Ecology of Plastic Flowers

Rusman, Q., Lucas-Barbosa, D., Poelman, E. H., & Dicke, M.

Please cite this publication as follows:

You can download the published version at:

https://doi.org/10.1016/j.tplants.2019.04.007

1 **Ecology of plastic flowers**

2

3 Quint Rusman[1], Dani Lucas-Barbosa[1,2], Erik H. Poelman[1], Marcel Dicke[1]

4

5 [1]Laboratory of Entomology, Wageningen University, P.O. Box 16, 6700 AA Wageningen, The

6 Netherlands

7 [2] Current address: Bio-communication & Ecology, ETH Zürich, Schmelzbergstrasse 9, 8092

8 Zürich, Switzerland

9 Correspondence: quint.rusman@wur.nl (Q Rusman).

10

13

14 **Abstract:**

15 Plant phenotypic plasticity in response to herbivore attack includes changes in flower traits.

16 Such herbivore-induced changes in flower traits have consequences for interactions with

17 flower visitors. Here, we synthesize current knowledge on the specificity of herbivore-induced

18 changes in flower traits, the underlying molecular mechanisms and the ecological

19 consequences for flower-associated communities. Herbivore-induced changes in flower traits

20 seem to be to a large extent herbivore-species-specific. The extensive plasticity observed in

21 flowers influences a highly connected web of interactions within the flower-associated

22 community. We argue that the adaptive value of herbivore-induced plant responses and

23 flower plasticity can only be fully understood from a community perspective, rather than from

24 pairwise interactions.

25

26 **Flowers and their environment**

27 The angiosperms, which comprise the majority of plant species, are characterized by an

28 incredible diversity in flowers that range from the tiny millimetre-long flowers of duckweed

29 (*Lemna minor*) to the giant meter-wide corpse flower (*Rafflesia arnoldi*) [1, 2]. The diversity of

30 shapes, colours and scents of flowers is largely a result of evolution with an even more diverse

31 flower-associated community [3, 4]. This community includes mutualists, such as **pollinators**

32 (see Glossary), predators and parasitoids, as well as antagonists, such as herbivores and

33 pathogens [5-7]. As flowers are the reproductive organs of the plant, their displays are under

34 selection to maximize reproduction under varying environmental conditions. Flowering plants

35 are therefore expected to respond to the environment, including visitation by antagonists and

36 mutualists. Indeed, flower traits readily change in response to herbivory or pathogen attack,

37 even when these antagonists attack plant organs other than flowers [8, 9]. Flower traits also

38 change in response to the activity of mutualists such as pollinators [10-13] and beneficial

39 microbes [14-16]. Here, we focus on herbivore-induced changes in flower traits, because

40 despite accumulating data on this topic, we still have important knowledge gaps. It is unclear

41 if there are general patterns in flower **phenotypic plasticity** to different types of herbivores,

42 and whether such plasticity is **adaptive** for the plant. Alternatively, herbivore-induced changes

43 that are non-adaptive may merely change as pleiotropic effects of herbivore-induced plant

44 responses *via* resource trade-offs, genetic, biochemical or functional linkage (see Box 1).

45 Because changes in flower traits mediate interactions with multiple flower-associated

46 community members, we need to adopt a community approach to understand flower trait

47 plasticity [6, 7, 17, 18]. In this review, we discuss 1) the current knowledge on the **specificity**

48 **of induction** and to what extent herbivore-induced changes affect flower traits, 2) what are

49 the underlying molecular mechanisms of flower plasticity, 3) the adaptive value of herbivore-

50 induced flower plasticity in mediating interactions with flower visitors, and 4) the ecological

51 consequences of floral plasticity for flower-associated communities.

52

53 **Specificity of herbivore-induced floral plasticity**

54 The influence of herbivore-induced changes on flower traits and consequences for flower

55 visitors was first recognized more than two decades ago [19] (Figure 1, Key Figure). Since then,

56 it has become apparent that floral plasticity in response to herbivory differs among plant

57 species, and ranges from limited to extensive plasticity [17, 20, 21] (Table 1). For example,

58 **folivory** by *Trichoplusia ni* affects flower morphology of *Campanula rotundifolia*, floral volatile

59 blend composition of *Heterotheca villosa*, whereas it does not affect flower traits of *Phacelia*

60 *hastata* or *Potentilla recta* [21]. In *Brassica nigra*, a range of herbivore species that commonly

61 attack this species change multiple traits simultaneously, including floral morphology,

62 volatiles, colour, nectar and pollen production [8]. Some flower traits are more plastic than

63 others, either because their expression is more plastic [22, 23], or because they are more

64 closely connected to physiological regulation of plant defences (Box 1). Especially flower

65 phenology, morphology, and volatile emission seem to be plastic in response to herbivory,

66 while nectar production changes in some cases, but not in others (Table 1). Few studies

67 investigated a set of multiple flower traits, *e.g.* flower colour, pollen production and chemistry

68 are rarely investigated. When measured, colour and pollen production show changes in

69 response to herbivory, but not necessarily so [8, 12, 24, 25]. For instance, the reflectance

70 spectrum of flowers might not change in response to herbivory [20, 24], or change by

71 reflecting higher or lower intensities of specific wavelengths like yellow and UV [8]. When

72 pollen production changes in response to herbivory, this is mostly by a reduction in the

73 amount of pollen produced [8, 25].

74 Besides variation in plant species and traits, herbivore-induced changes in flower traits vary

75 with herbivore identity and feeding behaviour (Table 1). Because herbivore-induced plant

76 responses often contain a systemic component, and defence and reproduction are

77 physiologically linked (Box 1), we expect similar patterns of specificity in the induction of

78 flower traits as for defence traits. Specificity of induction of foliar defence traits often includes

79 a general component based on the feeding mode and feeding site of the herbivore and a more

80 specific component based, among others, on herbivore identity [26-29]. The limited direct

81 evidence we have suggests that changes in flower traits are to a large extent herbivore-species

82 specific (Table 1). Indirect evidence gained by comparing different studies supports this. For

83 example, the application of jasmonic acid (JA) on leaves of *Brassica nigra*, which induces the

84 general component of herbivore-induced plant responses against chewing herbivores,

85 reduced nectar production in the flowers, whereas folivory by *Pieris rapae* or *P. brassicae*

86 caterpillars, two chewing herbivores that induce JA, increased nectar production or had no

87 effect [30, 31]. To explain differences in specificity of induction between foliar and floral

88 tissues, we need to consider the underlying physiological mechanisms.

89

90 **Physiological regulation of flower plasticity**

91 Herbivore-induced changes in plant leaves are well known to be mediated by phytohormonal

92 signal-transduction pathways [32]. Emerging evidence indicates that flowers, just as leaves,

93 respond to herbivory by activating phytohormonal signalling. Increased expression of the JA

