to TMSP at 0.0 ppm, using Topspin (version 2.1, Bruker). ^{1}H NMR spectra were reduced to ASCII files using AMIX (v. 3.7, Bruker Biospin). Spectral intensities were scaled to the intensity of the internal standard TMSP and reduced to integrated regions of equal width (0.04 ppm) corresponding to the region of δ 0.4-10. Regions in the range of δ 4.7-4.9 and δ 3.28-3.34 corresponding to residuals signals of water and methanol, respectively, were excluded from the analysis.

Hormone analysis

The concentration of the phytohormones 12-oxo-phytodienoic acid (OPDA), jasmonic acid (JA), jasmonic acid-isoleucine (JA-Ile), salicylic acid (SA), abscisic acid (ABA) and auxin (indole-3-acetic acid, IAA) was analyzed in leaflets taken from the third/fourth youngest leaf

from the apex by means of LC-MS/MS following the procedures described in Machado et al. (2013) and Schäfer et al. (2016) with minor modifications (Supplementary Methods S1).

Gene expression analysis

Total RNA was isolated as described in Verwoerd et al. (1989) and treated with DNase (Ambion). cDNA was synthesized from 4 µg of total RNA using M-MuLV Reverse Transcriptase (Fermentas) in a 20 µl reaction. qRT-PCR was performed in CFX96^{TM} Optics Module (BIO-RAD) using iQ^{TM} SYBR$^{®}$ Green Supermix (BIO-RAD) following the procedure described in Escobar-Bravo et al. (2017). Five biological replicates with two technical replicates were analyzed per treatment. *Actin* was used as a reference gene. The normalized expression (NE) data were calculated by the ΔCt method NE = - (PE_{target}^Ct_{target})/ ($PE_{reference}$ ^$Ct_{reference}$) (PE = primer efficiency; Ct = cycle threshold). The PEs were determined by fitting a linear regression on the Ct-values of a standard cDNA dilution series. To plot the relative expression, NE values were scaled the lowest average NE within the plot, being the lowest average in each plot set to 1. Transcript levels of the JA-marker genes *proteinase inhibitor-IIf* (*PI-IIf*) (formerly known as *WIPI-II*, *wound-inducible proteinase inhibitor-II*, in Farmer *et al*., 1992)*, jasmonate inducible protein-21* (*JIP-21*) and *threonine deaminase* (*TD-2*) (Alba *et al*., 2015) were analyzed. Gene-specific primers used for the qRT-PCRs are shown in Supplementary Table S1.

Statistical analysis

Data were analyzed using the SPSS software package (version 21; SPSS Inc., Chicago, IL, USA). Residuals were tested for normality and heteroscedasticity of variance. Effect of PAR, plant genotype and their interaction on silver damage, trichome density, phenolic compounds identified in leaf exudates, stem length, number of leaves, SLA, normalized gene expression and hormone levels were analyzed by two-way ANOVA. For this, 'plant genotype' and 'light treatment/PAR' were considered as fixed factors, and 'experimental replicate' as the random factor when pooled data from independent replicated experiments were analyzed. Differences among groups were tested by Fisher´s least significant difference (LSD) post-hoc test. Data on silver damage symptoms from whole plant bioassays, trichome density in the adaxial leaf side, SLA, normalized expression of *PI-IIf, TD-2* and *JIP-21* were log transformed prior to analysis to meet ANOVA assumptions. Data on trichome density in the abaxial leaf side and individual phenolic compounds were log (x + 1)- and square root (x + 1)-transformed, respectively, prior to analysis. Differences in total terpene content and levels of individual

