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16 **Knocking down of isoprene emission modifies the lipid matrix of thylakoid** 17 **membranes and influences the chloroplast ultrastructure in poplar**

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19 Violeta Velikova^{1,3}, Constanze Müller², Andrea Ghirardo³, Theresa Maria Rock², **Michaela Aichler4 , Axel Walch⁴ , Philippe Schmitt-Kopplin²** 20 **, and Jörg-Peter Schnitzler3** 21 **,***

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23 ¹ Institute of Plant Physiology, Bulgarian Academy of Sciences, Sofia 1113, Bulgaria

24 ² Research Unit Analytical BioGeoChemistry, Helmholtz Zentrum München, 85764

- 25 Neuherberg, Germany
- ³ 26 Research Unit Environmental Simulation, Institute of Biochemical Plant Pathology,
- 27 Helmholtz Zentrum München, 85764 Neuherberg, Germany
- 28 ⁴ Research Unit Analytical Pathology, Helmholtz Zentrum München, 85764 Neuherberg, 29 Germany
- 30

31 **Summary**

- 32 The biological function of isoprene emission in plants is closely associated with the structural
- 33 organization and functioning of plastidic membranes.

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35 **ABSTRACT**

36 Isoprene is a small lipophilic molecule with important functions in plant protection against 37 abiotic stresses. Here, we studied the lipid composition of thylakoid membranes and 38 chloroplast ultrastructure in isoprene emitting (IE) and non-isoprene emitting (NE) poplars. 39 We demonstrated that the total amount of mono- (MGDG), di-galactosyldiacylglycerols 40 (DGDG), phospholipids (PL), and fatty acids is reduced in chloroplasts when isoprene 41 biosynthesis is blocked. A significantly lower amount of unsaturated fatty acids, particularly 42 linolenic acid (18:3) in NE chloroplasts was associated with the reduced fluidity of thylakoid 43 membranes, which in turn negatively affects PSII photochemical efficiency (Φ_{PSII}) . The low Φ_{PSII} in NE plants was negatively correlated with non-photochemical quenching (NPO) and 45 the energy-dependent (qE) component of NPQ. Transmission electron microscopy revealed 46 alterations in the chloroplast ultrastructure in NE compared with IE plants. NE chloroplasts 47 were more rounded and contained less grana stacks and longer stroma thylakoids, more 48 plastoglobules, and larger associative zones between chloroplasts and mitochondria. These 49 results strongly support the idea that in isoprene-emitting species, the function of this 50 molecule is closely associated with the structural organization and functioning of plastidic 51 membranes.

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54 **INTRODUCTION**

55 Isoprene is globally the most abundant biogenic hydrocarbon constitutively emitted from 56 many plant species (Guenther et al., 2012). It has been proposed that leaf isoprene emission is 57 an important adaptation for plants, conferring tolerance to different environmental constraints 58 (Vickers et al., 2009; Loreto and Schnitzler, 2010; Loreto and Fineschi, 2014). However, 59 biogenic isoprene emission represents a non-trivial carbon loss in plants, particularly under 60 stress conditions (Fang et al., 1996; Brilli et al., 2007; Teuber et al., 2008; Ghirardo et al., 61 2014), and the reason(s) why plants emit isoprene are still ambiguous, and the true role of 62 isoprene emission remains elusive. Different approaches and techniques have been used to 63 determine whether and how the cost of this "expensive" carbon emission is matched by the 64 accomplishment of the physiological function *in planta*. It has been shown that isoprene 65 might quench and/or regulate reactive oxygen and nitrogen species formation (Behnke et al., 66 2010a; Velikova et al., 2012), therefore indirectly providing a general antioxidant action 67 (reviewed in Vickers et al., 2009; Loreto and Schnitzler, 2010) and stabilizing thylakoid 68 membrane structures due the lipophilic properties of this molecule (Sharkey et al., 2001; 69 Velikova et al., 2011).

70 Protein and pigment-protein complexes are assembled and embedded in a lipid matrix, 71 which has a unique lipid composition. The thylakoid lipid bilayer of chloroplasts is 72 characterized as a high proportion of galactolipids with one (monogalactosyldiacylglycerol, 73 MGDG) or two (digalactosyldiacylglycerol, DGDG) galactose molecules (Joyard et al., 2010). 74 MGDGs are the primary constituents (~50%) of thylakoid membrane glycerolipids, followed 75 by DGDGs (~30%), sulfoquinovosyl diacylglycerol (SQDG, ~5-12%) and 76 phosphatidylglycerol (PG, 5-12%) (Kirchhoff et al., 2002). Galactolipids contain a large 77 proportion of polyunsaturated fatty acids, and consequently the thylakoid membrane is a 78 relatively fluid system (Gounaris and Barber, 1983) compared with other biological 79 membranes. The fluidity of the thylakoid membrane is essential for photosynthetic processes.

80 The thylakoid membranes are highly organized internal membrane chloroplast systems that 81 conduct the light reactions of photosynthesis. These membranes comprise pigments and 82 proteins organized in complexes. Thylakoid membranes are arranged into stacked and 83 unstacked regions called grana and stroma thylakoids, respectively, differentially enriched in 84 photosystem I (PSI) and photosystem II (PSII) complexes (Mustárdy et al., 2008). The spatial 85 separation of the PSI and PSII complexes in the stacked and unstacked membrane regions and 86 the macromolecular organization of PSII in stacked grana thylakoids are self-organizing 87 processes and important features to maintain the functional integrity of the photosynthetic 88 apparatus (Kirchhoff et al., 2007).

89 It is not known how changes in the lipid matrix affect lipid-protein interactions and *vice* 90 *versa*, and how membrane macro-organization ensures the efficient diffusion of protein 91 complexes, associated with plant adaptation to the changing environment remains elusive. 92 The isoprene impact on thylakoid intactness and functionality has been assessed using 93 different biophysical techniques (Velikova et al., 2011). Thermoluminescence data 94 demonstrated that the position of the main peak (O_B peak) was up-shifted approximately 10^oC 95 in isoprene emitting plants, suggesting modifications in the lipid environment due to the 96 presence of isoprene in heterologous *Arabidopsis* plants expressing the isoprene synthase 97 gene from poplar. It was also shown that isoprene improves the stability of PSII light-98 harvesting complexes (LHCII-PSII) through the modification of pigment-protein complex 99 organization in thylakoid membranes (Velikova et al., 2011). Moreover, we recently showed 100 that knocking down isoprene emission in poplar remodels the chloroplast proteome (Velikova 101 et al., 2014). The lack of isoprene resulted in the down-regulation of proteins associated with 102 the light reactions of photosynthesis, redox regulation and oxidative stress defenses and 103 several proteins responsible for lipid metabolism (Velikova et al., 2014).

104 In the present study, we focused on the lipid composition of thylakoid membranes in 105 isoprene-emitting (IE) and non-emitting (NE) poplar leaves. Specifically, we determined 106 whether the translational suppression of isoprene synthase in NE leaves influences the lipid 107 matrix of thylakoids and how this phenomenon affects membrane structure and function. Here 108 we provided evidence that the suppression of isoprene biosynthesis in poplar (i) reduced total 109 galactolipids, phospholipids, and linolenic fatty acid (18:3), (ii) altered the chloroplast 110 ultrastructure, and (iii) stimulated photoprotective mechanisms.