biosynthesis gene *LIPOXYGENASE-2* (*LOX2*) can be induced in various floral tissues by exogenous methyl jasmonate [33], and leaf herbivory can induce the expression of JA biosynthesis genes, such as *ALLENE OXIDE SYNTHASE* (*AOS*) in the flowers [34, 35], with subsequent induction of JA [34, 36, 37]. In contrast to leaves, concentrations of floral salicylic acid (SA) have so far not been shown to change in response to herbivory, while for abscisic acid (ABA) evidence suggests that herbivory has either no effect or results in increased concentrations of ABA in flowers [34, 36]. Despite the apparently conserved phytohormonal signalling in leaves and flowers (Box 2), important tissue-specific patterns in the accumulation and regulation of signalling pathway components have been identified [38]. This may explain the discrepancy in specificity of herbivore induction between foliar and floral tissues. So far, the accumulation and regulation of foliar and floral tissue-specific components have mostly been documented for the JA-pathway. The constitutive accumulation of ALLENE OXIDE CYCLASE (AOC) mRNA and proteins was found to be higher in tomato flowers compared to leaves, and also differed between flower tissues [39]. The accumulation of AOC mRNA and proteins was accompanied by tissue-specific increases in the concentrations of JA, 12-oxo-phytodienoic acid (OPDA), and jasmonoyl-L-isoleucine (JA-Ile). When *AOC* was overexpressed in tomato, this increased JA and OPDA concentrations in buds and flowers, but not in leaves [40]. The increase in JA and OPDA concentrations differed among floral tissues, resulting in specific ratios of these compounds in various flower organs. Biosynthesis of JA in the stamens of *A. thaliana* starts with the expression of *DEFECTIVE IN ANTHER DEHISCENCE1*, which is not expressed in other flower tissues [41]. In pea (*Pisum sativum*), a *LOX* gene has been identified which is predominantly expressed in the flowers, and shows differential expression in flower tissues, with the highest expression in petals and carpels [42]. Together, these results suggest differential regulation of JA biosynthesis between leaves and flowers, and even different flower organs, *via* the tissue-specific accumulation of conserved pathway components and the presence of unique pathway components. Such tissue specificity is also present in the JA-induced part of the signalling pathway. Specific types of JASMONATE ZIM-DOMAIN (JAZ) and MYB proteins are found in flowers, that are not expressed in leaves [43-46]. These specific JAZ proteins are important for the accumulation of constitutive defences [43]. Moreover, JAZ proteins that occur both in leaves and flowers can serve different functions, with different regulatory targets [47]. Especially JAZ proteins and transcription factors (TFs) such as MYCs, MYBs and APs, may be important for tissue-specific regulation of particular processes, such as

flower development and defence [46, 48-50]. For example, in *Arabidopsis* flowers JAZ1, 3, 4 and 9 proteins interact with the TFs TOE1 and TOE2 to regulate *CORONATINE INSENSITIVE 1* (*COI1*)-dependent flowering, but not *COI1*-dependent defence gene expression [48]. Also, MYB and WRKY TFs, and multiple *CYP94*-genes – important in feedback mechanisms of JA-Ile – are differentially expressed in leaves and flowers, and even in different floral tissues [45, 51, 52].

Regarding the SA-pathway, leaves and flowers can contain different concentrations of free and total SA, which results in tissue-specific transcriptional responses of SA-regulated defence genes [36, 53]. Moreover, SA concentrations and gene transcription levels also differ between sepals and petals, although the differences are smaller compared to leaves. The TF HAHB10 is induced in sunflower leaves after SA treatment and pathogen attack, but repressed after wounding [54]. This TF increases the expression of multiple genes involved in flowering, and represses the expression of multiple genes involved in JA- and SA-mediated defence. Interestingly, this TF is mostly expressed in mature leaves, and almost absent in floral tissues, except for the carpels [54].

This suggests that regulation of development and defence is different in vegetative and floral tissues of flowering plants. Tissue-specific gene expression patterns and regulatory components likely lead to different plant responses in leaves versus flowers. Indeed, floral and foliar herbivory induce different changes in the plant [35, 55], and plant responses to foliar herbivory differ for foliar and floral tissues [12, 30, 37]. Flowers even respond differently to attack on different systemic tissues. For example, root and foliar herbivory induce different changes in flower traits [8, 56] (Figure 1). Moreover, the plant as an integrated phenotype can adopt different defence strategies depending on **plant ontogeny** [57], and specifically between vegetative and flowering stages [58, 59]. The timing of herbivory over plant ontogeny can therefore result in different patterns of herbivore-induced plant responses [60]. Taken together, tissue-specific and ontogeny-specific expression of genes and regulatory components with resultant differential expression of plant responses likely explain the differences in specificity of herbivore-induced changes in plant traits between leaves and flowers. Such knowledge on the underlying mechanisms allow us to manipulate the plant phenotype, while preserving the context of these complex interactions, to test effects of floral plasticity on other organisms present in the environment, and plant fitness.

Adaptiveness of floral plasticity

Flower traits that commonly change in response to herbivory are hypothesised to be adaptive by mediating interactions that maximize reproductive output, thus benefiting plant fitness (Figure 2). By now, we acknowledge that floral volatiles commonly change in response to herbivory and that these are exploited by natural enemies of herbivores [24, 61, 62]. Although plant fitness benefits through the attraction of natural enemies of herbivores are intuitive and have been shown for plants in interactions with herbivores and natural enemies in the vegetative stage [63], these remain largely elusive for flowering plants (but see [64]). Herbivore-induced changes can increase the attraction of pollinators [8, 65, 66], potentially *via* changes in floral volatile emission [67]. An increased attraction of pollinators can increase reproductive output [67, 68], but not necessarily [65], and this likely depends on conditions such as pollen and resource limitations. Herbivore-induced changes can lead to increased resistance to **florivores**, seed predators, and **nectar thieves** [66, 69], by changes in flower chemistry [7, 37, 70, 71]. Leaf-herbivore-induced resistance to seed predators benefits plants of *Oenothera biennis* by reducing seed predation to a large extent, whereas leaf herbivory itself had little impact on reproductive output [37]. Hence, herbivore-induced changes in flower traits that mediate interactions with mutualistic or antagonistic flower visitors may be adaptive for the plant.

In contrast to benefits, changes in flower traits may result in ecological costs [55, 72]. The most commonly reported ecological cost is a reduction in pollinator visitation [17, 55], mediated by herbivore-induced changes in floral volatiles, morphology, colour, and/or rewards (Figure 2) [8, 24, 55, 73]. Such reductions in pollinator visitation can negatively affect plant reproductive output [73], but not necessarily, again depending on conditions such as pollen and resource limitations [74, 75]. Herbivore-induced flower traits may also interfere with the optimization of pollination. For example, plants use honest signalling to increase flower constancy and pollination effectiveness [76]. With honest signalling, plants provide one or a few cues, such as volatile compounds or flower size, that are reliable indicators of flower rewards. By altering flower volatile emission, morphology, size, and nectar and pollen production, herbivores potentially interfere with honest signalling [8, 77]. Herbivory can also alter local changes in flower traits in response to visitation by flower visitors. Pollination often induces changes in flower volatile emission, colour and morphology, resulting in reduced

190 visitation by other pollinators to already pollinated flowers [10-13]. Pollination-induced

191 changes in, for example, floral volatiles can be dependent on whether the plant is

192 simultaneously attacked by herbivores [12], which might reduce pollination effectiveness.

193 Interestingly, ecological costs of changes in flower phenotype in terms of reduced pollination

194 can be compensated for by simultaneous changes in plant mating system [78], by, for

195 example, increasing **autogamous selfing** [79]. Herbivore-induced changes can increase the

196 attraction of florivores by changing apparency traits such as plant height, or flower colour and

197 volatile emission [69], with potential negative effects on plant reproduction [80]. Thus,

198 herbivore-induced changes in flower traits can be detrimental for plant reproduction by

199 altering interactions with flower visitors.

200

201 Herbivore-induced changes in interactions with flower visitors seem adaptive in some cases,

202 such as increased resistance to florivores, while maladaptive in others, such as the reduced

203 visitation by pollinators (Figure 2). Despite these insights, we lack studies that specifically

204 target fitness effects of plant responses to herbivory [81], and link these to altered interactions

205 with flower visitors. To understand the adaptive value of flower plasticity with contrasting

206 effects on pairwise interactions, it is important to adopt a community perspective.

207

208 **Consequences for flower-associated communities**

209 The flower-associated community is highly diverse and includes mutualists such as pollinators,

210 predators, parasitoids, and beneficial microorganisms as well as antagonists such as

211 herbivores and pathogenic microorganisms [5-7]. Flowers are visited by one or multiple

212 pollinator species, predominantly bees, flies, butterflies and moths, or beetles. The

213 composition of the pollinator community might be very specific for plant species, even when

214 those plants are part of the same plant community. Generalist predators such as crab spiders,

215 true bugs, and social wasps use flowers as hunting grounds [64, 82], whereas specialist

216 parasitoids may visit flowers to find their specific hosts [6, 24, 62]. Herbivores visit flowers

217 frequently, and as larvae or adults can consume specific organs or the complete flower [7].

