

Highlights, belonging to:

Predictability of biotic stress structures plant defence evolution

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- Sessile organisms such as plants strongly rely on external stimuli that predict the onset of stress to anticipate sub-optimal conditions and adjust their phenotype accordingly.
- By integrating correlations among attackers as well as predictable patterns in the timing, and order of arrival of attack in their defence strategies, plants can anticipate biotic stress and maximize life-time fitness. However, it is unclear under which ecological conditions such strategies are adaptive.
- Selection on plants to integrate predictable patterns of future stressors in their strategies when responding to current stress can lead to sub-optimal responses to each stressor in isolation. Explicitly including the predictability of co-occurrence and temporal patterns of stressors in theory on plant defence strategies is crucial in understanding the evolution of plant growth-defence and reproductive strategies.

1 **Predictability of biotic stress structures plant defence evolution**

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22 **Abstract**

23 To achieve ecological and reproductive success, plants need to mitigate a multitude of
24 stressors. The stressors encountered by plants are highly dynamic but typically vary predictably
25 due to seasonality or correlations among stressors. As plants face physiological and ecological
26 constraints in responses to stress, it can be beneficial for plants to evolve the ability to
27 incorporate predictable patterns of stress in their life histories. Here we discuss how plants
28 predict adverse conditions, which plant strategies integrate predictability of biotic stress, and
29 how such strategies can evolve. We propose that plants commonly optimize responses to
30 correlated sequences or combinations of herbivores and pathogens, and that the predictability
31 of these patterns is a key factor governing plant strategies in dynamic environments.

32 **Keywords**

33 Predictability, growth-defence strategy, risk perception, anticipatory responses, induced
34 defence

35 **Plants in a variable and multi-stressor environment**

36 Individual organisms use historical and current information to adapt their physiology and
37 behaviour to retain fitness under forthcoming conditions [1, 2]. For sessile organisms that
38 cannot evade suboptimal environments by moving, fitness is strongly determined by phenotypic
39 responses to changes in (a)biotic conditions. Plants serve as ideal model systems for
40 understanding how sessile organisms use information and adapt their phenotype in a community
41 context [3]. Over their lifetimes, plants cope with a range of stresses, such as daily changes in
42 insolation and temperature, low resource availability, unfavourable weather, competition, and
43 attack by pathogens or herbivores [4, 5]. In many cases, stressors are immediate and long lasting
44 [6]. However, probability of occurrence of biotic stressors as well as the sequence and
45 combination in which they occur can be highly variable [e.g. 7]. Consequently, plants have
46 evolved phenotypic plasticity to fine-tune their responses to the multiple stressors present in the
47 environment in which they develop and persist [5, 8, 9].

48 Most of our research on plant plasticity has focussed on how plants maximize resilience to
49 current stress. However, more recently plant physiological and ecological studies have
50 highlighted how plant responses to current stress not only affect plasticity in response to future
51 stress [10, 11] but also how this plasticity alters the likelihood of future stress [12, 13].
52 Importantly, even though stressors may vary greatly across and within seasons and over the life
53 cycle of plants, their occurrence is not random. Foreseeable patterns may emerge from the
54 phenology of insect herbivores and activity patterns of vertebrate herbivores associated with
55 optimal abiotic conditions [14], the responses of herbivores and pathogens to specific plant
56 (ontogenetic) phenotypes [15], or the increased likelihood of simultaneous or sequential attacks
57 by different plant-antagonists [13]. For example, open wounds in plant tissues caused by
58 chewing herbivores increase the risk of pathogen attack [16]. Such correlations provide plants
59 with an opportunity to adjust their phenotype in anticipation of sub-optimal conditions or

60 dynamics of stress. Even though it has been well established that **anticipatory responses** (see
61 Glossary) in plants are ubiquitous [17], we have little understanding of the ecological conditions
62 that promote the evolution of anticipatory strategies, especially in relation to biotic stress, or
63 under which conditions such strategies are adaptive [18]. Where most theory on plant growth-
64 defence strategies and their evolution thus revolves around responses to current stress,
65 predicting and anticipating forthcoming stress may be an adaptive strategy under various
66 ecological scenarios [19] and should be prominently included in our theories on plant plasticity.

67 Plants are likely to commonly optimize responses to correlated sequences or combinations
68 of herbivores and pathogens, rather than optimizing responses to current stress. We apply the
69 concept of ecological **forecast horizons**, developed to quantify the accuracy of predictions on
70 community and ecosystem processes, to plant defence strategies [20, 21]. We define a plant's
71 forecast horizon as the timespan measured from the (static) point in time at which the plant has
72 obtained information for which a plant can make more accurate predictions on, and hence
73 prepare for, forthcoming stress conditions than when following non-anticipatory strategies.
74 Plant defence strategies incorporate a forecast horizon to cope with attacks by herbivores and
75 pathogens following a gradient of predictability ranging from wholly unpredictable to highly
76 predictable. Anticipatory strategies fundamentally revolve around a cost – benefit balance [22],
77 but existing theory can be critically expanded by explicitly incorporating the **predictability of**
78 **biotic stress** in risk management strategies.

79 **Using information from the environment to predict future stress**

80 The forecast horizon of plants is determined by their ability to obtain information that
81 correlates with future environmental and ecological conditions [23]. The process of information
82 gathering in plants and the subsequent responses to stress involve numerous sensory
83 mechanisms and have been thoroughly reviewed [see e.g.: 17] (Table 1). As most stressors

84 persist over long periods of time, current conditions experienced by plants are likely to correlate
85 well with the environment that plants will experience in the near future. A simple example is
86 the daily variation in light levels caused by the Earth's rotation on its axis (night vs day).
87 Circadian rhythms evolved in response to this predictable diurnal flux in light (and temperature)
88 levels [24]. An example of a similar evolutionary response to biotic stress is that some plants
89 can detect oviposition by phytophagous insects, which correlates well with likely future
90 herbivory by larvae hatching from these eggs [1]. Plants that **prime** or **induce defences** in
91 response to eggs gain a fitness advantage over those plants without the ability to use this cue
92 [16].

