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1 **Cross Tolerance to Biotic and Abiotic Stresses in Plants: A Focus on Resistance**  
2 **to Aphid Infestation**

3

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5

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16

17 **Running title:** Aphid-abiotic stress interactions

18 **Number of tables:** 0

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21

22 **Highlight Summary:** Within natural environments plants respond to multiple biotic  
23 and abiotic stresses simultaneously, using an integrated signalling and response  
24 network that involves multiple points of reciprocal control. Here we explore how  
25 these multiple stress response pathways are managed and co-ordinated at a molecular

26 level to create short/medium term defences and long term memories of  
27 environmental hazards with a specific focus on how other biotic and abiotic stresses  
28 impact on plant-aphid interactions.

29 **Abstract**

30

31 Plants co-evolved with an enormous variety of microbial pathogens and insect  
32 herbivores under daily and seasonal variations in abiotic environmental conditions.  
33 Hence, plant cells display a high capacity to respond to diverse stresses through a  
34 flexible and finely balanced response network that involves components such as  
35 reduction-oxidation (redox) signalling pathways, stress hormones and growth  
36 regulators, as well as calcium and protein kinase cascades. Biotic and abiotic stress  
37 responses use common signals, pathways and triggers leading to cross tolerance  
38 phenomena, whereby exposure to one type of stress can activate plant responses that  
39 facilitate tolerance to several different types of stress. While the acclimation  
40 mechanisms and adaptive responses that facilitate responses to single biotic and  
41 abiotic stresses have been extensively characterised, relatively little information is  
42 available on the dynamic aspects of combined biotic/abiotic stress response. In this  
43 review, we consider how the abiotic environment influences plant responses to attack  
44 by phloem-feeding aphids. Unravelling the signalling cascades that underpin cross  
45 tolerance to biotic and abiotic stresses will allow the identification of new targets for  
46 increasing environmental resilience in crops.

47

48

49 **Key words:** aphids, secondary metabolites, nitrogen deficiency, drought, high light  
50 stress, UV irradiation, oxidative stress, reactive oxygen species

## 51 **Introduction**

52

53           Stress may be defined as any external factor that has a negative influence on  
54 plant growth and/or reproduction (Madlung and Comai, 2004). Environmental  
55 stresses have a significant negative impact on current agriculture. Under field  
56 conditions, commercially grown crops achieve an average of only about 50% of their  
57 potential yield due to the negative effects of abiotic environmental stresses such as  
58 drought, poor soil quality, temperature extremes and flooding (Hatfield and Walthall,  
59 2015). Biotic stress also contributes significantly to the yield gap with field losses to  
60 insect pests estimated at more than 10% (Kerchev et al., 2012a) a figure that rises to  
61 50-80% in the absence of control measures (Bruce, 2010).

62 In order to mitigate these diverse agricultural limitations, extensive effort has been  
63 expended examining the signalling and response pathways of plants to biotic and  
64 abiotic stresses. The majority of this work has necessarily focussed on single stresses  
65 in highly controlled environments in order to build our understanding of key  
66 processes and signalling elements. To date much less focus has been placed on the  
67 integrated response of plants to multiple stresses typically encountered under field  
68 conditions, however fundamental knowledge is now sufficiently advanced to tackle  
69 these questions. It is clear from studies on single stresses that there is significant  
70 overlap in signalling and response pathways to different biotic and abiotic stresses  
71 that include cellular redox status, reactive oxygen species, hormones, protein kinase  
72 cascades and calcium gradients as common elements (Atkinson and Urwin, 2012).  
73 This overlap in signalling pathways is associated with cross tolerance phenomena in  
74 which exposure to one type of stress enhances plant resistance to other biotic or  
75 abiotic stresses (Pastori and Foyer, 2002). These observations imply the possibility

76 of engineering or breeding for multiple stress resistance in crop plants. However, to  
77 achieve these goals a thorough understanding of how plants integrate information  
78 from multiple signals and optimise response to simultaneous stresses is required. In  
79 the present review we discuss knowledge concerning plant signalling and response to  
80 multiple stresses with particular reference to the impact of abiotic stresses on plant  
81 resistance to aphids.

82

### 83 **Factors that underpin multiple stress resistance**

84

85         Plants are able to withstand multiple mild and even severe environmental  
86 stresses simultaneously (Atkinson and Urwin, 2012). In a competitive growing  
87 environment a key factor underlying such resistance is the capacity of sessile plants  
88 to recognise, integrate and respond to biotic and abiotic environmental variables by  
89 constantly adjusting physiology and metabolism to optimise growth and reproduction  
90 in an ever changing environment. This capacity is facilitated by cross-tolerance  
91 phenomena, in which enhanced tolerance to a range of different environmental  
92 stresses is triggered by exposure to a single stress (Pastori and Foyer, 2002; Mittler,  
93 2006). Cross-tolerance is achieved by the synergistic co-activation of the plant innate  
94 immune system involving a network of non-specific stress-responsive pathways that  
95 cross biotic-abiotic stress boundaries (Bostock, 2005). The innate immune system of  
96 plants additionally facilitates the induction of the systemic acquired immune  
97 response (SAR) that primes the immune response of tissues distal to the site of  
98 pathogen attack in a process analogous to that of cross-tolerance. Both cross-  
99 tolerance and SAR comprise an arsenal of inducible defences activated by stress  
100 perception and associated cell signalling pathways (Figure 1). Cross-tolerance and

101 SAR are linked in many cases to an enhanced production of reactive oxygen species  
102 (ROS) such as superoxide ( $O_2^-$ ) and hydrogen peroxide ( $H_2O_2$ ) that are perceived via  
103 thiol-modulated redox- and nitric oxide-mediated (NO) signalling pathways (Foyer  
104 and Noctor, 2009). For example, exposure to the atmospheric pollutant ozone  
105 generates ROS in the apoplast of plant cells, activating a plethora of biotic and  
106 abiotic stress responses through interactions with plant hormones such as ethylene  
107 (ET), salicylic acid (SA), abscisic acid (ABA), auxin and JA (Baier et al., 2005;  
108 Fujita et al., 2006; Bartoli et al., 2013a). This redox-hormone signalling hub, which  
109 receives and integrates information from a wide range of environmental stimuli is  
110 linked to downstream changes in gene expression that are presumably optimised to  
111 meet the prevailing environmental conditions as well as the developmental stage of  
112 the plant. The concept that the transcriptional response of a plant results from  
113 integration of all of the prevailing external factors is often overlooked in experiments  
114 where researchers focus on responses to a single variable. This is illustrated by a  
115 recent meta-analysis of the transcriptional response of *Arabidopsis* to aphid  
116 infestation (Foyer et al., 2015). Highly limited overlap in gene expression changes  
117 were observed between experiments even when comparing identical interactions  
118 between *M. persicae* and the Col-0 genotype and these were reflective of variability  
119 in other environmental variables such as growth temperature, day length, light  
120 intensity and relative humidity between laboratories (Foyer et al., 2015).

