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1 **,Feeding guild determines strength of top-down forces in multitrophic system experiencing**
2 **bottom-up constraints**

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25 **Abstract**

26 Nitrogen (N) and water are crucial in crop production but increasingly scarce environmental resources.
27 Reducing their inputs can affect the whole plant-arthropod community including biocontrol agents. In a
28 multitrophic system, we studied the interaction of the bottom-up effects of moderately reduced N
29 concentration and/or water supply as well as the top-down effects of pests of different feeding guilds on plant
30 nutritional quality (N and carbon concentration), direct defense (alkaloids and phenolics), and indirect defense
31 (plant volatile organic compounds); on herbivore performance and host quality (N and carbon) to parasitoids
32 and the latter's performance. Studied organisms were tomato plants, the sap feeders *Macrosiphum euphorbiae*
33 and *Bemisia tabaci*, the leaf chewers *Tuta absoluta* and *Spodoptera littoralis*, and the parasitic wasps *Aphelinus*
34 *abdominalis* and *Necremnus tutaе*. Resource limitation affected plant quality, triggering bottom-up effects on
35 herbivore and parasitoid performance, except for *T. absoluta* and *N. tutaе*. Feeding guild had a major influence:
36 bottom-up effects were stronger on sap feeders; N effects were stronger on sap feeders while water effects
37 were stronger with leaf chewers (*S. littoralis*). Top-down effects of leaf chewer herbivory partly attenuated
38 bottom-up effects and partly suppressed plant defenses. Bottom-up effects weakened when cascading up
39 trophic levels. In summary, the interaction between plants, pests, and beneficial insects was modulated by
40 abiotic factors, affecting insect performance. Simultaneous abiotic and biotic impact shaped plant biochemistry
41 depending on the feeding guild: the biotic top-down effect of leaf chewer herbivory attenuated the bottom-up
42 effects of plant nutrition and hence dominated the plant biochemical profile whereas in sap feeder infested
43 leaves, it corresponded to the abiotic impact. This study highlights the plant's finely tuned regulatory system
44 facilitating response prioritization. It offers perspectives on how smart manipulation of plant nutrient solutions
45 might save resources while maintaining efficient biocontrol in crop production.

46 **Key words:** plant environment interactions; phenolics; alkaloids; plant VOC; herbivore; parasitoid

47 **Abbreviations:**

48 HN/LN: high nitrogen/low nitrogen

49 HW/LW: high water/low water

50 QARG = quercetin-3-(2"apiosyl-6"-rhamnosyl)glucoside)

51 KR = kaempferol rutinoside

52 1) Introduction

53 Food webs are shaped by trophic interactions, influenced by environmental factors and driven by network
54 forces. Bottom-up effects initially affect lower trophic levels and propagate up onto higher trophic levels while
55 top-down effects initially affect higher and cascade down onto lower trophic levels. Both top-down and
56 bottom-up effects can be of outstanding importance in multitrophic terrestrial ecosystems because of the
57 trophic interdependence between the levels (Ripple *et al.* 2016; Rosenblatt & Schmitz, 2016; Schuldt *et al.*,
58 2017). While bottom-up forces determine the energy that is available to a community, top-down forces
59 determine how that energy is redistributed among trophic levels (Terborgh, 2015). Resource limitation can
60 alter the nutritional value and/or concentration of toxins in plants (Le Bot *et al.*, 2009; Couture *et al.*, 2010; Han
61 *et al.*, 2015). These effects can propagate up to higher trophic levels, e.g. natural enemies of herbivores,
62 because the plant is the sole source of nutrition and water for herbivores and changes therein can alter their
63 biochemical composition and therefore their quality as insect hosts to natural enemies (Han *et al.*, 2019).

64 Tomato (*Solanum lycopersicum*) is the most cultivated vegetable crop worldwide (Schwarz *et al.*, 2014)
65 requiring high inputs of nitrogen (N) and water (Kempen, 2015). Yet, excessive fertilization threatens
66 ecosystems and human health (Galloway *et al.*, 2008) and freshwater resources decline due to human demand
67 and climate change (Elliott *et al.*, 2014). Nitrogen and water are important macronutrients in plants, crucial for
68 a plethora of processes and suboptimal supply can affect their primary and secondary metabolism (English-
69 Loeb *et al.*, 1997; Chaves *et al.*, 2002; Liu *et al.*, 2010; Han *et al.*, 2016). Such changes in plant chemistry can
70 have bottom-up effects on higher trophic levels (see Han *et al.* 2022 for a thorough review), mediated by
71 nutritional and/or defense compounds (Coqueret *et al.*, 2017; English-Loeb *et al.*, 1997; Huberty & Denno,
72 2004; Han *et al.*, 2014; Han *et al.*, 2016; Han *et al.*, 2019) or their interaction (Le Bot *et al.*, 2009; Couture *et al.*,
73 2010) but the effects vary between plant species and cultivars (Rivelli *et al.*, 2013; Han *et al.*, 2016) and with
74 insect species and their feeding guild (Huberty & Denno, 2004; Gutbrodt *et al.*, 2011; Stam *et al.*, 2014).

75 Quantitatively, the main defense compounds in tomato are glycoalkaloids and phenolics (Awmack & Leather,
76 2002; Cataldi *et al.*, 2005; Lariat *et al.*, 2014; Lariat *et al.*, 2016). They can have negative effects on insect
77 herbivore development (Lattanzio *et al.*, 2000; Friedman, 2002; Simmonds, 2003) and their concentrations can
78 increase with N and water limitation (English-Loeb *et al.*, 1997; Le Bot *et al.*, 2009; Han *et al.*, 2016; Lariat *et*
79 *al.*, 2016). Carbon (C) and N concentrations can be used as a proxy for nutritional quality because they are
80 especially important for herbivore performance (Awmack & Leather, 2002; Altieri & Nicholls, 2003; Lariat *et*

81 *al.*, 2016) as is plant water concentration (English-Loeb *et al.*, 1997). Drought spells often co-occur with
82 herbivore outbreaks (Mattson & Haack, 1987).

83 Volatile organic compounds (VOC) emitted by plants serve multiple ecological functions. Constitutively emitted
84 VOCs may help herbivores to locate suitable host plants while herbivory-induced plant volatiles (HIPV) can
85 attract natural enemies of the respective herbivore (Dicke & Baldwin, 2010; Tasin *et al.*, 2011). Both
86 constitutive VOCs as well as HIPV are potentially affected by abiotic conditions (Becker *et al.*, 2015).

87 The dilemma of plants is how to partition their finite resources between growth and defense-related processes
88 has been the subject of multiple “*plant defense*” hypotheses. The “*Optimal Defense hypothesis*”, for instance,
89 predicts that the degree of predation risk determines the level of plant defense which is restrained under
90 resource limitation because defense is costly (Rhoades, 1979; Stamp, 2003). The “*Growth-Differentiation*
91 *Balance hypothesis*” predicts that the availability of photosynthates and nutrients within plants, affected by
92 environmental factors, determines the allocation of resources – within the boundaries of genotype and
93 phenotypic plasticity – and that plants under moderate resource limitation are defended best (Herms &
94 Mattson, 1992). There are continuous attempts to refine these hypotheses and synthesize a common
95 framework (Herms & Mattson, 1982; Stamp, 2003; Züst & Agrawal, 2017).

96 Alterations in plant biochemistry can affect insect herbivores differently according to their feeding guild (Stam
97 *et al.*, 2014): sap-feeding herbivores are mainly in contact with compounds in the plant vascular system while
98 leaf chewers encounter all sorts of compounds in leaf tissue. The water concentration in plant tissue or sap
99 affects the concentration of toxins and the general food utilization efficiencies of herbivores (Mattson, 1980;
100 Zvereva & Kozlov, 2006). Several hypotheses predict how plant biochemical modifications affect herbivorous
101 insects. The “*Plant Vigor hypothesis*” (Price, 1991) predicts higher herbivore pressure on vigorous plants.
102 Similarly, the “*Nitrogen (N)-limitation hypothesis*” (White, 1993) predicts worse performances of insect
103 herbivores on low N plant tissue. The modified “*Plant Stress hypothesis*” differentiates between feeding guilds
104 and type of stress: sap feeders are predicted to perform better on stressed plants but leaf chewers on vigorous
105 plants because concentration of allelochemicals is lower in phloem sap than leaf tissue while nutritional value
106 is overall elevated by stress (Larsson, 1989; Huberty & Denno, 2004; White, 2009). Plant-mediated bottom-up
107 effects of manipulated N supply have been reported for both leaf chewers (Chen *et al.*, 2010) and sap feeders
108 (Kos *et al.*, 2012).

109 Furthermore, different herbivore feeding guilds trigger specific plant defense mechanisms, depending on their
110 mode of attack, causing only little tissue damage like sap feeders or destroy large areas of plant tissue like leaf
111 chewers (Dicke *et al.*, 2003; Stam *et al.*, 2014). These top-down effects include biochemical plant responses
112 resulting in induced resistance and defense against herbivores or induced susceptibility to them (Karban &
113 Myers, 1989).

114 Natural enemies of herbivores are pivotal elements of biological pest control, but their effectiveness can be
115 affected by network forces (Chailleux *et al.*, 2014; Desneux *et al.* 2019; Han *et al.*, 2019). For instance, high
116 insect host quality is crucial for good offspring development of parasitoids that lay their eggs onto or into
117 herbivores and are therefore completely dependent on the host for nutrients during larval development
118 (Turlings & Benrey, 1998; Ode, 2006; Desneux *et al.* 2009; Chen *et al.*, 2014; Stam *et al.*, 2014). Plant water
119 limitation can influence parasitoids (Romo & Tylianakis, 2013; Nguyen *et al.*, 2018). Despite the crucial role of
120 fertilizers, such as N, in crop production, little is known about their effect on parasitoids (Prado *et al.*, 2015).
121 Biological pest control is a key element in integrated pest management in greenhouses (Pilkington *et al.* 2010),
122 and parasitoids are crucial biological pest control agents (Hawkins *et al.* 1997).

123 Still, interactions in trophic webs are hardly unidirectional: both bottom-up and top-down processes occur
124 simultaneously (Hunter & Price, 1992). Plant quality is influenced by abiotic factors like nutrient availability and
125 by biotic impact like herbivory, regulated by interacting plant hormonal signaling networks (Atkinson & Urwin,
126 2012) and differences due to insect species and feeding guilds add heterogeneity (Hunter & Price, 1992). Giron
127 *et al.* (2018) highlighted the great challenge of integrating the diversity of factors that shape insect-plant
128 interactions, incorporating multiple factors, abiotic and biotic, and multiple partners, beneficial and
129 detrimental organisms.

130 In this spirit, we present this manuscript on the simultaneous biotic and abiotic impact on a tritrophic model
131 system. We aim to untangle the complexity of water- and nitrogen-related bottom-up effects on insect
132 herbivores of different feeding guilds, as well as on their parasitoids – while taking into account the
133 simultaneous bidirectional effects between the trophic levels.

134 The following hypotheses were investigated:

- 135 (1) Moderate water and nitrogen limitations affect leaf nutritional quality, *i.e.*, N and C concentration, as
136 well as leaf defensive quality, *i.e.*, concentrations of phenolics and alkaloids, and plant-emitted VOCs. As

137 predicted by the *Growth-Differentiation Balance hypothesis*, defense will increase with decreasing
138 nutrient availability in the plant.

139 (2) Herbivore feeding results in top down effects on leaf nutritional and defense quality.

140 (3) These changes affect the performance and nutritional quality of insect herbivores feeding on those
141 leaves, depending on the herbivores' feeding guild.

142 (4) These changes propagate up to the third trophic level, affecting parasitism of these herbivores feeding
143 on those leaves.

144 The chosen system is the agro-ecosystem of greenhouse tomatoes, involving two abiotic factors, four herbivore
145 species, and two natural enemies. Agro-ecosystems are often species-poor, especially in greenhouses.
146 Nonetheless, trophic interactions are of great importance, especially when plant growing conditions may affect
147 biological pest control.

148 The great strength of the presented study is that we actually followed the bottom-up and top-down effects
149 through the trophic levels on plants of the same culture, studying all herbivore and parasitoid species under
150 identical conditions. The experiment used fully grown plants in a greenhouse to obtain results of practical
151 relevance.