93 In addition to a direct interaction with specific stressors, plants can obtain information from
94 more indirect cues or from the correlations between different stressors [25]. As attacker
95 communities are structured over time because of differences in phenology, life history and niche
96 differentiation, interactions with specific attackers can become reliable predictors of future
97 biotic stress by different attackers. For example, leaf shelters constructed by caterpillars of the
98 genus *Pseudotelphusa* on white oak *Quercus alba* increase the species richness of subsequent
99 herbivores that colonize the new niches provided by these leaf shelters [12]. In addition to niche
100 construction, herbivore-induced changes in plants can generate **plant-mediated interaction**
101 linkages between herbivores. Plant responses to an initial attacker can thus affect the likelihood
102 of colonization by subsequent herbivores [13, 26]. These correlations among antagonists can
103 be immediate such as found for the correlated attack for pathogens spread by insect vectors
104 [27], or spanning over longer periods of time and even across seasons for perennial plants, such
105 as found for the correlations between transient attack by herbivores and their legacy effects on
106 future biotic stress [28]. Thus, by perceiving the current herbivore interaction as a cue for the
107 type of future attack, plants may incorporate likely future stress in their response to the current
108 attacker.

109 As the probability of interactions with a specific stressor is closely related to plant
110 phenotype, the **phenological and conditional state of the plant** can be an important source of
111 information that predicts to what type of stress it may get exposed. Moreover, transition
112 between ontogenetic or phenological stages of plants such as germination, leaf flushing, or
113 flowering are often initiated by similar abiotic conditions that trigger the release from dormancy
114 in insects or migration of vertebrate herbivores. Hence, phenologies of plants and their attackers
115 may strongly correlate [29]. The likelihood and impact of herbivore attack on plants may be
116 strongly dependent on the plant phenotype expressed at each ontogenetic stage [14, 30] and on
117 the ability of different ontogenetic stages of herbivores to cope with ontogenetic variation in
118 plant phenotypes [31].

119 When stress conditions for parental plants closely correlate with conditions that are likely
120 to be experienced by their offspring, it can be adaptive for parental plants to actively regulate
121 ontogenetic trajectories or trait plasticity in the next generation [32, 33]. Recent studies have
122 highlighted the important role of epigenetic trans-generational mechanisms in the regulation of
123 trait plasticity [34]. These mechanisms allow plants to alter the plasticity of offspring without
124 requiring direct genetic variation, greatly increasing the responsiveness of plants to their
125 environment over shorter trans-generational time scales (Box 1). Notably, such trans-
126 generational plasticity fits well into a traditional evolutionary framework. The ability to alter
127 the plasticity of a trait in offspring is likely a genetically encoded and heritable trait itself,
128 resulting from Darwinian adaptation [35].

129 **Plants evaluate and integrate information before expressing responses**

130 A significant problem for plants is that not all stimuli are relevant or can be used to
131 anticipate future conditions in the plant's environment [23]. Identifying reliable cues from a
132 background of environmental noise is thus a key challenge for plants using anticipatory defence

133 strategies involving a forecast horizon. The first difficulty in the perception of information is
134 that when the stimulus and the stress with which it correlates are separated over a wider
135 timespan or longer distance, variation increases due to stochastic processes in the environment.
136 Correlations between cues and the conditions they predict can rapidly deteriorate over spatial
137 or temporal scales. This creates spatio-temporal variation in cue reliability, in which plants may
138 be unable to correctly integrate or respond to the information they gather. A second challenge
139 is that the correlations between single cues and stressors are often context-dependent e.g. the
140 combination of the stressor with other cues. Exactly how accurate cues must be before they are
141 considered reliable depends on the balance between the asymmetric fitness cost of errors. If the
142 response threshold to a stimulus is too low, the costs of the defence response to a false alarm
143 may outweigh the cost of being unprepared for attack [22, 36].

144 Possible solutions to these issues are, on the one hand, the integration of multiple cues in
145 predictions, and, on the other hand, the selective weighting of more reliable cues over other by
146 the plant [37]. It is clear that plants are able to respond conditionally to cues [17]. For example,
147 repeated mechanical stimulation of leaflets by water droplets causes the sensitive plant, *Mimosa*
148 *pudica* to decrease sensitivity in leaf closure to the point where leaflets no longer respond to
149 the stimulus. After desensitisation to the stimulus, finger touch instead of water droplets elicited
150 leaflet closure in the plants, thus excluding the possibility that desensitisation was due to fatigue
151 [38].

152 **Opportunities and challenges when anticipating future conditions**

153 When abiotic or biotic cues or stresses are sufficiently well correlated with future
154 conditions that plants experience, it can be beneficial for plants to evolve anticipatory life-
155 history strategies [8, 39, 40]. Anticipatory induced responses to stimuli are ubiquitous in plants
156 and can involve a primed state or actual phenotypic change in a wide range of physiological,

157 chemical, or structural traits. These responses ultimately allow the plant to tolerate or avoid
158 future stress conditions within its reaction norm (Box 2). The adaptiveness of an anticipatory
159 response depends on opportunities and challenges in physiological regulation of the response,
160 as well as on the overall predictability of the environment [20] (Figure 1).

161 *Physiological dilemmas in plant responses to future stress*

162 Anticipatory strategies may be highly prevalent as they provide a solution to challenges
163 plants are likely to face when responding to different attacks by herbivores and/or pathogens.
164 First, even though early detection of stress by electrical signalling and reactive oxygen species
165 (ROS) takes seconds to minutes, actual metabolic changes in the network of phytohormones
166 and the formation of defence responses can take hours up to days to be realised [41, 42]. This
167 not only constraints plants in responding to current stress but also potentially makes the
168 response suboptimal by the time other stressors arrive. Second, cross-talk between regulatory
169 pathways may allow plants to fine-tune their responses to cope with simultaneous and
170 sequential arrival of stressors [43, 44]. However, it can also lead to a situation where the
171 response to one stressor compromises an optimal response to another [10, 43]. For example,
172 activation of the salicylic acid (SA) pathway in response to attack by sap-sucking herbivores or
173 biotrophic plant pathogens may impair jasmonic acid (JA)-based responses to chewing
174 herbivores, and *vice versa* [43]. For anticipatory strategies to be optimal, plant responses should
175 thus be effective against both the initial stress as well as the suite of future stressors the plant is
176 likely to encounter. Natural selection should favour plant ability to integrate the correlated
177 sequences of stressors in their physiological response to the initial attack, especially when the
178 optimal response to the initial stressor would constrain responses to (more costly) future
179 stressors. An emerging property is that plants may respond sub-optimally to stressors in
180 isolation to account for arrival of future stress this and is likely to contribute to the substantial
181 variation found in plant responses to biotic stress [11].