121 Changes in gene expression result in downstream consequences in plant  
122 developmental and defence programmes mediated via changes in protein and  
123 metabolite content. Plant metabolite composition is strongly impacted by the  
124 prevailing abiotic environment affecting the quality of plants as hosts for insect  
125 herbivores through both direct effects on the quality of the insect diet as well as

126 indirectly via their signalling function in plants. Conversely infestation by pathogens  
127 or pests can induce specific compounds that may play a role in abiotic stress  
128 signalling or adaptation.

129         The metabolite composition of leaves and other organs is considered to be an  
130 important determinant of the success of aphid infestation. Aphid feeding can exert a  
131 strong influence on leaf metabolite profiles (Foyer et al., 2012), greatly increasing  
132 the contents of some stress-associated primary and secondary metabolites such as  
133 trehalose (Hodges et al., 2013). Trehalose metabolism is important in sugar  
134 signalling and underpins the regulation of carbon partitioning during plant responses  
135 to abiotic stress (Nuccio et al., 2015). It also influences the resistance of *A. thaliana*  
136 plants to *M. persicae* where loss of *TREHALOSE PHOSPHATE SYNTHASE11*  
137 (*TPS11*) gene function, which is required for sugar signalling activities, prevented  
138 trehalose accumulation in aphid-infested leaves and decreased resistance to aphid  
139 infestation through modulation of the PAD4-dependent biotic stress response  
140 pathways (Singh et al., 2011). Interestingly trehalose plays a role in starch  
141 metabolism, where the external application of trehalose results in the accumulation  
142 of starch in plant tissues and in addition to promoting trehalose accumulation, *M.*  
143 *persicae* infestation of Arabidopsis results in local starch accumulation. In *tps11*  
144 mutant lines that exhibited lower resistance to *M. persicae* than wild-type lines,  
145 starch accumulation was impaired in response to aphid infestation. Similarly *pgm1*  
146 mutant plants that were unable to accumulate starch due to impaired glucose  
147 metabolism exhibited reduced *M. persicae* resistance (Singh et al., 2011). Taken  
148 together these data suggest that changes at the primary metabolic level can have  
149 broad pleiotropic effects on aphid susceptibility. Polyphenols are well known to  
150 respond to abiotic stresses such as nutrient availability, drought, salinity, light and



151 temperature (Nakabayashi and Saito, 2015). Polyphenols and their oxidation  
152 products are also considered important in aphid resistance (Miles and Oertli, 1993;  
153 Lattanzio *et al.*, 2000; Kerchev *et al.*, 2012b) through the nonspecific formation of  
154 radicals or by crosslinking of cell walls suggesting that certain abiotic environments  
155 might induce a relatively broad and non-specific basal aphid resistance. Conversely,  
156 many secondary metabolites are specific in their anti-aphid action. For example, the  
157 aphid-induced indole alkaloid gramine accumulated only in response to infestation  
158 by the aphid *Schizaphis graminum* on different barley genotypes with varying  
159 resistance characteristics. Feeding by the russian wheat aphid (*Diuraphis noxia*), the  
160 rose-grain aphid (*Metopolophium dirhodum*) or the bird cherry-oat aphid  
161 (*Rhopalosiphum padi*) failed to elicit gramine accumulation. Gramine accumulation  
162 was additionally triggered by exposure to abiotic drought stress or the addition of  
163 ABA (Larsson *et al.*, 2011) and drought stressed barley plants were a poorer host for  
164 *Schizaphis graminum* than control plants (Cabrera *et al.*, 1995).

165 Non-protein amino acids, such as 5-hydroxynorvaline that is induced in  
166 maize (*Zea mays*) leaves in response to herbivory by aphids (*Rhopalosiphum maidis*,  
167 the corn leaf aphid) and caterpillars (*Spodoptera exigua*, beet armyworm), and by  
168 abiotic stresses such as drought stress, can impede aphid reproduction (Yan *et al.*,  
169 2015). Moreover, glucosinolates and the products of their hydrolysis by myrosinases  
170 play important roles in constitutive and inducible defences in crucifers. In the  
171 absence of stress, myrosinases and their substrates are not localised in the same cell  
172 types, the enzymes are transported to the cells that contain glucosinolates in response  
173 to mechanical damage and other triggers such as jasmonic acid (Thangstad *et al.*,  
174 2004; Redovniković *et al.*, 2008). Furthermore, it has been demonstrated that  
175 feeding by *Myzus persicae* on *Arabidopsis* induces the accumulation of indole

176 glucosinolates and that the addition of indole glucosinolates to artificial diets reduces  
177 the fecundity of *M. persicae* (Kim and Jander, 2007). However the association  
178 between indole glucosinolates in plant tissues and aphid performance is less clear.  
179 For example, *atr1D* mutants of Arabidopsis that contain elevated levels of indole  
180 glucosinolates supported slower reproduction of *M. persicae* than wild-type plants  
181 (Kim *et al.*, 2008). Similarly, drought caused a significant increase in the indole  
182 glucosinolate content of Arabidopsis plants as well as reduced aphid fecundity  
183 (Pineda *et al.*, 2016). However a similar negative impact of drought treatment was  
184 observed in knockout mutant lines that were blocked in the production of indole  
185 glucosinolates (Pineda *et al.*, 2016). In our own experiments, treatment of kale with  
186 1 mM methyl-jasmonate (Me-JA) resulted in increases of glucobrassicin (indol-3-  
187 ylmethylglucosinolate) and neoglucobrassicin (1-methoxy-indol-3-  
188 ylmethylglucosinolate) of more than 35- and 550-fold, respectively. However, aphid  
189 fecundity on Me-JA treated plants was significantly higher (Student's t-test,  $p < 0.05$ )  
190 than that on untreated plants (Figure 2).