218 Florivores can feed exclusively on flowers, but also start feeding on leaves and move to the

219 flowers later in development, or switch diet when flowers become available [83]. In addition

220 to interactions with insects, flowers contain a rich microbial community consisting of fungi,

221 bacteria, archaea, and viruses [84]. These microbes can be antagonists by destroying flower

222 tissues, opportunists that exploit the transient habitat without benefits or detriments to the

223 flowers, or mutualists by competing for niche space with antagonistic microbes. The floral

224 microbial community shows considerable variation in space, various flower organs, and time

225 [84]. Some flower visitors use flower traits for host-plant location, whereas the growth and

226 survival of most of these organisms is affected by the chemical composition of the flowers [7,

227 84, 85]. Therefore, we expect herbivore-induced changes in flower traits to have major impact

228 on flower-associated community dynamics.

229

230 Herbivore-induced changes in flower traits have flower-community wide consequences.

231 Pollinator community composition can be different for herbivore-infested plants compared to

232 uninfested plants [20, 68, 86], but not necessarily [21, 83], and this may depend on the identity

233 and feeding guild or feeding site of the herbivore [68]. Florivore community assembly can be

234 affected by early-season leaf herbivory [87]. Interestingly, the florivore community of *Brassica*

235 *oleracea* was affected differentially by the sequence of arrival of two leaf-feeding herbivores

236 early in the season [87]. Although there is no direct evidence that herbivore-induced changes

237 in flower traits affect floral microbial community composition, this is most likely [88].

238 Herbivore-induced changes in flower traits include many characteristics that affect the

239 abundance and diversity of floral microbes such as nectar composition and volatile emission

240 [84]. Chemical properties of nectar are a prime determinant of microbial communities in

241 nectaries. For example, the composition of secondary metabolites such as pyridine-type

242 alkaloids affect bacterial community richness, diversity and composition in the nectar [89],

243 and herbivory can increase nectar alkaloid levels [90]. Therefore, we expect that changes in

244 flower traits in response to herbivory affect floral microbial communities.

245 Flower plasticity can link multiple interactions between flower visitors. Flowers are generally

246 short-lived [91]. Flower-associated organisms all interact with flowers during this short time

247 window. Flower visitors that respond to herbivore-induced changes in flower traits, so-called

248 receivers, can become inducers themselves when their activities induce additional changes in

249 flower traits (Figure 3). Such flower-visitor-induced changes in flower traits can subsequently

250 affect other flower visitors [12-16, 66], and even feedback to leaf herbivores [69]. Changes in

251 flower phenotype in response to each interacting flower visitor will result in multiple linked

252 indirect interaction units, where one interaction unit comprises an inducer, the mediator (the

253 flower(s)), and a receiver (Figure 3) [92]. For example, herbivory can induce changes in nectar

composition and volatile emission [30, 90], which subsequently affect nectar microbial community composition and pollinator visitation [12, 30, 68, 89]. Different nectar microbial communities may induce further changes in nectar composition and volatiles, which affect parasitoid foraging and performance [14, 16], and pollinator visitation [15]. Indeed, artificial florivory, pollination, and nectar robbery have been shown to affect multiple subsequent flower visitors at the same time, including pollinators, nectar thieves and **robbers**, florivores, and predators [66, 69]. Interestingly, most effects were non-additive which suggests that the effect of one flower visitor can depend on the presence or behaviour of other flower visitors. Taken together, the extensive plasticity of flowers likely results in a highly connected web of interactions within the complete flower-associated community.

Although flower plasticity most likely has community-wide effects, broader patterns are difficult to predict. We still lack detailed knowledge on flower plasticity in response to the community; *e.g.* how flowers respond to sequential induction by different interactors or multiple interactors at the same time. Different interactors may vary in the magnitude of induced changes in flowers, with supposedly varying community-wide effects. Leaf and root herbivory induce systemic changes in the plant, likely affecting all flowers in the inflorescences, with high potential to affect temporal or spatially displaced flower visitors [68, 73]. For floral herbivory, herbivore-induced changes can be local, which would restrict the effects to visitors of that specific flower or a specific inflorescence. For example changes in flower phenotype due to feeding damage by florivores can be restricted to individual flowers, and damaged flowers subsequently receive fewer pollinator visits [93, 94]. Moreover, the tissue/organ that is damaged can influence how the flower appears to flower visitors [95, 96]. For example, nectar-guide removal in *Alstroemeria ligtu* reduced pollinator visitation, whereas lateral red tepal removal did not [96]. Interestingly, damaged flowers can also reduce visitation to undamaged flowers in the inflorescence [97], either due to systemic changes in the whole inflorescence, or because pollinators judge potential food plants on the plant level and therefore avoid damaged plants as a whole. Pollinator- and microbe-induced changes in flower traits are expected to be mostly local. Some of these local effects, such as pollinator-induced changes in flower longevity, affect plant appearance as a whole, and thereby pollinator and florivore visitation to non-induced flowers [13, 98]. Thus, community-wide

285   effects of flower plasticity likely vary considerably depending on the type of inducer, and
286   whether induction is local or systemic.

287   It is also worth considering how such effects will vary depending on plant phenological traits
288   such as flower longevity and abundance. Plant species can differ greatly in flower longevity
289   and abundance, from having just a few flowers that can last multiple months, to having
290   hundreds of flowers that last for a few days or less [91]. Community-wide effects of local
291   induction are probably much more extensive for plant species with a few long-lived flowers
292   compared to plant species with a high floral turn-over. The extent of floral plasticity can also
293   vary depending on flower longevity and abundance. Long-lived flowers are expected to be
294   more plastic to continuously adapt to environmental variation [13, 91]. Orchids with their
295   relatively long-lived flowers, for example, alter flower longevity depending on variation in the
296   biotic environment, *i.e.* the presence of pollinators which pollinate the flower [91]. Although
297   potentially less affected by local pollinator-induced changes, short-lived flowers still readily
298   change in response to systemic induction by herbivores [56]. Local microbe-induced changes
299   might affect short- and long-lived flowers to the same extent, because microbes directly
300   modulate flower traits rather than indirectly *via* changes in plant physiology [84, 99]. The
301   consequences of such microbe-induced changes will be more apparent for plants with long-
302   lived flowers, however, due to the lower rate of flower turn-over and smaller numbers of
303   flowers [91]. Hence, flower longevity and abundance can be important for community-wide
304   effects of local and systemic induction.

305   Lastly, responses of certain groups of flower visitors to flower plasticity are better understood
306   than others, and we specifically lack fundamental knowledge on if and how herbivore-induced
307   changes affect floral microbial community composition, differential responses of microbe
308   species, and differential effects on microbes inhabiting different floral organs. Although it
309   seems likely that flower plasticity has community-wide effects, we still have important gaps in
310   our knowledge with respect to flower plasticity, to what extent such plasticity may be
311   explained by plant life-history traits, and what the consequences for flower visitors are.

312

313   **Concluding remarks and future perspectives**
314   To understand the ecology of flower plasticity, we need to adopt a community context
315   approach. The evolution of flowers cannot be fully explained by focussing solely on pollinators,
316   but rather by combined selection of the flower-associated community, e.g. pollinators,

317 florivores, and microbes [3, 66]. Likewise, the evolution of plant defences cannot be fully

318 explained by focussing solely on herbivores, and theories on plant defence evolution will

319 benefit from including plant reproduction. For example, outcrossing *Nicotiana* species have

320 lower nicotine concentrations in leaves, flowers, and nectar compared with selfing species

321 [100]. Defensive traits may evolve from pre-existing traits with reproductive functions, and

322 hence reproductive evolutionary history may help to explain the current defence phenotype

323 [101]. Moreover, communities are characterized by ample indirect interactions among their

324 members. These indirect interactions are as important as direct interactions are in shaping

325 evolution [72, 102-104]. Hence, organisms such as herbivores not directly associated with the

326 flowers can contribute to flower evolution by indirectly affecting interactions with flower

327 visitors (**non-additive selection**). The herbivore-species-specific nature of flower plasticity in

328 response to herbivory suggests a high number of potential selective agents, but also large

329 temporal and spatial fluctuations in selection pressure exhibited by such indirect interactions.