183 How well plant responses match the actual conditions they anticipate and experience is
184 highly dependent on the correlations between cues and stressors [45]. Even though dynamics
185 in herbivore communities are often structured in their broad sense and offer plants the
186 opportunity to anticipate stress, most plant interactions are characterised by high levels of
187 stochasticity. This stochasticity affects the strength of the correlation between cues and
188 stressors, shaping the degree of statistical predictability or **intrinsic predictability** of the
189 plant's environment. In addition to stochastic processes, a discrepancy in plant responses and
190 anticipated conditions can be caused by the delayed rate of change in communities of
191 antagonists in response to changes in the local environment [20]. Such mismatches are
192 promoted by the persistence of relatively long-lived individuals, the absence of better matching
193 species in the local species pool, or due to priority effects in the assembly of communities [46].

194 Together with physiological and developmental constraints, and incomplete or unreliable
195 information when mounting responses, stochastic processes and community lags limit plants in
196 how well and for which timespan they can anticipate and match plastic responses to stress.
197 While physiological and developmental constraints determine the minimal timespan needed to
198 form anticipatory plastic responses, stochastic processes and incomplete information determine
199 the timespan for which predictions are reliable (Figure 1). Finally, specific plant responses can
200 be the result of targeted manipulation of plant metabolism by herbivores, with gall forming
201 herbivores as a prominent case [37]. Non-galling herbivores can also manipulate plant
202 metabolism. For example, Colorado potato beetles *Leptinotarsa decemlineata* contain bacteria
203 in their oral secretions which cause tomato plants, *Solanum lycopersicum*, to greatly increase
204 levels of SA, which down-regulate JA-dependent defences required for resistance against the
205 beetles [47]. This suggests that plants identify the stress as related to pathogens rather than

206 related to stress by chewing herbivores. Hence, biotic interactions can cause plants to mismatch
207 their responses to stress [48].

208 **Predictability of biotic stress is integrated in plant strategies**

209 Despite the physiological constraints and ecological stochasticity, there is substantial
210 evidence that plants do integrate predictability in their strategies. The nature of these strategies
211 is determined by the accuracy and timespan of the forecast horizon. We may expect that specific
212 anticipatory strategies that are commonly found across populations of a plant species match
213 processes that act on large spatial or temporal scales such as climatic conditions or migration
214 patterns of herbivores [49, 50]. More uncommon or plant-population-specific anticipatory
215 strategies include adaptations to local dynamics in herbivore communities.

216 *Ontogenetic trajectories*

217 When probability and patterns of herbivore attack change in a predictable way throughout
218 the lifetime of plants, defensive traits can be expressed through fixed ontogenetic trajectories
219 which allow the optimization of resources and functions across plant development [15]. These
220 trajectories can have significant genetic variation and/or be phenotypically variable within
221 populations, influenced by plastic responses to different stressors. Thus, natural selection
222 should favour plants allocating resources to specific defensive traits only when most needed or
223 when other functions with a greater impact on fitness are not compromised [51, 52]. The genes
224 underlying these allocation trade-offs, such as those between defence and growth, are now
225 being identified [53, 54].

226 Ontogenetic changes in resistance and tolerance are found in systems in which interactions
227 with herbivores affecting plant fitness are relatively predictable [53]. For example, once boreal
228 plants outgrow the height browsed by mammals, they reduce their investment in phenolic
229 compounds, a natural deterrent against these herbivores [55]. Analogous to ontogenetic

230 expression of direct defences, it is common to see dynamics in indirect defences that enhance
231 herbivore predation by their natural enemies. Plants tend to increase domatia and extrafloral
232 nectaries as plants develop [56]. This increased emphasis on indirect defences during ontogeny
233 could be driven by the likelihood of encountering natural enemies that are foraging for plant
234 rewards, the resources available to produce such traits, mutualism management strategies,
235 and/or trade-offs between processes regulating reproduction and direct plant defences [57, 58].
236 The adaptive value of ontogenetic changes in defence strategies matches patterns that act on
237 longer-term scales of development (i.e. weeks to months for annuals, years for perennials) [59].

238 *Steering development of communities*

239 On shorter time scales, priming and induced responses can allow plants to cope with low
240 predictability of herbivory or allow them to influence the sequence in which different types of
241 herbivores occur on the plant. Induced responses to biotic and abiotic stress frequently involve
242 fundamental changes in both primary and secondary metabolism and alter the plant as an
243 environment for current and subsequent attackers [60, 61]. Hence, the pool of herbivore species
244 that interact with the plant after the first attacker is in part a function of the induced phenotype
245 of the plant [62]. Plants in environments with multiple fitness-impacting herbivore species can
246 thus be hypothesized to be under selection to predict and influence attacker sequences through
247 their induced responses to minimize overall fitness impact (Figure 2). A major expectation of
248 this hypothesis is that herbivore communities interacting with a plant change in their
249 predictability after the plant interacts with antagonists. In extreme cases this could mean that
250 plants are under selection to be attractive to herbivores that themselves have little or no
251 significant negative fitness impact on the plant but make the plant more resistant to other, more
252 damaging herbivores [26, 63]. More generally, these ecological phenomena allow plants to fine
253 tune their responses to current attack while optimising this response in function of the plant's
254 community-wide context (Figure 2).