191 Camalexin, a characteristic indole alkaloid of Arabidopsis, is considered to be  
192 important in plant defences against bacteria, fungi and insects (Rogers *et al.*, 1996;  
193 Kettles *et al.*, 2013). For example, aphid reproductive performance was decreased on  
194 the *dcl1* Arabidopsis mutants, which accumulate high levels of camalexin (Kettles *et*  
195 *al.*, 2013). However, aphid fecundity was increased in the *A. thaliana* phytoalexin-  
196 deficient *pad3* relative to the wild type plants (Glazebrook and Ausubel, 1994;  
197 Kettles *et al.*, 2013). Camalexin accumulation has been observed under conditions  
198 that cause amino acid starvation or those inducing oxidative stress (Zhao *et al.*,  
199 1998).

200

## 201 **Plant responses to aphid infestation**

202           Aphids, which are the largest group of phloem feeding insects, are major  
203 agricultural pests causing extensive damage to crop, garden and wild plants (Foyer et  
204 al., 2015). During feeding, aphids secrete metabolites, proteins, pathogenic bacteria  
205 and viruses into the host plant (Furch et al., 2015; Sugio et al., 2015; Whitfield et al.,  
206 2015). While the feeding process is thought to cause relatively little damage to the  
207 host plant tissues, the impact of feeding on vigour and productivity depend largely on  
208 the intensity of infestation. In agricultural environments, aphid-induced damage  
209 generally results in crop losses of about 15% (Leather et al., 1989). The majority of  
210 damage is associated with their role as vectors for more than 100 disease-causing  
211 viruses such as potato leaf roll virus and cucumber or cauliflower mosaic virus (van  
212 Emden et al., 1969). Furthermore, because aphids feed exclusively on the phloem,  
213 their diet is rich in sugar but relatively poor in nitrogen requiring the ingestion of  
214 large volumes so that the insects can acquire sufficient nitrogen (Douglas 2006).  
215 These large volumes of phloem sap are secreted as honeydew, which attracts  
216 saprophytic fungi which colonise the leaf surface inhibiting photosynthetic  
217 performance (Dedryver *et al.*, 2010).

218           In order to feed, aphids penetrate the leaf epidermis and probe between the  
219 mesophyll cells with their piercing-sucking mouthparts that are called stylets to reach  
220 the phloem sieve elements from which they feed (Figure 3). Along the stylet track  
221 mesophyll cells are regularly probed and small amounts of cell content are ingested,  
222 a behaviour that is believed to orientate the aphid stylet towards the phloem (Hewer  
223 et al., 2011). Aphids produce a rapidly-gelling “sheath saliva” around the stylets  
224 during probing activity which is rich in conjugated carbohydrates, phospholipids,  
225 pectinases, phenoloxidases and  $\beta$ -glucosidases, all of which have the potential to

226 induce plant defence responses (Miles, 1999) however it remains unclear whether  
227 aphid sheath components are recognised by plant hosts (Bak *et al.*, 2013). In addition  
228 to the rapidly-gelling sheath saliva, aphids also secrete “watery saliva” at the  
229 puncture points and feeding locations (Tjallingii, 2006). The enzymes present in the  
230 watery saliva prevent the induction of the plant wound responses in the penetrated  
231 tissues and so impede the repair of feeding-associated damage (Will *et al.*, 2009).  
232 However, aphid saliva also contains components that act as elicitors that induce plant  
233 defence responses (Miles, 1999; de Vos and Jander, 2009). For example, Mp10, an  
234 elicitor present in green peach aphid saliva induces chlorosis and local cell death in  
235 *Nicotiana benthamiana* (Bos *et al.*, 2010). Moreover, oligogalacturonides are  
236 released from the plant cell walls as a result of the action of enzymes secreted by the  
237 stylet sheath. Oligogalacturonides and other products of the cell wall breakdown  
238 have the potential to induce defence responses that limit aphid infestation (Heil,  
239 2009). Proteins derived from endosymbiotic bacteria that have been found in aphid  
240 saliva may also participate in the elicitation of plant defence responses, for example  
241 GroEL a chaperonin associated with the obligate aphid endosymbiont *Buchnera*  
242 *aphidicola* triggers plant immunity resulting in reduced aphid fecundity on hosts  
243 (Chaudhary *et al.*, 2014).

244         Plants perceive the presence of fungal pathogens mainly through the presence  
245 of chitin in the fungal cell wall, which acts as an elicitor. Chitin is also a major  
246 constituent of the insect exoskeleton and chitin oligosaccharides act as microbe-  
247 associated molecular patterns (MAMP), inducing a suite of responses which play  
248 important roles in defence against fungal pathogens (Boller and Felix, 2009; Wan *et*  
249 *al.*, 2008). In *Arabidopsis*, plant perception of chitin is dependent on LysM  
250 RECEPTOR-LIKE KINASE 1 (LysM RLK1) that specifically binds

251 chitooligosaccharides released from fungal cell walls and insect exoskeletons by the  
252 action of chitinases. These important pathogenesis-related (PR) proteins are induced  
253 not only by biotic but also by abiotic stress (Ahmed et al., 2012). It has been  
254 suggested that in addition to catalysing chitin oligosaccharide release from pests and  
255 pathogens, plant chitinases may also release similar polysaccharides from  
256 endogenous glycoproteins. In support of this hypothesis *Arabidopsis* plants  
257 engineered to express *Trichoderma* endochitinase and hexoaminidase exhibit  
258 enhanced tolerance to several abiotic stresses however tolerance was lost in a LysM  
259 RLK1 mutant background (Brotman et al., 2012). The significance of endogenous  
260 chitinases was highlighted in a study in *Malus hupehensis* where infection by the  
261 fungal pathogen *Botryosphaeria berengeriana*, infestation by the apple aphid *Aphis*  
262 *citricota*, as well as treatment with SA, methyl jasmonate, and 1-aminocyclopropane-  
263 1-carboxylic acid increased the expression of *MHCHIT1*, a class I chitinase gene  
264 (Zhang et al., 2012). Transgenic tobacco plants that constitutively over-expressed  
265 *MHCHIT1* had enhanced resistance to *Botrytis cinerea* and to treatment with the  
266 drought-inducing compound, polyethylene glycol, suggesting that the pathways  
267 induced by the *MHCHIT1* gene product were involved in cross tolerance responses  
268 to abiotic and biotic stresses (Zhang et al., 2012).