152 **2) Material and Methods**

153 **2.1 Experimental setup and plant cultivation**

154 Tomato plants (*Solanum lycopersicum*, Solanaceae; cultivar, "San Marzano Nano", BAVICCHI S.p.A., Perugia,
155 Italy) were cultivated in four compartments of a climate-controlled greenhouse (min 15.8 °C, max 32.6 °C,
156 mean 24.4 ± 3.3 °C; mean relative humidity 80.6 ± 13.6 %; mean daytime global irradiance inside the
157 greenhouse: 449.5 W m^{-2}). Plants of all insect-treatments were distributed randomly over three compartments
158 while non-infested plants were cultivated in a separate one to avoid airborne priming effects. Plants were
159 cultivated hydroponically in an inert substrate (perlite) and automatically supplied with one of four nutrient
160 solutions: standard (10 mM) or reduced (2.5 mM) N concentrations, and standard (320 mL) or reduced
161 (160 mL) volumes of water per irrigation event (Table S1; Table S2). These treatments were designed based on
162 published results (Adamowicz *et al.*, 2008, Bénard *et al.*, 2009, Le Bot *et al.*, 2009, Han *et al.*, 2014). We
163 monitored the nutrient solution during the whole experiment (July 7th-August 31st, 2016) and adjusted settings
164 if necessary. All plants had entered the reproductive stage when insect infestation started and leaf quality was

165 significantly affected by the manipulated nutrient solutions (Table S4). For more details on plant cultivation,
166 please see supplemental materials.

167 2.2 Herbivores

168 We studied two sap-feeders, the potato aphid *Macrosiphum euphorbiae* (Thomas) (Hemiptera: Aphididae) and
169 the silverleaf whitefly *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) and two leaf-chewers, the African
170 cotton leafworm *Spodoptera littoralis* (Boisduval) (Lepidoptera: Noctuidae) and the tomato leaf miner
171 *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae). All four herbivore species have the potential to inflict
172 major economic damage on tomato crops (Byrne & Bellows, 1991; Desneux *et al.*, 2010; Biondi *et al.*, 2018;
173 Hulle *et al.*, 2020; Pavela *et al.* 2020). They were reared in caged colonies, located in climatic chambers
174 (*B. tabaci*, *M. euphorbiae*, *T. absoluta*; day/night = 12 h/12 h; T = 23 ± 1°C, RH = 65 %) or in the lab (*S. littoralis*;
175 day/night: 16 h/8 h; T = 23 ± 1°C; RH = 70 %). The colonies of *M. euphorbiae*, *S. littoralis*, and *T. absoluta* were
176 initiated using individuals naturally infesting tomato plants in the INRAE Sophia Antipolis experimental station
177 while the *B. tabaci* colony was provided by INRAE Montpellier. *Macrosiphum euphorbiae* were transferred from
178 potato to tomato plants two weeks before infestation. *Bemisia tabaci* were reared on tobacco plants until
179 infestation. *Spodoptera littoralis* were kept on a variety of plants (faba bean, peppermint, tomato) for three
180 generations. The last 10 days before infestation, they were reared on tomato plants only. *Tuta absoluta* was
181 reared on tomato plants.

182 The three front leaflets of the first fully expanded leaf from the top were infested with one of the four insect
183 species on 10 plants per nutrient solution (n = 10). For *T. absoluta* and *M. euphorbiae*, we cut pieces of leaves
184 from the colonies containing six 2nd-3rd-instar larvae and 30 individuals of mixed nymph stages and adults,
185 respectively, and placed them on the leaf to be infested where they moved to on their own. We used a fine
186 brush to gently transfer one *S. littoralis* 1st-2nd instar larvae on the leaf to be infested. Approximately 100 adult
187 *B. tabaci* were caught from the colony and transferred onto the leaflets. Concerning *T. absoluta* and
188 *M. euphorbiae*, we additionally infested the second fully expanded leaf from the top, in the same manner
189 described above, to study parasitism (see section 3.3). Infested leaves were covered with mesh cage to prevent
190 insect dispersal. Infestation duration was seven and 10 days for *M. euphorbiae* and *B. tabaci*, respectively, and
191 only two days for *T. absoluta* and *S. littoralis* (Table S3) because the latter cause larger damage to the plants.

192 We counted *M. euphorbiae* and *B. tabaci* individuals to assess their abundance. Additionally, eggs and nymphs
193 of *B. tabaci* were counted in an area of 1 cm² (repeated five times on five different parts of leaf) using a

194 microscope (Leica EZ 4, Leica Microsystems, Switzerland). The fecundity was determined as the ratio of
195 offspring over adults. We chose six *T. absoluta* larvae and one *S. littoralis* larva (mean total weight \pm sd:
196 4.0 ± 0.8 mg and 10.6 ± 2.4 mg, respectively) to approximate the inflicted damage on the plant. Consumed leaf
197 area was measured from photographs (ImageJ 1.49v, Wayne Rasband, National Institute of Health, USA).

198 The respective herbivore load was chosen based on previous experience: enough to elicit a detectable plant
199 defense response but not too many in order to have sufficient plant material left to conduct biochemical
200 analyses.

201 **2.3 Parasitism**

202 The parasitoid colonies were tended to according to the protocol of Biondi *et al.* (2013) in a climatic chamber
203 (day/night = 12 h/12 h; T = $23 \pm 1^\circ\text{C}$, RH = 65 %). The *Aphelinus abdominalis* (Dalman) (Hymenoptera:
204 Aphelinidae) colony, a widely used endoparasitoid biological control agent for *M. euphorbiae* (Mölk & Wyss,
205 2001; Shrestha *et al.*, 2015), was initiated from parasitoids naturally colonizing *M. euphorbiae* on
206 *S. lycopersicum* and reared on *Acyrtosiphon pisum* (Harris) aphids on faba bean plants. The *Necremnus tutae*
207 (Ribes & Bernardo) (Hymenoptera: Eulophidae) colony, a highly promising ectoparasitoid biological control
208 agent for *T. absoluta* (Gebiola *et al.*, 2015; Naselli *et al.*, 2017; Campos *et al.*, 2020), originated from field
209 collected material and was maintained on *T. absoluta* on tomato. A wide insect host range is reported for
210 *A. abdominalis* (Shrestha *et al.*, 2014) and suspected for *N. tutae* (personal experience).

211 As described above, on plants infested with *M. euphorbiae* and *T. absoluta*, respectively, a second leaf was
212 infested with the respective herbivores in the same manner and at the same time as the first one. Herbivores
213 on this second leaf were exposed to the parasitoids in 2nd-3rd instar larvae of leaf miners and mixed stages of
214 aphids, respectively.

215 Seven days after herbivore infestation, two male and two female *A. abdominalis* were released into the mesh
216 cage with *M. euphorbiae* and killed after 24h. After nine days, mummified aphids were counted, separated and
217 kept in the laboratory until they hatched. Similarly, two couples of *N. tutae* were added into the mesh cage
218 after *T. absoluta* larvae had been feeding for two days and killed after 48h. After 10 days, dead and parasitized
219 larvae were counted, the latter were separated and kept in the laboratory until they hatched. The sum of
220 *T. absoluta* larvae parasitized or killed inside the leaf by *N. tutae* were counted as successful biocontrol.

221 **2.4 Biochemical analyses**

222 Before infestation, the first fully developed leaf from the top was harvested from 10 plants per nutrient
223 solution treatment to assess leaf quality. Afterwards, leaves infested with insects and control leaves were
224 harvested on the same day the herbivore performance was assessed. Control leaves were taken from non-
225 infested plants in a separate compartment. Herbivores were removed from infested leaves to avoid
226 contaminations and stored separately. Leaves and herbivores were immediately frozen in liquid nitrogen and
227 stored at -80°C, lyophilized, and ground (Retsch ball mill MM301, Germany). For more details on biochemical
228 analyses, please see supplemental materials.

229 **2.4.1 Leaf water, nitrogen, and carbon concentrations**

230 The first and second fully developed leaves from six plants were harvested before infestation and weighed
231 before and after drying in an oven at 80°C for three days to determine their water concentrations (Table S4).
232 This was only done before infestation because large quantities of leaf material were needed. Leaf N and C
233 concentrations (gram per 100g of dry mass) were measured in aliquot samples using an elemental analyzer
234 (Flash EA1112 Series, ThermoFinnigan, Milan, Italy). The leaf C/N ratio was calculated as the ratio between leaf
235 C and leaf N concentrations.

236 **2.4.2 Leaf alkaloid and phenolics concentrations**

237 Leaves were harvested as described above in section 2.4. The concentrations of alkaloids and phenolic
238 compounds were analyzed as described in Han *et al.* (2020). In short, dry matter was extracted with extraction
239 solvent (75% MeOH, 0.1% formic acid, 24.9% H₂O; containing 100 µg mL⁻¹ of caffeine as internal standard) and
240 analyzed via UHPLC on an Acquity UPLC system coupled to a XEVO-G2-QTOF (Quadrupole-Time of flight;
241 Waters Corporation, Manchester, United Kingdom) with an Acquity UPLC BEH C18 column. The eluents were
242 H₂O with 0.1% formic acid and acetonitrile with 0.1% formic acid. The ionization mode was positive
243 electrospray. In a targeted approach, we tentatively identified alkaloids and phenolic compounds by comparing
244 the fragmentation patterns to literature data (Cataldi *et al.* 2005; Larbat *et al.* 2014). The internal standard
245 caffeine was used for quantification.

246 **2.4.3 Plant VOC collection**

247 Locally emitted VOCs of infested or non-infested tomato leaves were collected via solid phase micro-extraction
248 fibers (SPME; 50/30 µm, DVB/CAR/PDMS, 24 Ga; Supelco, Bellefonte, USA), as described in Han *et al.* (2020). In
249 short, headspaces of comparable sizes were created around the leaves using Nalophan bags (15 x 30 cm,
250 20 µm, Kalle). Volatiles were collected by inserting the SPME-fibers in the bags for 30 min in three or four

251 replicates per treatment, between 10-12 h. SPME-fibers were analyzed by GC-MS (Hewlett Packard, HP 6890
252 Series: Gas Chromatograph and Mass Selective Detector). Peaks were tentatively identified via Agilent
253 Enhanced ChemStation (E.02.02.1431), using several libraries (in-house based on standard compounds; NIST 98
254 by the National Institute of Standards and Technology, Wiley6n by Wiley), previous publications (Adams 2004;
255 Anastasaki *et al.*, 2015), and retention indices obtained using an alkane-mixture (C6-C15; SIGMA ALDRICH, St.
256 Quentin Fallavier, France).

257 2.4.4 Herbivore nitrogen and carbon concentrations

258 Freeze-dried and milled herbivores that had been removed from the harvested leaves were pooled into three
259 samples to measure their N and C concentrations (gram per 100g of dry mass) using an elemental analyzer
260 (Flash EA1112 Series, ThermoFinnigan, Milan, Italy). The herbivore C/N ratio was calculated as the ratio
261 between herbivore C and herbivore N concentrations (g g^{-1}).

262 2.5 Data Evaluation

263 The impact of herbivores, N, and water on leaf quality was evaluated by 3-factorial analyses including
264 interactions, using ANOVA followed by Tukey's honest significance test (HSD) or Kruskal-Wallis test followed by
265 Dunn's test, depending on data distribution (checked by Shapiro-Wilk and Bartlett tests). The performance of
266 leaf chewers was evaluated similarly by 2-factorial analyses. The performance of sap feeders was evaluated by
267 generalized Poisson-log distribution models, followed by "General Linear Hypotheses" (GLHT) for multiple
268 comparisons. Parasitism data were evaluated in the same way as sap feeder performance. Herbivore
269 nutritional value was evaluated by linear models. Correlations were analyzed using Spearman's rank
270 coefficients. Regarding plant VOC, peak areas were treated as suggested by Hervé *et al.* (2018), *i.e.* subjected to
271 fourth-root transformation and mean centered. Using MetaboAnalyst 4.0 (The Metabolomics Innovation
272 Centre and Mc Gill University, Montreal, Canada; Xia & Wishart, 2016), the data were then analyzed via
273 projection on latent structures discriminant analysis (PLS-DA). Model reliability was checked by 1000
274 permutations. A significance level of $\alpha = 0.05$ was applied. Except for VOC, data were evaluated using R
275 statistics (R, 2014).

276 3) Results

277 3.1 First trophic level: leaf quality

278 We detected two glycoalkaloids, α -tomatine and dehydrotomatine, one alkaloid aglycone, tomatidine, three
279 flavonoid glycosides, rutin, quercetin-3-(2''apiosyl-6''-rhamnosylglucoside) – in the following abbreviated as
280 QARG – and kaempferol rutinoside, and two phenolic acids, chlorogenic acid and feruloyl quinic acid.

281 3.1.1 Bottom-up effects: Abiotic factors modulate plant traits

282 **Nutritional value.** Nitrogen and water supplies significantly affected the nutritional value of non-infested
283 leaves. Nitrogen had a stronger impact, affecting leaf N and C concentrations, and the C/N ratio (Table 1;
284 Fig. 1). Water supply weakly interacted with the effect of N supply, regarding C concentration and C/N ratio,
285 (Table 1; Fig. 1).

286 **Defense compounds.** Concentrations of defense compounds in non-infested leaves were affected by leaf N
287 concentration and, to a lesser degree, by leaf water concentration (mostly in interaction with N, potentiating
288 its effect; Table 1). Leaves with lower leaf N (LN) concentration contained higher concentrations of α -tomatine,
289 dehydrotomatine, tomatidine, rutin, QARG, kaempferol rutinoside, chlorogenic acid, and feruloyl quinic acid
290 than those with higher leaf N concentration (Table 1). This effect was aggravated by water limitation regarding
291 α -tomatine, dehydrotomatine, and chlorogenic acid (interaction of the effect of water and N, Table 1). Water
292 limitation significantly increased foliar concentrations of tomatidin and feruloyl quinic acid (Table 1).