330 Particular plant traits such as flower longevity and abundance, or the ability to separate foliar

331 from floral plant responses, or defence and reproduction for the plant as a whole, may

332 determine the extent of non-additive selection by indirect interactions. Separation of foliar

333 from floral plant responses, and defence and reproduction, can partly be achieved by tissue-

334 specific gene expression and regulatory components, and plant ontogenetic trajectories in

335 growth-defence-reproduction strategies. Still, it might be difficult for plants to completely

336 separate processes in leaves and flowers, and defence and reproduction, due to various

337 physiological links that allow plants to function as one integrated entity. Exploring the ecology

338 of plastic flowers will extend our understanding of the evolution of plant defence and

339 reproduction.

340

341 To better understand flower plasticity in response to herbivory, we need to deepen our

342 knowledge on specificity of induction, for example by using combinations of herbivores that

343 show patterns of induction of changes in foliar and/or root traits related to feeding guild,

344 feeding site, or host plant specialization. Such studies should measure a multitude of flower

345 traits because specificity of induction can only be judged when considering the complete

346 flower phenotype. We have just started to unravel the molecular mechanisms underlying

347 specificity in flower plasticity, especially how phytohormones, secondary metabolites, and

348 defence genes are expressed in the flowers [43, 47, 48, 51, 53]. More insight into such tissue-

349 specific plant responses will shed light on which of the potential links between defence and

350 reproduction (Box 1) are common and important in flower plasticity in response to herbivory.

351 Moreover, research on specificity of induction will provide broader insights in how flowering

352 plants deal with ecological variation, and optimize the attraction of mutualists while dealing

353 with antagonists. The consequences of floral plasticity should be investigated in a community

354 context, and should consider adaptive plasticity, with consequences for plant reproduction.

355 An interesting approach would be to focus on keystone herbivores: herbivores that have a

356 large effect on the interaction network with associated fitness consequences for the plant

357 [72]. Keystone herbivores that especially affect the flower-visitor community can be compared

358 with keystone herbivores that have large effects on foliar and/or root communities, and non-

359 keystone herbivores to identify how such herbivores drive selection in complex communities,

360 and what the contribution of flower plasticity and the flower-associated community is.

361 Another interesting approach will be to compare responses of flower-associated communities

362 varying in their overall degree of host plant specialization [17], because these might

363 differentially impact plant fitness, and open up different evolutionary trajectories. In addition

364 to systemic induction, the role of local flower plasticity in response to herbivory, but also

365 pollination and microbial induction, needs further attention (See Outstanding Questions). The

366 community-wide effects of local compared to systemic flower plasticity have so far not been

367 explored, and it will be interesting to compare flower plasticity of plants with particular traits,

368 such as flower longevity and abundance, in this perspective. Comparing plants with particular

369 defensive flower traits, and applying explicit hypothesis from theories on the evolution of

370 plant defence will reveal if we can generalize patterns of defences in flowering plants as we

371 have done for plants in the vegetative stage [105]. For example, do plants with apparent

372 flowers invest more in constitutive defences in the flowers whereas plants with unapparent

373 flowers invest more in inducible defences in the flowers? Answers to such questions will

374 facilitate the integration of evolutionary theories on plant defence and reproduction and help

375 explain flower plasticity in response to herbivory (see also outstanding questions).

376

380

References

1. Soltis, P.S. and Soltis, D.E. (2014) Flower diversity and angiosperm diversification. In Flower Development: Methods and Protocols (Riechmann, J.L. and Wellmer, F. eds), pp. 85-102, Springer New York.

2. Moyroud, E. and Glover, B.J. (2017) The evolution of diverse floral morphologies. Curr Biol 27, R941-R951.

3. Strauss, S.Y. and Whittall, J.B. (2006) Non-pollinator agents of selection on floral traits. In Ecology and evolution of flowers (Harder, L.D. and Barrett, S.C.H. eds), pp. 120-138, Oxford Univ. Press.

4. Schiestl, F.P. and Johnson, S.D. (2013) Pollinator-mediated evolution of floral signals. Trends Ecol Evol 28, 307-315.

5. Junker, R.R. and Keller, A. (2015) Microhabitat heterogeneity across leaves and flower organs promotes bacterial diversity. FEMS Microbiol Ecol 91, fiv097.

6. Lucas-Barbosa, D. et al. (2011) The effects of herbivore-induced plant volatiles on interactions between plants and flower-visiting insects. Phytochemistry 72, 1647-1654.

7. McCall, A.C. and Irwin, R.E. (2006) Florivory: the intersection of pollination and herbivory. Ecol Lett 9, 1351-1365.

8. Rusman, Q. et al. (2019) Floral plasticity: Herbivore-species-specific-induced changes in flower traits with contrasting effects on pollinator visitation. Plant, Cell Environ, In press.

9. McArt, S.H. et al. (2014) Arranging the bouquet of disease: floral traits and the transmission of plant and animal pathogens. Ecol Lett 17, 624-636.

10. Rodriguez-Saona, C. et al. (2011) Variation in highbush blueberry floral volatile profiles as a function of pollination status, cultivar, time of day and flower part: implications for flower visitation by bees. Ann Bot 107, 1377-1390.

406   11. Willmer, P. et al. (2009) Bidirectional flower color and shape changes allow a second

407   opportunity for pollination. Curr Biol 19, 919-923.

408   12. Lucas-Barbosa, D. et al. (2016) Visual and odour cues: plant responses to pollination and

409   herbivory affect the behaviour of flower visitors. Funct Ecol 30, 431-441.

410   13. van Doorn, W.G. (1997) Effects of pollination on floral attraction and longevity. J Exp Bot

411   48, 1615-1622.

412   14. Lenaerts, M. et al. (2017) Nectar bacteria affect life history of a generalist aphid

413   parasitoid by altering nectar chemistry. Funct Ecol 31, 2061-2069.

414   15. Rering, C.C. et al. (2018) Nectar-inhabiting microorganisms influence nectar volatile

415   composition and attractiveness to a generalist pollinator. New Phytol 220, 750-759.

416   16. Sobhy, I.S. et al. (2018) Sweet scents: Nectar specialist yeasts enhance nectar attraction

417   of a generalist aphid parasitoid without affecting survival. Front Plant Sci 9, 1009.

418   17. Lucas-Barbosa, D. (2016) Integrating studies on plant–pollinator and plant–herbivore

419   interactions. Trends Plant Sci 21, 125-133.

420   18. Jacobsen, D.J. and Raguso, R.A. (2018) Lingering effects of herbivory and plant defenses

421   on pollinators. Curr Biol 28, R1164-R1169.

422   19. Strauss, S.Y. et al. (1996) Foliar herbivory affects floral characters and plant

423   attractiveness to pollinators: implications for male and female plant fitness. Am Nat 147,

424   1098-1107.

425   20. Hoffmeister, M. et al. (2016) Herbivore-induced changes in flower scent and morphology

426   affect the structure of flower-visitor networks but not plant reproduction. Oikos 125, 1241-

427   1249.

428   21. Burkle, L.A. and Runyon, J.B. (2016) Drought and leaf herbivory influence floral volatiles

429   and pollinator attraction. Global Change Biol 22, 1644-1654.

430   22. Siebenkäs, A. et al. (2015) Phenotypic plasticity to light and nutrient availability alters

431   functional trait ranking across eight perennial grassland species. AoB PLANTS 7, plv029.

432 23. Rozendaal, D.M.A. et al. (2006) Plasticity in leaf traits of 38 tropical tree species in
433 response to light; relationships with light demand and adult stature. Funct Ecol 20, 207-216.

434 24. Schiestl, F.P. et al. (2014) Herbivory and floral signaling: phenotypic plasticity and
435 tradeoffs between reproduction and indirect defense. New Phytol 203, 257-266.

436 25. Poveda, K. et al. (2005) Floral trait expression and plant fitness in response to below- and
437 aboveground plant–animal interactions. Perspect Plant Ecol Evol Syst 7, 77-83.