269 The induction of MAMP-type responses is not specific to the detection of  
270 micro-organisms. Similar molecular patterns and related responses such as the  
271 hypersensitive response (HR) can be triggered by a range of abiotic and biotic  
272 stresses, including aphid feeding (Klinger et al., 2009; Villada et al., 2009). The  
273 oxidative burst that is characteristic of HR involves the production and accumulation  
274 of reactive oxygen species (ROS) as well as changes in calcium fluxes, leading to the  
275 production of pathogenesis-related (PR) proteins linked to genetically-programmed

276 cell suicide responses (Smith and Boyko, 2007). Relatively little is known about the  
277 resistance responses that are mediated by the plant disease resistance (R) genes  
278 involved in aphid resistance. Incompatible plant-pathogen interactions involve the  
279 recognition of the products of avirulence genes produced by the attacking or  
280 invading organism by R genes, most of which encode nucleotide-binding site  
281 leucine-rich repeat (NBS-LRR) proteins (Martin et al., 2003; McHale et al., 2006).  
282 For example, an NBS-LRR gene is thought to be involved in the incompatible  
283 interaction between potato aphid (*Macrosiphum euphorbiae*) and tomato that leads to  
284 poor aphid growth and reproductive performance (Rossi et al., 1998). Furthermore,  
285 the *AIN* gene that mediates the hypersensitive response of *Medicago trunculata* to  
286 *Acyrtosiphon kondoi* and *A. pisum* as well as the *AKR* and *TTR* genes which  
287 specifically provide resistance to *A. kondoi* and *Therioaohis maculate* respectively all  
288 map to a genomic region containing a cluster of NBS-LRR coding sequences  
289 (Klinger et al., 2009). Similarly, the *VAT* gene encodes a NBS-LRR protein, which is  
290 implicated in the resistance response of melon to the aphid *Aphis gossypii* (Villada et  
291 al., 2009). Resistance responses dependent on the presence of the *VAT* gene included  
292 apoplastic callose production, lignin decomposition and localised programmed cell  
293 death (Villada et al., 2009; Dogimont et al., 2014).

294 In other plant species although R genes against insects have been defined  
295 through genetic studies individual genes have not been identified and cloned. For  
296 example, while several genes that confer resistance to fungi and rusts have been  
297 cloned from wheat and mostly identified as NBS-LRRs, none of the 65 R genes  
298 providing resistance to insects have been identified (Harris et al., 2015). In contrast,  
299 a number of genes that act downstream of R genes in wheat have been identified and  
300 functionally characterised. For example, the wheat genes *Hfr-1* and *Wci-1* encoding

301 lectins thought to interfere with feeding are expressed in response to Hessian fly  
302 (*Mayetiola destructor*) or bird cherry-oat aphid (*Rhopalosiphum padi*) in a biotype  
303 specific manner. Both of these genes additionally respond to treatment with SA or its  
304 analogue benzothiadiazole while *Wci-1* was also responsive to MeJA and ABA  
305 (Subramanyam et al., 2006). Within the context of abiotic-biotic stress crosstalk an  
306 interesting additional observation was that expression of *Wci-1* was upregulated by  
307 mechanical wounding while *Hfr-1* upregulation was observed following water-  
308 deficit. Similarly, the presence of the *Rag1* aphid resistance gene in soybean led to  
309 the constitutive expression of many defence-related transcripts, including those  
310 associated with ABA signalling. In resistant cultivars containing the *Rag1* gene,  
311 aphid feeding triggered the significant expression of only one additional gene,  
312 whereas aphid feeding in the susceptible cultivar caused increased abundance of  
313 many transcripts (Studham and MacIntosh, 2013).

314         The SA, ABA and JA signalling network is considered to be particularly  
315 important in triggering appropriate responses against herbivory (de Vos et al., 2005;  
316 Kerchev et al., 2013; Studham and MacIntosh, 2013; Hillwig *et al.*, 2016). While  
317 each hormone has a defined role to play in activating defences, the dynamic  
318 adjustment of the relative contribution of each pathway is required to ensure that  
319 elicited defence responses are appropriate to prevailing biotic and abiotic  
320 environments. SA is required for the induction of effective defences against  
321 biotrophic and hemi-biotrophic pathogens. Plants exposed to pathogens, herbivores  
322 and to abiotic stresses accumulate SA and PR proteins such as  $\beta$ -1,3-glucanase  
323 (Loake and Grant, 2007). However, SA does not provide an effective defence against  
324 necrotrophic pathogens (Coquoz et al., 1995; Yu, et al., 1997), which require  
325 activation of JA-dependent responses. The NON-EXPRESSOR OF PR1

326 (NPR1) protein is important in the elaboration of SA-mediated defence responses  
327 (Kinkema et al., 2000; Mou et al., 2003). *NPR1* and *NPR1*-related transcripts such as  
328 *MhNPR1* in apple were increased in response to a range of different abiotic and  
329 biotic stresses including aphid infestation (Zhang et al., 2014). Although  
330 overexpression of AtNPR1 decreased dehydration and salt tolerance in rice (Quilis et  
331 al., 2008), the constitutive expression of *MhNPR1* in tobacco enhanced tolerance to  
332 salinity and drought stresses, together with increasing resistance to *Botrytis cinerea*  
333 (Zhang et al., 2014).

334 In addition to its functions in protection against invasion by necrotrophic  
335 pathogens, the JA-dependent pathways of defence are associated with wounding and  
336 responses to herbivory (Creelman and Mullet, 1995; Devoto and Turner, 2005).  
337 Although many studies show that JA and SA act in an antagonistic manner in the  
338 regulation of plant defences (Spoel et al., 2003), abiotic stress-associated oxidative  
339 signalling can induce both pathways together (Han et al., 2013a). ABA has roles in  
340 oxidative signalling and protection against aphids (Kerchev et al., 2013, Studham  
341 and MacIntosh, 2013). ABA, which can act antagonistically to SA (Ton et al., 2009;  
342 Zabala et al., 2009), is important in drought and key physiological responses such as  
343 stomatal closure, via the activation of NADPH oxidases (Kwak et al., 2003; Petrov  
344 and Van Breusegem, 2012). Mutants defective in ABA biosynthesis such as *aba2* fail  
345 to accumulate JA or associated oxylipins following pathogen challenge (Adie et al.,  
346 2007). Furthermore *aba2* mutants support smaller aphid colonies than the wild type  
347 controls (Kerchev et al., 2013). The *aba1* mutant also supported reduced aphid  
348 colonisation associated with increased accumulation of the indole glucosinolates  
349 glucobrassicin and 4-methoxy glucobrassicin (Hillwig et al., 2016). Both of these  
350 compounds and particularly 4-methoxy glucobrassicin are toxic when provided in



351 artificial diets (Kim and Jander, 2007). However, as discussed above *M. persicae* can  
352 tolerate high concentrations of indole glucosinolates *in planta* (Figure 2).