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113 **RESULTS**

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115 **Lipid, fatty acid and malondialdehyde analyses**

116 Chloroplast membranes isolated from NE poplar had significantly lower (-53%, P<0.01) 117 lipid contents than the membranes of IE plants (Fig. 1). In both NE and IE plants, the major 118 molecular species of MGDG were 18:2-18:3 and 18:3 dimers. In DGDG the major molecular 119 species were n16:0-18:3 and 18:3 dimers. Linolenic acid (18:3) was the major fatty acid of 120 both IE and NE chloroplast membranes, but the content of this fatty acid was consistently 121 much lower in NE than in IE plants (Table 1, Fig. S1). The fatty acid analysis also revealed 122 significantly lower palmitic (n16:0), linoleic (18:2) and stearic (n18:0) acid contents in NE 123 plants compared with IE plants. In the fraction of the phospholipids (PL) the phosphatidic 124 acid (18:1) levels were lower in NE plants.

125 The concentration of malondialdehyde (MDA), the principal product of polyunsaturated 126 fatty acid peroxidation, was lower in chloroplasts isolated from NE plants than in those 127 isolated from IE poplars (Fig. 2), associated with a lower concentration of polyunsaturated 128 fatty acids in NE chloroplasts (Table 1, Fig. S1).

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130 **Chloroplast ultrastructure observations and protein abundance in photosynthetic** 131 **membranes**

132 To determine whether the different lipid concentrations and changes in lipid composition 133 affect the chloroplast structure, thin leaf segments obtained from the middle region of IE and 134 NE leaves were subjected to Transmission Electron Microscopy **(**TEM) analyses.

135 Representative micrographs of chloroplasts from IE and NE specimens are shown in Fig. 3 136 and 4.

137 The typical elliptic shape of mesophyll chloroplasts was more oval in NE than in IE 138 specimens (Fig. 3). The mesophyll cells of IE leaves are characterized by a well-developed 139 inner membrane system, comprising grana of different sizes and relatively long stromal 140 thylakoids. IE chloroplasts contained single, midsize starch granules, less numerous 141 peroxisomes, and these organelles were associated with relatively small-sized mitochondria 142 (Fig. 3A, B and 4A, B).

143 Conversely, the chloroplasts of NE plants were characterized by a less developed 144 membrane system, with shorter and fewer grana stacks and longer stroma thylakoids (Fig. 4 C, 145 D, E). NE chloroplasts contained more plastoglobules and smaller starch grains than IE 146 chloroplasts (Fig. 3C, D). NE chloroplasts were also in close structural contact with 147 mitochondria through relatively large associative regions (Fig. 4C). A relatively large number 148 of NE chloroplasts were undeveloped (data not shown).

149 To further understand how the structural changes were related with the protein enrichment 150 in photosynthetic membranes we extracted MS data from our recent proteome study 151 (Velikova et al., 2014). The concentrations of PSI-RCI and PSII-RCII were strongly 152 decreased in NE chloroplasts compare to IE (Fig. 5A, B). Lower protein abundance of PSII-153 RCII correlated with less number of stacks (Fig. 4F). Chlorophyll concentrations in the NE 154 lines RA1 and RA2 were also significantly reduced (Fig. 5C).

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156 **Chlorophyll fluorescence**

157 We measured light- and dark-adapted states of chlorophyll fluorescence in IE and NE 158 poplar plants grown under ambient greenhouse conditions (Fig. 6). There was no significant 159 difference in maximal PSII activity between IE and NE plants (data not shown), suggesting 160 that the efficiency of PSII, when all reaction centers were open, was similarly high in both 161 groups of plants. However, NE leaves exhibited significantly lower Φ_{PSII} and qL and higher 162 NPQ (non-photochemical quenching) and qE (energy-dependent quenching) (Fig. 6). 163 Importantly, the true efficiency of PSII (Φ_{PSII}) was lower in NE compared with IE, indicating 164 that a smaller fraction of the absorbed light energy was used for photochemistry. Indeed, the 165 accurate indicator of the PSII redox state, qL, (Baker, 2008), was significantly lower in NE, 166 suggesting that the fraction of open PSII reaction centers was much lower in these mutants 167 (Figs 5, 7, Fig. S2).

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169 **Multivariate data analyses**

170 We examined the involvement of lipid content and fatty acid compositions in NE and IE 171 chloroplasts, compared with chlorophyll fluorescence measurements, MDA contents and 172 previously described proteomic differences (Velikova et al., 2014). The principal component 173 (PC) analysis showed that the isoprene emission traits reflected the largest variance of the 174 measured data, indicated by the separation between NE and IE samples in the first two 175 principal components (Fig. S2; explained variance: PC1=51%, PC2=16%). Additionally, 176 there were no appreciable differences within the two groups, as both RA1 and RA2 lines and 177 WT and EV lines clustered together in the NE and IE groups, respectively.

178 We performed a discriminant analysis to determine which of the analyzed parameters were 179 significantly affected by the suppression of isoprene biosynthesis and assess the relative 180 importance of these parameters in distinguishing NE from IE plants (Fig. 7). The OPLS 181 analysis indicated, overall, that differences between NE and IE chloroplasts reflect the lipid 182 composition, fatty acid and MDA content, chlorophyll fluorescence parameters and 183 chloroplastic proteins associated with photosynthesis or cell structure. Each singular factor 184 had a different importance (Fig. 7C). Specifically, the most important (high VIP values) 185 variables negatively correlated with NE (positive and high correlation coefficient values) 186 were MDA, qL, PL, saturated and unsaturated fatty acids, the MGDG and DGDG, and 187 photosynthetic proteins (Fig. 7B, C). Importantly, the unsaturated fatty acid 18:3 (linolenic 188 acid) was strongly negatively correlated with NE in all lipids (MGDG, DGDG and PL). 189 Additionally, linolenic acid was well correlated with the lipid degradation product MDA, 190 detected in both MGDG and DGDG. The PL content was highly correlated with 191 photosynthetic proteins, namely PSI proteins, ATP synthase, cytochrome $b₆f$ and PsbP. 192 Conversely, NPQ and qE were strongly and positively correlated with the NE genotype.

193 The computed OPLS model was reliable, resulting in a significant (P = 0.00061, CV-194 ANOVA) cross-validated predictive ability of $Q^2(Y) = 84\%$ to distinguish NE from IE 195 samples and a cross-validated goodness of $R^2(X) = 44\%$, $R^2 = 93\%$, $R^2(Y) = 100\%$ using only 196 the first PC.

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199 **DISCUSSION**

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201 **Suppression of isoprene biosynthesis decreases the chloroplastic lipid content and alters** 202 **chloroplast ultrastructure**

203 One of the proposed biological functions of isoprene is the stabilization of thylakoid 204 membrane structures through the modification of the lipid environment and organization of 205 the pigment-protein complexes in thylakoid membranes (Velikova et al., 2011). Indeed, 206 several clear alterations were evident in thylakoid membrane lipids and fatty acid composition 207 due to the translational suppression of isoprene synthase activity in poplar plants. The most 208 important changes in NE chloroplasts were the absolute decrease in the contents of 209 galactolipids (MGDG, DGDG) and phospholipids (PL) through the down-regulation of the 210 unsaturated fatty linolenic acid (18:3). The functional role of MGDGs in the bioactivity of 211 various membrane proteins is well known (Lee 2003, 2004): a mutant with a defective 212 MGDG synthase 1 (*mgd1*) is unable to produce photosynthetically active membranes 213 (Kobayashi et al., 2013). MGDGs are essential for the efficient activity of violaxanthin de-214 epoxidase (VDE) (Yamamoto and Higashi, 1978). The ability of the lipid mixture to 215 segregate into bilayer and non-bilayer phases might regulate the protein content in chloroplast 216 membranes (Garab et al., 2000). Indeed, we could demonstrate that the proteins related to 217 photosynthesis were strongly down-regulated in NE compared to IE plants (Fig. 7 and Fig. 8; 218 Velikova et al., 2014).

