Delayed chemical defense: timely expulsion of herbivores can reduce competition with neighboring plants

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Abstract

Time delays in plant responses to insect herbivory are thought to be the principal disadvantage of induced over constitutive defenses, suggesting that there should be strong selection for rapid responses. However, observed time delays between the onset of herbivory and defense induction vary considerably among plants. We postulate that strong competition with conspecifics is an important co-determinant of the cost-benefit balance for induced responses. There may be a benefit to the plant to delay mounting a full defense response until the herbivore larvae are mobile enough to leave, and large enough to cause severe damage to neighboring plants. Thus, delayed responses could reduce the competitive pressure on the focal plant. To explore this idea, we developed an individual-based model using data from wild tobacco, *Nicotiana attenuata*, and its specialized herbivore, *Manduca sexta*. Chemical defense was assumed to be costly in terms of reduced plant growth. We used a genetic algorithm with the plant's delay time as a heritable trait. A stationary distribution of delay times emerged, which under high herbivore densities peaked at higher values, which were related to the time larvae need to grow large enough to severely damage neighboring plants. Plants may thus tip the competitive balance by expelling insect herbivores to move to adjacent plants when the herbivores are most damaging. Thereby herbivores become part of a plant's strategy for reducing competition and increasing fitness.

Keywords: induced defense, intra-specific competition, plant-herbivore interactions, trait diversity, individual based model, simulation

Introduction

Optimal defense theories predict that inducible defenses in plants are less costly than constitutive defenses, because the defenses are produced only when they are actually needed (Karban and Baldwin, 1997, Karban et al. 1999). As long as there are no herbivores, plants

with inducible defenses can allocate their resources to primary, fitness-enhancing processes such as growth and reproduction, and hence out-compete plants with constitutive defenses (Clark and Harvell, 1992; Herms and Mattson, 1992). The time lag between the environmental cue and optimal adjustment of a plant to its current environment is considered to be one of the greatest disadvantages of inducible defenses and other forms of phenotypic plasticity (Moran and Hamilton, 1980; Padilla and Adolph, 1996; DeWitt et al., 1998). This time lag is particularly detrimental for induced responses because herbivores may remove substantial amounts of biomass before the defenses are effective. Consequently, a strong selection pressure should exist for short time lags, or delay times, between herbivory and the production of effective chemical defenses. However, observed delay times for inducible defenses vary considerably within plant species (Schuman, 2012, Mathur et al. 2011). This suggests that there is little selection pressure for short delay times and even that under certain environmental conditions slower responses might actually increase fitness. To test this hypothesis, we explored the potential for neutral or even positive selection for longer delay times using a model parameterized with new and existing data for an annual plant attacked by a caterpillar.

To generate a better understanding of the concepts underlying the model, imagine two adjacent, conspecific plants which are in severe competition. When one of the plants is attacked by an herbivore (caterpillar), there are three possible scenarios (Fig. 1): first, the attacked plant does not respond to feeding damage by increasing its defenses, allowing the caterpillar to complete its life cycle on the plant. In this scenario, the plant will suffer substantial damage or may even be entirely destroyed (Fig. 1a). For an annual species this constitutes a severe fitness loss.

Second, the attacked plant may increase its defense levels very rapidly. A fast response may deter or kill the herbivore by producing direct defenses, e.g. nicotine and protease inhibitors (Steppuhn and Baldwin 2007). Rapid induction may have several benefits:

the direct defenses may deter or kill non-specialized herbivores very quickly, thereby reducing leaf loss. This may not apply to specialist herbivores that can tolerate or detoxify their host plant's specific defenses (Ali and Agrawal, 2012). However, even specialist herbivores show significantly slower growth rates and higher mortality when feeding on well defended host plants (Steppuhn and Baldwin, 2007; Harvey et al 2007). In addition, indirect defenses such as volatile organic compounds (VOCs) that attract predators or parasitoids may be induced (Kessler and Baldwin 2001, Fig. 1b). A rapid induction of volatiles may be beneficial because parasitoids and insect predators usually prefer the early developmental stages. On the other hand, individual plants may not incur an immediate benefit from parasitoids, if parasitized larvae feed more to sustain the endoparasitoids or even go through a supernumeral (thus sixth) instar (Beckage et al, 1994). In addition, there are also costs for inducing defenses, as they may reduce the plant's competitive ability by decreasing vegetative growth due to an investment tradeoff between chemical defense and vegetative growth (Louda et al., 1990; Augner et al., 1997; Nötzold et al., 1998, Redman et al., 2001). In environments with high plant growth rates, small differences in competitive ability may lead to large differences in plant size and eventually plant fitness (Nicotra and Rodenhouse, 1995; Schwinning and Fox, 1995; van Dam and Baldwin, 2001). Plants treated with the induction hormone methyl-jasmonate (MeJA) or genotypes that over-expressed MeJA, produced up to 50% less seed mass than their untreated neighbors (van Dam and Baldwin, 1998; van Dam and Baldwin, 2001; Cipollini, 2002; Cipollini, 2007). Because the wound signal was applied without damaging the plant, these costs are independent of leaf loss (Baldwin, 1996; van Dam and Baldwin, 1998; Cipollini, 2007). Thus, if herbivore feeding immediately elicits an induced response, the induced plant suffers a fitness decrease compared to its non-induced neighboring competitor, regardless of how little damage the herbivore has done.