terpene compounds in leaf exudates of low and high PAR-treated wild-type plants were analyzed by *t*-test, or when transformation was not possible, by non-parametric Mann-Whitney U tests. Thrips feeding preference tested in leaf disc dual-choice bioassays obtained from three independent experiments were pooled and analyzed by Wilcoxon signed rank test. For this, data from the three independent experiments were tested for heterogeneity using contingency tables and associated chi-squared test. Patterns of chemical signals detected by NMR in leaf extracts of low and high PAR-treated wild-type and *od-2* plants were subjected to multivariate analysis using the SIMCA-P 13 software package (Umetrics, Sweden). A supervised partial least squares discriminant analysis (PLS-DA) was used to determine the variation in X variables (metabolites) modeled by the Y explanatory variable corresponding to PAR levels. The cumulative variations in X and Y explained by the model are reported as R2X and R2Y, respectively. The resulting model was fit to the minimum number of latent variables showing the highest value of predicted variation (Q2). The important X variables were selected based on a VIP (variable importance in projection) score > 1. Effect of plant genotype, PAR and their interaction on the relative peak intensity of identified compounds with VIP score > 1 was then tested using a two-way ANOVA followed by LSD post-hoc test.

Acknowledgements

This work was supported by the STW Perspective program "Green Defense against Pests" (GAP) (Ref.13553). We thank the companies involved in the GAP project: Rijk Zwaan, Dummen Orange, Deliflor, Dekker Chrysanten, and Incotec for financial support. Katharina Grosser and Nicole M. van Dam gratefully acknowledge the support of the German Center for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig funded by the German Research Foundation (FZT 118).

Disclosures

The authors have no conflicts of interest to declare.

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Legends

Figure 1. Effect of low and high PAR treatments on tomato resistance to the Western flower thrips *F. occidentalis,* tested in a whole plant no-choice bioassay, at 35 days after initial light treatments. Silver damage caused by thrips feeding was measured in low and high PAR-treated wild-type (wt) and *odorless-2* (*od-2*) plants at 12 days after thrips infestation. Values represent the mean (+ SEM) of 26 plants from three independent experiments. Different letters above bars denote significant differences among groups (ANOVA followed by Fisher´s LSD test, $P \leq 0.05$).

Figure 2. Feeding preference of the Western flower thrips *F. occidentalis* for low and high PAR-treated wild-type (wt) and *odorless-2* (*od-2*) plants tested in leaf disc dual-choice bioassays. Leaf discs were taken from leaflets belonging to the third/fourth youngest leaf at 35 days after initial light treatments. Silver damage (mean + SEM, n = 25-30) caused by thrips feeding was evaluated at 72 h after thrips release in the following pair-wise comparisons: (a) low PAR versus high PAR-treated wild-type plants, (b) low PAR versus high PAR-treated *od-2* plants, (c) high PAR-treated wild-type versus high PAR-treated *od-2* plants, and (d) low PAR-treated wild-type versus low PAR-treated *od-2* plants. Pooled data from three independent experiments were analyzed. Asterisks denote significant differences tested by Wilcoxon signed rank test ($P \leq 0.05$). n.s. = not significant.

Figure 3. Effect of low and high PAR treatments on type VI leaf trichome-associated defenses in wild-type (wt) and *odorless-2* (*od-2*) plants. Type-VI trichome density was evaluated on (a) adaxial and (b) abaxial leaf sides of leaflets taken from the third/fourth youngest leaf at 35 days after initial light treatments. Values represent the mean (+ SEM) of 28-29 plants from three independent experiments. (c) Main phenolic compounds identified in leaf exudates of low or high PAR-treated wild-type and *od-2* plants. Values represent the mean (+ SEM) of 9 plants from two independent experiments. (d) Total terpene content (mean + SEM, n = 4-5) measured in leaf exudates of leaflets taken from the third/fourth youngest leaf and (e) levels (mean + SEM, n = 4-5) of individual terpene compounds.

Asterisks denote significant differences between low and high PAR-treated wild-type plants analyzed by *t-test* or Mann-Whitney U tests ($P \leq 0.05$). Different letters above bars denote significant differences among groups (ANOVA followed by Fisher´s LSD test, $P \leq 0.05$). n.s. = not significant. n.d. = not detected.