293 **Correlations.** In non-infested leaves, the concentration of most defense compounds was negatively correlated
294 with leaf N and leaf water concentration (Table 2).

295 **Constitutive VOCs.** The composition of constitutively emitted plant VOC blends was affected by N and water
296 limitation in interaction: the effect of water-limitation was stronger in High N (HN) leaves (Fig. 2a, $P = 0.04$).
297 Water and N limitation alone did not yield significant PLS-DA models (Fig. 2b, $P = 0.86$, and 2c, $P = 0.31$).

298 3.1.2 Top-down effects: Herbivory modulates plant traits

299 **Nutritional value.** Herbivory significantly affected leaf N and C concentrations and the C/N ratio, independent
300 of leaf N and water (Table 3). The average leaf N concentration tended to decrease in infested compared to
301 non-infested leaves but this was only significant regarding *B. tabaci*-infestation (Fig. 3). The average leaf C
302 concentration tended to decrease with leaf chewer but not with sap feeder infestation (Fig. 3) resulting in
303 higher C concentration in sap feeder than in leaf chewer-infested leaves ($P=0.0004$). Compared to non-infested
304 leaves, the C/N ratio increased in sap feeder- ($P=0.002$) but not in leaf chewer-infested leaves (Fig. 3).

305 **Defense compounds.** Like in non-infested leaves, lower leaf N and water concentrations generally increased
306 the concentrations of defense compounds in infested leaves, although there were some notable exceptions for

307 leaf chewer-infested leaves (Table 2). Herbivory affected the concentration of tomatidine, rutin, QARG,
308 chlorogenic acid, and feruloyl quinic acid in varied ways, often depending on leaf N and/or leaf water
309 concentration (Table 3): the only significant difference regarding tomatidine concentration was between
310 *T. absoluta*- and *M. euphorbiae*-infested leaves (0.16 and 0.13 mg g⁻¹ dry matter, respectively). Feruloyl quinic
311 acid concentration was significantly reduced in *S. littoralis*-infested compared to non-infested leaves (0.059 and
312 0.076 ng g⁻¹ dry matter, respectively). In HN leaves, *B. tabaci*-herbivory reduced the rutin concentration (21.2
313 compared to 28.9 ng g⁻¹ dry matter in non-infested leaves). In LN leaves, *T. absoluta*- and *S. littoralis*-herbivory
314 reduced the rutin (41.3 and 41.3 compared to 59.0 ng g⁻¹ dry matter in non-infested leaves) and the
315 chlorogenic acid concentration (28.0 and 25.0 compared to 34.7 ng g⁻¹ dry matter in non-infested leaves). In LN
316 leaves, *T. absoluta*-herbivory reduced the concentration of α -tomatine (16.9 compared to 19.4 mg g⁻¹ dry
317 matter in non-infested leaves). In LN-LW leaves, *T. absoluta*-herbivory reduced the concentration of
318 dehydrotomatine in LN-LW leaves (3.3 compared to 3.9 mg g⁻¹ dry matter in non-infested leaves).

319 **Correlations.** In non-infested and sap feeder-infested leaves, there was a significant negative correlation
320 between the concentrations of all measured defense compounds and leaf N as well as most compounds and
321 leaf water (Table 2). In leaf chewer-infested leaves, however, these correlations were weaker or not significant
322 in many cases (Table 2).

323 **HIPV.** Compositions of HIPV blends emitted from sap feeder-infested leaves were affected by N and, to a lesser
324 degree, by water limitation (Figs 2e-2f, respectively) but not their interaction (Fig. 2d). The composition of leaf-
325 chewer associated HIPV blends was neither affected by N nor water limitation (Figs 2g-i). A complete list of
326 detected compounds and their ranking among important features for PLS-DA can be found in supplementary
327 materials (tabs. S5 and S6). PLS-DA models and important features showing the separation of constitutive VOC,
328 leaf chewer and sap feeder-associated HIPV, of constitutive VOC and leaf chewer-associated HIPV, and of
329 constitutive VOC and sap feeder-associated HIPV ($P=0.04$, $P>0.001$, and $P=0.01$, respectively) can also be found
330 in supplementary materials (Fig. S7, Table S8).

331 **3.2 Second trophic level**

332 **3.2.1 Herbivore performance**

333 **Sap feeders.** The number of *M. euphorbiae* was largest on HN-LW leaves and smallest on LN-LW leaves (Fig. 4).
334 Correlation analyses indicated that the higher leaf nutritional value promoted population development while it
335 was impeded by high concentrations of some alkaloid and phenolic defense compounds, especially chlorogenic

336 acid but also rutin, feruloyl quinic acid, QARG, and α -tomatine (Table 4, Table 5). However, the leaf water
337 concentration had no effect on its own but interacted with the effect of leaf N (Table 4). The number of
338 *B. tabaci* adults, nymphs, and eggs was significantly influenced by leaf N*water concentration (Fig. 4, Table 4).
339 The correlation analyses indicate that the lowest number of adults on less nutritional leaves may be due to a
340 high concentration of the alkaloid defense compound tomatidine (Table 5). The number of nymphs and the
341 number of eggs were not significantly affected by leaf N or leaf water concentration (data not shown).

342 **Leaf chewers.** *Tuta absoluta* larvae were not significantly affected by leaf N or water concentrations (Table 4,
343 Fig. 5). Correlation analyses suggest, however, that larval weight gain was impeded by tomatidine ($P=0.04$) and
344 promoted by rutin ($P=0.05$), two defense compounds occurring in rising concentrations when leaf water or leaf
345 N concentration decline (Table 3, Table 5). There was no significant correlation between consumed leaf area
346 and leaf nutritional value or leaf defense compounds (Table 5) or larval weight increase (data not shown). The
347 leaf area consumed by *S. littoralis* larvae increased significantly in LW leaves (Table 4, Fig. 5). Although the
348 larval weight increase followed the same pattern the difference was only approaching significance ($P=0.07$;
349 Table 4, Fig. 5). There was a significant positive correlation between consumed leaf area and larval weight
350 increase for *S. littoralis* feeding on HN as well as HW leaves (Fig. 6). No significant correlations between larval
351 weight increase or consumed leaf area and leaf nutritional quality or leaf defense compounds were detected
352 (Table 5).

353 3.2.2 Herbivore nutritional quality

354 **Sap feeders.** The nutritional quality of *M. euphorbiae* was affected by plant N and water supply with a
355 significant negative correlation between plant N and insect N concentration (Table 6, Fig. 7). The C and N
356 concentration of *B. tabaci* was not measured due to their small size.

357 **Leaf chewers.** The nutritional quality of *T. absoluta* larvae was affected by plant N but not by plant water
358 supply while it was the other way around for *S. littoralis* larvae (Table 6, Fig. 7). There were no significant
359 correlations between leaf and insect nutritional quality (Table 6).

360 3.3 Third trophic level: Parasitism

361 **Parasitism on sap feeder.** Leaf N concentration had an impact on parasitism of *A. abdominalis* on
362 *M. euphorbiae* (Fig. 8, Table 7). The number of successfully formed mummies and the number of emerged
363 parasitoids was significantly higher on HN than on LN leaves (10.1 compared to 6.8 mummies and 7.7
364 compared to 5.7 emerged parasitoids, respectively; $P=0.003$ and 0.03, respectively; Table 7). The interactive

365 effect of N and water limitation on both parameters was approaching significance ($P=0.07$ and 0.09 ,
366 respectively; Table 7), indicating a lower number of mummies and emerged parasitoids on LW compared to
367 HW leaves when N concentration was reduced at the same time. Correlation analyses indicated that successful
368 mummy formation was reduced by plant rutin and kaempferol-rutinoside; the latter also had the tendency to
369 reduce parasitoid emergence (Table 8). A high insect host C/N ratio had the tendency to promote mummy
370 formation (Table 8).

371 **Parasitism on leaf chewer.** Regarding parasitism of *N. tutae* on *T. absoluta*, we did not detect any significant
372 effects (Table 7) but the average number of emerged parasitoids was higher on HN-HW and LN-LW leaves (0.7
373 and 0.8, respectively) than on HN-LW and LN-HW leaves (0.2 and 0.3, respectively), highlighting the tendency
374 of these two factors to have an interactive effect ($P=0.06$; Table 7). Also, high concentrations of chlorogenic
375 acid in the leaves tended to promote parasitoid emergence ($P=0.06$; Table 8). Still, the lack of significant results
376 indicates that there was no strong impact of leaf N and leaf water on parasitism of *N. tutae* on *T. absoluta*
377 larvae.

378 **4) Discussion**

379 Moderate limitations of water and N did affect leaf quality in terms of nutritional and defense compounds, thus
380 confirming **hypothesis 1**. Similarly, constitutive VOC blends were affected. The *Growth-Differentiation Balance*
381 *hypothesis* is partly supported by our results as the trade-off was clear in non-infested and sap feeder-infested
382 leaves but not so much in leaf chewer-infested leaves.

383 **Hypothesis 2** was partly confirmed since the concentration of several leaf nutritional and defense compounds
384 changed due to herbivory. Yet, the direction of these top down effects varied. The reduced N concentration
385 and increased C/N ratio in *B. tabaci*-infested leaves are probably to the herbivores' detriment and can be
386 interpreted as plant defense. However, the various cases of reduced concentrations of leaf defense compounds
387 due to herbivore infestation are probably to their benefit.

388 We could partly confirm **hypothesis 3**: plant-mediated bottom-up effects were detected on three out of four
389 herbivore species – the exception being *T. absoluta*. The herbivores' feeding guild played an important role
390 regarding bottom-up as well as top-down effects. Likewise, we can partially confirm **hypothesis 4**: while
391 parasitism on aphids was affected by N limitation, parasitism on leaf miners was not affected by bottom-up
392 effects, *i.e.*, when the effect was already weak on the second trophic level, there was no effect on the third.

393 **4.1 First trophic level: tomato plants**

394 **4.1.1 Bottom-up effects of N and water manipulation**

395 The increasing concentrations of phenolics and alkaloids in our non-infested LN and/or LW leaves are in line
396 with previous publications (English-Loeb *et al.*, 1997; Royer *et al.*, 2013; Larbat *et al.*, 2014; Han *et al.*, 2016).

397 The increased resource allocation to direct defense under moderately limited resource supply, as reported
398 previously for young tomato plants (Le Bot *et al.*, 2009), is in line with the “*Growth-Differentiation Balance*
399 *hypothesis*” (Herms & Mattson, 1992). In contrast, our data do not support the “*Optimal Defense hypothesis*”
400 (Rhoades, 1979) as interpreted by Stamp (2003), predicting that plants with a limited supply of resources will
401 reduce their defense. Yet, Le Bot *et al.* (2009) suggest that it is rather a gradual shift between growth and
402 defense than a hard threshold and Züst & Agrawal (2017) propose a complex regulatory network enabling
403 plants to prioritize one process over another.

404 The effect of water and/or N limitation on the composition of constitutive VOC blends emitted by non-infested
405 leaves that we detected agrees with a previous study showing that N limitation affects tomato VOCs (Coqueret,
406 2017) and experiments on other plants (Becker *et al.*, 2015). From an evolutionary perspective, this variability
407 of constitutive VOC blends might be of advantage to plants because it might hamper detection by herbivores –
408 as long as herbivores are not able to interpret this variation as additional information on the plants’ nutritional
409 status. The latter has been suggested by an experiment on variable moth oviposition on grapevine (Tasin *et al.*,
410 2011). In further experiments, it would be very interesting to investigate if the different constitutive VOC
411 blends we observed are able to attract and arrest different herbivores in order to estimate the ecological
412 consequences.

413 **4.1.2 Top-down effects of herbivory**

414 We observed a more or less pronounced reduction of the leaf nutritional value in infested leaves, depending on
415 the herbivore. The low N concentration in *B. tabaci*-infested leaves could slow down their development
416 because it reduces their nutrient intake. The elevated C concentration in sap feeder-infested leaves could
417 strengthen this effect because it further dilutes the available N, as shown by the associated elevated C/N ratio.
418 Sap feeders on these leaves have to ingest larger quantities of plant sap to obtain the necessary amounts of N.
419 This can be interpreted as successful plant defense. However, remarkably this was not the case for leaf chewer-
420 infested leaves. Yet, we have to keep in mind that we analyzed the complete leaf tissue and not only the sap.
421 Hence, the actual nutritional quality of the ingested plant part might vary between the feeding guilds.