255 **Predictability in an eco-evolutionary context**

256 While predicting dynamics in stress can provide plants with a means to better match
257 responses to the environment, it is unlikely that plants achieve a perfect prediction of future
258 conditions given pleiotropic constraints and the lack of a guarantee of a future environment that
259 is predicted by the past. However, fitness differences between plants that anticipate stress
260 relative to less informed conspecifics should be sufficient to select for plant strategies that allow
261 for increased predictability, even if dynamics in stress are uncertain. As individual plants rarely
262 interact with all potential antagonists in the local environment, plants may reduce their
263 responses to only the more likely and most severe fitness-limiting stressors and anticipate the
264 most predictable responses of other community members to the induced plant phenotype.
265 Variation in predictability of herbivore assembly on individual plants is likely to drive the
266 evolution of (herbivore specific) induced defences. This may include maintenance of genetic
267 variation in plant populations by frequency-dependent selection in which genotypes are selected
268 to optimise resistance strategies to subsets of the community consisting of strongly correlated
269 antagonists [64]. An emerging evolutionary consequence may be that heritability of traits in
270 resistance to different herbivores becomes linked. For example, correlation between leaf
271 chewing herbivore attack and subsequent arrival of seed predators may yield induced responses
272 to leaf chewers that include changes in traits of reproductive organs [63].

273 Rather than accurately predicting arrival of individual stressors, it is likely that plants
274 optimise a more general cost – benefit balance to deal with multiple stressors, while managing
275 risk by making adaptive errors under conditions of uncertain but, if realised, costly attack [22].
276 This suggests that a plant strategy that maximises the predictability of individual stressors is
277 not adaptive by default: a developmental trajectory associated with higher levels of uncertainty
278 will be selected over a developmental trajectory with predictable dynamics if the latter is
279 associated with a lower overall fitness (Figure 1). Nevertheless, the predictability of stressors

280 could help plants to anticipate future dynamics in costs, benefits and risks and ultimately
281 optimise life-history strategies [65]. The readiness of plants to respond to stimuli is likely to be
282 dynamic over plant ontogeny, as some plant life-stages may be more vulnerable to specific
283 stressors than other stages [66].

284 Finally, high levels of gene flow may prevent plants from incorporating patterns that are
285 predictable at the local scale due to trait mismatching. However, the lack of sustained
286 directional change towards integrating predictability in plant strategies is not indicative of the
287 absence of selection. For example, alternative strategies can evolve within populations through
288 balancing selection. Conversely, while we observe that many mechanisms can increase the
289 predictability of stress in the plants' environment, not all traits involved are necessarily shaped
290 by processes where predictability is the selective agent. It remains challenging to disentangle
291 selective agents, as phenotypes that are selected by other stressors are likely to overlap with
292 changes in the overall predictability of future conditions plants experience. For example,
293 drought stress can alter plant phenotypes in ways that affect their subsequent interactions with
294 herbivores. Even though the expressed phenotype under drought stress may increase the
295 predictability of, and resistance against future biotic stress, it is unlikely that the induced
296 phenotype is selected to increase predictability.

297 **Concluding remarks**

298 Anticipatory responses are ubiquitous in plants, demonstrating that the integration of
299 correlations between stimuli and stressors in plant strategies can provide fitness benefits relative
300 to plants with uninformed strategies [17]. Over recent years there has been a growing interest
301 in the role such correlations play across larger (transgenerational) scales in modulating the
302 plasticity of plant development and responses to stress, which itself may evolve [67, 68].
303 However, a continuing challenge is to identify the ecological conditions under which such

304 strategies are adaptive, and how variation in the predictability of the environment in which
305 plants grow affects intraspecific variation in plant strategies (see Outstanding questions) [69].
306 We propose that, even if dynamics in stress for the greater part remain uncertain, predictable
307 patterns are readily integrated in plant strategies. Hence, the predictability of (sequences of)
308 stressors is likely to be a key component governing inter and intra-specific variation in plant
309 responses and strategies maximising life-time fitness [64]. While studying plant interactions
310 with stressors in isolation provides fundamental insights in the mechanisms underlying plant
311 responses to stress, integrating predictability to the framework of plant-stressor interactions will
312 yield important new insights in the evolution of plant defence strategies.

313 **Figure 1: Plant strategies in the framework of forecast horizons**

314 **Community:** Plants interact with multiple biotic stressors in sequence. Stressors may
315 strongly correlate (indicated by R^2) such as when caterpillars cause open wounds that promote
316 pathogen infections, or correlate only weakly such as illustrated by attack by a different
317 herbivore species. **Plant strategy:** To deal with variation in predictability and the risk of
318 incurring fitness costs, plants follow different strategies. The green line illustrates a trajectory
319 in which the plant only responds to an initial stimulus and does not follow an anticipatory
320 strategy. The red and blue lines illustrate trajectories with an anticipatory strategy, but in which
321 plants differ in their proneness to take risk: The phenotypic trajectory illustrated by the blue
322 line tracks the most probable antagonist community. The phenotypic trajectory illustrated by
323 the red line is a risk averse strategy, where the plant anticipates a less likely, but if realized
324 while unprepared, more costly scenario. **Match in phenotype with the predicted community:**
325 Plant strategies vary in how well the plant phenotype will match with the predicted
326 environment, represented by the coloured lines. The y-axis represents how well the plant
327 phenotype is predicted to match the future environment. From our vantage point at time zero
328 (t_0), we consider how well the plant will match the predicted communities of the future. Shaded
329 areas indicate the increasing uncertainty in how well the phenotype will match the future
330 community of antagonists due to stochastic processes, lag in community responses, and
331 incorrect or incomplete information transferred by the initial attack. **Time lag:** Plants need time
332 to detect and start responding to the stimulus or stress, defined by physiological constraints.
333 **Plant response to initial stress:** Time needed to fully form responses to the initial stress or
334 stimulus. Anticipatory strategies match the changing antagonist community (red and blue lines),
335 while non-anticipatory strategies only respond to the initial stressor or stimulus (green line).
336 Developmental constraints and the integration of potential future stress in plant responses may
337 limit how well plants following anticipatory strategies will match their phenotype with the

338 environment. **Phenotype to predicted community:** Time frame where plants following
339 anticipatory strategies try to match the future antagonistic community, and in which uncertainty
340 increases until the forecast horizon is met, indicated by the solid black line. **Forecast horizon**
341 **with increasing uncertainty:** In the period after the forecast horizon is met, predictions of
342 plants following anticipatory strategies are not more accurate than non-informed / non-
343 anticipatory strategies.