Figure 4. Effect of low and high PAR treatments on plant growth parameters. Graphs depict (a) stem length, (b) specific leaf area (SLA), and (c) number of leaves determined in low and high PAR-treated wild-type (wt) and *odorless-2* (*od-2*) plants at 35 days after initial light treatments. Values of stem length and number of leaves represent the mean (+ SEM) of 52-56 plants, while for SLA values represent the mean (+ SEM) of 24-28 plants from three independent experiments. Different letters above bars denote significant differences among groups tested by ANOVA followed by Fisher´s LSD test ($P \leq 0.05$). (d) Representative photographs of five weeks old wild-type and *od-2* plants exposed to low or high PAR conditions.

Figure 5. Metabolomic responses in wild-type (wt) and *odorless-2* (*od-2*) plants under low or high PAR conditions. Leaf metabolites were analyzed by NMR at 35 days after initial light treatments on leaflets collected from the third/fourth youngest leaf. Projection to latent structures-discriminant analysis (PLS-DA) was performed on the obtained ^{1}H NMR spectra, and resulted in three latent variables (LVs) that cumulatively explained 82% of the total metabolomic variation and 84.6% of the light treatment response, with a 76.3% total model predictability. (a) Score plot showing the first two latent variables (LV). (b) Loading plot showing metabolites contributing most to the model (VIP score > 1). (c) Relative spectral intensities (mean + SEM, n = 4-5), scaled to the internal standard, of selected metabolites (VIP score > 1) identified in the ^{1}H NMR spectra. Different letters above bars denote significant differences among groups (ANOVA followed by Fisher´s LSD test, $P \leq 0.05$).

Figure 6. Concentrations of (a) indole-3-acetic acid (IAA), (b) abscisic acid (ABA), (c) salicylic acid (SA), (d) 12-oxo-phytodienoic acid (OPDA), (e) jasmonic acid (JA) and (f) jasmonic acid-isoleucine (JA-Ile) determined in low and high PAR-treated wild-type (wt) and *odorless-2* (*od-2*) plants at 35 days after the initial light treatments. The analysis was performed on leaflets collected from the third/fourth youngest leaf. Values represent the mean (+ SEM) of five individual plants. Different letters above bars denote significant differences among groups (ANOVA followed by Fisher´s LSD test, $P \leq 0.05$). n.s. not significant.

Figure 7. Relative transcript levels of the JA-responsive genes (a) *proteinase inhibitor-IIf* (*PI-IIf*), (b) *threonine deaminase-2* (*TD-2*), and (c) *jasmonate inducible protein-21* (*JIP-21*) measured in low and high PAR-treated wild-type (wt) and *odorless-2* (*od-2*) plants at 35 days after the initial light treatment. The analysis was performed on leaflets collected from the third/fourth youngest leaf. Values represent the mean (+ SEM) of relative expression of each treatment group (n = 5 biological replicates, two technical replicates). Different letters above bars denote significant differences among groups (ANOVA followed by Fisher´s LSD test, at $P \leq 0.05$.

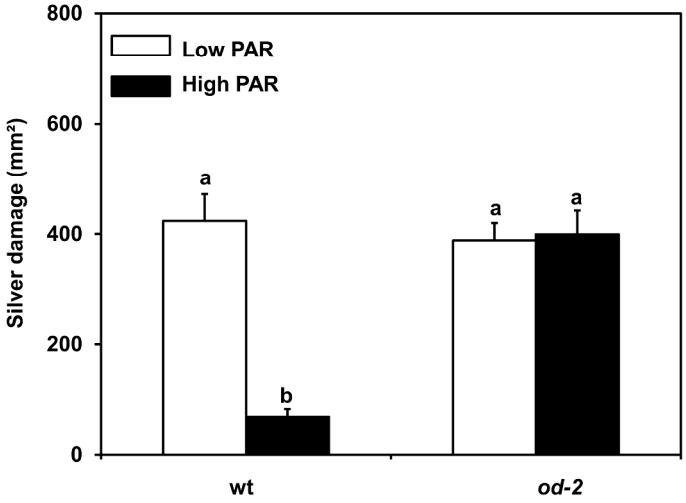

Figure 1. Effect of low and high PAR treatments on tomato resistance to the Western flower thrips F. occidentalis, tested in a whole plant no-choice bioassay, at 35 days after initial light treatments.