As illustrated above, short delay times may not be uniformly beneficial to the plant. This opens the possibility of a third scenario in which the attacked plant delays its defense

response by a certain amount of time. If the costs of losing competitive capacity are larger than the costs of leaf loss due to herbivory, this can lead to a net increase of fitness (Fig. 1c). A similar idea, but applied to constitutive defense strategies, was first proposed by Tuomi et al. (1994). They hypothesized that plants with less effective defenses may gain an associational protection when growing close to well defended plants. If the well defended plants kill most of the herbivores, they might then easily be outcompeted by less defended plants (Tuomi et al., 1994). Although their model applies to constitutive defense polymorphisms and plants of different species, we propose that a similar strategy may pertain to herbivore-induced plants competing with conspecifics. Under these conditions, we postulate that plants should optimize the timing of their defense production to induce herbivore movement to a neighboring plant when the herbivore is the most damaging. This optimal delay time would be determined by larval developmental rates. In a plant-caterpillar system, later instars consume the majority of the biomass, with 90% consumed during their last instar. Thus, there is an optimal time for "sending" a larva to a neighboring plant so that the costs of induced defense will be offset by the gains in fitness resulting from reduced competition from the attacked neighbor.

To further explore our hypothesis and test its relevance on the population level, we developed an individual-based model representing fast growing plants competing in dense cohorts with different densities of their mobile herbivores. We used an existing model of intraspecific plant competition (Lin et al. 2013, 2014) and included plant defenses, fitness costs, herbivory, as well as growth, survival, and movement of individual larvae. Our model is based on observations and data on *Nicotiana attenuata* (Solanaceae) and an important specialized invertebrate herbivore, *Manduca sexta* (Lepidoptera: Sphingoidae). We chose this interaction because it is one of the best studied models for induced defenses, from chemical mechanisms to ecological effects, with over 20 years of data, providing realistic parameter values for the model.

N. attenuata is a fast-growing annual plant from the Great Basin desert (south-western USA) whose seeds germinate synchronously after a fire has destroyed the dominant vegetation (Baldwin and Morse 1994; Young and Evans, 1978; Koniak, 1985; Preston and Baldwin, 1999). The fire pyrolizes litter and removes negative regulators of germination and releases smoke cues, which seeds use to synchronize their germination from long-lived seed banks (Baldwin and Morse, 1994; Baldwin et al., 1994). The synchronization of seed germination results in dense cohorts of even-aged plants of more or less the same size, so intra-specific competition is a common factor affecting plant performance even under the high nutrient levels after a fire (Lynds and Baldwin 1998). The most limiting resource is water, which is present at the beginning of the season but runs short after some time and thus limits the length of the growth season.

In the first year after a large fire, the herbivore community is dominated by arthropod herbivores such as *M. sexta*, while later in the succession vertebrate browsers will cause extensive damage (Baldwin, 1998). Occasionally, *M. sexta* and its close relative *M. quinquemaculata* can reach outbreak densities and completely defoliate *N. attenuata* (A. Kessler, pers. comm.). *M. sexta* moths oviposit single eggs on the leaves of *N. attenuata* on which the larvae feed for about 3 weeks until they have reached the prepupal stage and leave the plant to pupate in the soil (Gilmore, 1938; Madden and Chamberlin, 1945). During this time the larvae grow exponentially: while neonate larvae weigh a few milligrams, the prepupal stage may weigh 8 to 10 g (van Dam et al., 2001a).