422 Top-down effects on leaf defense compounds by leaf chewers were stronger than those of sap feeders. Leaf
423 chewer infestation even interfered with the bottom-up effects of limited resources on some foliar defense
424 compounds. Remarkably, many foliar defense compounds were reduced by herbivory, especially in resource-
425 limited leaves and especially when infested by leaf chewers. While plant defense suppression by pathogens and
426 phytophagous mites is well characterized, it is less studied for herbivores (Kant *et al.*, 2015). There are
427 indications for plant defense suppression by oral secretions for *M. euphorbiae* and *B. tabaci* on tomato
428 (Atamian *et al.*, 2013; Su *et al.*, 2015), and *S. littoralis* on *Arabidopsis thaliana* (Consales *et al.*, 2012), but no
429 evidence was found for *T. absoluta* (Larbat *et al.*, 2016). Yet, a different leaf miner species can alter leaf
430 phenolics to its favor (Giron *et al.*, 2016). Still, we know of no previous study reporting the effect of
431 *M. euphorbiae*, *S. littoralis*, and *B. tabaci* on phenolics or alkaloids in tomato plants.

432 **4.1.3 Interactive, bidirectional effects**

433 In our experiment, we applied a sequence of abiotic and biotic impact factors. The plant hormonal signaling
434 networks involved are prone to interact, adding a degree of complexity to the observed plant response
435 (Atkinson & Urwin, 2012). Studying the plant transcriptome under sequential stresses, Coolen *et al.* (2016)
436 suggested that the most recent stress largely overrides the effects of previous ones and dominates the plant
437 biochemical profile. Our results agree with this regarding leaf chewers but not regarding sap feeders.
438 Phytohormones are key components for plants to integrate information on their biotic and abiotic
439 environment. Nitrogen as well as water limitation triggers salicylic acid (SA) signaling (Rubio *et al.*, 2009;
440 Weldegergis *et al.*, 2015), while plant defense against leaf chewers is mainly mediated by jasmonic acid (JA).
441 Since JA has been suggested as a potent inhibitor of SA-dependent signaling (Beckers & Spoel, 2006), the leaf
442 chewer-related JA-response might suppress the N- and water-related SA-response – balancing the cost of
443 resource allocation to the ecological costs of herbivory. The SA-JA crosstalk has been suggested to serve as a
444 powerful mechanism to plants, allowing them to fine-tune their defense responses and possibly prioritize one
445 over the other (Mur *et al.*, 2005; Beckers & Spoel, 2006; Spoel & Dong, 2008; Pieterse *et al.*, 2012; Züst &
446 Agrawal, 2017). From this perspective, our results could be interpreted as plants prioritizing the biotic impact
447 of feeding leaf chewers over the abiotic impact of moderate resource limitation. Moderate resource limitation,
448 as applied here, may not pose as big a threat to plants as leaf chewing herbivores, potentially destroying large
449 leaf areas quickly. This hypothesis is further supported by the high resilience of leaf chewer-associated HIPV
450 blends towards resource limitation we observed (Figs 2g-i). However, further studies are necessary to

451 investigate whether these changes of the blends translate into behavioral changes with herbivores and natural
452 enemies. Also, further studies into the crosstalk of biotic and abiotic impacts of plant hormone status and
453 global plant defense should give very interesting insights into this issue.

454 **4.2 Bottom-up effects on the second trophic level: herbivores**

455 **4.2.1 Sap feeders**

456 ***Macrosiphum euphorbiae*** – Aphid abundance was shaped by both leaf nutritional quality and leaf defense
457 compounds, albeit in opposite directions (Table 5). This might, on the one hand, be due to increased phloem
458 sap quality under water limitation, providing higher concentrations of free amino acids and sugars (Mewis *et*
459 *al.*, 2012), in line with the modified “*Plant Stress hypothesis*” (White, 2009). On the other hand, on LN-LW
460 leaves, this nourishing effect might be overruled by high concentrations of defense compounds as indicated by
461 the negative correlation between individual abundance and plant defense compounds (Table 5). Earlier studies
462 report a negative impact of α -tomatine and tomatidine on *M. euphorbiae* (Güntner *et al.*, 1997). Alkaloids have
463 previously been detected in phloem sap (Wink & Witte, 1984) and can harm sap feeders (Güntner *et al.*, 1997).
464 Such steroidal alkaloids lead to membrane disruption and cell death in insects (Friedman, 2002), while phenolic
465 compounds can harm insects by forming reactive oxygen species in their guts (Simmonds, 2003).

466 The nutritional value of *M. euphorbiae* was affected by plant-mediated bottom-up effects in a counter-intuitive
467 way: their N concentration was higher on LN leaves (Fig. 7, Table 6). A previous study on *Aphis nerii*
468 (Fonscolombe) (Hymenoptera: Aphididae) on the milkweed *Asclepias curassavica* found higher aphid N on
469 higher N concentration plants (Couture *et al.*, 2010). This discrepancy shows that results are not easily
470 transferrable from one system to another. Moreover, the total leaf N concentration does not reveal the N
471 form, whether it is available to the herbivores as amino acids, unavailable as nitrate or in structural elements,
472 or even in defense compounds like alkaloids. On LN leaves, sap feeders may have had to ingest a lot of sap in
473 order to reach the necessary levels of essential amino acids while ingesting nitrate-N or alkaloids. Alternatively,
474 the high N concentrations could be amino acids since resource-limited plants can contain higher levels of N in
475 this readily bioavailable form, as reported for water-limited leaves (Ximénez-Embún *et al.*, 2016). Analyzing the
476 concentration of nitrate, amino acids and allelochemicals, in the herbivores would be a very interesting next
477 step.

478 The negative correlation between many foliar phenolics and *M. euphorbiae* population size suggests that they
479 are not able to sequester them. While this may be an obvious disadvantage, it could be beneficial from a

480 multitrophic perspective if parasitoids were vulnerable to these compounds. Our data suggest that this might
481 show if our species were studied on a community level study system since the negative correlation with plant
482 kaempferol-rutinoside was significant on parasitoids (Table 8) but not on aphids (Table 5).

483 ***Bemisia tabaci*** – Our results are largely in line with previous reports that the number of adult whitefly on
484 tomato plants decreases with reduced N supply and/or water concentration (Jauset *et al.*, 1998; Žanić *et al.*,
485 2011). In our experiment, however, the effect only manifested if both leaf N and water concentration were
486 reduced - probably because our reductions were only moderate. A possible explanation might be tomatidine
487 ingestion with phloem sap. Leaf anatomy and plant primary metabolites would be an important factor to be
488 included in future experiments as they have been linked to *B. tabaci* abundance (Žanić *et al.*, 2018).

489 In their meta-analysis, Huberty & Denno (2004) reported a distinct negative impact of drought on phloem
490 feeders. In our study, plants were only experiencing water limitation not drought, highlighting that the severity
491 of a limitation or stress can modulate its effect. Our results partly support the “*Plant Vigor Hypothesis*” (Price,
492 1991) and the “*N-limitation hypothesis*” (White, 1993) predicting a worse performance of insect herbivores on
493 stressed and low N plant tissue, respectively.

494 **4.2.2 Leaf chewers**

495 ***Tuta absoluta*** – *Tuta absoluta* was not sensitive to bottom-up effects (Fig. 5), which agrees with some
496 previously published results (Dong *et al.*, 2018) but not with others (Han *et al.*, 2014; Coqueret *et al.*, 2017).
497 However, these studies used different tomato cultivars, growth systems, limitation levels, and assessed other
498 life-history traits over a different time span than we did, which may all contribute to the divergent results.
499 Furthermore, we cannot exclude that leaf density varied due to the treatments, *i.e.*, the amount of ingested
500 tissue could actually vary although the consumed leaf area did not. The opposing correlation of tomatine and
501 rutin with larval weight gain we observed might explain the neutral net-effect on larval weight gain. This
502 balance might be different in other cultivars as their alkaloid and flavonoid concentrations vary (Larbat *et al.*,
503 2014). In our experiment, the short duration was chosen in order to have sufficient leaf material left over to
504 conduct chemical analyses. It was sufficient to affect the insect host quality but not the performance.
505 Interestingly, *T. absoluta* performance was less susceptible to host plant quality changes than *S. littoralis*.

506 ***Spodoptera littoralis*** – The observation that *S. littoralis* compensated lower leaf water concentration with
507 higher consumption (Fig. 5) is in line with previous reports (Mattson, 1980; Gutbrodt *et al.*, 2011). It is
508 remarkable that such a small difference in leaf water (1.3%) leads to such a large difference in consumption

509 (29.6%). Again, we have to be careful interpreting these results as we did not measure leaf thickness.
510 Nevertheless, losing leaf area is in itself relevant as plants are losing photosynthetically active leaf surface.
511 Leaves only limited in N concentration apparently provided enough N for good larval development. On LW
512 leaves, however, the otherwise positive correlation between food intake and larval weight gain was decoupled
513 (Fig. 6), indicating a bottom-up effect of leaf water on the larvae's capacity to metabolize the ingested leaf
514 tissue. Water itself is important for insect development and plant tissue digestibility and N availability for insect
515 herbivores strongly depend on water, too (Mattson, 1980; Fajer, 1989; Zvereva & Kozlov, 2006).
516 The lack of bottom-up effects due to altered leaf defense chemistry is in line with the "*Plant Stress hypothesis*"
517 (White, 1984) but not the "*N limitation hypothesis*" (White, 1993). It is possible, that low leaf N concentration
518 and direct defense compounds would have affected larval development if larvae fed for a longer period. Yet,
519 the lack of effects of plant allelochemicals is in line with a previous study on *S. littoralis*, suggesting successful
520 detoxification of tomato phenolics and alkaloids (Ferrerres *et al.*, 2011).

521 **4.3 Bottom-up effects on the third trophic level: parasitoids**

522 ***Aphelinus abdominalis* on *M. euphorbiae*** – The negative effect of low plant and insect host quality on
523 *A. abdominalis* parasitism is in line with previous studies on aphid parasitoids (Aqueel *et al.*, 2015, Prado *et al.*,
524 2015). Our data suggest plant defense compounds ingested by aphids can negatively affect mummy formation
525 and parasitoid emergence (Table 8). This is in line with Prado *et al.* (2015), summarizing how low plant quality
526 can impede parasitism. Females of the koinobiont endoparasitic *A. abdominalis* lay their eggs inside their host
527 that continues to live for a considerable time after oviposition (Shrestha *et al.*, 2015). There are several steps at
528 which parasitism can fail/ be averted by the aphid, behavioral and physiological, as summarized by Monticelli
529 *et al.* (2019). Our results suggest that somewhere in this chain of events, rutin and kaempferol rutinoside
530 interfere with *A. abdominalis* development. These interpretations, however, need further investigation on a
531 physiological level. Previous studies found effects of plant water limitation on aphid parasitoid performance
532 (Romo & Tylianakis, 2013; Nguyen *et al.*, 2018), while we did not, which might be due to differing water
533 limitation severity.

534 ***Necremnus tutae* on *T. absoluta*** – The lack of bottom-up effects of water or N limitation on *N. tutae* parasitism
535 is mostly in line with previous results (Dong *et al.*, 2018). The nutritional value of *T. absoluta* was affected by
536 plant-mediated bottom-up effects (Fig. 7, Table 6) but the absence of effects on parasitism (Tables 7, 8)
537 suggests that the host C concentration is not crucial for *N. tutae* development. Like Dong *et al.* (2018), we

538 conclude that the bottom-up effects did not negatively affect the parasitoids because the effects were not
539 strong enough on the herbivore level to propagate up to higher trophic levels.

540 **4.4 Conclusions and Outlook**

541 Overall, we did find evidence that moderate reductions of water and/or N supply to tomato plants in the
542 greenhouse did trigger bottom-up effects that can reach the third trophic level but this propagation depends
543 on the nature and the intensity of modulations. Leaf chewer-associated top down-forces attenuated the
544 nutrition-related bottom-up effects on plant quality and hence dominated their biochemical profile. In sap
545 feeder-infested leaves, however, the abiotic impact shaped the biochemical profile. This suggests a very
546 intricate system of impact prioritization in plants.

547 Aphid parasitism was reduced under N limitation while leaf miner parasitism was not, indicating that N and/or
548 water inputs in crop production could be reduced without jeopardizing biocontrol. Yet, it has to be done wisely
549 and to be adapted to the species – possibly even the cultivar of the plant. Here, more information is necessary.
550 As a next step, studies on community dynamics and more species of each feeding guild and further parasitoid
551 species with different strategies, *i.e.*, koino- and idiobiont endo- and ectoparasitoids, should be conducted.
552 Omnivorous predatory bugs could be directly affected by changes on the first as well as the second trophic
553 level. This way, we might come closer to predicting the impact of bottom-up forces on biocontrol services
554 which could be a crucial step towards more sustainable agriculture.