344

345 **Figure 2. Interactions with an antagonist require anticipatory responses to subsequent**
346 **conditions and results in linkages in the evolution of traits**

347 Attack by an initial stressor induces responses in the plant with physiological and ecological
348 consequences for the plant, with the potential to ultimately change the selective pressure on
349 plant traits. **Blue:** Induced responses involve (local or systemic) changes in the chemical
350 composition of plant tissues and require the regulation of underlying phytohormonal pathways.
351 In addition, herbivores themselves may manipulate the responses of plants on a molecular level.
352 These changes in the plant's defensive phenotype may prove effective against subsequent
353 attackers due to cross resistance but may also cause the plant to become more susceptible to
354 subsequent attackers. Anticipatory responses should thus integrate, or at least not inhibit,
355 responses to likely subsequent attack at the level of the plant's physiology. **Green:** Induced
356 responses to initial stress often lead to systemic changes in the plant's phenotype. In addition,
357 herbivores themselves may manipulate the phenotype of plants through niche construction (e.g.
358 leaf-rolling caterpillars). The overall changes in the phenotype of the plant presented to the
359 community can affect the likelihood of colonization by subsequent herbivores, effectively
360 partitioning the antagonist community into subsets of strongly correlated antagonists. Plants
361 may thereby anticipate the nature of future attack when interacting with the current herbivore.
362 **Orange:** The interaction with an initial antagonist may result in the enhanced probability of
363 interacting with a subsequent antagonist which has direct impacts on plant fitness. For example,
364 a leaf feeding caterpillar enhances probability of seed weevil attack. Plant responses induced
365 by initial herbivory may thus culminate to indirectly affect plant fitness. Plant traits that are key
366 in mediating the initial and subsequent interactions are thus under the same selection pressure.
367 This may result in heritability (h) of defence traits against different herbivores to be strongly
368 linked.

369

Table 1. Overview of different plant states or stimuli that plants respond to, which may correlate with dynamics in future stress conditions.

Plant state or stimulus	Example	Reference
a. Plant intrinsic state		
<i>Intra-generational</i>		
Architecture	Apical stem bending alters susceptibility to aphids and gall-forming herbivores in late goldenrod (<i>Solidago altissima</i>)	[30]
Biomass	Leaf biomass determines leaf-chewing insect abundance across tropical forest host species	[70]
Chemical composition	Insect community structure covaries with host plant chemistry in pedunculate oak (<i>Quercus robur</i>)	[71]
Ontogenetic state	Floral volatiles attract specialist herbivores in the <i>Cucurbita</i> genus	[72]
<i>Transgenerational</i>		
Seed composition	Parental stress directly affects the metabolome of seeds in thale cress (<i>Arabidopsis thaliana</i>)	[73]
Seed germination	Regulation of seed dormancy following maternal herbivory in <i>Arabidopsis thaliana</i>	[74]
Trait plasticity	Abiotic stress enhances competitive ability of progeny in lady's thumb (<i>Polygonum persicaria</i>)	[75]
b. External cues or stressors		
<i>Abiotic</i>		
Photoperiod	Light quality affects flavonoid production in wheel wingnut (<i>Cyclocarya paliurus</i>)	[76]
	Altered photoperiod induces stress in <i>Arabidopsis thaliana</i>	[77]
Temperature	Heat stress alters shock - factor - responsive gene expression in <i>Arabidopsis thaliana</i>	[78]
	Rapid and gradual decreases in temperature trigger different pathways in <i>Arabidopsis thaliana</i>	[79]
	Fire induced heat alleviates dormancy across grassland species in South-Eastern Australia	[80]
Salinity	Salinity reduces the capacity of the photosynthetic system in cabbage (<i>Brassica oleracea</i>)	[81]
Touch	Rapid leaflet-closure responses to mechanical stimulation in <i>Mimosa pudica</i>	[38]
	Obstacle avoidance by self-inhibition in pea (<i>Pisum sativum</i>)	[82]
Vibrations	Sound vibrations increase expression of genes related to mechanical stimulation in <i>Arabidopsis thaliana</i>	[83]
Wind	Air flow increases height, while stem flexure reduces height in common sunflowers (<i>Helianthus annuus</i>)	[84]
Gravitropism	Gravity reception is used to regulate organ straightening and plant posture in <i>Arabidopsis thaliana</i>	[85]
Humidity gradients	Hydrotropism is regulated by auxin and abscisic acid in <i>Arabidopsis thaliana</i>	[86]
Plant state or stimulus	Example	Reference