219 DGDGs are the predominant bilayer lipid species in thylakoid membranes of higher plants 220 (Joyard et al., 2010). They exert structural functions and improve the thermal stability of 221 membranes, particularly at high temperatures (Krumova et al., 2010). DGDGs bind to PSII 222 (Loll et al., 2007) through the formation of hydrogen bonds with tyrosine in PSII (Gabashvili 223 et al., 1998), and DGDGs are also important for binding of extrinsic proteins required for the 224 stabilization of the oxygen-evolving complex (Sakurai et al., 2007). Our data clearly indicate 225 that the suppression of isoprene biosynthesis significantly diminished the level of DGDGs in 226 poplar chloroplasts, which was accompanied with a reduction of the RCI and RCII 227 concentration (Fig. 5A, B), PsbP and PsbQ protein subunits of PSII, and LHCI and LHCII 228 (Velikova et al., 2014). When the thylakoid membrane protein complexes were resolved by 229 blue native-PAGE, the protein patterns of the two groups of poplar lines looked quite similar 230 in content and intensity of the individual bands (Velikova et al., 2014, see supporting 231 information). However, semi-quantitative analysis of the individual protein bands showed that 232 the levels of PSI, the PSII dimer, ATP synthase, the PSII monomer, and the cytochrome $b₆f$ 233 complex were slightly reduced in NE compared with IE chloroplasts (Velikova et al., 2014). 234 Decreased lipid and protein levels were associated with changes in the ultrastructure of the

235 chloroplasts from NE plants, suggesting a role for isoprene biosynthesis in the structural 236 organization of plastidic membranes. These results are consistent with previous studies that

237 indicated a role for MGDGs and DGDGs in the structure of thylakoid membranes (Dörmann 238 et al., 1995; Jarvis et al., 2000). In the present study we observed significant reduction of 239 grana stacks per chloroplasts in NE compare to IE poplar lines (Fig. 4E, F), which was related 240 to important decrease in PSI and PSII proteins (Fig. 5A, B). Alterations in protein 241 stoichiometry could exert a direct influence on the thylakoid membrane ultrastructure (Pribil 242 et al., 2014), in particular, the assembly of PSII and LHCII into super- and megacomplexes 243 (Kouřil et al., 2012). It was demonstrated (Labate et al., 2004) that the constitutive expression 244 of the pea *Lhcb 1* gene in transgenic tobacco plants leads to increased grana stacking 245 indicating that increased concentrations of LHCII results in more stacking.

246 Typically, chloroplast membranes have a unique lipid composition characterized by a high 247 proportion of galactolipids containing a large portion of tri-unsaturated fatty acids $(C_{16}$ or $C_{18})$ 248 (Joyard et al., 2010). The high content of tri-unsaturated fatty acids guarantees the high 249 fluidity of the thylakoid membranes and the precise allocation of the photosynthetic 250 machinery to efficiently acquire light energy (Gounaris and Barber, 1983). The level of 251 membrane viscosity is an important factor for the photosynthetic performance, e.g., providing 252 the optimal conditions for the diffusion of hydrophobic molecules, such as plastoquinol 253 (Kirchhoff et al., 2000, 2002) or membrane intrinsic protein complexes (e.g., during state 254 transitions) (Allen and Forsberg, 2001; Tikkanen et al., 2008). The low linolenic acid (18:3) 255 content in all lipid fractions from NE chloroplasts indicates that in the absence of isoprene, 256 the thylakoid membrane fluidity is reduced, which in turn negatively affects the efficiency of 257 PSII photochemistry (Fig. 6). A low level of unsaturation in thylakoid membranes makes PSII 258 extremely susceptible to photoinhibition and causes a significant reduction in the content of 259 D1 protein (the reaction center protein) at high irradiance (Kanervo et al., 1995), suggesting 260 that membrane fluidity is a critical factor for PSII D1 protein turnover. Moreover, we detected 261 in NE chloroplast lower amounts of phosphatidic acid (18:1), an important intermediate in 262 lipid biosynthesis (Joyard et al., 2010) with functions as signaling lipid (Testerink and 263 Munnik, 2005, 2011; Horváth et al., 2012; McLoughlin and Testerink, 2013).

264 We observed that the lower level of linolenic acid (18:3) detected in NE chloroplasts was 265 associated with significantly lower MDA chloroplast content in NE compared with IE poplars 266 (Fig. 2, Table 1). Previous studies have reported that MDA is primarily derived from tri-267 unsaturated fatty acids in chloroplasts (Yamauchi et al., 2008; Schmid-Siegert et al., 2012). 268 MDA can be used as an oxidative stress marker when plants are exposed to unfavorable 269 conditions (Esterbauer et al., 1991), but is also present in healthy plants (Weber et al., 2004; 270 Mène-Saffrané et al., 2007, 2009). On a whole leaf extract level, MDA levels were found 271 higher in NE (Behnke et al., 2010b), which agree with their higher concentrations of linolenic 272 acid (Way et al., 2013).The production of MDA from tri-unsaturated fatty acids serves to 273 adsorb a portion of the reactive oxygen species (ROS) (Mène-Saffrané et al., 2009) and 274 therefore MDA is a by-product in the mechanism of cell protection.

275 Another remarkable observation in the present study was the increased abundance of 276 plastoglobules in NE compared with IE chloroplasts. Plastoglobules are lipoprotein particles 277 containing isoprenoid-driven metabolites (primarily prenylquinones, including plastoquinone 278 and phylloquinone), tocopherols (Vidi et al., 2006) and structural proteins (plastoglobulins) 279 (Bréhélin et al., 2007). The increased number of plastoglobules in NE compared with IE 280 chloroplasts might reflect the higher levels of α -tocopherol in leaves of these lines as 281 previously demonstrated (Behnke et al., 2010b).

282 Electron tomography revealed that plastoglobules are physically coupled to thylakoid 283 membranes via a half-lipid bilayer, providing a direct lipid conduit for metabolite channeling 284 between plastoglobules and thylakoid membranes (Austin et al., 2006). Moreover, 285 plastoglobules are involved in different secondary metabolism pathways, stress responses, and 286 in the development of thylakoids (Bréhélin et al., 2007). In a previous study, we showed that 287 the PAP fibrillin content, comprising lipid-associated proteins (PAPs) and fibrillins, is 288 negatively correlated with the NE plants (Velikova et al., 2014). This observation suggests the 289 involvement of isoprene in the maintenance of thylakoid membranes.