353 Many hormones such as auxin and ABA promote ROS production as part of  
354 their mechanism of action through the activation of superoxide-producing enzymes  
355 such as NADPH oxidases, also called respiratory burst oxidase homologues (RBOH)  
356 (Bartoli et al., 2013b; Xia et al., 2015). For example, the RbohD and RbohF proteins  
357 were found to be important in generating a ROS burst and long-distance systemic  
358 signal following aphid infestation (Miller et al., 2009; Jaouannet et al., 2015).  
359 Together with cell wall peroxidases that also produce ROS, germin-like oxalate  
360 oxidases, and polyamine oxidases these enzymes generate an oxidative burst in the  
361 apoplast (Bolwell et al., 2002; Torres et al., 2002; Apel and Hirt, 2004; Sierla et al.,  
362 2013). The steady state concentrations of ROS within the cytoplasm are generally  
363 very low because of the activity of an elaborate network of low molecular weight  
364 antioxidants and antioxidant enzymes (Noctor and Foyer, 1998; Foyer and Noctor,  
365 2009). Plant cells contain many low molecular weight antioxidants such as ascorbic  
366 acid and glutathione. The capacity of the cellular antioxidant defences including the  
367 activities of enzymes such as superoxide dismutases (SOD), ascorbate peroxidases  
368 (APX), glutathione peroxidases (GPX), catalases (CAT) and peroxiredoxins (PRX)  
369 (Noctor and Foyer, 1998; Foyer and Noctor, 2005) are important in regulating the  
370 innate immune response to aphids and other pathogens. Mutants that are defective in  
371 antioxidant enzymes, or that have a low abundance of ascorbate, show enhanced  
372 resistance to biotrophic pathogens (Pavet et al., 2005). For example, mutants lacking  
373 the major leaf form of catalase (*CAT2*) exhibit enhanced resistance to bacterial  
374 pathogens (Chaouch et al., 2010), together with constitutive activation of  
375 pathogenesis-related (PR) genes and lesion development linked to SA accumulation

376 (Chen et al., 1993; Chamnongpol et al., 1998). Similarly, leaves with low ascorbate  
377 show enhanced resistance to aphid infestation (Kerchev et al., 2013).

378 ROS signals are in part mediated through GSH-dependent post-translational  
379 modifications of signalling proteins (Mhamdi et al., 2013; Han et al., 2013 a, b) as  
380 well as through protein kinase signalling cascades (Apel and Hirt, 2004; Foyer et al.,  
381 2015). Different components of mitogen-activated protein kinase (MAPK) cascades  
382 that comprise of MAPK, MAPK kinase (MAPKK/MKK) and MAPKK kinase  
383 (MAPKKK/MEKK) are activated by H<sub>2</sub>O<sub>2</sub>. For example, the MEKK1–  
384 MKK4/MKK5–MPK3/MPK6 signalling cascades that regulate pathogen defences  
385 via regulation of transcription factors such as WRKY22 and WRKY29 (Asai et al.,  
386 2002) are responsive to oxidative signalling (Rentel et al., 2004; Nakagami et al.,  
387 2005; Xing et al., 2008; Pitzschke et al., 2009;). There are more than 80 MAPKKK  
388 genes in the *A. thaliana* genome and most have been implicated in plant defence  
389 responses (Taj et al., 2010). Furthermore, systematic transcriptional analyses of  
390 aphid infestation in Arabidopsis revealed a significant role for MAPK cascades in  
391 plant responses to this stress (Foyer et al., 2015). The roles of cell wall associated  
392 kinases (WAKS) and Domain of Unknown Function (DUF)26 receptor-like kinases  
393 in the responses of Arabidopsis leaves to aphid infestation was highlighted in a  
394 recent metadata analysis of available transcriptome responses to aphid infestation  
395 (Foyer *et al.*, 2015).

396 Protein phosphatases, which regulate the degree of protein phosphorylation,  
397 participate in cell signalling, particularly in oxidative and stress-regulated pathways  
398 (He et al. 2004; Nakagami et al., 2005; Segonzac et al. 2014), as well as in wounding  
399 responses (Rojo et al. 1998). Protein phosphatase (PP)2A, which has been shown to  
400 regulate oxidative signalling leading to the elaboration of pathogen responses (Li et

401 al., 2014), also plays a role in plant resistance to aphids (Rasool et al., 2014). PP2A-  
402 B'γ was found to function downstream of metabolic ROS signals and act as a  
403 negative control of SA-linked responses in *A. thaliana* (Trotta et al., 2011; Li et al.,  
404 2014). Moreover, metabolite profiling analysis indicated that PP2A-B'γ modulates  
405 amino acid and secondary metabolism, particularly camalexin synthesis under  
406 oxidative stress (Li et al., 2014).

407 Biotic and abiotic factors alter the expression of a large number of  
408 transcription factors. For example, the *A. thaliana* homeodomain-leucine zipper  
409 (HD-Zip) transcription factor, ATHB13 influences resistance to both biotic and  
410 abiotic stresses (Gao et al., 2014; Cabello et al., 2012; Cabello and Chan, 2012).  
411 While Arabidopsis plants in which this transcription factor was overexpressed by  
412 activation tagging had a similar susceptibility to *Pseudomonas syringae*, they were  
413 found to exhibit a higher resistance to *M. persicae* and downy mildew (Gao et al.,  
414 2014). Similarly, the WRKY53 transcription factor, which is expressed in response  
415 to biotic and abiotic stress triggers in cereals, contains upstream *cis*-acting regulatory  
416 elements responsive to environmental cues such as drought and ultraviolet radiation  
417 (Van Eck, et al., 2014). Downstream targets of WRKY53 include components  
418 involved in HR such as the ORK10/LRK10 Ser/Thr receptor kinase and the  
419 apoplastic peroxidase POC1, which are expressed in response to pathogens and  
420 aphids (Van Eck, et al., 2014).

421 The expression of Redox Responsive Transcription Factor1 (RRTF1) is  
422 increased by ROS-generating necrotrophic pathogens but not by biotrophic and  
423 mutualistic infections (Matsuo et al., 2014). Moreover, transgenic lines  
424 overexpressing RRTF1 showed increased susceptibility to *Alternaria brassicae*  
425 infection (Matsuo et al., 2014). In contrast, aphid fecundity was reduced on null

426 mutants deficient in the RRTF1 protein compared to that on the wild type controls,  
427 even though RRTF1 transcripts were greatly increased within the first hours of aphid  
428 feeding (Kerchev et al., 2014).