Abiotic

Chemicals in atmosphere	Ozone modifies plant responses to biotic stresses in charlock mustard (<i>Sinapis arvensis</i>)	[87]
	Smoke and ash induce germination across functional groups in Northern European heathlands	[88]
Chemicals in soil	Root tip contact with low-phosphate media reprograms plant root architecture in <i>Arabidopsis thaliana</i>	[89]
<u>Biotic</u>		
Mycelia	Common mycelial networks warn neighbouring plants of aphid attack in faba bean (<i>Vicia faba</i>)	[90]
Bioacoustics	Flowers respond to pollinator sound by increasing nectar sugar concentration in the evening primrose (<i>Oenothera drummondii</i>)	[91]
Volatiles	Volatiles from damaged neighbours increase resistance against herbivores across plant species	[92]
	The parasitic plant fiveangled dodder (<i>Cuscuta pentagona</i>) exhibits directed growth toward volatiles of the potential plant host	[93]
Non-volatile exudates	Root-secreted JA is involved in neighbour detection and plant-plant communication in common wheat (<i>Triticum aestivum</i>)	[94]
Herbivore damage	Specific tobacco hawk moth (<i>Manduca sexta</i>) elicitor shows highly specialised herbivore-detection system in solanaceous plants	[95]
Vibrations	Vibrations caused by insect feeding elicit chemical defences in <i>Arabidopsis thaliana</i>	[96]
Herbivore oviposition	Oviposition by <i>Leptinotarsa decemlineata</i> beetles causes hypersensitivity and egg drop in <i>Solanum</i> spp.	[97]
	Leaf contact cues associated with oviposition by the large cabbage white (<i>Pieris brassicae</i>) arrest parasitoids in black mustard (<i>Brassica nigra</i>)	[98]
Herbivore excretion	Proteins from fall army worm (<i>Spodoptera frugiperda</i>) frass induces wound-responsive defense genes in maize (<i>Zea mays</i>)	[99]
	Exogenous honeydew deposition by pea aphids <i>Acyrtosiphon pisum</i> alters JA and SA accumulation in <i>Vicia faba</i>	[100]
Antagonist interactions	Barley yellow dwarf virus alters likelihood of herbivory by bird cherry-oat aphids (<i>Rhopalosiphum padi</i>) in <i>Triticum aestivum</i>	[101]
	Herbivore damage increases attraction of generalist herbivores in creeping cucumber (<i>Solena amplexicaulis</i>)	[102]
	Induced plant responses attract oviposition by the specialist small cabbage whites (<i>Pieris rapae</i>) in radish (<i>Raphanus raphanistrum</i>)	[103]
	Order of herbivore arrival influences subsequent community development in <i>Brassica oleracea</i>	[13]
	Infection with <i>Pseudomonas</i> spp. bacteria in leaves predicts prevalence and damage by <i>Scaptomyza flava</i>	[48]

373 **BOX 1: Epigenetic modulation of plant trait plasticity across generations**

374 Variation in most plant traits is quantitative (continuously variable) and the heritable
375 component of this variation is polygenic in architecture – many genes each contribute a small
376 effect to the phenotype. However, the expression of plant traits can be regulated by (heritable
377 or transient) molecular mechanisms such as DNA methylation, small RNAs, or histone
378 modifications affecting gene transcription. The epigenetic regulation of protein-coding genes is
379 essential for general plant functions such as development or the silencing of transposable
380 elements [104]. In addition to these general functions, epigenetic mechanisms play a key role
381 in acclimation to stress and rapid plastic responses in plants [105]. Importantly, epigenetically
382 controlled variation in trait plasticity exists without the need to deviate from a genetic blueprint
383 – natural selection acts on the *ability* of a plant to epigenetically control trait expression –
384 regulation of gene expression being a simple example [106, 107]. Non-genetic inheritance
385 through the transfer of epigenetic states can have major consequences on offspring resistance
386 to (a)biotic stress [105]. These effects can be limited to one generation or persist for multiple
387 generations by so called soft inheritance [108]. A critical need is to study the levels of biological
388 organization from individual to populations and species that produce these ontogenetically
389 extended phenotypes. In addition, fully addressing this question requires identifying ultimate
390 mechanisms at the genetical level that may drive the origin and persistence of transgenerational
391 phenotypes.

392 Even though the mechanisms underlying epigenetic regulation of gene expression are
393 becoming increasingly well studied, the effects of transgenerational phenotypic plasticity on
394 plant responsiveness to environmental conditions and ultimately plant fitness are poorly
395 understood. This is in great part due to complexity: A plant's phenotype is the result of
396 interactions between its genotype, the inherited epigenetic elements, environmental conditions,
397 within-generation epigenetic regulation, and other regulatory elements involved in plant

398 development. Moreover, evidence suggests that non-genetical inherited elements that confer a
399 fitness advantage are often and rapidly reversed, nuancing the implications of epimutations for
400 long-term fitness of individuals. Despite its complexity, transgenerational phenotypic plasticity
401 can be key to understanding the short-term integration of predictable patterns into plant life-
402 history strategies. For example, information obtained by the maternal plant or both parental
403 plants may correlate well with stress experienced by their progeny through spatial or temporal
404 autocorrelation of stress.

405 **BOX 2: Plant anticipatory strategies to deal with (un)predictable stress**

406 In anticipatory strategies, plants adapt their phenotype in preparation of forthcoming adverse
407 conditions. These strategies entail a range of genotypic and phenotypic regulations to match
408 predictable arrival patterns of stress. The genetic regulation of anticipatory strategies is
409 illustrated by ontogenetic trajectories of plants in expression of traits that are adaptive to stress.
410 For example, seedlings that are heavily attacked by herbivores express stronger resistance to
411 herbivory, because the costs of herbivory early in the development of plants are large. When
412 plant biomass increases, the same degree of herbivore damage can be tolerated, and resources
413 may be used for growth and reproduction. The adaptive value of ontogenetic changes in defence
414 strategies match patterns that act on longer-term scales of development. Phenotypically, plants
415 may use abiotic conditions to match seasonal variation in resistance to the likelihood of
416 herbivore attack due to the correlation of seasonality and herbivore activity [29]. Over shorter
417 time scales, plants may use reliable cues of presence of antagonists to anticipate actual attack
418 by these antagonists. These cues may come from the environment, such as neighbouring plants
419 that release volatiles when attacked by herbivores, or from direct interactions of the plant with
420 stressors that predict forthcoming attack such as the oviposition of eggs by herbivorous insects
421 on plant tissues [1, 109]. Plants may anticipate the forthcoming stress by priming, a
422 physiological process by which a plant prepares to respond to future biotic or abiotic stress
423 more quickly or intensively, without the formation of resistance in the absence of the actual
424 occurrence of stress. Alternatively, when the cue is highly reliable it pays plants to increase
425 resistance through induced resistance [8]. The induced resistance may be tailored directly and
426 primarily to the stressor associated with the cue, but we argue that these induced responses may
427 also anticipate attack across longer temporal scales when the initial stressor is a good predictor
428 for the arrival of other stressors. Across generations, plants may prepare offspring for
429 forthcoming conditions by epigenetic mechanisms (Box 1).