290 Interestingly, we observed larger associative zones between chloroplasts and mitochondria 291 in NE plants. Mitochondria are instrumental for the generation of metabolic energy in 292 eukaryotic cells, and these organelles deliver intermediates to support different metabolic 293 pathways, including photosynthesis (Jacoby et al., 2012). One of the important benefits of 294 mitochondria-chloroplast interactions is the optimization of photosynthetic carbon 295 assimilation through the coordinated production and utilization of ATP and NADPH, the 296 induction of photosynthesis, the activation of enzymes and the maintenance of metabolite 297 levels (Raghavendra and Padmasree, 2003). We propose that the larger associative zones 298 between chloroplasts and mitochondria in NE plants reflect a higher demand for assimilatory 299 power (ATP and NADPH) compared with IE. Indeed, the down-regulation of the cytochrome 300 *b6f* complex in NE chloroplasts indicates the inhibition of ATP production, associated with 301 the down-regulation of extrinsic subunits of ATP synthase in isoprene-suppressed lines 302 (Velikova et al., 2014). Because isoprene functions as protective molecule against oxidative 303 stress (Loreto and Schnitzler, 2010), the isoprene suppression in NE plants might be balanced 304 by enhancing other compensatory protective mechanisms such as photorespiration and 305 oxidative electron transport, which are both mediated by mitochondria.

306 Recent analyses demonstrated that the suppression of isoprene biosynthesis dramatically 307 reduces carbon fluxes throughout the MEP pathway (Ghirardo et al., 2014), followed by the 308 re-allocation of carbon to other pathways, which in turn induces profound metabolic changes, 309 particularly in lipid biosynthesis (Way et al., 2013; Kaling et al., 2015). Thus, at the cellular 310 level, lipid metabolism is up-regulated in NE leaves, whereas at the subcellular level, as 311 shown herein, low levels of galactolipids and phospholipids comprise the structure of NE 312 chloroplasts. These results suggest that the crucial needs of NE plants to maintain the correct 313 fluidity of thylakoid membranes induces the up-regulation of lipid metabolism, including lipid 314 intermediates, likely compensating for the low levels of galactolipids and phospholipids 315 packed into chloroplast membranes. Thus, isoprene might (i) directly improve the fluidity of 316 thylakoid membranes in synergy with galactolipids or (ii) indirectly affect lipid biosynthesis 317 or trafficking into the chloroplast. Whether, the lack of isoprene function or the alteration of 318 the plastidic isoprenoid pathway itself induces changes in the chloroplastidic lipid levels, 319 thereby affecting membrane fluidity, should be examined in future studies.

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321 **Functional changes relate to structural alterations in NE chloroplasts**

322 We measured light- and dark-adapted states of chlorophyll fluorescence in IE and NE 323 poplar plants grown under unstressed conditions in order to assess whether the structural 324 changes have functional significance as regards the differences in ability to emit isoprene. Our 325 results showed that Φ_{PSII} was lower in NE plants than in IE plants, consistent with previous 326 observations that the proteins involved in photosynthetic processes are down-regulated in NE, 327 potentially decreasing the efficiency of photochemistry of photosynthesis (Fig. 5; Velikova et 328 al., 2014). The lower Φ_{PSII} values in NE were negatively correlated to NPQ, a protective 329 mechanism for the removal of excess excitation energy within pigment complexes and the 330 inhibition of the formation of free radicals (Demmig-Adams and Adams, 2006).

331 Higher NPQ levels in concert with restricted ETR between both photosystems and a 332 reduced plastoquinone pool has been shown (Härtel et al., 1998) to be accompanied by 333 DGDG modifications in the *Arabidopsis* mutant (*dgd1*). Moreover, in this mutant PSI showed 334 an increased capacity for cyclic electron transfer and a reduced capacity for state transitions 335 (Ivanov et al., 2006). Similar to the *dgd1* mutant (Dörmann et al., 1995), the NE poplar plants 336 showed a lower DGDG content, modified chloroplastic ultrastructure, increased NPQ, 337 restricted ETR (Behnke et al., 2007), and decreased total chlorophyll content (Fig. 5C) 338 (Behnke et al., 2013; Way et al., 2013; Ghirardo et al., 2014).

339 The NPQ comprises energy-dependent (i.e., dependent on the energization of thylakoid 340 membranes) quenching (qE), state transitions (qT) (Minagava, 2011), photoinhibition 341 quenching (qI) (Müller et al., 2001), and zeaxanthin-dependent quenching (qZ) (Nilkens et al., 342 2010). Energy-dependent quenching is the most important and well-characterized component 343 of NPQ. This transition is triggered through the acidification of the thylakoid lumen (Ruban et 344 al., 2012), which in turn leads to the protonation of VDE, for the conversion of violaxanthin 345 to zeaxanthin, and PsbS, a polypeptide of the PSII-associated LHC (Kiss et al., 2008; Murchie 346 and Niyogi, 2011).

347 Here we showed higher values of qE in NE plants, which might reflect a particular 348 conformation of the LHCII complex resulting from chlorophyll and/or xanthophyll/protein 349 interactions (Horton et al., 2005). Indeed, we observed that many proteins associated with 350 photosynthesis are less abundant in NE chloroplasts (Fig. 5 and Fig. 7; for detail see Velikova 351 et al., 2014). This lack of photosynthetic proteins could lead to specific conformational 352 changes, which in turn could determine the higher qE in NE poplars. However, the 353 supramolecular organization of the PSII antenna involves numerous interactions between 354 proteins, suggesting that the changes in these interactions (Garab and Mustardy, 1999; Horton 355 et al., 2005) could be responsible for the increase in NPQ we observed in NE plants. Indeed, 356 with CD spectroscopy it has been shown that isoprene deficiency inhibits the formation of the 357 chirally organized macrodomains. This effect in turn decreases the thermal stability of 358 thylakoid membranes (Velikova et al., 2011). We also observed the significant down-359 regulation of the cytochrome *b6f* complex in NE lines (Velikova et al., 2014), which might 360 inhibit the production of ATP in isoprene-suppressed plants. The increase of qE in NE lines 361 might reflect the optimization of electron transport and ATP synthesis through the modulation 362 of the cyclic electron transfer around PSI, the activation state of ATP synthase, and the 363 partitioning of the proton motive force between ΔpH and the membrane electrical potential 364 (Horton et al., 2005).