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565 **Author’s contribution**

566 CB, AVL, and TM designed the experiment with the supporting expertise of JLB, SA, RB, XF, and ND. PH and
567 MRC likewise contributed to planning and conducting the experiment together with CB, AVL, ET, RB, and PB.
568 Insects were reared and provided by PB, ET, MRC, CB, and PH. Plants were reared, provided and tended to by
569 PB, CB, and PH. CB, PH, AVL, and ET analyzed the plant nutritional and defense compounds as well as volatiles.
570 JLB, SA and XF provided facilities for these analyses. CB analyzed the data, CB, TM, and AVL interpreted and
571 discussed the results, CB and AVL led the writing of the manuscript. Funding was acquisitioned by ND, AVL, and
572 CB. All authors contributed critically to the draft and gave their final approval for publication.

573 **Data availability statement**

574 All data will be made available at the DRYAD digital repository.

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915

916 **Figure legends**

917 Figure 1: Nutritional value of leaves from different nutrient solution treatments before infestation. Displayed
918 are the carbon nitrogen ratio (C/N ratio) and water concentration of first fully expanded leaves from the top
919 (mean ± standard error). Identical letters indicate that values do not differ significantly. Large and small N-
920 symbols indicate leaves with high and low leaf N concentration, respectively. Large and small drop-symbols
921 indicate leaves with high and low leaf water concentration, respectively.

922 Figure 2: Abiotic impact on volatile organic compounds released by plants constitutively or during infestation
923 with herbivores, illustrated by PLS-DA models. a, d, g: effect of water and N limitation on emitted blends; b, e,
924 h: effect of N limitation on emitted blends; c, f, i: effect of water limitation on emitted blends. VOC: volatile
925 organic compounds, HIPV: herbivory-induced plant volatiles, PLS-DA: projection on latent structures -
926 discriminant analysis, *P*: p-value of PLS-DA model, HN/LN: high/low leaf nitrogen concentration, HW/LW:
927 high/low leaf water concentration.

928 Figure 3: Nutritional value of leaves from different infestation scenarios (non-infested control leaves, infested
929 with *Macrosiphum euphorbiae*, *Bemisia tabaci*, *Tuta absoluta*, or *Spodoptera littoralis*) as affected by top-down
930 forces. Displayed are the leaf nitrogen concentration, leaf carbon concentration, and leaf carbon/nitrogen ratio
931 (mean ± standard error). Identical letters indicate that values do not differ significantly.

932 Figure 4: Performance of sap feeding insect herbivores that fed on leaves with different N and water
933 concentration; left: *M. euphorbiae* population size, right: number of adult *B. tabaci* (mean ± standard error).
934 Identical letters indicate that values do not differ significantly. Large and small N-symbols indicate insects that

935 fed on leaves with high and low leaf N concentration, respectively. Large and small drop-symbols indicate
936 insects that fed on leaves with high and low leaf water concentration, respectively.

937 Figure 5: Performance of leaf chewing insect herbivores that fed on leaves with different N and water
938 concentration; top left: larval weight increase of *T. absoluta*, top right: larval weight increase of *S. littoralis*,
939 bottom left: leaf area consumed by *T. absoluta*, bottom right: leaf area consumed by *S. littoralis* (mean \pm
940 standard error). Identical letters indicate that values do not differ significantly. Large and small N-symbols
941 indicate insects that fed on leaves with high and low leaf N concentration, respectively. Large and small drop-
942 symbols indicate insects that fed on leaves with high and low leaf water concentration, respectively.

943 Figure 6: Correlation between larval weight increase and consumed leaf area of *S. littoralis*, on leaves with high
944 and low nitrogen and water concentration, respectively. The correlation is described by spearman's correlation
945 coefficient (R) and the *p*-value (P).

946 Figure 7: Carbon nitrogen ratio (C/N ratio) of insect herbivores as proxy of their host quality for higher trophic
947 levels; from left to right: *M. euphorbiae*, *T. absoluta*, or *S. littoralis*, that fed on leaves with different N and
948 water concentration (mean \pm standard error). Identical letters indicate that values do not differ significantly.
949 Large and small N-symbols indicate insects that fed on leaves with high and low leaf N concentration,
950 respectively. Large and small drop-symbols indicate insects that fed on leaves with high and low leaf water
951 concentration, respectively.

952 Figure 8: Parasitism of *A. abdominalis* on *M. euphorbiae* that fed on leaves with different N and water
953 concentration (mean \pm standard error). Identical letters indicate that values do not differ significantly. Large
954 and small N-symbols indicate insects that fed on leaves with high and low leaf N concentration, respectively.
955 Large and small drop-symbols indicate insects that fed on leaves with high and low leaf water concentration,
956 respectively.

957 **Supplementary data**

958 Table S1: nutrient solution recipe, standard (10 mM) compared to reduced N (2.5 mM).

959 Table S2: pH value, electric conductivity (EC, dS m^{-1}) and volume of nutrient solution supplied per plant and
960 irrigation event (mL) of the four different nutrient solutions, monitored over the duration of the experiment.

961 Table S3: Duration of infestation before volatile sampling.

962 Table S4: Bottom-up effects on leaf nutritional value and defense compound concentration, before infestation.

963 Table S5: Complete list of detected volatile compounds emitted by tomato leaves.

964 Table S6: Importance of the volatile organic compounds in the PLS-DA models displayed in manuscript fig. 2.

965 Figure S7: PLS-DA models of constitutive VOC, sap feeder- and leaf chewer-associated HIPV

966 Table S8: Importance of volatile organic compounds in the PLS-DA models of constitutive VOC, sap feeder- and

967 leaf chewer-associated HIPV displayed in fig. S7

968 Details on Material & Methods, experimental setup and biochemical analyses

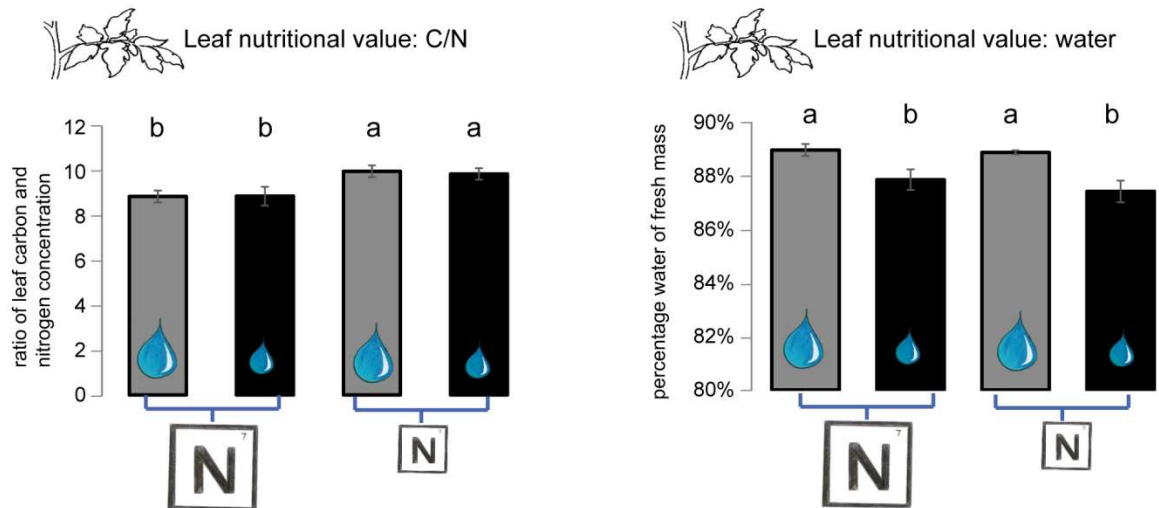


Figure 1: Nutritional value of leaves from different nutrient solution treatments before infestation. Displayed are the carbon nitrogen ratio (C/N ratio) and water concentration of first fully expanded leaves from the top (mean \pm standard error). Identical letters indicate that values do not differ significantly. Large and small N-symbols indicate leaves with high and low leaf N concentration, respectively. Large and small drop-symbols indicate leaves with high and low leaf water concentration, respectively.

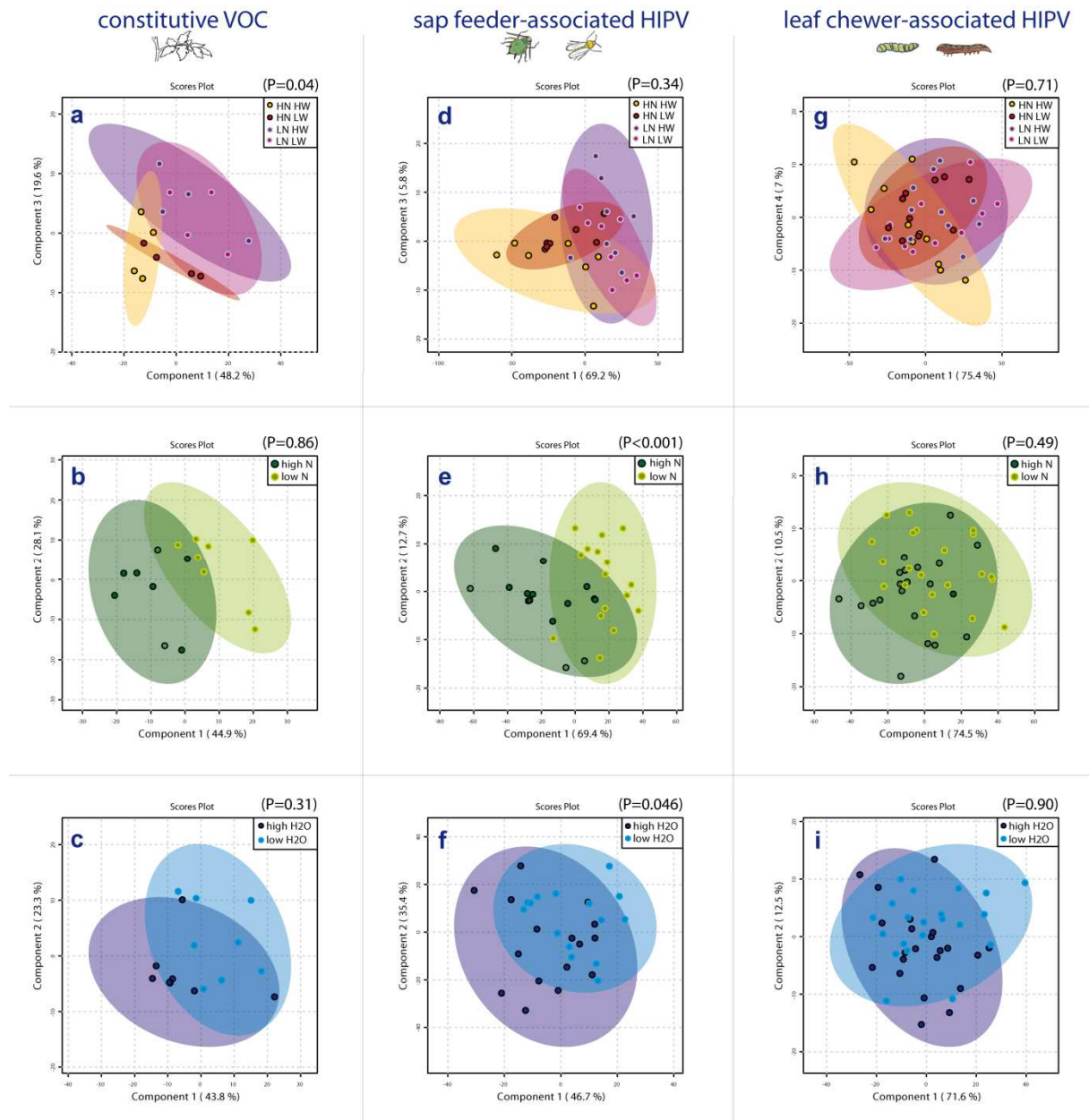


Figure 2: Abiotic impact on volatile organic compounds released by plants constitutively or during infestation with herbivores, illustrated by PLS-DA models. a, d, g: effect of water and N limitation on emitted blends; b, e, h: effect of N limitation on emitted blends; c, f, i: effect of water limitation on emitted blends. VOC: volatile organic compounds, HIPV: herbivory-induced plant volatiles, PLS-DA: projection on latent structures - discriminant analysis, *P*: p-value of PLS-DA model, HN/LN: high/low leaf nitrogen concentration, HW/LW: high/low leaf water concentration.