429

### 430 **Effects of the abiotic environment on plant responses aphids**

431 While it has been postulated that abiotic stress increases herbivory, a meta-  
432 analysis of insect performance on woody plants subjected to drought, pollution,  
433 and/or shading, showed that overall these stresses had few significant effects on  
434 insect growth rates or other parameters such as colonization density (Koricheva et  
435 al., 1998). However, this analysis also revealed that abiotic stresses adversely  
436 affected chewing insects and that the reproductive potential of phloem feeding  
437 insects was reduced by drought (Koricheva et al., 1998). Moreover, much uncertainty  
438 remains concerning how climate change will alter the performance of insect  
439 herbivores and influence plant resistance to aphids and other insects. The  
440 development of the *Brassica* specialist feeder, *Brevicoryne brassicae* was not greatly  
441 altered by elevated plant growth temperatures, such as those that might be predicted  
442 to occur as a result of climate change. However, the weights of *M. persicae* adult and  
443 progeny were lower at the higher temperatures and the development time was  
444 decreased (Himanen et al., 2008).

445 Like global temperatures, atmospheric carbon dioxide (CO<sub>2</sub>) levels are  
446 increasing annually. Growth under high atmospheric CO<sub>2</sub> typically decreases plant  
447 tissue N contents while increasing C/N ratios but these effects had little impact on  
448 aphid performance on oilseed rape (Himanen et al., 2008). However, in a free air  
449 enrichment (FACE) study of pea aphid (*Acyrtosiphon pisum*) performance on *Vicia*

450 *faba*, the atmospheric composition had a significant impact on aphid performance in  
451 a genotype-dependent manner. One genotype was unaffected by enrichment of  
452 either CO<sub>2</sub>, O<sub>3</sub> or both gasses together however, a second genotype was significantly  
453 more abundant when CO<sub>2</sub> and O<sub>3</sub> were enriched simultaneously although enrichment  
454 of either gas in isolation had either no (CO<sub>2</sub>) or a negative (O<sub>3</sub>) impact on aphid  
455 abundance (Mondor et al., 2005). However, it was unclear whether differences in  
456 aphid fecundity were due to the direct impact of altered atmospheres or via indirect  
457 influences on the host plant. In a recent report, *M. trunculata* plants grown at  
458 ambient temperature (26°C) with CO<sub>2</sub> fertilisation (640 µmol mol<sup>-1</sup>) were observed  
459 to have a significant increase in both total and essential amino acids relative to plants  
460 grown at ambient CO<sub>2</sub> (400 µmol mol<sup>-1</sup>) concentrations. Plants grown under  
461 elevated CO<sub>2</sub> were more suitable hosts for *A. pisum* than those grown at ambient  
462 CO<sub>2</sub>; however, when plants were grown at elevated temperature (30°C) the effect of  
463 CO<sub>2</sub> fertilisation on amino acid content was lost as was the enhanced susceptibility of  
464 plants to aphid infestation (Ryalls et al., 2015) suggesting that at least under some  
465 conditions effects may be plant mediated. These data further illustrate the complexity  
466 of biotic-abiotic crosstalk under variable environmental conditions and demonstrate  
467 potential difficulties in predicting herbivore pest status under changing  
468 environments. Considerable cross talk exists between plant responses to ozone and to  
469 aphids leading to speculation that future selection of ozone-resistant cultivars may  
470 also influence the ability of plant defences to prevent infestation (Menendez et al.,  
471 2009).

472 While the relative importance of abiotic and biotic soil components can differ  
473 between plants and their herbivores, a study of the interactions between the aphid  
474 *Schizaphis rufula* and its host dune grass *Ammophila arenaria* revealed that aphid

475 population characteristics were dependent on the abiotic properties of the soils in  
476 different growing regions, irrespective of whether soil biota were present  
477 (Vandegheuchte et al., 2010). Moreover, herbivore-induced resistance is likely to be  
478 constrained in plants growing on degraded soils because of JA-linked responses to  
479 prevailing abiotic and biotic stresses (Held and Baldwin, 2005). Of the abiotic  
480 properties of the soils, the availability of water and essential nutrients such as  
481 nitrogen and phosphate are the most important in determining plant growth and  
482 productivity (Comadira et al., 2015).

### 483 *Nitrogen availability*

484 Soil nitrogen contents can have a strong influence on aphid fecundity (Gash,  
485 2012), as well as influencing the competition between phytophagous species. For  
486 example, the presence of leaf-chewing insects had a negative impact on aphid  
487 infestation on plants growing on all fertilizer treatments, except for ammonium  
488 nitrate fertilizer treatment (Staley, et al., 2011). The availability of essential nutrients  
489 in the soil is likely to have a significant impact on the success of herbivores because  
490 of direct effects of host nutrient availability on the diet, as well as on plant  
491 composition of secondary metabolites and on the nature of preformed and inducible  
492 defences. Herbivore feeding itself can cause carbon and nitrogen allocation changes  
493 in plants that are exacerbated under conditions of nitrogen deficiency. Moreover, the  
494 emission of volatiles is decreased in plants grown with low fertilization (Gouinguene  
495 and Turlings, 2002). In situations where essential resources such as nitrogen and  
496 phosphate are scarce, one might predict that the plant response to aphids is adjusted  
497 by shortages in essential metabolites. The specialist aphid *Rhopalosiphum padi*  
498 performed more poorly on N-limited barley seedlings, with aphids taking longer to  
499 locate the phloem (Ponder *et al.*, 2000). Similarly, the generalist feeder *M. persicae*

500 was unable to establish a successful infestation of nitrogen-deficient barley plants  
501 even though the leaves were found to be rich in amino acids, sugars and tricarboxylic  
502 acid cycle intermediates (Comadira et al., 2015). Nitrogen deficiency has a large  
503 impact on leaf transcriptome profiles, such that transcripts encoding cell wall, sugar  
504 and nutrient signalling, protein degradation and secondary metabolism are over-  
505 represented in nitrogen-deficient leaves. The extensive reorganisation of leaf  
506 metabolism and gene expression that occurs under nitrogen deficiency induces  
507 defences that protect the metabolite-rich nitrogen-deficient leaves from *M. persicae*  
508 attack (Comadira et al., 2015). Some significant similarities were observed between  
509 the gene expression profiles of N-deficient barley leaves and those of *A. thaliana*  
510 leaves infested by *M. persicae* (Foyer et al., 2015). For example, transcripts encoding  
511 WRKY 18, 33, 40, 51 and 53 were significantly induced following either N-  
512 limitation in barley or by aphid infestation in Arabidopsis leaves. Conversely, while  
513 the transcript data show that N-limitation resulted in higher levels of flavonoid  
514 metabolism transcripts in barley, flavonoid metabolism was effectively suppressed  
515 by *M. persicae* feeding in *A. thaliana* leaves (Foyer et al. 2015). Transcripts  
516 encoding WAKs and DUF26 kinases were significantly abundant in both stress  
517 situations, adding support to the hypothesis that WAKs, DUF26 kinases and WRKY  
518 transcription factors play important roles for basal resistance to aphids (Foyer et al.,  
519 2015).