365

366 **CONCLUSION**

367 The proposed biological functions of isoprene in plants have been associated with the 368 ability of this molecule to affect thylakoid membrane organization and reduce the formation 369 of ROS, conferring tolerance to heat and oxidative stress. It has been hypothesized that 370 isoprene improves the thermal stability of thylakoid membranes by affecting the membrane

371 lipid composition (Velikova et al., 2011). Herein, we provided direct evidence of the 372 relationship between isoprene emission and the level of main lipid classes and their fatty acid 373 composition, and we characterized the structural organization of the photosynthetic 374 machinery in IE and NE poplar genotypes. The suppressed isoprene production in NE plastids 375 was associated with the reduced amount of galacto- and phospholipids, lower level of the 376 major fatty acid (18:3), and altered chloroplast ultrastructure (Fig. 8). The suppression of 377 isoprene biosynthesis causes considerable metabolic changes, particularly in lipid 378 biosynthesis (Way et al., 2013; Kaling et al., 2015) and significant alterations in the 379 chloroplast proteome (Velikova et al., 2014). The majority of the plastidic and mitochondria 380 proteome is encoded in the nuclear genome, and there is a continuous exchange of "forward" 381 information from nucleus-to-organelle (anterograde) and of "backward" information from 382 organelle-to-nucleus (retrograde) (Pfannschmidt, 2010). According to the retrograde signaling 383 concept, based on the available experimental data, signals originating in chloroplasts and/or 384 mitochondria modulate nuclear gene expression (Leister, 2012). These signals originate from 385 carotenoid biosynthesis, ROS, photosynthetic redox processes, and changes in the pool of 386 metabolites (Pfannschmidt, 2010; Leister, 2012). The plastidic signals identified so far have 387 been associated with specific stress conditions. It is likely that the comprehensive changes in 388 the metabolome (e.g., Way et al., 2013; Kaling et al., 2015), liposome, proteome (Velikova et 389 al., 2014) and ultrastructure of the chloroplasts in non-isoprene emitting poplars (Fig. 8) as 390 well as the distinct physiological behavior of these plants reflects finely tuned retrograde 391 signaling. The precise mechanism(s) for the transmission of the changes in chloroplast to the 392 nucleus in NE plant cells remain elusive.

393

394 **MATERIAL AND METHODS**

395 **Plant material**

396 In the present study, we used the same gray poplar (*Populus* x *canescens; syn. Populus* 397 *tremula* x *P. alba*) genotypes as utilized in previous chloroplast proteome research (Velikova 398 et al., 2014), namely two isoprene-emitting lines (IE: wild type and empty vector control, 399 WT/EV) and two non-isoprene emitting (NE: RA1/RA2) lines. EV was used to ensure that 400 the differences between NE and IE reflected specific alterations in the isoprene synthase gene 401 and not to a more general genetic manipulation effect. The plants were grown in a greenhouse 402 as previously described (Velikova et al., 2014). Briefly, the ambient temperature was 25/20°C, 403 with a relative humidity of 50/60% and a photoperiod of 16/8 h (day/night). The plants were 404 fertilized weekly with Triabon (Compo, Münster, Germany) and Osmocote (Scotts Miracle-405 Gro, Marysville, OH) (1:1 v/v; 10 g per liter of soil).

406 Four-month-old plants were used for the experiments. Fully expanded leaves $(9th$ node 407 from the apical meristem) from 6-7 different plants, considered as biological replicates, were 408 used for physiological, biochemical and structural studies. The chloroplasts were isolated as 409 previously described (Velikova et al., 2014) and used for lipid and malondialdehyde (MDA) 410 analyses.

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412 **Lipid extraction procedure**

413 The total lipids from chloroplasts were extracted according to Bligh and Dyer (1959). All 414 procedures were performed in dim light using chilled solvents (containing BHT, 0.01% w/v) 415 and glassware. The chloroplast samples (0.5 mL) were mixed with chloroform/methanol (1:2 416 v/v; 1.9 mL) for approximately 2 min, and subsequently 0.625 mL of chloroform and 0.625 417 mL of distilled water were added. The lower chloroform phase, containing the lipids, was 418 removed, and aliquots were transferred into vials and exsiccated under $N₂$. The residues were 419 weighed and calculated for total lipids.

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421 **GC-MS analysis of phospholipid fatty acid composition**

422 Phospholipid fatty acids (PLFAs) were analyzed as previously described (Way et al., 2013; 423 Behnke et al., 2013). Briefly, the PLFAs were separated from other lipids using a silica 424 bonded phase column (MEGA-BE-SI, 2 g 12 mL⁻¹, 20/PK, Bond ELUT, Agilent 425 Technologies, CA, USA). Fatty acid methyl esters (FAMEs) were obtained after mild alkaline 426 hydrolysis. Myristic acid was used as internal standard for gas chromatography analysis. Un-427 substitute FAMEs were measured using a 5973MSD GC-MS (Agilent Technologies, 428 Oberhaching, Germany) coupled with a combustion unit to an isotope ratio mass spectrometer 429 (DeltaPlus; Thermo Electron Corporation, Bremen, Germany) and identified using the 430 established fatty acid libraries and characteristic retention times of pure standards. The fatty 431 acids were named according to the total number of C atoms and double bonds. Saturated 432 straight-chain fatty acids are indicated as 'n'.

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434 **UPLC-ESI-Qq-ToF-MS of galactolipids**

436 Lipids were dissolved in 1 mL of LC-MS grade methanol (Fluka). MGDG and DGDG 437 contents were analyzed using the UPLC-ESI Qq-ToF-MS System (Ultra performance liquid 438 chromatography electrospray time of flight mass spectrometry, maXis Bruker, Bremen, 439 Germany). Aliquots of 2.5 µL of each sample were analyzed in three technical replicates in 440 randomized order.

441 The chromatographic separation was achieved on a C₁₈ ACQUITYUPLC BEH column, 50 442 mm, 2.1 mm, and 1.7 µm (Waters), using a gradient elution. The composition was changed 443 from 50% to 92% B for 10 min and maintained for an additional 10 min, then change to 100% 444 B for 1 min and maintained for 5 min. The flow was set to 0.4 mL h^{-1} . Mobile phase A 445 comprised water/isopropyl alcohol (95:5, v/v), and mobile phase B comprised 446 acetonitrile/isopropyl alcohol (95:5, v/v). A format of 0.001 mM sodium (Sigma-Aldrich, 447 Taufkirchen, Germany) was added to both mobile phases. This method has been previously 448 published for profiling photosynthetic glycerol lipids (Xu et al., 2010).

449 MGDGs and DGDGs were detected as sodium adducts through positive electrospray 450 ionization. The instrument was calibrated with ESI tune mix (Agilent Technologies). 451 Acquired spectra were internally calibrated and exported to GENEDATA software for 452 chromatographic alignment and peak picking. MGDGs and DGDGs were identified based on 453 the retention time and detected exact mass (mass error < 0.01 Da).

454 MGDG and DGDG standards (Larodan) were used to evaluate the analytical performance 455 and determine the QC, which was injected 10 times in the beginning for column conditioning 456 and after every 10^{th} sample to validate the measuring performance.

457

458 **Malondialdehyde (MDA) content**

459 The lipid peroxidation level in extracted chloroplast samples was quantified after 460 measuring the MDA content using the thiobarbituric acid-reactive substances (TBARS) assay 461 according to Hodges et al. (1999). The chloroplast sample (0.100 mL) was mixed with 1.2 mL 462 of 80% ethanol (containing 0.01% BNT w/v) and sonicated in a water bath sonicator for 3 463 min, followed by centrifugation at 5,000 *g* for 10 min at 4ºC. An aliquot of the obtained 464 supernatant (0.5 mL) was mixed with the same volume of 0.65% (w/v) thiobarbituric acid 465 (TBA) solution containing 20% (w/v) trichloroacetic acid (TCA). Another aliquot of the 466 supernatant (0.5 mL) was mixed with 0.5 mL of 20% (w/v) TCA, representing the zero-467 control. The mixture was heated at 95ºC for 30 min. The reaction was terminated after 468 incubation in an ice bath. The cooled mixture was centrifuged at 10,000 *g* for 10 min at 4ºC, 469 and the absorbance of the supernatant was measured at 532, 600 and 440 nm (Perkin Elmer, 470 Walthman, MSC, USA). MDA equivalents were calculated according to Hodges et al. (1999), 471 namely:

472 1) $[A_{532+\text{TBA}} - A_{600+\text{TBA}} - (A_{532-\text{TBA}} - A_{600+\text{TBA}})] = A$

473 2) $[(A_{440+TBA} - A_{600+TBA}) \times 0.0571] = B$

474 3) MDA equivalents (nmol ml⁻¹) = $(A - B)/157000$) x 10⁶

475

476 **Protein and chlorophyll analysis**

477 For the calculation of the abundance of reaction center proteins in PSI and PSII we used 478 the chloroplast proteome data published in Velikova et al. (2014). Peak intensities of peptides 479 identified as RCI (protein accession numbers: POPTR_0008s15100.1, POPTR_0006s27030.1, 480 POPTR_0003s14870.1, POPTR_0002s25510.2) and RCII (protein accession numbers: 481 POPTR_0011s03390.1, POPTR_0004s03160.1, POPTR_0005s22780.1, POPTR_0002s05660.1, 482 POPTR_0005s01430.1, POPTR_0005s27800.3, POPTR_0002s05720.1, POPTR_0002s25810.1, 483 POPTR_0001s44210.1, POPTR_0006s26270.1), respectively, were summed, and expressed per 484 mg chlorophyll.

485 The chlorophyll content was measured in isolated chloroplast suspension after extraction 486 with 80% of ice-cold acetone. Absorbance at 663 and 646 nm was detected to determine 487 chlorophyll a and chlorophyll b concentrations, calculated according to Porra et al. (1989).

488

489 **Chlorophyll fluorescence measurements**

490 The chlorophyll fluorescence parameters were measured on intact leaves using a MINI-491 PAM Photosynthesis Yield Analyzer (Heinz Walz GmbH, Effeltrich, Germany). The leaves 492 were dark-adapted for 15 min prior to the determination of the minimal (F_0) and maximal (F_m) 493 chlorophyll fluorescence, and subsequently the leaves were exposed to actinic light (430 μmol 494 m⁻² s⁻¹). After steady-state fluorescence was obtained, a saturating pulse was applied to 495 determine the maximum fluorescence in the light (F_m) . The operating efficiency of PSII 496 photochemistry (Φ_{PSII}) was calculated from $(F_m^{\prime} - F^{\prime})/F_m^{\prime}$ (Genty et al., 1989). The redox 497 state of PSII was assessed based on the parameter $qL = (F_q/F_v) / (F_o/F^2)$, where F' is the 498 fluorescence emission from the light-adapted leaf, F_v ^{\cdot} - variable fluorescence from the light-499 adapted leaf, and F_q ' is the difference in fluorescence between F_m ' and F' (Baker, 2008); F_0 ' 500 was estimated using the following equation: $F_o' = F_o/[(F_v/F_m) + F_o/F_m']$ (Oxborough and 501 Baker, 1997). The non-photochemical quenching (NPQ) was calculated as NPQ = $(F_m -$ 502 Fm')/Fm' (Bilger and Björkman, 1991). The NPQ relaxation kinetics in the dark was used to 503 calculate energy-dependent (qE) quenching. qE was assigned as a fast-relaxing component 504 (within the first 2 minutes of dark relaxation after switching off the actinic light), calculated 505 as $qE = (F_m' - F_m')/F''_{m.2min dark}$ (Zaks et al., 2013).

506

507 **Transmission Electron Microscopy (TEM)**

508 Leaf segments (1 mm^2) were cut from the middle of the leaves for TEM analyses. The 509 segments were fixed in 2.5% (v/v) glutaraldehyde (electron microscopy grade) in 0.1 M 510 sodium cacodylate buffer, pH 7.4 (Science Services, Munich, Germany), post-fixed in 2% 511 (v/v) aqueous osmium tetraoxide (Dalton, 1955), dehydrated in gradual ethanol (30–70%), 512 stained with uranyl acetate (2% in 70% ethanol), dehydrated in gradual ethanol (70-100%) 513 and propylene oxide (100%), embedded in Epon (Merck, Darmstadt, Germany) and cured for 514 24 h at 60°C. Semi-thin sections (300 nm) were cut and stained with toluidine blue. Ultrathin 515 sections of 50 nm were collected onto 200 mesh copper grids before examination using 516 transmission electron microscopy (Zeiss Libra 120 Plus, Carl Zeiss NTS GmbH, Oberkochen, 517 Germany). The images were acquired using 'Slow Scan CCD-camera' and 'iTEM' software 518 (Olympus Soft Imaging Solutions, Münster, Germany).

519

520 **Statistical analyses**

521 Correlation analyses between different data sets of phospholipid (PL) and galactolipid 522 (MGDG, DGDG) contents, fatty acid compositions, chlorophyll fluorescence parameters, 523 MDA content, the data groups and IE or NE genotypes were performed using Principal 524 Component Analysis (PCA) and Orthogonal Partial Least Square regression (OPLS) from the 525 software package 'SIMCA-P' (v13.0.0.0, Umetrics, Umeå, Sweden). In addition, we included 526 the chloroplastic protein contents associated with photosynthesis and structure (Velikova et al., 527 2014) to correlate lipids to proteins. Because the proteomic data originated from 3 samples for 528 each plant genotype (containing 6 - 7 different leaves each of the three samples), multivariate 529 analyses were performed using only the data matching the same 3 samples used for both 530 proteomic and PL analyses. Galactolipids, MDA, and chlorophyll fluorescence measurements 531 were obtained from more and different extracts, and therefore only the data from 3 samples 532 were taken randomly and used for these analyses. We added the means of all biological 533 replicates to examine the correlations between genotypes using data originating from different 534 leaf extracts. The resulting matrix size was therefore 78-by-16 (variables-by-observations). 535 Thus, the present analyses could correlate any data value with an isoprene emission trait 536 (plant genotype IE and NE), but correlations between/within variables could be achieved only 537 using data from the same leaf material, i.e., within PL and proteins, MGDG, DGDG and 538 MDA, and within chlorophyll fluorescence data.

539 The multivariate data analyses followed the established procedures to analyze MS data as 540 previously described (Ghirardo et al., 2005; Ghirardo et al., 2012; Kreuzwieser et al., 2014; 541 Vanzo et al., 2014; Velikova et al., 2014). The isoprene emission trait was selected as the Y-

542 variable for the OPLS analysis by setting $NE = 1$ and $IE = 0$. The X variables were centered, 543 and each type of data was block-wise scaled with 1 sd^{-1} , considering the different number of 544 X-variables in each group of data. Each calculated significant principal component was 545 validated using 'full cross validation', with 95% confidence level on parameters. The 546 regression model OPLS was further tested for significance using CV-ANOVA (Eriksson et al., 547 2008). Variables showing variable of importance for the projection (VIP) values greater than 548 1 and jack-knifing method uncertainty bars smaller than the respective VIP values were 549 defined as discriminant variables to distinguish IE from NE samples. For the proteomics data, 550 containing a much higher number of variables, the VIP threshold was set to 0.5. The statistical 551 significance of the differences between the means of discriminant variables and the functional 552 and structural parameters measured in NE and IE plants were additionally evaluated using 553 Student's *t*-test and at an α level of 0.05, unless otherwise stated.