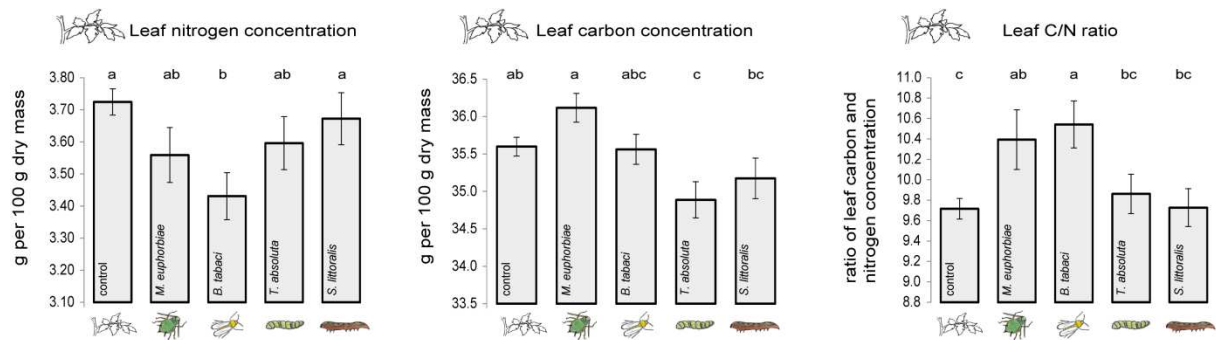
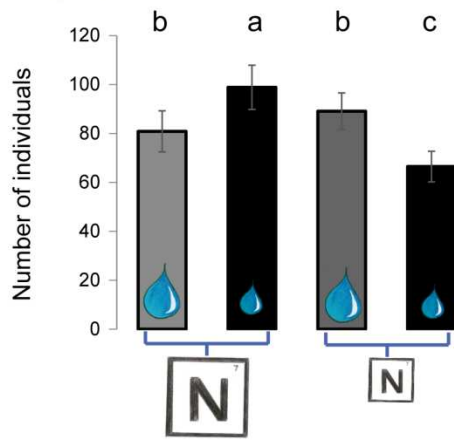


Figure 3: Nutritional value of leaves from different infestation scenarios (non-infested control leaves, infested with *Macrosiphum euphorbiae*, *Bemisia tabaci*, *Tuta absoluta*, or *Spodoptera littoralis*) as affected by top-down forces. Displayed are the leaf nitrogen concentration, leaf carbon concentration, and leaf carbon/nitrogen ratio (mean \pm standard error). Identical letters indicate that values do not differ significantly.



Macrosiphum euphorbiae



Bemisia tabaci

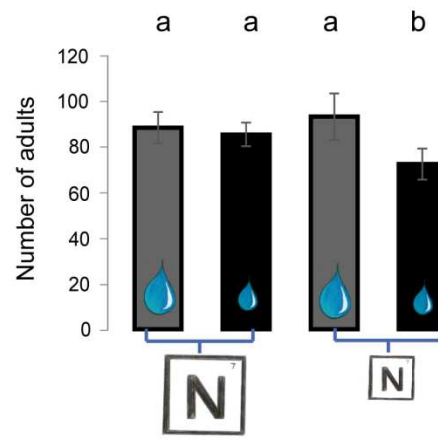


Figure 4: Performance of sap feeding insect herbivores that fed on leaves with different N and water concentration; left: *M. euphorbiae* population size, right: number of adult *B. tabaci* (mean \pm standard error). Identical letters indicate that values do not differ significantly. Large and small N-symbols indicate insects that fed on leaves with high and low leaf N concentration, respectively. Large and small drop-symbols indicate insects that fed on leaves with high and low leaf water concentration, respectively.

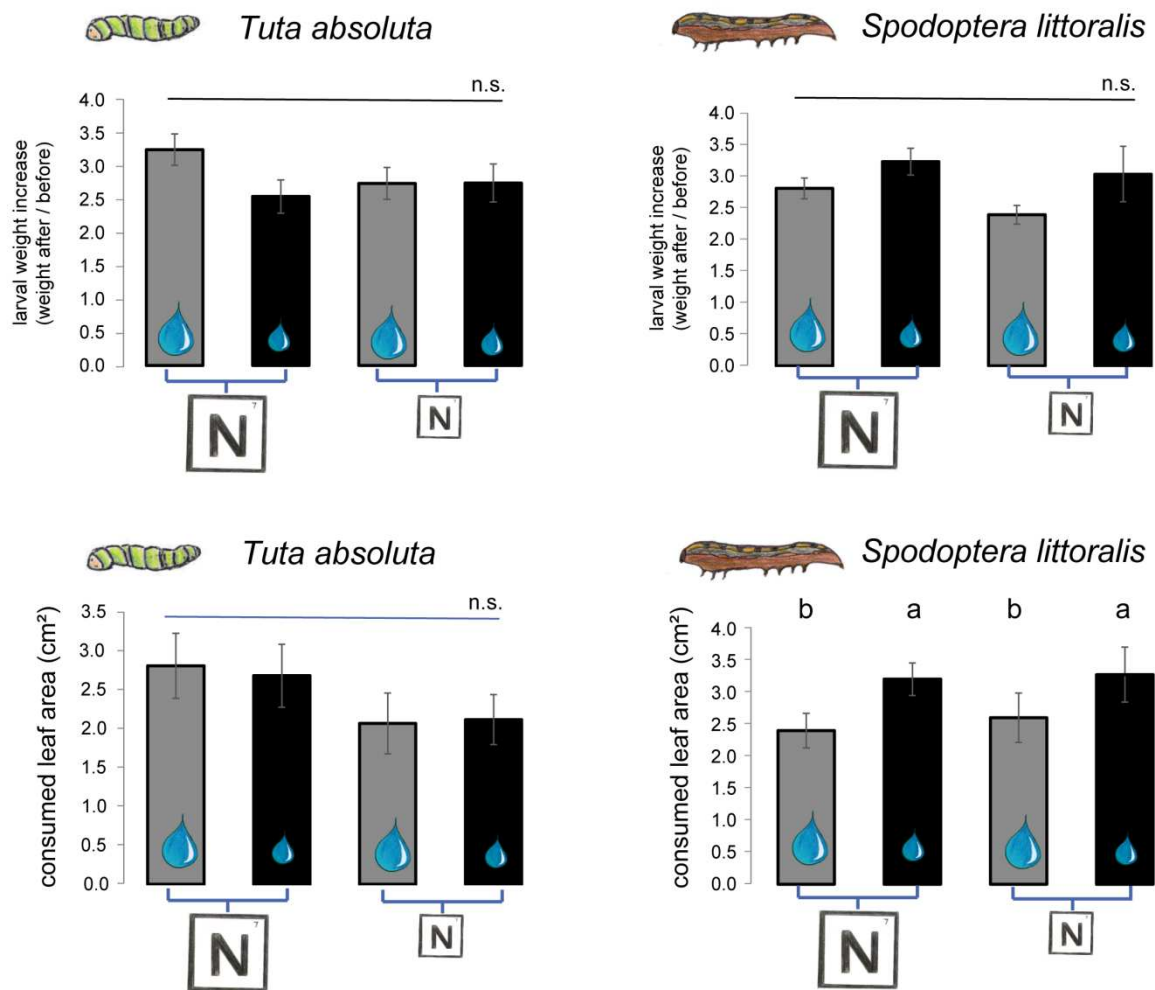


Figure 5: Performance of leaf chewing insect herbivores that fed on leaves with different N and water concentration; top left: larval weight increase of *T. absoluta*, top right: larval weight increase of *S. littoralis*, bottom left: leaf area consumed by *T. absoluta*, bottom right: leaf area consumed by *S. littoralis* (mean \pm standard error). Identical letters indicate that values do not differ significantly. Large and small N-symbols indicate insects that fed on leaves with high and low leaf N concentration, respectively. Large and small drop-symbols indicate insects that fed on leaves with high and low leaf water concentration, respectively.

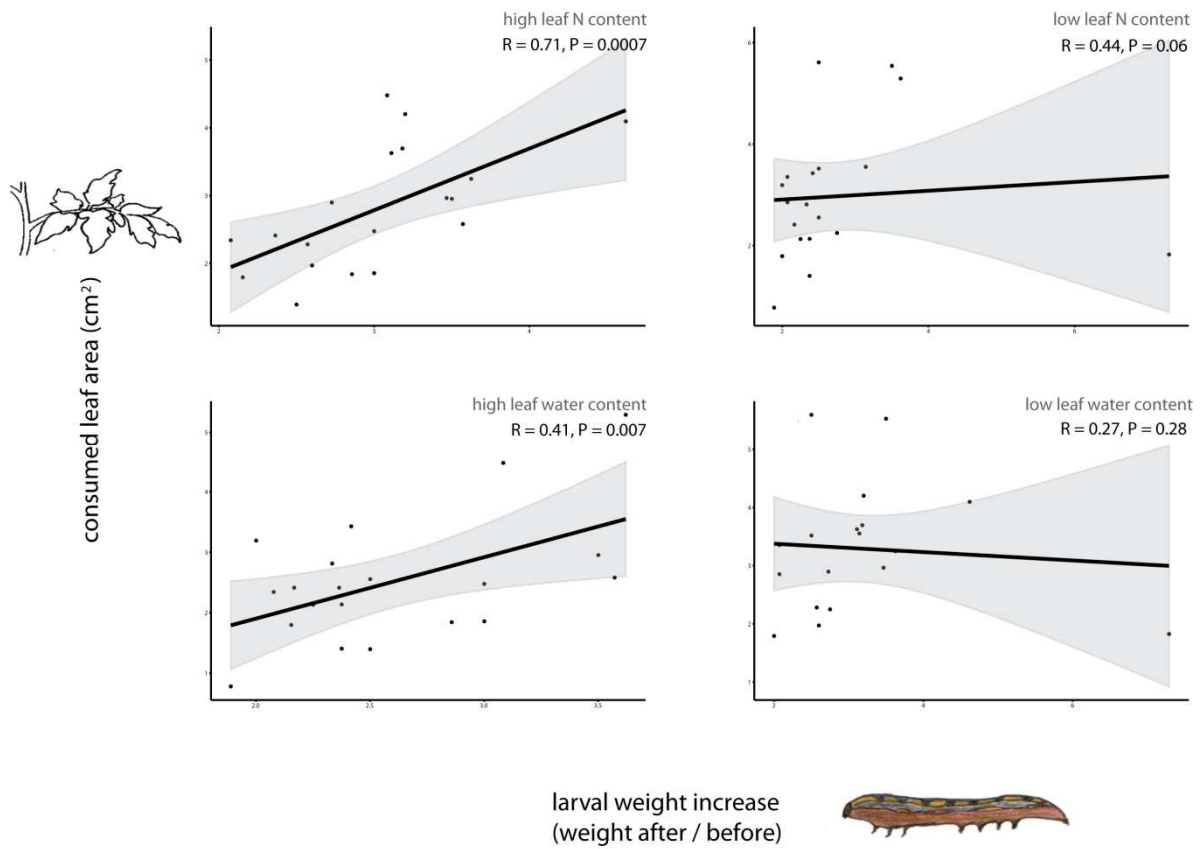
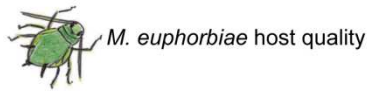
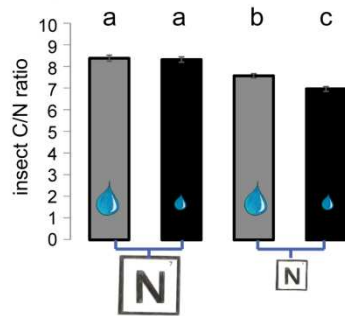


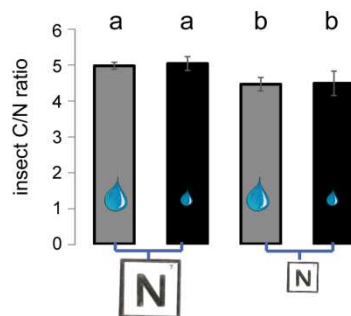
Figure 6: Correlation between larval weight increase and consumed leaf area of *S. littoralis*, on leaves with high and low nitrogen and water concentration, respectively. The correlation is described by spearman's correlation coefficient (R) and the p -value (P).



M. euphorbiae host quality



T. absoluta host quality



S. littoralis host quality

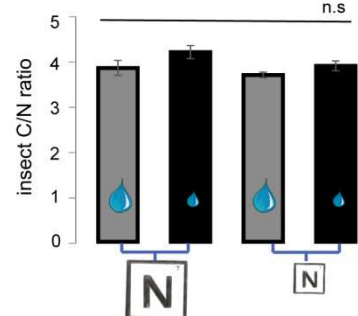


Figure 7: Carbon nitrogen ratio (C/N ratio) of insect herbivores as proxy of their host quality for higher trophic levels; from left to right: *M. euphorbiae*, *T. absoluta*, or *S. littoralis*, that fed on leaves with different N and water concentration (mean \pm standard error). Identical letters indicate that values do not differ significantly. Large and small N-symbols indicate insects that fed on leaves with high and low leaf N concentration, respectively. Large and small drop-symbols indicate insects that fed on leaves with high and low leaf water concentration, respectively.