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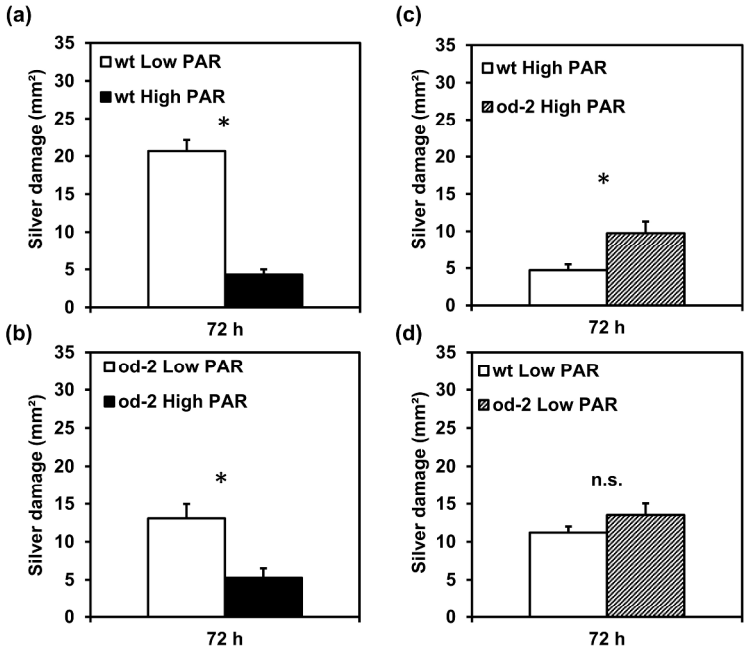

Figure 2. Feeding preference of the Western flower thrips F. occidentalis for low and high PAR-treated wild-type (wt) and odorless-2 (od-2) plants tested in leaf disc dual-choice bioassays.

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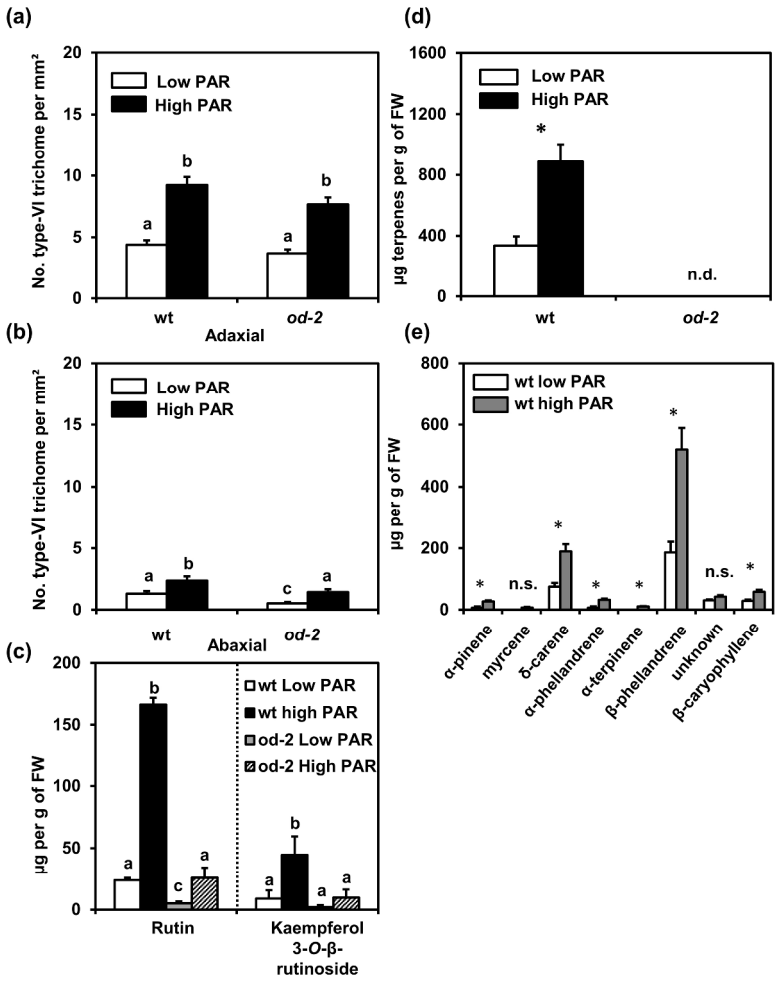