520         The presence of the root nematode, *H. schachtii* decreased aphid performance  
521 on *A. thaliana* when nitrate levels were low but not under conditions of higher nitrate  
522 fertilization (Kutyniok et al., 2014). While host choice by the aphids was not  
523 influenced by the presence of nematodes under the higher nitrate fertilization regime,  
524 the aphids preferred nematode-free plants to nematode-infested plants under the

525 lower nitrogen conditions (Kutyniok et al., 2014). The presence of aphids on the  
526 shoots enhanced nematode infestation compared to controls under the low but not  
527 high nitrate availability, (Kutyniok and Müller, 2013), suggesting that the carbon-  
528 nitrogen interactions in the roots and shoots exert a strong influence on herbivore  
529 preferences and the susceptibilities of roots and shoots to herbivory.

### 530 *Water availability, drought and salinity*

531 Drought can have a strong negative influence on the success of phloem  
532 feeding insects (Koricheva et al., 1998) although it has additionally been proposed  
533 that under conditions of pulsed water stress such insects can perform better than on  
534 unstressed plants (Huberty and Denno, 2004). Interestingly, aphid performance was  
535 found to be highest in *Brassica* plants subjected to moderate drought stress (Tariq et  
536 al., 2013). Moreover, plant water status in *B. oleracea* did not have a great influence  
537 on the ability of the specialist *Brevicoryne brassicae* to induce leaf glucosinolate  
538 accumulation although it was significant with respect to glucosinolate accumulation  
539 following feeding by the generalist *M. persicae*. While the responses of plants  
540 infested with *B. brassicae* were not changed by water availability (flooding or  
541 drought), the ability of plants to induce this response following *M. persicae*  
542 infestation was negatively affected by both treatments (Khan et al., 2011). High  
543 salinity led to a significant decrease in aphid fecundity on cotton plants, an effect that  
544 was linked to increased levels of secondary metabolites such as flavonoids (Wang et  
545 al., 2015).

546 Any negative impact of drought on aphid performance is likely to be related  
547 to increases in ABA and ABA-signalling pathways that are known to decrease aphid  
548 fecundity (Kerchev et al., 2013). Protein elicitors such as harpin are able to induce  
549 plant SAR and HR responses, including resistance to the green peach aphid and can



550 also trigger drought tolerance through ABA-dependent pathways. For example,  
551 constitutive over-expression of the harpin-encoding gene, *HRF1* in rice enhanced  
552 drought tolerance through abscisic acid (ABA) signalling (Zhang et al., 2011).

553

#### 554 *Light intensity and quality, including UV irradiation*

555         Although light is an essential driving force for photosynthesis, excess light  
556 has a damaging impact on photosynthetic efficiency by inducing photoinhibition and  
557 producing transcriptome changes indicative of a wide-ranging stress response (Foyer  
558 et al., 1994; Niyogi, 1999; Suzuki et al., 2012). Signals concerning light availability  
559 arise in the chloroplast and are transmitted to the nucleus in order to regulate gene  
560 expression (Karpinski et al., 2013). High light stress triggers oxidative signalling,  
561 MPK3/MPK6, lipoxygenase and hormone signalling, particularly through SA, ABA  
562 and auxin-dependent pathways (Mühlenbock et al. 2008; Suzuki et al. 2012). For  
563 example, singlet oxygen ( $^1\text{O}_2$ ) generated by the photosynthetic electron transport  
564 chain triggers signalling pathways leading to defence responses including  
565 programmed cell death (Lee et al., 2007). The plant response to high light is  
566 qualitatively similar to HR (Chang et al. 2009; Frenkel et al. 2009) leading to SAR  
567 (Nomura et al., 2012) and systemic acquired acclimation (SAA) responses (Mateo et  
568 al. 2004; Rossel et al. 2007). Moreover, plants pre-treated with high light retain a  
569 “memory” of the high light stress that persists when plants are returned to low light  
570 conditions (Szechyńska-Hebda et al., 2010; Zhao et al., 2014). The creation of such  
571 “light memory” signalling pathways is poorly understood but ROS, hormonal and  
572 electrophysiological signalling are thought to have important roles (Szechyńska-  
573 Hebda et al., 2010). Growth under high light also increases the levels of secondary  
574 metabolites, raffinose, polyamines and glutamate in leaves (Edreva et al., 2008;

575 Zavala and Ravetta, 2001; Wulff-Zottele et al., 2010; Jänkänpää et al., 2012) and  
576 light quality also has a marked effect on leaf metabolite profiles (Kopsell and Sams,  
577 2013). *M. persicae* fecundity was similar on tobacco plants when infestation  
578 occurred in plants grown under high or low light levels, presumably because the  
579 high-light grown leaves had more amino acids and sugars compared to those grown  
580 under low light (unpublished data). In contrast, aphid fecundity was decreased when  
581 infection took place on *Arabidopsis* plants that had previously been grown under  
582 high light ( $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) and returned to low light ( $250 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) conditions  
583 (Rasool et al., 2014).

584         The content of UV-B radiation within the light spectrum can also have an  
585 impact on herbivory. Growth under UV-irradiation altered the attractiveness *B.*  
586 *oleracea* plants to herbivorous insects such as thrips, whiteflies, and aphids  
587 (Kuhlmann and Müller, 2009). However, the fecundity of the green peach aphid was  
588 significantly decreased on the *B. oleracea* plants grown under high (80%) and low  
589 (4%) UV-B levels compared to ambient UV-B (Kuhmann and Müller, 2010). In  
590 contrast, the reproduction of specialist cabbage aphid (*Brevicoryne brassicae*) was  
591 decreased only under high UV-B (80%) levels (Kuhmann and Müller, 2010).