438 26. Thaler, J.S. et al. (2012) Evolution of jasmonate and salicylate signal crosstalk. Trends
439 Plant Sci 17, 260-270.

440 27. Ali, J.G. and Agrawal, A.A. (2012) Specialist versus generalist insect herbivores and plant
441 defense. Trends Plant Sci 17, 293-302.

442 28. Johnson, S.N. et al. (2016) Roots under attack: contrasting plant responses to below-and
443 aboveground insect herbivory. New Phytol 210, 413-418.

444 29. Erb, M. et al. (2012) Role of phytohormones in insect-specific plant reactions. Trends
445 Plant Sci 17, 250-259.

446 30. Bruinsma, M. et al. (2014) Folivory affects composition of nectar, floral odor and
447 modifies pollinator behavior. J Chem Ecol 40, 39-49.

448 31. Bruinsma, M. et al. (2008) Differential effects of jasmonic acid treatment of *Brassica*
449 *nigra* on the attraction of pollinators, parasitoids, and butterflies. Entomol Exp Appl 128,
450 109-116.

451 32. Pieterse, C.M.J. et al. (2012) Hormonal modulation of plant immunity. Annu Rev Cell Dev
452 Biol 28, 489-521.

453 33. Jensen, A.B. et al. (2002) Fusion genetic analysis of jasmonate-signalling mutants in
454 *Arabidopsis*. The Plant Journal 29, 595-606.

455 34. Zhou, Y. et al. (2017) Insects (*Thrips hawaiiensis* (Morgan)) change the stereochemical
456 configuration of 1-phenylethanol emitted from tea (*Camellia sinensis*) flowers. RSC Advances
457 7, 32336-32343.

458   35. Peng, Q. et al. (2018) Functional characterization of an allene oxide synthase involved in

459   biosynthesis of jasmonic acid and its influence on metabolite profiles and ethylene

460   formation in tea (*Camellia sinensis*) flowers. Int J Mol Sci 19, 2440.

461   36. Chrétien, L.T.S. et al. (2018) Caterpillars induce jasmonates in flowers and alter plant

462   responses to a second attacker. New Phytol 217, 1279-1291.

463   37. McArt, S.H. et al. (2013) Leaf herbivory increases plant fitness via induced resistance to

464   seed predators. Ecology 94, 966-975.

465   38. Schmid, M. et al. (2005) A gene expression map of *Arabidopsis thaliana* development.

466   Nat Genet 37, 501-506.

467   39. Hause, B. et al. (2000) Tissue-specific oxylipin signature of tomato flowers: allene oxide

468   cyclase is highly expressed in distinct flower organs and vascular bundles. The Plant Journal

469   24, 113-126.

470   40. Miersch, O. et al. (2004) Constitutive overexpression of allene oxide cyclase in tomato

471   (*Lycopersicon esculentum* cv. Lukullus) elevates levels of some jasmonates and

472   octadecanoids in flower organs but not in leaves. Phytochemistry 65, 847-856.

473   41. Ishiguro, S. et al. (2001) The DEFECTIVE IN ANTHER DEHISCENCE1 gene encodes a novel

474   phospholipase A1 catalyzing the initial step of jasmonic acid biosynthesis, which

475   synchronizes pollen maturation, anther dehiscence, and flower opening in *Arabidopsis*. The

476   Plant Cell 13, 2191-2209.

477   42. Rodríguez-Concepción, M. and Beltrán, J.P. (1995) Repression of the pea lipoxygenase

478   gene loxg is associated with carpel development. Plant Mol Biol 27, 887-899.

479   43. Li, R. et al. (2017) Flower-specific jasmonate signaling regulates constitutive floral

480   defenses in wild tobacco. Proc Nat Acad Sci USA 114, E7205-E7214.

481   44. Reeves, P.H. et al. (2012) A regulatory network for coordinated flower maturation. PLoS

482   Genet 8, e1002506.

483   45. Stitz, M. et al. (2014) Jasmonoyl-L-Isoleucine coordinates metabolic networks required

484   for anthesis and floral attractant emission in wild tobacco (*Nicotiana attenuata*). The Plant

485   Cell 26, 3964-3983.

486   46. Sherif, S. et al. (2015) A stable JAZ protein from peach mediates the transition from

487   outcrossing to self-pollination. BMC Biol 13, 11.

488   47. Oh, Y. et al. (2013) A jasmonate ZIM-domain protein NaJAZd regulates floral jasmonic

489   acid levels and counteracts flower abscission in *Nicotiana attenuata* plants. PLoS ONE 8,

490   e57868.

491   48. Zhai, Q. et al. (2015) Transcriptional mechanism of jasmonate receptor COI1-mediated

492   delay of flowering time in *Arabidopsis*. The Plant Cell 27, 2814-2828.

493   49. Yu, X. et al. (2018) The jasmonate ZIM-domain protein gene SlJAZ2 regulates plant

494   morphology and accelerates flower initiation in *Solanum lycopersicum* plants. Plant Sci 267,

495   65-73.

496   50. Wang, H. et al. (2017) The bHLH transcription factors MYC2, MYC3, and MYC4 are

497   required for jasmonate-mediated inhibition of flowering in *Arabidopsis*. Mol Plant 10, 1461-

498   1464.

499   51. Bruckhoff, V. et al. (2016) Functional characterization of CYP94-genes and identification

500   of a novel jasmonate catabolite in flowers. PLoS ONE 11, e0159875.

501   52. Wagstaff, C. et al. (2009) A molecular and structural characterization of senescing

502   *Arabidopsis* siliques and comparison of transcriptional profiles with senescing petals and

503   leaves. The Plant Journal 57, 690-705.

504   53. Ederli, L. et al. (2015) *Arabidopsis* flower specific defense gene expression patterns affect

505   resistance to pathogens. Front Plant Sci 6.

506   54. Dezar, C.A. et al. (2011) HAHB10, a sunflower HD-Zip II transcription factor, participates

507   in the induction of flowering and in the control of phytohormone-mediated responses to

508   biotic stress. J Exp Bot 62, 1061-1076.

509   55. Kessler, A. and Halitschke, R. (2009) Testing the potential for conflicting selection on

510   floral chemical traits by pollinators and herbivores: predictions and case study. Funct Ecol

511   23, 901-912.

512   56. Barber, N.A. et al. (2011) Effects of above-and belowground herbivory on growth,

513   pollination, and reproduction in cucumber. Oecologia 165, 377-386.

514   57. Barton, K.E. and Boege, K. (2017) Future directions in the ontogeny of plant defence:

515   understanding the evolutionary causes and consequences. Ecol Lett 20, 403-411.

516   58. Diezel, C. et al. (2011) Mechanisms of optimal defense patterns in *Nicotiana attenuata*:

517   Flowering attenuates herbivory-elicited ethylene and jasmonate signaling. J Integr Plant Biol

518   53, 971-983.

519   59. Desurmont, G.A. et al. (2015) Floral volatiles interfere with plant attraction of

520   parasitoids: Ontogeny-dependent infochemical dynamics in *Brassica rapa*. BMC Ecol 15, 17.

521   60. Barton, K.E. and Koricheva, J. (2010) The ontogeny of plant defense and herbivory:

522   Characterizing general patterns using meta-analysis. Am Nat 175, 481-493.

523   61. Dannon, E.A. et al. (2010) Effects of volatiles from *Maruca vitrata l*arvae and caterpillar-

524   infested flowers of their host plant *Vigna unguiculata* on the foraging behavior of the

525   parasitoid *Apanteles taragamae*. J Chem Ecol 36, 1083-1091.

526   62. Silveira, T.A. et al. (2018) Phloem-feeding herbivory on flowering melon plants enhances

527   attraction of parasitoids by shifting floral to defensive volatiles. Arthropod Plant Inte 12, 751-

528   760.

529   63. Schuman, M.C. et al. (2012) Herbivory-induced volatiles function as defenses increasing

530   fitness of the native plant *Nicotiana attenuata* in nature. Elife 1, e00007.