- 554
- 555 **Legend to figures:**
- 556 557

558 **Figure 1.** Lipid content in isolated chloroplasts of isoprene emitting (IE, WT/EV) and non-559 isoprene emitting (NE, RA1/RA2) poplar. Error bars display the SE (n=4). Asterisks indicate 560 significant differences with WT; $** P < 0.01$.

561

562 **Figure 2.** MDA level in isolated chloroplasts of isoprene emitting (IE, WT/EV) and non-563 isoprene emitting (NE, RA1/RA2) poplar. Error bars display the SE (n=4). Asterisks indicate 564 significant differences with WT; $* P < 0.05$.

565

566 **Figure 3.** Transmission electron micrographs of representative chloroplast cross-sections 567 taken from the intact leaves of isoprene emitting (IE, WT/EV) (A, B) and non-isoprene 568 emitting (NE, RA1/RA2) (C, D) poplar. Height / Length ratio (E) and average number of 569 starch grains in IE and NE chloroplasts (F). CW - cell wall; GT - granal thylakoids; M, 570 mitochondrion; P, plastoglobuli; S, stroma; SI, starch gain. Scale bar = 1 μ m in A, B, C and D; 571 at x 6,300 magnification.

572

573 **Figure 4.** Transmission electron micrographs of representative chloroplast cross-sections 574 taken from the intact leaves of isoprene emitting (IE, WT/EV) (A, B) and non-isoprene 575 emitting (NE, RA1/RA2) (C, D) poplar. Average number of stacks per chloroplast (E) and 576 correlation between PSII – RCII protein abundance (10 peptides; for protein accession 577 numbers see Materials and Methods) and number of stacks (F). CW - cell wall; GT - granal

- 578 thylakoids; M, mitochondrion; P, plastoglobuli; S, stroma; SI, starch gain. Scale bar = 500 nm
- 579 in A, and C, at x10,000 magnification; and 200 nm in B and D, at magnification x20,000.
- 580

581 **Figure 5.** Protein abundance of PSI-RCI (4 peptides; for protein accession numbers see 582 Materials and methods) (A), PSII-RC (10 peptides; for protein accession numbers see 583 Materials and methods) (B) and chlorophyll content (C) in isoprene emitting (IE, WT/EV) 584 and non-isoprene emitting (NE, RA1/RA2) poplar plants. Protein abundance represents sum 585 of MS data extracted from our proteome study (Velikova et al., 2014). Error bars display the 586 SE (n=4). Asterisks indicate significant differences with WT; ** *P* < 0.01; *** *P* < 0.001.

587

588 **Figure 6.** PSII photochemical efficiency (A), redox state of PSII (B), non-photochemical 589 quenching (C) and NPQ energy-dependent component (D) of isoprene emitting (IE, WT/EV) 590 and non-isoprene emitting (NE, RA1/RA2) poplar plants at growth conditions. Values 591 represent means of 5-7 different plants out of three independent experiments ($n = 15-21, \pm SE$ 592 is given). Photosynthetic parameters are described in "Material and Methods". Asterisks 593 indicate significant differences with WT; $* P < 0.05$, $* P < 0.01$, $* * P < 0.001$.

594

595 **Figure 7.** Score (A), loading (B) and correlation coefficient plots (C) of Orthogonal Partial 596 Least Squares (OPLS) of lipid classes, fatty acid composition and MDA contents in isolated 597 chloroplasts, chlorophyll fluorescence parameters measured in intact leaves (NPQ, Φ_{PSII} , qE 598 and qL), and chloroplast proteins related to photosynthesis and proteins with structural 599 activity. (A) IE (WT/EV), grey circles; NE (RA1/RA2), white triangles. (B) Each parameter 600 is indicated with different symbol. Dark grey circles, MGDG; dark gray square, DGDG; gray 601 triangle, PL; dark gray circles with a dot, MGDG – fatty acids; dark gray square with a dot – 602 DGDG – fatty acids; gray triangle with a dot, PL – fatty acids; green diamond, MDA; red star, 603 NPQ; red triangle-down, qE; blue square, qL; blue star, proteins with structural activity; green 604 star, proteins related to photosynthesis. (C) Parameter colors as plot legend B. Only 605 discriminant data with VIP > 1 (for all except proteins) and VIP > 0.5 (proteins) are presented. 606 Model fitness: $Q^2(Y) = 84\%$; $R^2(X) = 44\%$, $R^2 = 93\%$, $R^2(Y) = 100\%$ using one PC; P = 607 0.00061, CV-ANOVA. 608

609 **Figure 8.** Schematic overview of the changes in chloroplast ultrastructure, lipid composition, 610 change, protein abundance and PSII fluorescence triggered by the suppression of isoprene 611 biosynthesis and emission in poplar plants. 612 613 614 615 **Acknowledgements** 616 617 This research was supported by a grand awarded by the Alexander von Humboldt Foundation 618 to V.V. 619 620 621 **Supporting information** 622 Supplemental Figure S1 provides lipid content and fatty acid composition in isolated 623 chloroplasts of isoprene emitting (IE, WT/EV) and non-emitting (NE, RA1/RA2) poplar. 624 Supplemental Figure S2 provides score and loading plots of PCA all parameters analyzed 625 (lipid and fatty acid composition, MDA, NPQ, Φ_{PSII} , qE, qL, proteins related to 626 photosynthesis and proteins with structural activity. 627 628 629 **LITERATURE CITED** 630 631 **Allen JF, Forsberg J** (2001) Molecular recognition in thylakoid structure and function. 632 Trends Plant Sci **6:** 317-326 633 **Austin JR, Frost E, Vidi P-A, Kessler F, Staehelin LA** (2006) Plastoglobules are 634 lipoprotein subcompartments of the chloroplast that are permanently coupled to thylakoid 635 membranes and contain biosynthetic enzymes. Plant Cell **18:** 1693–1703 636 **Baker NR** (2008) Chlorophyll fluorescence: a probe of photosynthesis in vivo. Ann Rev 637 Plant Biol **59:** 89–113 638 **Behnke K, Ehlting B, Teuber M, Bauerfeind M, Louis S, Hänsch R, Polle A, Bohlmann** 639 **J, Schnitzler JP** (2007) Transgenic, non-isoprene-emitting poplars don't like it hot. Plant 640 J **51:** 485-499 641 **Behnke K, Ghirardo A, Janz D, Kanawati B, Esperschütz J, Zimmer I, Schmitt-**642 **Kopplin P, Niinemets Ü, Polle A, Schnitzler JP, Rosenkranz M** (2013) Isoprene 643 function in two contrasting poplars under salt and sunflecks. Tree Physiol **33:** 562-578 644 **Behnke K, Kaiser A, Zimmer I, Brüggemann N, Janz D, Polle A, Hampp R, Hänsch R,** 645 **Popko J, Schmitt-Kopplin P,Ehlting B, Rennenberg H, Barta C, Loreto F, Schnitzler**

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Table 1. Fatty acid composition (μ g mg⁻¹ Chl) of the main lipid classes in C₁₆-C₂₃ saturated (:0) and unsaturated (:1,:2,:3) compounds in chloroplasts of isoprene emitting (IE, WT/EV) and non emitting (NE, RA1/RA2) poplar plant lines (n16:0, palmitic acid; 16:1, palmitoleic acid; n18:0, stearic acid; 18:1, oleic acid; 18:2, linoleic acid; 18:3, linolenic acid; n23:0, tricosanoic acid).. Fatty acids are designated as the total number of C atoms followed by the number of double bonds and their location (omega) after the colon. Saturated straight-chain fatty acids are indicated by 'n'. Means ± SE and shown; n=4. Asterisks indicate significant differences with WT; * *P* < 0.05, ** *P* < 0.01, *** *P* < 0.001.