Figure 3. Effect of low and high PAR treatments on type VI leaf trichome-associated defenses in wild-type (wt) and odorless-2 (od-2) plants.

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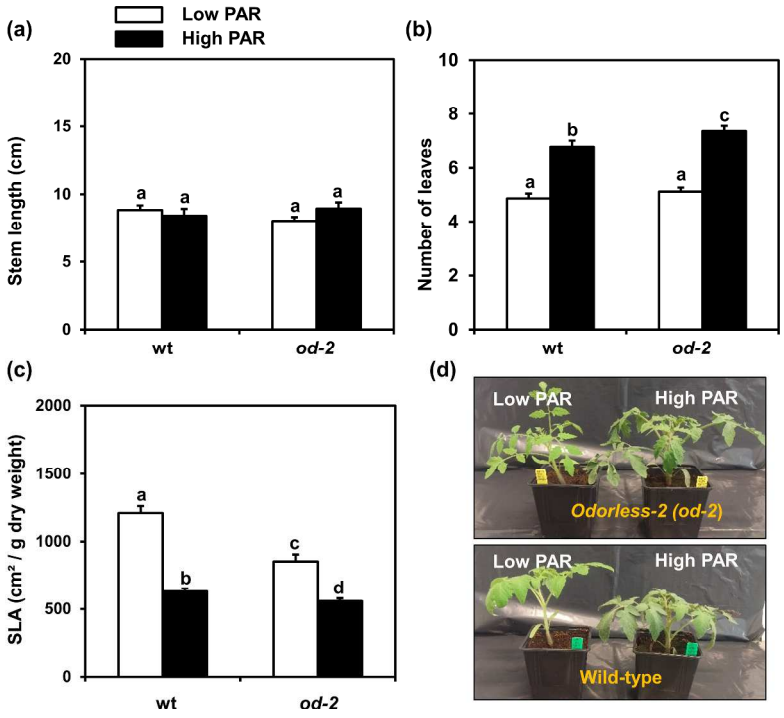

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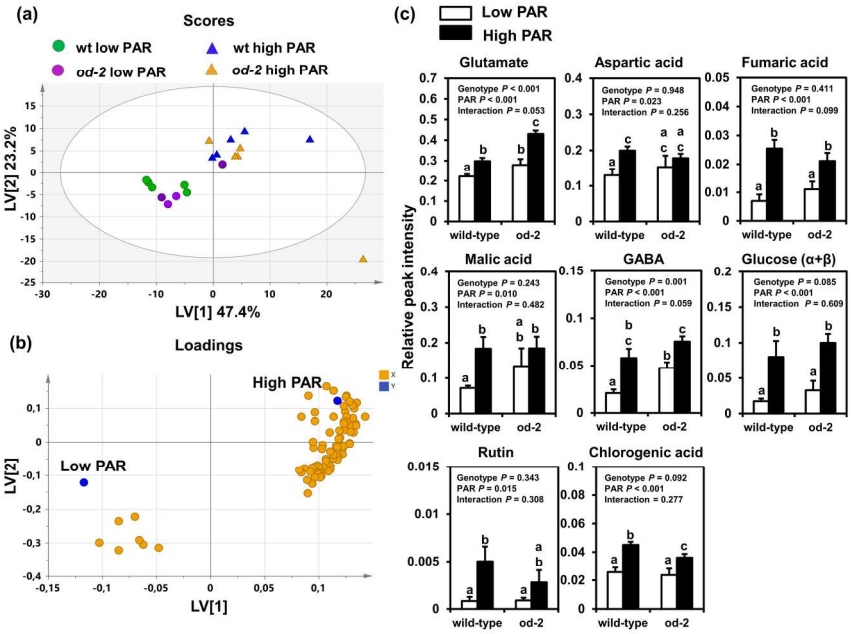