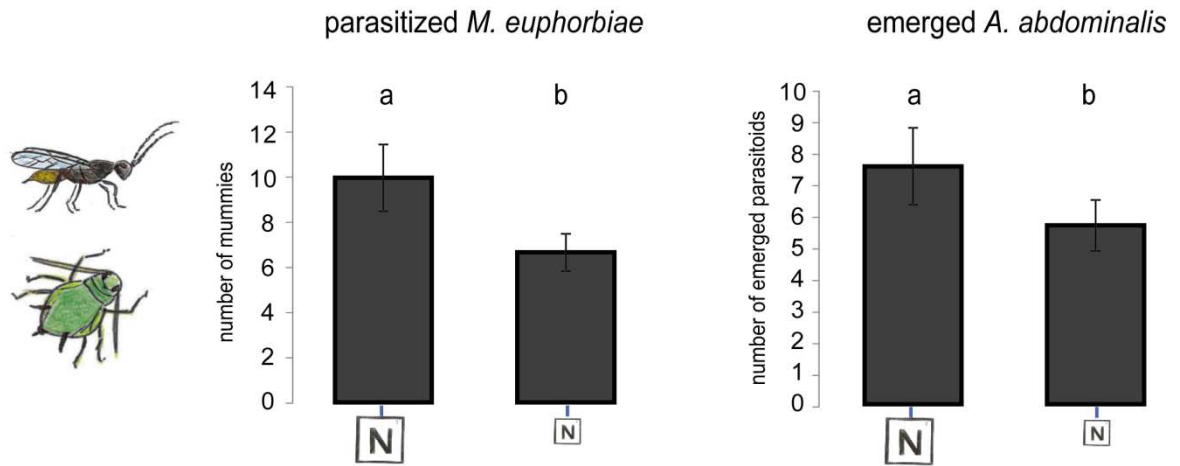


Figure 8: Parasitism of *A. abdominalis* on *M. euphorbiae* that fed on leaves with different N and water concentration (mean \pm standard error). Identical letters indicate that values do not differ significantly. Large and small N-symbols indicate insects that fed on leaves with high and low leaf N concentration, respectively. Large and small drop-symbols indicate insects that fed on leaves with high and low leaf water concentration, respectively.

1 Table 1: Bottom-up effects of plant nutrition on quality of non-infested leaves, in terms of nutritional value and
 2 defense compound concentration (means, n = 10; alkaloids are given in mg g⁻¹, phenolics in ng g⁻¹ dry matter).
 3 Additionally, *p*-values, degrees of freedom, and F-values, describing the impact of nitrogen (N), and water (H₂O)
 4 supply and the interaction thereof (N*H₂O) are listed. Identical upper- or lower-case letters indicate that values
 5 do not significantly differ from each other. HN/LN: high/low leaf N concentration, HW/LW: high/low leaf H₂O
 6 concentration. C = carbon, QARG = quercetin-3-(2''apiosyl-6''-rhamnosylglucoside), KR = kaempferol rutinoside.

	leaf N	leaf C	leaf C/N
HN-HW	4.0 a	36.4 a	9.1 b
HN-LW	4.1 a	36.1 a	8.9 b
LN-HW	3.4 b	34.6 b	10.2 a
LN-LW	3.3 b	35.3 b	10.7 a
N	<0.0001, F=(1, 150)=118.1	<0.0001, F=(1, 150)=34.0	<0.0001, F=(1, 150)=91.1
H₂O	0.95, F=(1, 150)=0.0	0.42, F=(1, 150)=0.6	0.51, F=(1, 150)=0.1
N*H₂O	0.16, F=(1, 150)=2.0	0.04, F=(1, 150)=4.2	0.03, F=(1, 150)=5.3
	α-tomatine	dehydrotomatine	tomatidine
HN-HW	17.5 c	2.8 c	0.11 a B
HN-LW	16.7 c	2.6 c	0.12 a A
LN-HW	19.5 b	3.4 b	0.17 b B
LN-LW	22.1 a	3.9 a	0.21 b A
N	<0.0001, F=(1, 150)=63.3	<0.0001, F=(1, 150)=100.8	<0.0001, F=(1, 150)=106.8
H₂O	0.06, F=(1, 150)=3.5	0.20, F=(1, 150)=1.6	0.0003, F=(1, 150)=13.4
N*H₂O	0.0003, F=(1, 150)=13.2	0.0006, F=(1, 150)=12.2	0.26, F=(1, 150)=1.3
	rutin	QARG	KR
HN-HW	30.6 b	8.9 b	5.9 b
HN-LW	27.2 b	8.5 b	4.5 c
LN-HW	59.0 a	28.9 a	12.4 a
LN-LW	59.1 a	32.3 a	12.9 a
N	<0.0001, F=(1, 150)=234.7	<0.0001, F=(1, 150)=277.7	<0.0001, F=(1, 150)=174.8
H₂O	0.46, F=(1, 150)=0.6	0.37, F=(1, 150)=0.8	0.16, F=(1, 150)=2.0
N*H₂O	0.42, F=(1, 150)=0.7	0.31, F=(1, 150)=1.1	0.03, F=(1, 150)=5.1
	chlorogenic acid	feruloyl quinic acid	
HN-HW	23.3 c	56.0 b B	
HN-LW	20.8 c	58.6 b A	
LN-HW	31.4 b	84.1 a B	
LN-LW	38.0 a	107.2 a A	
N	<0.0001, F=(1, 150)=115.9	<0.0001, F=(1, 150)=67.2	
H₂O	0.14, F=(1, 150)=2.2	0.005, F=(1, 150)=8.3	
N*H₂O	0.0007, F=(1, 150)=12.1	0.09, F=(1, 150)=2.9	

7 Table 2: Correlation between defense compound concentration and leaf nitrogen (N) as well as leaf water
 8 (H₂O) concentration. R = Spearman's correlation coefficient, P = p-value. QARG = quercetin-3-(2''apiosyl-6''-
 9 rhamnosylglucoside), KR = kaempferol-rutinoside

	α-tomatine		dehydrotomatine		tomatidine	
	R	P	R	P	R	P
correlation to leaf N						
non-infested leaves	-0.34	<0.0001	-0.41	<0.0001	-0.35	<0.0001
sap feeder-infested leaves	-0.54	<0.0001	-0.57	<0.0001	-0.54	<0.0001
leaf chewer-infested leaves	-0.20	0.09	-0.20	0.004	-0.45	<0.0001
correlation to leaf H₂O						
non-infested leaves	-0.28	0.0004	-0.24	0.003	-0.35	<0.0001
sap feeder-infested leaves	-0.31	0.006	-0.34	0.002	-0.47	<0.0001
leaf chewer-infested leaves	0.09	0.43	0.05	0.68	-0.35	0.001
	rutin		QARG		KR	
	R	P	R	P	R	P
correlation to leaf N						
non-infested leaves	-0.54	<0.0001	-0.55	<0.0001	-0.42	<0.0001
sap feeder-infested leaves	-0.51	<0.0001	-0.61	<0.0001	-0.51	<0.0001
leaf chewer-infested leaves	-0.47	<0.0001	-0.61	<0.0001	-0.36	0.0002
correlation to leaf H₂O						
non-infested leaves	-0.15	0.07	-0.23	0.004	-0.13	0.10
sap feeder-infested leaves	-0.32	0.004	-0.37	0.0008	-0.19	0.09
leaf chewer-infested leaves	-0.13	0.26	-0.23	0.04	0.07	0.19
	chlorogenic acid		feruloyl quinic acid			
	R	P	R	P		
correlation to leaf N						
non-infested leaves	-0.56	<0.0001	-0.53	<0.0001		
sap feeder-infested leaves	-0.70	<0.0001	-0.66	<0.0001		
leaf chewer-infested leaves	-0.54	<0.0001	-0.55	<0.0001		
correlation to leaf H₂O						
non-infested leaves	-0.26	0.001	-0.33	<0.0001		
sap feeder-infested leaves	-0.25	0.03	-0.37	0.0007		
leaf chewer-infested leaves	-0.15	0.19	-0.32	0.005		

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15 Table 3: Bidirectional effects of plant nutrition (bottom-up) and herbivory (top-down) on quality of insect
 16 infested leaves, in terms of nutritional value and defense compound concentration. Listed are the *p*-values as
 17 well as degrees of freedom and χ^2 or F-values, describing the impact of herbivory, nitrogen (N), and water (H₂O)
 18 supply and the interaction thereof (N*H₂O) are listed. C = carbon, QARG = quercetin-3-(2''apiosyl-6''-
 19 rhamnosylglucoside), KR = kaempferol rutinoside.

	leaf N	leaf C	leaf C/N
herbivory	0.0006 , F=(4, 292)=5.1	<0.0001 , F=(4, 292)=6.2	<0.0001 , F=(4, 292)=6.6
N	<0.0001 , F=(1, 292)=138.9	<0.0001 , F=(1, 292)=111.7	<0.0001 , F=(1, 292)=85.6
H ₂ O	0.96, F=(1, 292)=0.0	0.22, F=(1, 292)=1.5	0.63, F=(1, 292)=0.2
herbivory*N	0.73, F=(4, 292)=0.5	0.08, F=(4, 292)=2.1	0.47, F=(4, 292)=0.9
herbivory*H ₂ O	0.89, F=(4, 292)=0.3	0.13, F=(4, 292)=1.8	0.88, F=(4, 292)=0.3
N*H ₂ O	0.0009 , F=(1, 292)=11.3	0.01 , F=(1, 292)=6.1	<0.0001 , F=(1, 292)=20.8
herbivory*N*H ₂ O	0.46, F=(4, 292)=0.9	0.46, F=(4, 292)=0.9	0.56, F=(4, 292)=0.8
	α -tomatine	dehydrotomatine	tomatidine
herbivory	0.22, F=(4, 292)=1.4	0.62, $\chi^2_4=2.7$	0.01 , F=(4, 292)=3.3
N	<0.0001 , F=(1, 292)=83.4	<0.0001 , $\chi^2_1=120.6$	<0.0001 , F=(1, 292)=147.5
H ₂ O	0.71, F=(1, 292)=0.1	0.98, $\chi^2_1=0.0$	<0.0001 , F=(1, 292)=27.4
herbivory*N	0.04 , F=(4, 292)=2.5	<0.0001 , $\chi^2_7=130.3$	0.59, F=(4, 292)=0.7
herbivory*H ₂ O	0.02 , F=(4, 292)=3.0	0.40, $\chi^2_7=7.3$	0.23, F=(4, 292)=1.4
N*H ₂ O	<0.0001 , F=(1, 292)=25.3	<0.0001 , $\chi^2_3=136.4$	0.12, F=(1, 292)=2.5
herbivory*N*H ₂ O	0.88, F=(4, 292)=0.3	<0.0001 , $\chi^2_{15}=154.7$	0.77, F=(4, 292)=0.5
	rutin	QARG	KR
herbivory	<0.001 , F=(4, 292)=10.8	0.02 , F=(4, 292)=2.9	0.31, $\chi^2_4=4.7$
N	<0.001 , F=(1, 292)=243.4	<0.001 , F=(1, 292)=318.4	<0.001 , $\chi^2_1=158.8$
H ₂ O	0.58, F=(1, 292)=0.3	0.04 , F=(1, 292)=4.2	0.06, $\chi^2_1=3.6$
herbivory*N	0.004 , F=(4, 292)=3.9	0.07, F=(4, 292)=2.2	<0.0001 , $\chi^2_7=171.1$
herbivory*H ₂ O	0.17, F=(4, 292)=1.6	0.10, F=(4, 292)=2.0	0.17, $\chi^2_7=10.3$
N*H ₂ O	0.07, F=(1, 292)=3.2	<0.001 , F=(1, 292)=17.1	<0.0001 , $\chi^2_3=169.0$
herbivory*N*H ₂ O	0.60, F=(4, 292)=0.7	0.14, F=(4, 292)=1.7	<0.0001 , $\chi^2_{15}=185.3$
	chlorogenic acid	feruloyl quinic acid	
herbivory	0.002 , F=(4, 292)=5.7	<0.001 , F=(4, 292)=4.8	
N	<0.001 , F=(1, 292)=96.7	<0.001 , F=(1, 292)=70.7	
H ₂ O	0.42, F=(1, 292)=0.7	<0.001 , F=(1, 292)=17.3	
herbivory*N	0.02 , F=(4, 292)=3.1	0.21, F=(4, 292)=1.5	
herbivory*H ₂ O	0.58, F=(4, 292)=0.7	0.63, F=(4, 292)=0.6	
N*H ₂ O	<0.001 , F=(1, 292)=21.4	0.009 , F=(1, 292)=6.9	
herbivory*N*H ₂ O	0.96, F=(4, 292)=0.2	0.68, F=(4, 292)=0.6	

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23 Table 4: Bottom-up effect of leaf nutritional quality on herbivore performance. Statistical analyses of the impact
 24 of leaf nitrogen (N) and leaf water (H₂O) concentration and the interaction thereof (N*H₂O) on population
 25 dynamics of *Macrosiphum euphorbiae* and *Bemisia tabaci* as well as developmental data of *Tuta absoluta* and
 26 *Spodoptera littoralis*. Listed are the *p*-values as well as degrees of freedom and χ^2 or F-values, describing the
 27 impact of leaf nitrogen (N) and/or water (H₂O) concentrations.