592

### 593 **Discussion and perspectives**

594         It has long been supposed that plants experiencing adverse environmental  
595 conditions are likely to be more susceptible to attack by herbivores and pathogens.  
596 Certainly herbivore performance and behaviour are affected by the quality of their  
597 host plants, which in turn is determined by the prevailing environmental conditions.  
598 However, in many cases even mild exposures to abiotic stresses trigger innate  
599 immune responses and so enhance plant defences. Each stress influences the

600 morphological, metabolic, transcript and protein landscapes of the leaves and other  
601 organs in ways that show a high degree of overlap with the responses to other  
602 stresses allowing for cross tolerance phenomena. In reality, relatively few stress-  
603 specific signalling pathways have been found in plant responses to biotic and abiotic  
604 triggers. The use of common signalling pathways that enhance general defences to a  
605 wide range of stresses dictates that exposure to a single environmental stress is  
606 sufficient to trigger rapid defence responses to a range of stresses as well as  
607 generating epigenetic memories of stress that can persist from generation to  
608 generation. Plant responses to aphids therefore involve overlap and interaction  
609 points between hormone, redox, nitric oxide, kinase and calcium signalling pathways  
610 that have common features with abiotic stress responses. The analysis of current  
611 literature discussed above suggests that few stresses pre-dispose plants to aphid  
612 infestation.

613         Most of the common plant defence responses to the imposition of abiotic  
614 stress such as decreased growth and enhanced production of secondary metabolites  
615 are likely to have a negative impact on the ability of aphids to colonise and thrive on  
616 their plant hosts. In particular, abiotic stresses that lead to strengthening of the cell  
617 wall and/or altered accumulation of assimilate in the phloem are likely to impede  
618 aphid feeding. It is therefore important to understand the impact of abiotic stress on  
619 factors that are crucial to aphid success. Climate change factors such as elevated  
620 atmospheric CO<sub>2</sub> concentrations might diminish aphid success, particularly if the  
621 higher capacity for carbon gain achieved by the inhibition of photorespiration is  
622 accompanied by nitrogen limitation and limitations on primary nitrogen assimilation  
623 (Foyer et al., 2009).

624 Redox regulation and signalling through different pathways, particularly  
625 thiol-mediated post-translational modification processes, is important in the  
626 regulation of growth and defence responses because it is intrinsically linked to the  
627 action of hormones such as ABA, SA and JA that facilitate resistance to different  
628 pathogens and herbivores. Redox regulation is also likely to participate in a raft of  
629 different epigenetic control mechanisms that influence the plant response to aphids.  
630 For example, processes such as S-glutathionylation of histones and GSTs, together  
631 with GSH - and glutaredoxin-dependent mechanisms for the reductive activation of  
632 methionine sulfoxide reductases that facilitate the reduction of methionine sulfoxide  
633 to methionine, provide an additional layer of stress-mediated control of gene  
634 regulation. We have previously highlighted the importance of ascorbate as a major  
635 redox buffer in priming leaf local and systemic transcript profile responses to aphids  
636 (Kerchev et al. 2013). Ascorbate is also an important co-factor for the 2-oxoglutarate  
637 dehydrogenase family of enzymes that includes the ten-eleven translocation (TET)  
638 methylcytosine dioxygenases. These enzymes catalyze the conversion of 5-methyl  
639 cytosine (5-mC) to 5-hydroxymethyl cytosine (5-hmC), which is considered to be the  
640 initial step of active DNA methylation. Moreover, ascorbate has been shown to be a  
641 reprogramming enhancer in animals because of its ability to induce a blastocyst-like  
642 state in embryonic stem cells, promoting widespread DNA demethylation in gene  
643 promoters by modulating epigenetic modifiers (Gao et al., 2015). In this way, the  
644 impacts of biotic and abiotic stresses on the cellular ascorbate pool and the redox  
645 state of the cell can therefore generate molecular memories of stress with lasting  
646 consequences.

647 Recent advances in molecular genetic techniques mean that we are close to  
648 the identification of receptors and the associated cell signalling pathways that

649 underpin many stress-induced responses that influence aphid performance. For  
650 example, a better understanding of the stress-dependent regulation and functions of  
651 wall-associated kinases is likely to provide new insights into the biotic/abiotic stress  
652 interactions that influence aphid fecundity.

653

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## Figure Legends

**Figure 1** Schematic model of the perception and common signalling pathways that trigger enhanced biotic and abiotic stress cross tolerance. Biotic threats are frequently perceived by the recognition of pathogen associated molecular patterns (PAMP) by receptor-like kinases (RLK) which in turn activate respiratory burst oxidase homologues (RBOH) via  $\text{Ca}^{2+}$  and kinase signalling cascades (not shown) leading to the accumulation of apoplastic ROS that diffuse across the plasma membrane to enter the cytoplasm. Unfavourable abiotic environments similarly result in the accumulation of ROS primarily produced in organelles such as the chloroplasts (Chl), mitochondria (Mit) and peroxisomes (not shown). ROS accumulation promotes NO production and NO can react with  $\text{O}_2^-$  to produce other reactive nitrogen species (RNS). ROS and RNS react with protein thiol groups providing one of the perception mechanisms for redox signals that promote hormonal signalling leading to the combined activation of stress associated genes and subsequent tolerance to biotic and abiotic stress.

**Figure 2** The impact of methyl-jasmonate treatment on indole glucosinolate content and aphid fecundity on curly kale. Plants were grown under glass for three weeks prior to treatment with 1 mM methyl-jasmonate or water (control) as a foliar spray. Five days after treatment 5 plants were harvested and the relative quantity of indole glucosinolate estimated by LC/MS as previously described (Panel A, Viger *et al.*, 2015). Ten further plants were transferred to controlled environment chambers and a single one-day *M. persicae* nymph (genotype G) was applied to each plant which were caged as previously described (Kerchev *et al.*, 2012b). Following 15 days, the total number of aphids present were recorded (panel B). Bars represent mean values  $\pm$  SE.

**Figure 3** Schematic of potential elicitor release during aphid feeding. Hydrolytic enzymes in gelling sheath saliva have the capacity to release cell wall oligosaccharides allowing ‘damaged self’ recognition and furthermore, sheath proteins and peptides can be recognised by the plant immune system and will be present both in the apoplast and through the function of sheath saliva in sealing cell puncture wounds small amounts will also be present intracellularly. proteins and

peptides from watery saliva will be primarily present in cells punctured epidermal, mesophyll and companion cells punctured during location of the sieve element as well as within the sieve elements themselves. Similarly, proteins of bacterial symbiont origin will be localised within these cells.