N. attenuata employs a variety of inducible chemical defenses in response to damage or herbivore feeding, such as nicotine, proteinase inhibitors, phenolics and volatile emissions (Keinanen et al., 2001; Kessler and Baldwin, 2001; van Dam et al., 2001b). Despite the fact that *M. sexta* is a specialist herbivore and possesses several physiological mechanisms to deal with the nicotine in tobacco plants (Murray et al., 1994; Snyder et al., 1994), both its performance and its behavior are negatively affected by high levels of nicotine (Harvey et al.

2007) and other jasmonate-induced responses (Steppuhn and Baldwin 2007). Larvae that are reared on leaves of induced plants grow significantly slower and suffer a higher mortality than larvae on control leaves (van Dam et al., 2000). Moreover, if larvae are placed on jasmonate-treated plants growing adjacent to an untreated plant, the larva will move to the non-induced plant and the sooner it moves and feeds on it; the larger it grows (van Dam et al., 2000).

Our model explores, whether delaying chemical defense of herbivores can improve individual fitness of plants growing in dense cohorts. We tailored our model in terms of parameter values and functional relationships to mimic a specific system, but also perform simulation experiments that explore a wider range of settings, and will discuss implications for general theory.

Methods

The Model

A full and detailed description of our model, dubbed TIMELY (short for TIME deLaY), following the ODD (Overview, Design concepts, Details) protocol (Grimm et al. 2006, 2010) is provided in the Supplementary Material. Below we present a summary description. Further information on the model is given in the TRACE (TRAnsparent and Comprehensive model Evaludation) document (Schmolke et al. 2010, Grimm et al. 2014) in the Supplementary Material. TRACE documents contain evidence that a model was thoughtfully designed, correctly implemented, thoroughly tested, well understood, and appropriately used for its intended purpose.

We used an existing, well-established model of intraspecific plant competition (Lin et al. 2013, 2014) which combines a two-layer zone of influence approach (May at al. 2009) with an ontogenetic growth model for plants. Two layers were used because below-ground competition for nutrients and water was found to be size-symmetric (Casper and Jackson 1997), while above-ground competition for light is largely asymmetric (Schwinning and

Weiner 1998). We adapted the model parameters to match values obtained on wild tobacco (*N. attenuata*) growth and competition data. The most important parameters and variables are given in Table 1.

We used this model for simulations of two plants and one larva ("two-plant scenario") to test the main idea of this publication. The two-plant scenario helped demonstrating and exploring the consequences of delayed chemical defense in a highly simplified setting. However, in real plant populations, several factors will strongly affect the fitness consequences of delayed defense, in particular the density of plants and herbivores, the spatial distribution of plants, and the frequency distribution of delay times within the plant population. Therefore, we also extended this model to whole plant populations of several hundred plants and larvae ("400 plants scenario").

The model comprises 250 x 250 square grid cells, corresponding to a total area of 15 x 15 m². Grid cells were used to represent zones of influence in a discretized way (Weiner et al. 2001, May et al. 2009). Time proceeded in discrete steps of 4 h; simulations were run for 27 days, thus the full life cycle of the caterpillars. Plants were characterized by their position, their above- and below-ground biomass, their defense level, and the delay time, τ, defined as the time between the attack of a larva and start of defense production of the plant. We assumed that τ was also the time between the larva leaving the plant and the stop of defense compound production by the abandoned plant. The plants were assigned to random positions and their delay time differed within the population but stayed constant for each plant over the simulation. Plants grow, compete for resources, produce defense compounds when being attacked, and die if they are eaten entirely by a caterpillar.

Intraspecific plant-plant competition for resources was represented separately for both roots and shoots by a two-layer zone-of influence model. Plants obtain resources only within the area of their zones of influence (ZOI), with the above-ground area representing competition mainly for light and the belowground area for water, nitrogen, and other

nutrients. The ZOI's radii were allometrically related to the respective above- and belowground biomasses. Competition only occurred where zones of influences overlapped. In simulations including genetic algorithms, plant reproduction was represented as well (see corresponding section below).

Larvae were characterized by their biomass, age and position. Initially they were distributed on randomly chosen plants. They first stayed on their host plant, where they fed and grew. After having reached a certain age and weight (3rd instar), they became mobile enough to switch host plant if needed, i.e., in response to the host plants chemical defense (larval movement between host plants has been observed in the field: Kessler and Baldwin, 2002 and in the laboratory: Van Dam et al., 2000 and Casey, 1977). Caterpillars grew exponentially and consumed plant mass proportionally to their weight; this assumption is based on two studies which show that *M. sexta* larvae reared on *Nicotiana* feed proportionally to their body weight (Gilmore 1938; Madden and Chamberlin 1945). In reality, the relationship between body mass and consumption might be nonlinear because the efficiency of assimilation might change with body mass, but we do not expect strong nonlinearity and therefore, also to reduce model complexity, used a linear relationship. When the larvae reached their maximum size, they left the plants for pupation and were thus inactive in the model. Caterpillar growth and instar progression was negatively affected by plant defense compounds (Fig. 2).