531   64. Knauer, A.C. et al. (2018) Crab spiders impact floral-signal evolution indirectly through

532   removal of florivores. Nat Commun 9, 1367.

533   65. Poveda, K. et al. (2003) Effects of below-and above-ground herbivores on plant growth,

534   flower visitation and seed set. Oecologia 135, 601-605.

535   66. Soper Gorden, N.L. and Adler, L.S. (2018) Consequences of multiple flower–insect

536   interactions for subsequent plant–insect interactions and plant reproduction. Am J Bot 105,

537   1-12.

538   67. Cozzolino, S. et al. (2015) Herbivory increases fruit set in *Silene latifolia*: A consequence

539   of induced pollinator-attracting floral volatiles? J Chem Ecol 41, 622-630.

540   68. Rusman, Q. et al. (2018) Dealing with mutualists and antagonists: Specificity of plant-

541   mediated interactions between herbivores and flower visitors, and consequences for plant

542   fitness. Funct Ecol 32, 1022-1035.

543   69. Soper Gorden, N.L. and Adler, L.S. (2016) Florivory shapes both leaf and floral

544   interactions. Ecosphere 7, e01326.

545   70. McCall, A.C. et al. (2018) Leaf herbivory induces resistance against florivores in *Raphanus*

546   *sativus*. Botany 96, 337-343.

547   71. Li, R. et al. (2018) Jasmonate signaling makes flowers attractive to pollinators and

548   repellant to florivores in nature. J Integr Plant Biol 60, 190-194.

549   72. Poelman, E.H. and Kessler, A. (2016) Keystone herbivores and the evolution of plant

550   defenses. Trends Plant Sci 21, 477-485.

551   73. Chautá, A. et al. (2017) Leaf herbivory imposes fitness costs mediated by hummingbird

552   and insect pollinators. PLoS ONE 12, e0188408.

553   74. Ghyselen, C. et al. (2016) Is there a missing link? Effects of root herbivory on plant-

554   pollinator interactions and reproductive output in a monocarpic species. Plant Biol 18, 156-

555   163.

556   75. Krupnick, G.A. and Weis, A.E. (1999) The effect of floral herbivory on male and female

557   reproductive success in *Isomeris arborea*. Ecology 80, 135-149.

558   76. Wright, G.A. and Schiestl, F.P. (2009) The evolution of floral scent: the influence of

559   olfactory learning by insect pollinators on the honest signalling of floral rewards. Funct Ecol

560   23, 841-851.

561   77. Junker, R.R. et al. (2018) Covariation and phenotypic integration in chemical

562   communication displays: biosynthetic constraints and eco-evolutionary implications. New

563   Phytol 220, 739-749.

564   78. Johnson, M.T.J. et al. (2015) Evolutionary interactions between plant reproduction and

565   defense against herbivores. Annu Rev Ecol Evol Syst 46, 191-213.

566   79. Penet, L. et al. (2009) Florivory increases selfing: an experimental study in the wild

567   strawberry, *Fragaria virginiana*. Plant Biol 11, 38-45.

568   80. Theis, N. and Adler, L.S. (2012) Advertising to the enemy: enhanced floral fragrance

569   increases beetle attraction and reduces plant reproduction. Ecology 93, 430-435.

570   81. Erb, M. (2018) Plant defenses against herbivory: Closing the fitness gap. Trends Plant Sci

571   23, 187-194.

572   82. Lucas-Barbosa, D. et al. (2014) Caught between parasitoids and predators – Survival of a

573   specialist herbivore on leaves and flowers of mustard plants. J Chem Ecol 40, 621-631.

574   83. Lucas-Barbosa, D. et al. (2013) Reproductive escape: annual plant responds to butterfly

575   eggs by accelerating seed production. Funct Ecol 27, 245-254.

576   84. Aleklett, K. et al. (2014) The microbial ecology of flowers: an emerging frontier in

577   phyllosphere research. Botany 92, 253-266.

578   85. Dötterl, S. and Vereecken, N.J. (2010) The chemical ecology and evolution of bee–flower

579   interactions: a review and perspectives. Can J Zool 88, 668-697.

580   86. Steets, J.A. et al. (2006) Consequences of vegetative herbivory for maintenance of

581   intermediate outcrossing in an annual plant. Ecology 87, 2717-2727.

582   87. Stam, J.M. et al. (2018) Order of herbivore arrival on wild cabbage populations influences

583   subsequent arthropod community development. Oikos 127, 1482-1493.

584   88. Allard, S.M. et al. (2018) Insect exclusion limits variation in bacterial microbiomes of

585   tomato flowers and fruit. J Appl Microbiol 125, 1749-1760.

586   89. Aizenberg-Gershtein, Y. et al. (2015) Pyridine-type alkaloid composition affects bacterial

587   community composition of floral nectar. Sci Rep UK 5, 11536.

588   90. Adler, L.S. et al. (2006) Leaf herbivory and nutrients increase nectar alkaloids. Ecol Lett 9,

589   960-967.

590   91. Ashman, T.-L. (2004) 24 - Flower Longevity. In Plant Cell Death Processes (Noodén, L.D.

591   ed), pp. 349-362, Academic Press.

592   92. Utsumi, S. et al. (2010) Linkages among trait-mediated indirect effects: a new framework

593   for the indirect interaction web. Popul Ecol 52, 485-497.

594   93. Cardel, Y.J. and Koptur, S. (2010) Effects of florivory on the pollination of flowers: an

595   experimental field study with a perennial plant. Int J Plant Sci 171, 283-292.

596   94. Muola, A. et al. (2017) Direct and pollinator-mediated effects of herbivory on strawberry

597   and the potential for improved resistance. Front Plant Sci 8.

598   95. Oguro, M. and Sakai, S. (2009) Floral herbivory at different stages of flower development

599   changes reproduction in *Iris gracilipes* (Iridaceae). Plant Ecol 202, 221-234.

600   96. Botto-Mahan, C. et al. (2011) Floral herbivory affects female reproductive success and

601   pollinator visitation in the perennial herb *Alstroemeria ligtu* (Alstroemeriaceae). Int J Plant

602   Sci 172, 1130-1136.

603   97. Sõber, V. et al. (2010) Florivores decrease pollinator visitation in a self-incompatible

604   plant. Basic Appl Ecol 11, 669-675.

605   98. Harder, L.D. and Johnson, S.D. (2005) Adaptive plasticity of floral display size in animal-

606   pollinated plants. Proc R Soc B 272, 2651-2657.

607   99. Junker, R.R. et al. (2011) Composition of epiphytic bacterial communities differs on

608   petals and leaves. Plant Biol 13, 918-924.

609   100. Adler, L.S. et al. (2012) Reliance on pollinators predicts defensive chemistry across

610   tobacco species. Ecol Lett 15, 1140-1148.

611   101. Armbruster, W.S. et al. (2009) Macroevolutionary patterns of defense and pollination in

612   *Dalechampia* vines: Adaptation, exaptation, and evolutionary novelty. Proc Nat Acad Sci USA

613   106, 18085-18090.

614   102. Guimarães Jr, P.R. et al. (2017) Indirect effects drive coevolution in mutualistic

615   networks. Nature 550, 511-514.

616   103. Siepielski, A.M. and Benkman, C.W. (2004) Interactions among moths, crossbills,

617   squirrels, and lodgepole pine in a geographic selection mosiac. Evolution 58, 95-101.

618   104. Haloin, J.R. and Strauss, S.Y. (2008) Interplay between ecological communities and

619   evolution. Ann N Y Acad Sci 1133, 87-125.

620   105. Agrawal, A.A. (2007) Macroevolution of plant defense strategies. Trends Ecol Evol 22,

621   103-109.

622   106. Zangerl, A. and Berenbaum, M. (2009) Effects of florivory on floral volatile emissions

623   and pollination success in the wild parsnip. Arthropod Plant Inte 3, 181-191.

624   107. Ivey, C.T. and Carr, D.E. (2005) Effects of herbivory and inbreeding on the pollinators

625   and mating system of *Mimulus guttatus* (Phrymaceae). Am J Bot 92, 1641-1649.