430 **Glossary**

431 **Anticipatory responses:** a plant response to information indicative of stress in which the
432 phenotype is adjusted in anticipation of sub-optimal conditions or arrival of stress.

433 **Forecast horizon:** the maximal length of time into the future from the point in time at which
434 information is gathered for which plants can make predictions about, and hence anticipate,
435 forthcoming stress conditions.

436 **Induced response:** the phenotypic change of a plant in response to stress that may lead to
437 decreased performance of the stressor (induced resistance) and result in a plant fitness benefit
438 by the response (induced defence).

439 **Phenological and/or conditional state of the plant:** the intrinsic state of the plant determined
440 by ontogenetic and physiological phenotype formed by prior interactions with the (a)biotic
441 environment.

442 **Plant-mediated interaction:** the indirect effects of spatially or temporally separated organisms
443 on each other's performance or behaviour through induced responses of their shared host plant.

444 **Predictability of stress:** the level of certainty in arrival patterns of stress such as the timing and
445 order of arrival of herbivore or pathogen species over a plant's lifetime.

446 **Intrinsic predictability:** the maximal degree of statistical predictability among successive
447 environmental states within a local environment.

448 **Priming:** the phenomenon whereby a temporally limited environmental (priming) stimulus
449 prepares and modifies the response to a future stress incident (the triggering stimulus)

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458

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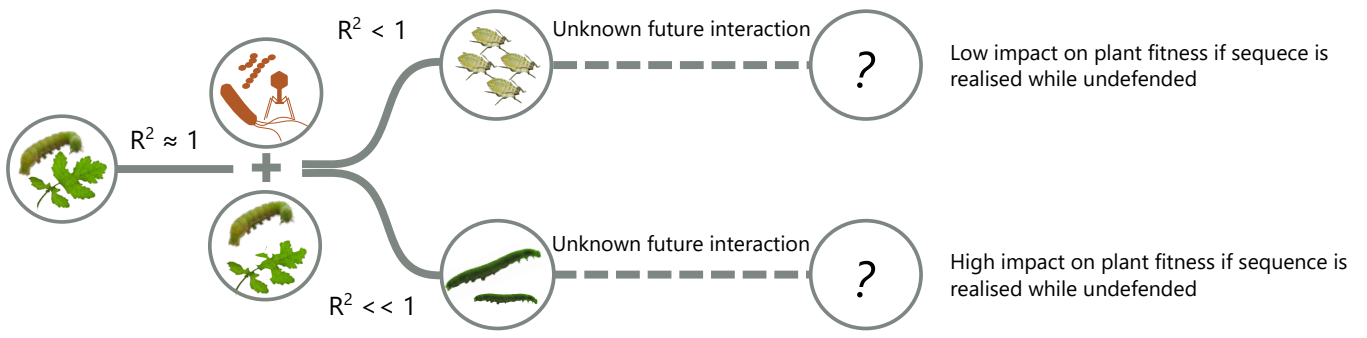
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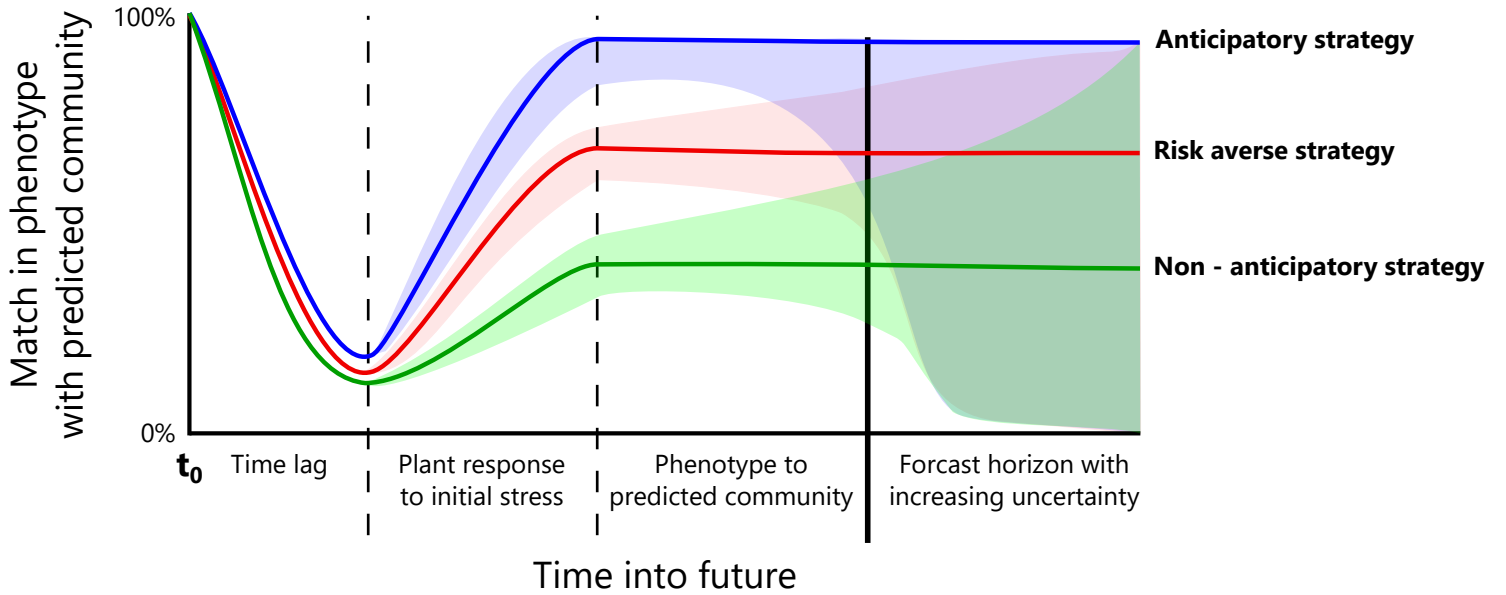
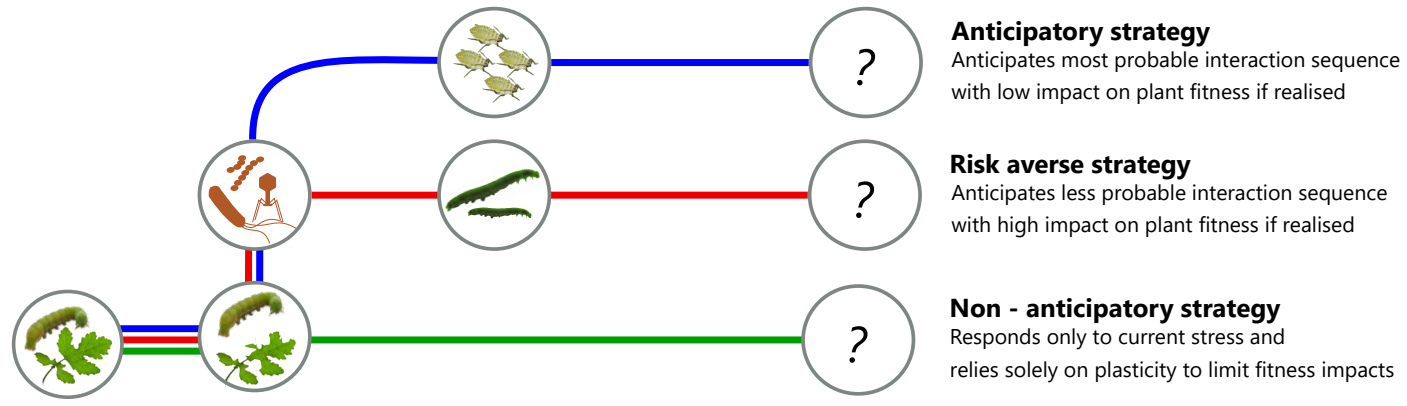
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Community