In each time step caterpillars had a certain probability to die. Their mortality rate scaled proportionally with their current host plant's defense level and inversely with the logarithm of the caterpillar's body mass. This means that at the beginning of simulations, caterpillar mortality risk was very high but decreased as the caterpillars grew larger.

If the plant defense level reached a certain threshold, caterpillars which were heavy enough moved to another nearby plant. Caterpillars which were too small were not able to move and thus remained on their host plant. The next host plant was chosen randomly among

all plants within the movement radius of the larva. The probability of being chosen decreased exponentially with its distance to the larva's previous host plant. Caterpillars which were in the process of switching plants had a higher probability to die than caterpillars feeding on a plant.

When a caterpillar encountered a new host plant it immediately started feeding and thereby inducing defense with the delay time, τ. When a plant is induced, 30% of the plant's metabolic resources are invested in defense production; the rest is invested in growth and reproduction.

Parameterization

Most of the parameter values were taken from experimental data on *N. attenuata* and *M. sexta*. Model parameters and variables are summarized in Tab. 1. *M. sexta* larvae reared on N. *attenuata* leaves grow exponentially in time and feed proportionally to their body weight (Gilmore 1938; Madden and Chamberlin 1945). The average conversion factor of plant to larval biomass is 0.19 and the largest pre-pupal larval mass observed is 10.11 g (van Dam et al., 2001a.), hence we set the maximal biomass to 10 g (van Dam et al., 2001a.)

Shoot growth rates were derived from non-induced and undamaged soil-grown and hydroponic *N. attenuata* plants grown for 50 and 20 days in climate rooms, respectively (van Dam and Baldwin, 1998; Glawe et al., 2003). Both soil and hydroponically grown plants grew exponentially during those periods and attained relative growth rates (RGRs) of 0.25 and 0.16 g per g and day, respectively. Accordingly, we chose a maximal growth RGR of 0.2 g per g and day. The maximal fresh weight of the above-ground biomass of a plant in the field was estimated to be 500 g (Table 1, A. Keßler, *pers. comm.* and TRACE document Fig. T6: field data of *A. Weinhold*,). The parameter value for allocation to defense production is difficult to estimate, since there are only few data to quantify the magnitude of investment on a whole plant basis. Induced *N. attenuata* plants allocate 6% of their whole plant nitrogen to *de novo*

nicotine production alone (Baldwin, 1998b). Induced *N. attenuata* plants, however, also produce significantly more protease inhibitors (van Dam et al., 2001b), volatiles (Halitschke et al. 2000; Kahl et al. 2000), phenolics and sugar esters (Keinänen et al., 2001). Thus the total allocation to defense production may well be much higher than 6% and therefore we tested the model for allocation values ranging from 10% - 40% (Fig. S5). In the default case, we assumed that induced plants temporarily allocate 30% of their growth to the production of defensive compounds when attacked by an herbivore.

We used the commonly seen response times as assessed in the many experiments carried out in the Baldwin lab (Baldwin, 1988, Baldwin 1989, Ziegler 2001) and also response times measured for different plants (Agrell et al. 2003, Karban 1989, Underwood 1998, Kant 2004) as potential range for the delay time τ.

We chose 27 days for the simulation of one generation, because we concentrated on the time where interaction between larvae and plants occurred. As M. *sexta* is both the main herbivore and pollinator of *N. attenuata*, both pollination services and oviposition are motivated by floral scent and nectar (Kessler, 2012). Our simulations thus started with plants already being in an early flowering stage, because at this time oviposition rates started rising.

Field experiment

In a field experiment, we compared the growth trajectories of *M. sexta* larvae feeding on defenseless plants with larvae feeding on well-defended plants. We therefore recorded the growth trajectories of 30 larvae of *M. sexta* per treatment in their native environment in the Great Basin Desert (Utah, United States). We recorded larval growth on two different plant lines: either well defended, "wild type" plants, or plants of the jasmonate-deficient inverted repeat allene-oxide cyclase (irAOC) line. Jasmonic acid accumulation and perception are critical for the activation of most defense responses and the irAOC line we used in the field study shows a reduction of herbivory-induced jasmonate levels of more than 95% (Kallenbach, 2012, Machado, 2013) (for further information see Fig. S1 and section 4.3:

Data evaluation in the Supplementary document). The results were used to parameterize larval growth.