626   108. Irwin, R.E. and Adler, L.S. (2006) Correlations among traits associated with herbivore

627   resistance and pollination: implications for pollination and nectar robbing in a distylous

628   plant. Am J Bot 93, 64-72.

629   109. Herms, D.A. and Mattson, W.J. (1992) The dilemma of plants: to grow or defend. Q Rev

630   Biol 67, 283-335.

631   110. Rivas-San Vicente, M. and Plasencia, J. (2011) Salicylic acid beyond defence: its role in

632   plant growth and development. J Exp Bot 62, 3321-3338.

633   111. Yuan, Z. and Zhang, D. (2015) Roles of jasmonate signalling in plant inflorescence and

634   flower development. Curr Opin Plant Biol 27, 44-51.

635   112. Avanci, N. et al. (2010) Jasmonates are phytohormones with multiple functions,

636   including plant defense and reproduction. Gen Mol Res 9, 484-505.

637   113. Rasmann, S. et al. (2018) Pleiotropic effect of the *Flowering Locus C* on plant resistance
638   and defence against insect herbivores. J Ecol 106, 1244-1255.

639   114. van Es, S.W. et al. (2018) Novel functions of the *Arabidopsis* transcription factor TCP5 in
640   petal development and ethylene biosynthesis. The Plant Journal 94, 867-879.

641   115. Hemm, M.R. et al. (2003) The Arabidopsis *ref2* mutant is defective in the gene encoding
642   CYP83A1 and shows both phenylpropanoid and glucosinolate phenotypes. The Plant Cell 15,
643   179-194.

644   116. Kaufmann, K. et al. (2009) Target genes of the MADS transcription factor SEPALLATA3:
645   Integration of developmental and hormonal pathways in the *Arabidopsis* flower. PLoS Biol 7,
646   e1000090.

647   117. Nagpal, P. et al. (2005) Auxin response factors ARF6 and ARF8 promote jasmonic acid
648   production and flower maturation. Development 132, 4107-4118.

649   118. Pajoro, A. et al. (2014) The (r)evolution of gene regulatory networks controlling
650   Arabidopsis plant reproduction: a two-decade history. J Exp Bot 65, 4731-4745.

651   119. Fineblum, W.L. and Rausher, M.D. (1997) Do floral pigmentation genes also influence
652   resistance to enemies? The W locus in *Ipomoea purpurea*. Ecology 78, 1646-1654.

653   120. Muhlemann, J.K. et al. (2014) The monolignol pathway contributes to the biosynthesis
654   of volatile phenylpropenes in flowers. New Phytol 204, 661-670.

655   121. Adler, L.S. (2000) The ecological significance of toxic nectar. Oikos 91, 409-420.

656   122. Borghi, M. et al. (2017) The sexual advantage of looking, smelling, and tasting good: The
657   metabolic network that produces signals for pollinators. Trends Plant Sci 22, 338-350.

658   123. Gronquist, M. et al. (2001) Attractive and defensive functions of the ultraviolet
659   pigments of a flower (*Hypericum calycinum*). Proc Nat Acad Sci USA 98, 13745-13750.

660   124. Sanders, P.M. et al. (2000) The *Arabidopsis* DELAYED DEHISCENCE1 gene encodes an
661   enzyme in the jasmonic acid synthesis pathway. The Plant Cell 12, 1041-1061.

662   125. Chini, A. et al. (2016) Redundancy and specificity in jasmonate signalling. Curr Opin

663   Plant Biol 33, 147-156.

664   126. Inouye, D.W. (1980) The terminology of floral larceny. Ecology 61, 1251-1253.

665   127. Whitman, D.W. and Agrawal, A.A. (2009) What is phenotypic plasticity and why is it

666   important? In Phenotypic plasticity of insects: Mechanisms and consequences (Whitman,

667   D.W. and Ananthakrishnan, T.N. eds), pp. 1-63, Science Publishers, Inc.

668

669   **Figure legends**

670   Figure 1. Illustration of the potential effects of herbivore-induced plant responses on flower

671   traits and consequences for flower-associated organisms. Plant responses to herbivory involve

672   the systemic activation of phytohormonal signalling pathways. Overall patterns illustrate that

673   above- and belowground chewing herbivores induce the jasmonic acid (JA) pathway, whereas

674   sap-feeding herbivores induce the salicylic acid (SA) pathway. Both defence and reproduction

675   are mediated by phytohormones such as JA and SA, but also others. Moreover, defence and

676   reproduction are physiologically linked *via* various mechanisms. Both defence- and

677   reproduction-related processes affect the expression of flower traits. Flower traits mediate

678   interactions with flower-associated community members such as floral microbes, florivores

679   (including seed predators, and nectar or pollen thieves and robbers), pollinators, and

680   predators and parasitoids. Photograph credits: Dani Lucas-Barbosa, Jitte Groothuis, Erik

681   Poelman, and Quint Rusman.

682

683   Figure 2. Schematic representation of herbivore-induced changes in flower traits that mediate

684   interactions with flower-associated organisms. Solid lines indicate direct evidence, while

685   dashed lines are based on indirect evidence. The sign in the circle represents the direction of

686   effect, where + = positive effects, - = negative effects, +/- = both positive and negative effects,

687   on the attraction, abundance, or performance of the insects and microbes. The term florivore

688   here includes seed predators, and nectar and pollen thieves and robbers. Photograph credits:

689   Erik Poelman and Quint Rusman.

690

691   Figure 3. Theoretical framework of how plant-mediated species interactions form a network
692   of trait-mediated species interactions within flowers (A), the whole plant (B), or both (C, D).
693   (A) A flower feeding herbivore that induces a local plant response (inducer) affects floral
694   microbes (receiver), that in turn may affect the same or different flower traits that are
695   received by a pollinator. (B) A leaf feeding herbivore that induces systemic plant responses
696   (inducer) affects a flower feeding herbivore (receiver), that in turn also induces systemic plant
697   responses and affects the same or different flower traits that are perceived by a pollinator. (C)
698   A leaf feeding herbivore that induces systemic plant responses (inducer) affects a pollinator
699   (receiver), that in turn induces local plant responses and affect the same or different flower
700   traits that are received by a predator. (D) Local or systemic induced changes may affect
701   multiple receivers at the same time and have flower-community wide consequences.
702   Photograph credits: Erik Poelman and Quint Rusman.
703
704

Table 1. Phenotypic plasticity of flowers in response to herbivory with its effects on subsequent flower visitation by other organisms.

Feeding guild or site	Insect herbivore	Plant species	Flower abundance	Flower phenology	Flower morphology								Flower volatiles		Flower colour			Petal quality		Flower rewards					Behavioural responses						Refs
					Petal/Corolla size	Petal/Corolla length	Petal/Corolla width	Petal roundness	Flower display size	Anther Length	Style Length	Herkogamy	Total volatile emission	Volatile blend	Reflectance spectrum	Yellow reflectance	UV reflectance	Defensive chemistry	Nutritional	Nectar volume	Nectar sugar conc.	Nectar chemistry	Pollen grains	Pollen chemistry	Syrphid fly	Butterfly behaviour	Hummingbird	Bee behaviour	Predators and	Florivores	
Chewing herbivores	*Athalia rosae*	Bn	O	.	O	_	O	_	O	.	.	.	O	C	C	_	O	.	.	_	.	.	.	.	O	O	.	.	.	.	[8]
	Depressaria pastinacella	Ps	_	.	.	.	.	.	_	.	.	.	+	C	.	.	.	.	.	.	.	.	.	.	_	.	.	.	.	.	[106]
	Manduca sextra	Sp	O	.	.	.	.	.	O	O	_	_	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	_	.	_	[55]
	Phaedon cochleariae	Sa	O	+/O	.	.	+/O	.	O	.	.	.	O/?	O/?	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	[20]
	Pieris brassicae/	Br	.	+	.	.	.	.	O	.	.	.	_	?	O	.	.	O	.	.	.	.	.	.	.	.	.	_	+	.	[24]
	Pieris brassicae	Bn	.	.	.	.	.	.	.	.	.	.	.	C	O	O	O	C	.	.	.	.	.	.	_	O	.	.	.	.	[12]
	Pieris brassicae	Bn	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	O	C	O	.	.	_	_	.	_	.	.	[30]
	Pieris rapae	Rr	O	_	.	_	_	.	.	.	.	.	.	.	.	.	.	.	.	_	.	.	_	.	_	.	.	_	.	.	[19]
	Plutella xylostella	Bn	O	.	O	O	+	_	+	.	.	.	O	C	C	O	O	.	.	.	.	.	.	.	O	_	.	.	.	.	[8]
	Spodoptera littoralis	Br		_	.	.	.	.	O	.	.	.	_	?	O	.	.	.	.	.	.	+	.	.	.	.	.	_	.	.	[24]
	Spodoptera littoralis	Sa	O	_	_	.	.	.	_	.	.	.	.	.	.	.	.	.	.	O	.	.	.	.	.	.	.	.	.	.	[25]
	Spodoptera littoralis	Sl	O	.	.	O	O	.	.	.	.	.	?/+	?	.	.	.	.	.	O	O	.	.	.	.	.	.	.	.	.	[67]
	Trichoplusia ni	Cr	O	.	.	.	.	.	_	.	.	.	O	O	.	.	.	.	.	.	.	.	.	.	.	.	.	O	.	.	[21]