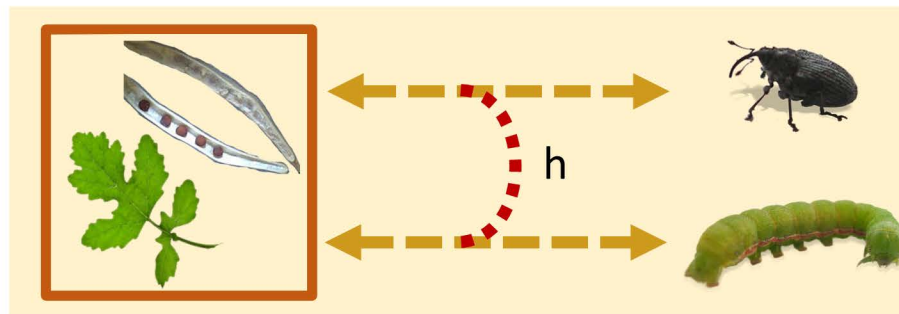
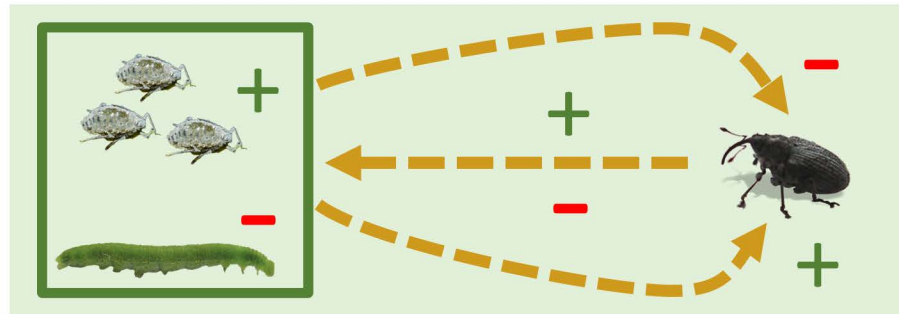
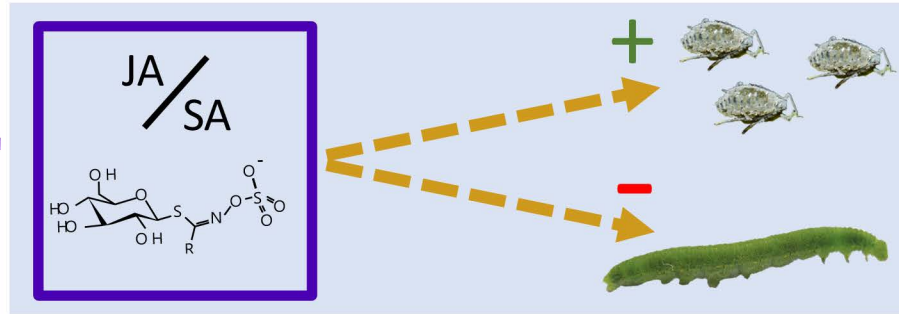
Plant strategy



Current interaction



Anticipating



Emerging property

Plant response to current herbivore includes response to future stress

Physiology

Plant response to current herbivore partitions attacker community to influence likelihood of attack

Ecology

Linkages in trait evolution of defence to current and future attacker

Evolution

Outstanding questions, belonging to:

Predictability of biotic stress structures plant defence evolution

Authors: Daan Mertens^{1*}, Karina Boege², André Kessler³, Julia Koricheva⁴, Jennifer S. Thaler⁵, Noah K. Whiteman⁶, and Erik H. Poelman¹

- What characteristics of ecological systems underly variation in the intrinsic predictability of stress and how does this affect plant life-history strategies?
- What are the plant traits that perceive and process predictive environmental cues?
- How plastic are plants in their sensitivity to cues and what is their tendency to take risks? Do plants exposed to a more predictable antagonist community anticipate arrival of new stressors in their plastic response to current stress, and do plants in unpredictable environments respond to each stressor in isolation when it arrives?
- Does selection by a local predictable order of stressors lead to rapid evolution in plant populations in which plant traits become linked to maximize resistance to multiple stressors?