Simulation experiments

At the start of our simulation, all plants had the same weight of 30 g and the neonate larvae started with a body mass of 1 mg on randomly selected plants. For the robustness analysis (see Appendix and Supplementary Material) we also run simulations where caterpillars started at any time point on randomly selected plants.

We ran simulations with two plants, for test purposes, and for 400 plants. The model was implemented in NetLogo (Wilensky, 1999, Tisue and Wilensky, 2004). Field data and model output were analyzed with R (R Core Team, 2016). The NetLogo program is provided on GITHUB:**https://github.com/PiaBackmann/TIMELY-MODEL**, data are available from the Dryad Digital Repository: **https://doi.org/10.5061/dryad.gh2m22t**.

Two-plants scenario

We ran simulations with only two plants and one larva to visualize the scenario discussed in the Introduction. Both plants had the same delay time and one plant, plant A, received a newly hatched caterpillar. We performed simulations with three different delay times: no delay time ($\tau = 0$), intermediate ($\tau = 4$ days) and long ($\tau = \infty$ days); the latter option equals no defense response.

Main simulations (400 plants scenario)

All 400 plants were either given the same delay time for all plants (for the experiments conducted for Figs. 3 and 4) or random delay times, with $\tau \in [0,\ldots 10]$(for the results shown in Fig. 5). Caterpillars were placed randomly on the plants, according to their chosen density.

Genetic algorithm

The heritable trait for the genetic algorithm (GA) was the plant's delay time, τ. At initialization, the delay times of all plants were drawn from a uniform distribution between 0 and 10 days. The plants that had the largest average shoot biomass at the end of a simulation, or generation, are considered to have the largest fitness, assuming that larger plants produce more seeds (Aarssen and Taylor, 1992, TRACE document, Fig. T6). Therefore, in the following generation, the 400 plants were assigned to genotypes (delay times τ) proportional to their total shoot biomasses at the end of the preceding generation. This was repeated for 300 generations with 27 days per simulation. To prevent being caught in local fitness maxima, we represented mutation by adding, every generation, a random number r, with $-3 < r < 3$, to every assigned value of τ. Simulation experiments were conducted with different densities of larvae (0 – 500 larvae). Per larvae density, the genetic algorithm was repeated 100 times.

We compared our genetic algorithm with a different one (Stonedahl and Wilensky 2008; see TRACE document) to see whether the results were persistent. We also started the Genetic Algorithm with all plants having the same delay time, to see whether initial setting would affect the final distribution of delay times.

Results

Field study

Larvae feeding on low defense plants showed significantly higher growth rates (Fig. 2) than larvae feeding on high defense plants. Furthermore, their instar progression was faster. The 5th instar, for example, was reached four days earlier (Tab. S1). Additionally, the maximal weight attained in each instar (Tab. S1) and survival rates of larvae raised on low defense plants were higher; 53 % of the larvae survived on low defense plants and 20 % on well defended plants, showing that there is a fitness cost for larvae to stay on a well defended plant

Two-plants scenario

For the scenario with immediate defense production ($\tau = 0$ days), the larva died after seven days, thus before it would have been able to switch plants. The final biomass of plant A was significantly lower than the biomass of its uninfected competitor (Fig. 3, left panel). For the scenario with long delay time (corresponding to no defense at all), the larva stayed on plant A until pupation and the biomass of the infested plant was reduced by larval feeding, resulting in a lower biomass than the other plant (Fig. 3, right panel). For the $\tau = 5$ days scenario, the larva was driven from the first host plant to the neighboring plant on the 11th day of the simulation. The final mass of plant A was higher than the mass of plant B (Fig. 3, center panel).

Main simulations (400 plants scenario)

We conducted simulations with populations of 400 plants having all the same delay time and 300 larvae to record average larval mortality for different τ values. For $\tau = 0$, on average 21.7%, and for $\tau = \infty$, on average 45.8% of all larvae survived until pupation stage. For an intermediate delay time ($\tau = 4$) on average 50.3% survived until pupation and 57.4% of all caterpillars reached the third instar, which is the instar in which larvae can switch their host plants.