Figure 5. Multivariate analysis of NMR metabolomic data

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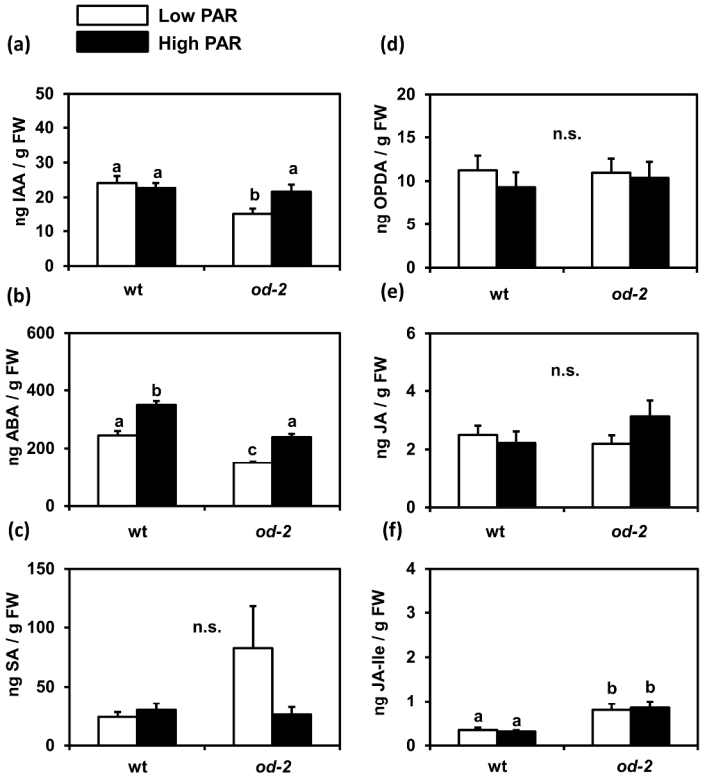

Figure 6. Levels of growth and defense-related hormones

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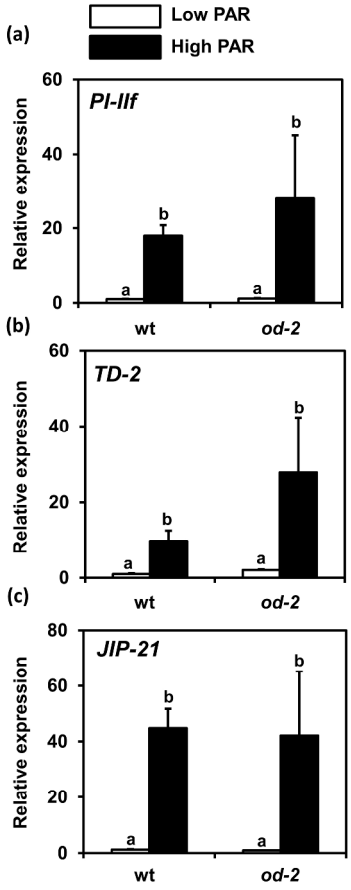

Figure 7. Expression analysis of JA-associated defensive genes

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