	<i>M. euphorbiae</i>		<i>B. tabaci</i>	
	individuals	(adults)	(nymphs)	(eggs)
N	<0.0001, $\chi^2_1=15.6$	0.21, $\chi^2_1=1.54$	<0.0001, $\chi^2_1=19.4$	<0.0001, $\chi^2_1=19.2$
H₂O	0.88, $\chi^2_1=0.0$	0.0001, $\chi^2_1=15.0$	0.02, $\chi^2_1=5.0$	0.73, $\chi^2_1=0.1$
N*H₂O	<0.0001, $\chi^2_1=36.0$	<0.0001, $\chi^2_1=10.1$	<0.0001, $\chi^2_1=79.3$	<0.0001, $\chi^2_1=59.1$
	<i>T. absoluta</i>		<i>S. littoralis</i>	
	consumed leaf area	larval growth rate	consumed leaf area	larval growth rate
N	0.16, F=(1, 34)=1.11	0.34, F=(1, 34)=0.92	0.62, F=(1, 34)=0.2	0.36, F=(1, 34)=0.9
H₂O	0.80, F=(1, 34)=0.93	0.33, F=(1, 34)=0.99	0.04, F=(1, 34)=4.8	0.07, F=(1, 34)=3.4
N*H₂O	0.60, F=(1, 34)=0.97	0.31, F=(1, 34)=1.04	0.94, F=(1, 34)=0.0	0.65, F=(1, 34)=0.2

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40 Table 5: Correlation between herbivore performance and leaf nutritional quality and defense compound
 41 concentration. R = Spearman's correlation coefficient, P = p-value. N = nitrogen, C = carbon, QARG = quercetin-
 42 3-(2''apiosyl-6''-rhamnosylglucoside), KR = kaempferol-rutinoside, CA = chlorogenic acid, FQA = feruloyl quinic
 43 acid.

	<i>M. euphorbiae</i> individuals		<i>B. tabaci</i> (adults)	
	R	P	R	P
leaf N	0.37	0.02	0.06	0.73
leaf C	-0.01	0.94	-0.15	0.39
leaf C/N	-0.45	0.005	-0.14	0.41
α-tomatine	-0.33	0.045	-0.24	0.16
dehydrotomatine	-0.25	0.13	-0.21	0.22
tomatidine	-0.05	0.73	-0.37	0.03
rutin	-0.42	0.01	0.06	0.74
QARG	-0.37	0.02	-0.11	0.51
KR	-0.18	0.28	-0.14	0.42
CA	-0.56	0.0003	-0.21	0.23
FQA	-0.38	0.02	-0.08	0.64

	<i>T. absoluta</i> larval weight increase		<i>T. absoluta</i> consumed leaf area		<i>S. littoralis</i> larval weight increase		<i>S. littoralis</i> consumed leaf area	
	R	P	R	P	R	P	R	P
leaf N	0.03	0.88	0.17	0.32	0.01	0.94	0.22	0.18
leaf C	0.12	0.49	0.17	0.30	-0.11	0.51	0.19	0.23
leaf C/N	0.00	1.00	-0.12	0.48	-0.01	0.96	-0.19	0.26
α-tomatine	0.02	0.91	-0.21	0.21	-0.17	0.31	-0.25	0.14
dehydrotomatine	-0.07	0.69	-0.03	0.86	-0.17	0.31	-0.30	0.07
tomatidine	-0.34	0.04	0.00	0.98	0.02	0.92	-0.23	0.17
rutin	0.32	0.05	-0.19	0.25	0.05	0.75	-0.04	0.81
QARG	0.16	0.35	-0.12	0.47	0.07	0.70	-0.13	0.44
KR	0.15	0.36	-0.11	0.53	-0.01	0.97	-0.26	0.12
CA	0.07	0.69	-0.12	0.46	-0.08	0.65	-0.02	0.91
FQA	0.05	0.76	-0.10	0.55	0.14	0.39	0.03	0.84

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50 Table 6: Carbon and nitrogen concentration of insect herbivores that fed on leaves with varying water and
 51 nitrogen concentration (mean \pm standard deviation) and correlation between insect host quality and leaf host
 52 quality, i.e. their N and C concentration and the respective ratio. R = Spearman's correlation coefficient, P = *p*-
 53 value, C = carbon concentration in percent of dry weight, N = nitrogen concentration in percent of dry weight.
 54 HN/LN: high/low leaf N concentration, HW/LW: high/low leaf H₂O concentration. Identical letters indicate that
 55 the values do not differ significantly.

	<i>M. euphorbiae</i>		<i>T. absoluta</i>		<i>S. littoralis</i>	
	C	N	C	N	C	N
HN-HW	48 \pm 0.5 a	6 \pm 0.1 b	46 \pm 0.2 a	9 \pm 0.1 a	37 \pm 0.4 b	9 \pm 0.3 a
HN-LW	47 \pm 0.2 a	6 \pm 0.1 b	46 \pm 0.8 a	9 \pm 0.2 a	38 \pm 0.3 a	9 \pm 0.3 a
LN-HW	45 \pm 1.4 b	6 \pm 0.2 b	43 \pm 0.9 b	10 \pm 0.3 a	36 \pm 0.2 b	10 \pm 0.2 a
LN-LW	46 \pm 0.4 b	7 \pm 0.1 a	44 \pm 1.3 b	10 \pm 0.4 a	37 \pm 0.2 a	9 \pm 0.2 a
correlations	R	P	R	P	R	P
insect N – leaf N	-1.0	<0.0001	-0.6	0.4	-0.8	0.2
insect C – leaf C	0.8	0.2	0.8	0.2	0.0	1.0
insect C/N – leaf C/N	-0.8	0.2	-0.8	0.2	-0.4	0.6

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69 Table 7: Bottom-up effect of leaf nutritional quality on parasitism. Statistical analyses of the impact of leaf (N)
 70 and water (H₂O) concentration and the interactions thereof (N*H₂O) on the number of mummies and emerged
 71 parasitoids of *Aphelinus abdominalis* on *Macrosiphum euphorbiae* as well as the biocontrol success of *Necremnus*
 72 *tutae* on *Tuta absoluta* as well as the number of emerged parasitoids. Listed are the *p*-values as well as degrees
 73 of freedom and χ^2 -values, describing the impact of leaf nitrogen (N) and/or water (H₂O) concentrations.
 74 Biocontrol success = number of larvae parasitized or killed inside the leaf.

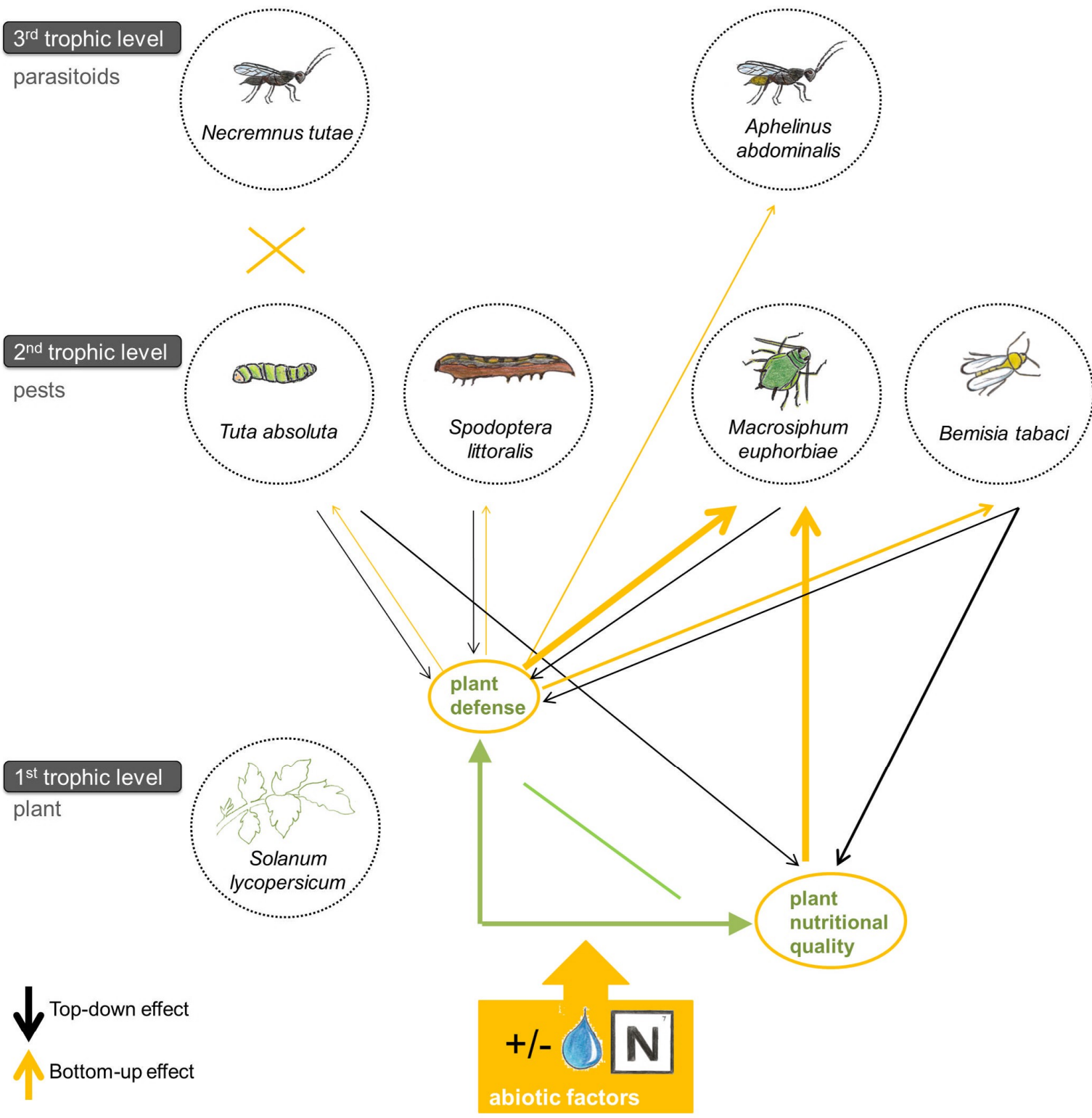
<i>A. abdominalis</i> on <i>M. euphorbiae</i>		
	mummies	parasitoids emerged
N	0.003, $\chi^2_1=8.5$	0.04, $\chi^2_1=4.1$
H₂O	0.39, $\chi^2_1=0.7$	0.48, $\chi^2_1=0.5$
N*H₂O	0.09, $\chi^2_1=2.9$	0.07, $\chi^2_1=3.2$
<i>N. tutae</i> on <i>T. absoluta</i>		
	biocontrol success	parasitoids emerged
N	0.84, $\chi^2_1=0.1$	0.79, $\chi^2_1=0.1$
H₂O	0.78, $\chi^2_1=0.1$	0.92, $\chi^2_1=0.0$
N*H₂O	0.23, $\chi^2_1=2.2$	0.05, $\chi^2_1=5.8$



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88 Table 8: Correlation between parasitism and leaf nutritional quality and defense compound concentration.
 89 R = Spearman's correlation coefficient, P = *p*-value. N = nitrogen, C = carbon, QARG = quercetin-3-(2''apiosyl-6''-
 90 rhamnosylglucoside), KR = kaempferol-rutinoside, CA = chlorogenic acid, FQA = feruloyl quinic acid.

	<i>A. abdominalis</i>				<i>N. tutae</i>			
	mummies		emerged		biocontrol success		emerged	
	R	P	R	P	R	P	R	P
leaf N	-0.01	0.98	-0.04	0.83	-0.17	0.30	-0.17	0.30
leaf C	0.26	0.13	0.20	0.25	-0.08	0.65	0.01	0.95
leaf C/N	0.06	0.74	0.08	0.65	0.19	0.25	0.20	0.22
α-tomatine	-0.06	0.74	-0.06	0.71	-0.01	0.95	0.20	0.22
dehydrotomatine	-0.27	0.11	-0.25	0.15	-0.01	0.97	0.15	0.38
tomatidine	-0.14	0.41	-0.08	0.64	0.01	0.55	0.05	0.76
rutin	-0.35	0.03	-0.31	0.07	0.10	0.57	0.12	0.45
QARG	-0.27	0.11	-0.26	0.13	0.09	0.60	0.18	0.27
KR	-0.36	0.03	-0.33	0.05	0.01	0.95	0.04	0.81
CA	-0.11	0.51	-0.12	0.48	0.14	0.39	0.31	0.06
FQA	-0.06	0.73	0.08	0.65	0.11	0.52	0.17	0.31
host C/N	0.53	0.07	0.42	0.17	-0.31	0.35	0.20	0.22
host N	-0.37	0.23	-0.27	0.39	0.35	0.30	0.35	0.29
host C	0.51	0.09	-0.38	0.22	-0.40	0.22	-0.32	0.34

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 Top-down effect
 Bottom-up effect