Figure 1. Lipid content in isolated chloroplasts of isoprene emitting (IE, WT/EV) and nonisoprene emitting (NE, RA1/RA2) poplar. Error bars display the SE (n=4). Asterisks indicate significant differences with WT; ** *P* < 0.01.

Figure 2. MDA level in isolated chloroplasts of isoprene emitting (IE, WT/EV) and nonisoprene emitting (NE, RA1/RA2) poplar. Error bars display the SE (n=4). Asterisks indicate significant differences with WT; * *P* < 0.05.

Figure 3. Transmission electron micrographs of representative chloroplast cross-sections taken from the intact leaves of isoprene emitting (IE, WT/EV) (A, B) and non-isoprene emitting (NE, RA1/RA2) (C, D) poplar. Height / Length ratio (E) and average number of starch grains in IE and NE chloroplasts (F). CW - cell wall; GT - granal thylakoids; M, mitochondrion; P, plastoglobuli; S, stroma; SI, starch gain. Scale bar = 1 μ m in A, B, C and D; at x 6,300 magnification.

Figure 4. Transmission electron micrographs of representative chloroplast cross-sections taken from the intact leaves of isoprene emitting (IE, WT/EV) (A, B) and non-isoprene emitting (NE, RA1/RA2) (C, D) poplar. Average number of stacks per chloroplast (E) and correlation between PSII – RCII protein abundance (10 peptides; for protein accession numbers see Materials and Methods) and number of stacks (F). CW - cell wall; GT - granal thylakoids; M, mitochondrion; P, plastoglobuli; S, stroma; SI, starch gain. Scale bar = 500 nm in A, and C, at $x10,000$ magnification; and 200 nm in B and D, at magnification x20,000.

Figure 5. Protein abundance of PSI-RCI (4 peptides; for protein accession numbers see Materials and methods) (A), PSII-RC (10 peptides; for protein accession numbers see Materials and methods) (B) and chlorophyll content (C) in isoprene emitting (IE, WT/EV) and non-isoprene emitting (NE, RA1/RA2) poplar plants. Protein abundance represents sum of MS data extracted from our proteome study (Velikova et al., 2014). Error bars display the SE (n=4). Asterisks indicate significant differences with WT; ** *P* < 0.01; *** *P* < 0.001.

Figure 6. PSII photochemical efficiency (A), redox state of PSII (B), non-photochemical quenching (C) and NPQ energy-dependent component (D) of isoprene emitting (IE, WT/EV) and non-isoprene emitting (NE, RA1/RA2) poplar plants at growth conditions. Values represent means of 5-7 different plants out of three independent experiments ($n = 15-21$, \pm SE is given). Photosynthetic parameters are described in "Material and Methods". Asterisks indicate significant differences with WT; * *P* < 0.05, ** *P* < 0.01, *** *P* < 0.001.

Figure 7. Score (A), loading (B) and correlation coefficient plots (C) of Orthogonal Partial Least Squares (OPLS) of lipid classes, fatty acid composition and MDA contents in isolated chloroplasts, chlorophyll fluorescence parameters measured in intact leaves (NPQ, Φ_{PSII} , qE and qL), and chloroplast proteins related to photosynthesis and proteins with structural activity. (A) IE (WT/EV), grey circles; NE (RA1/RA2), white triangles. (B) Each parameter is indicated with different symbol. Dark grey circles, MGDG; dark gray square, DGDG; gray triangle, PL; dark gray circles with a dot, MGDG – fatty acids; dark gray square with a dot – DGDG – fatty acids; gray triangle with a dot, PL – fatty acids; green diamond, MDA; red star, NPQ; red triangle-down, qE; blue square, qL; blue star, proteins with structural activity; green star, proteins related to photosynthesis. (C) Parameter colors as plot legend B. Only discriminant data with VIP > 1 (for all except proteins) and VIP > 0.5 (proteins) are presented. Model fitness: $Q^2(Y) = 84\%$; $R^2(X) = 44\%$, $R^2 = 93\%$, $R^2(Y) = 100\%$ using one PC; P = 0.00061, CV-ANOVA.

Figure 8. Schematic overview of the changes in chloroplast ultrastructure, lipid composition, change, protein abundance and PSII fluorescence triggered by the suppression of isoprene biosynthesis and emission in poplar plants.

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Figure S1. Lipid content and fatty acid composition in isolated chloroplasts of isoprene emitting (IE, WT/EV) and non-emitting (NE, RA1/RA2) poplar. (A) Monogalactosyldiacylglycerols (MGDG), (B) digalactosyldiacylglycerols (DGDG), (C) phospholipids (PL). Error bars display the SE (n=4). Asterisks indicate significant differences with WT; $* P < 0.05$, $* P < 0.01$, $* * P < 0.001$.

Supplemental Figure 2

Fig. S2. Score and loading plots of PCA all parameters analyzed (lipid and fatty acid composition, MDA, NPQ, Φ_{PSII} , qE, qL, proteins related to photosynthesis and proteins with structural activity. (A) IE (WT/EV), grey circles; NE (RA1/RA2), white triangles. (B) Each parameter is indicated with different symbol. Dark grey circles, MGDG; dark gray square, DGDG; gray triangle, PL; dark gray circles with a dot, MGDG – fatty acids; dark gray square with a dot – DGDG – fatty acids; gray triangle with a dot, PL – fatty acids; green diamond, MDA; red star, NPQ; red triangle-down, qE; blue square, qL; blue star, proteins with structural activity; green star, proteins related to photosynthesis. Data with VIP > 1 (all data except proteins) and VIP > 0.5 (proteins) are presented.

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Figure S1. Lipid content and fatty acid composition in isolated chloroplasts of isoprene emitting (IE, WT/EV) and non-emitting (NE, RA1/RA2) poplar. (A) Monogalactosyldiacylglycerols (MGDG), (B) digalactosyldiacylglycerols (DGDG), (C) phospholipids (PL). Error bars display the SE (n=4). Asterisks indicate significant differences with WT; * *P* < 0.05, ** *P* < 0.01, *** *P* < 0.001.

Supplemental Figure 2

Fig. S2. Score and loading plots of PCA all parameters analyzed (lipid and fatty acid composition, MDA, NPQ, Φ_{PSII} , qE, qL, proteins related to photosynthesis and proteins with structural activity. (A) IE (WT/EV), grey circles; NE (RA1/RA2), white triangles. (B) Each parameter is indicated with different symbol. Dark grey circles, MGDG; dark gray square, DGDG; gray triangle, PL; dark gray circles with a dot, MGDG – fatty acids; dark gray square with a dot – DGDG – fatty acids; gray triangle with a dot, PL – fatty acids; green diamond, MDA; red star, NPQ; red triangle-down, qE; blue square, qL; blue star, proteins with structural activity; green star, proteins related to photosynthesis. Data with VIP > 1 (all data except proteins) and VIP > 0.5 (proteins) are presented.