Group	Species	Plant																														Ref
	Trichoplusia ni	Hv	O	.	.	.	.	.	O	.	.	.	O	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	_	.	.	[21]
	Trichoplusia ni	Ph	O	.	.	.	.	.	O	.	.	.	O	O	.	.	.	.	.	.	.	.	.	.	.	.	.	.	O	.	.	[21]
	Trichoplusia ni	Pr	O	.	.	.	.	.	O	.	.	.	O	O	.	.	.	.	.	.	.	.	.	.	.	.	.	.	O	.	.	[21]
	Zeromastax selenesii	Pa	.	.	.	O	.	.	.	O	_	.	O	O	.	.	.	.	.	_	+	.	.	.	.	.	.	_	O	.	.	[73]
Sap-feeding herbivores	*Brevicoryne brassicae*	Bn	O	.	O	_	O	_	O	.	.	.	O	C	C	O	+	.	.	_	.	.	.	.	.	_	_	.	.	.	.	[8]
	Lipaphis erysimi	Bn	O	.	+	O	+	_	O	.	.	.	O	C	C	O	+	.	.	O	.	.	O	.	.	+	+	.	.	.	.	[8]
	Philaenus spumarius	Mg	O	.	_	_	O	.	O	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	O	.	.	O	.	.	[107]
Root-feeding herbivores	*Agriotes* sp.	Sa	O	O	O	.	.	.	.	O	.	.	.	.	.	.	.	.	.	.	O	.	.	.	.	.	.	.	.	[25]
	Delia radicum	Bn	O	.	+	O	+	_	O	.	.	.	O	C	C	O	O	.	.	O	.	.	_	.	+	O	.	.	.	.	[8]1

---

1 Compared to uninfested plants, herbivory may increase (+), decrease (-), or have neutral (O) effects on plant traits and flower visitors, or herbivory may change traits in a specific direction (C). A dot (.) indicates that the trait/insect response was not assessed for the respective herbivore. Question mark indicates that no exact data was presented or accessible, or no proper statistical analysis was done. We only included studies that assessed 3 or more trait groups. Plant species: Bn = *Brassica nigra*, , Br = *B. rapa*, Pa = *Palicourea angustifolia*, Sa = *Sinapis arvensis*, Sl = *Silene latifolia*, Cr = *Campanula rotundifolia*, Hv = *Heterotheca villosa*, Ph = *Phacelia hastata*, Pr = *Potentilla recta*, Mg = *Mimulus guttatus*, Sp = *Solanum peruvianum*, Rr = *Raphanus raphanistrum*, Ps = *Pastinaca sativa*.

706

Box 1: Physiological links between defence and reproduction

Plant defence and reproduction appear to be linked because defensive and reproductive traits are correlated [90, 108] and the expression of flower traits changes in response to herbivore attack. Various mechanisms have been proposed to explain these links [17, 18]. All traits share resources from the limited nutrient pool of the plant and <u>reallocation</u> of resources to defence can impair reproduction [109]. Defence and reproductive traits share <u>phytohormonal signalling pathways</u> including e.g. jasmonic acid (JA) and salicylic acid (SA) [26, 29, 110-112], and herbivore-induced increases or decreases in any of these phytohormones potentially alter the expression of flower traits [111]. Downstream of phytohormonal signalling, the expression of both flower and defence traits is controlled by <u>genetic</u> and <u>biochemical pathways</u>. Genetic pleiotropy *via* gene regulatory networks and shared transcription factors, or individual genes involved in multiple regulatory pathways can connect defence and reproduction [113-118]. Biochemical pleiotropy can occur *via* changes in pools of shared precursors or enzymes [77, 78, 119, 120]. Other <u>physiological constraints</u> can lead to co-expression of defence and reproductive traits, such as the passive diffusion of defensive metabolites from the phloem to flower organs [18, 121], or herbivory-induced changes in the chemical environment of the cell, which are important for phytohormonal signalling [29], but can also change the redox state of pigments, leading to a shift in light absorbance [122]. Finally, individual traits can have <u>multiple functions</u> and be involved in defence and reproduction [24, 123]. For example, flowering plants use floral volatiles to attract pollinators, but also natural enemies of herbivores [24]. Redirection of flower traits to a defensive function upon herbivore attack with associated changes can render these traits sub-optimal for reproductive functions.

Box 2: Defence regulation in flowers: What can we learn from leaves?

Research on flower development suggests that the gene regulatory networks for various phytohormones, and jasmonic acid (JA) in particular, is conserved in leaves and flowers [52, 111]. Flowers show expression of multiple JA biosynthesis genes and products similar as in leaves, such as *LIPOXYGENASE* (*LOX*), *ALLENE OXIDE SYNTHASE* (*AOS*), 12-oxo-phytodienoic acid (OPDA), and *OPDA REDUCTASE* (*OPR*), and produce JA locally [43, 44, 52, 124]. Later steps in JA signalling also seem to work similarly in leaves and flowers, with essential roles for CORONATINE INSENSITIVE 1 (COI1) and JASMONATE ZIM-DOMAIN (JAZ) proteins and WKRY and MYB TFs [45, 48]. In addition, this is evident from similar expression patterns in leaves

739 and flowers for three *NAC* genes encoding JA regulatory proteins [52] and some *JAZ* genes:
740 *JAZ5* and *JAZ7* [44, 125]. Thus, the backbone of phytohormone signalling, and for JA in
741 particular, appears conserved in leaves and flowers.

742

743 **Glossary:**

744 **Adaptive:** enhancing fitness, *i.e.* the contribution of an individual to the gene pool of the
745 next generation

746 **Autogamous selfing**: Self-pollination within a flower

747 **Folivores**: Consumers of aboveground vegetative tissues.

748 **Florivores**: Consumers of developing flower buds or mature flowers before the development
749 of the seed coat and including consumers of bracts, sepals, petals, stamens, pistils, pollen
750 and ovules [7]. Also includes sap-feeding consumers that feed from floral stalks.

751 **Nectar thief**: flower visitor that collects nectar without damaging flowers, but does not
752 contribute to pollination [126].

753 **Nectar robber**: flower visitor that damages flowers while collecting nectar, but does not
754 contribute to pollination [126].

755 **Non-additive selection**: Selective effect of a community member depends on the presence
756 of other community members [104].

757 **Pollinator**: Flower visitor that contributes to successful pollination, *i.e.* to the transfer of
758 pollen from one flower to another conspecific flower.

759 **Plant ontogeny**: Development of a plant from seed to mature seed-producing plant [57].

760 **Phenotypic plasticity**: The capacity of a single genotype to display different phenotypes in
761 response to different environments [127].

762 **Specificity of induction**: differential changes in phenotype in response to different inducers.

763