As next step, we calculated the mean number of inter-plant movements of larvae per simulation. These switches were either motivated by a high defense level of the host plant or because the host plant was entirely consumed by the larva. For our analysis, we only counted switches motivated by a high defense level as those were a larval reaction to the plants defense mechanism. The mean number of switches peaked when the delay time of plants was intermediate ($3d <= \tau <= 5d$, Fig. 4). If the plant defended immediately ($\tau = 0$) or after a very long delay time, the number of switches was significantly smaller (Fig. 4).

The higher the defense levels of the host plant, the shallower the growth curves of larvae. As a result, if a larva encountered mostly fast-defending plants during its development,

it needed 2-3 days longer to reach its final size and go into pupation stage (Fig. S2, Supplementary Material).

Larvae are sufficiently mobile to switch host plants when they have reached a certain size. In our simulations, the larvae moved earliest after eight days from one plant to another (Fig. 5 bottom). Larvae were only mobile that fast when the delay time of their host plant was intermediate ($\tau = 4$ days). In case of feeding on a plant with a delay time of $\tau = 0$ days, caterpillars needed in average 2 days longer (10 days) to reach a size where inter-plant movement was possible, because their growth was inhibited by the fast rising defense levels in their host plants during the early instar phases.

In most of the cases, when switching, larvae moved to one of the other plants in the closer neighborhood – thus direct competitors of the originally infested plant (Fig. S3). A single larva, which survived until pupation, visited on average 4-5 plants per simulation. Reasons for switching were complete consumption of the host plant (in ca. 70 % of cases) or that the host plant defense level increased over the threshold level (in ca. 30% of cases). If a plant was infested by a larva and started inducing defense, the critical defense level to repel larvae was reached approximately 4-7 days after induction (Fig. 5, top). This time depended on the current growth rate of the plant and of the size of the plant when induction had started.

Genetic algorithm

Starting from the random initialization of delay times in generation 1, variance of the delay times decreased and the distribution started to peak around a maximum value. In all cases a specific dominant delay time, τ, emerged. However, it never fully suppressed other delay times. Average delay time depended on initial herbivore density (Fig. 6, left panel); for high densities, the mean of the delay times increased over the generations, for low densities, the mean delay time decreased. For higher initial herbivore densities, variance of delay times decreased more rapidly and the final stationary distribution developed more pronounced peaks

(Fig. 6, right panel; see also video of the development of the delay time distribution over time in the Supplementary Material). More or less the same final distributions where obtained when the genetic algorithm started with the same delay time for all plants (TRACE document, Fig. ST18). All these results were also obtained when using the alternative genetic algorithm (see TRACE document).

To test whether inter-plant competition was one important driver for longer delay times, we also run the genetic algorithm for plants which were not affected by inter-plant competition. Here it showed that without competition, optimal delay times should be as short as possible (Fig. S4 of the Supplement).

Discussion

Our results show that in highly competitive environments plants can realize a fitness benefit by delaying induction of defenses. Expelling an herbivore to one of the neighbors may be the best chance for an infested plant competing with uninduced conspecifics to compensate for the costs of induction, despite the amount of leaf loss. Consequently, there is no strong selection for reducing response times, which may explain the large variety in delay times found in plants. Therefore, the postulation that the delay in deploying anti-herbivore defenses is unequivocally costly (Herms and Mattson, 1992) can be rejected.

Our results indicate that instead of being as fast as possible, it is more important that defense induction is timely. For *N. attenuata*, the peak in defense production should co-occur with a "window of sensitivity" for the herbivores. Behaviour of *M. sexta* larvae is most sensitive to the induced defenses of *N. attenuata* when they are in their third instar (van Dam et al 2001a). From this instar onwards, the larvae start to cause significant damage to the plant and are large enough to reduce the risks of starvation or predation while searching for a less defended host plant (Gilmore 1938; Haccou and Hemerik 1985; Figure 2). For the host plant it would be most beneficial if larvae in this instar are driven to the neighbor plants and start

feeding on their competitor. We could also show that for plants which are not exposed to inter-plant competition, the opposite is true and shorter delay times are preferable (Fig. S4).

Not producing defense at all results in a higher plant lethality: larvae would stay on the host plant during their whole life cycle and cause severe damage (Fig. 6, right panel). In our simulations, on average, 171 out of 400 plants die due to herbivory and competition if no defense is produced whereas only 117 plants die if plants immediately produce defense. However, for a plant inducing defense immediately after an attack, the defense level peaks too early and more larvae will die before reaching the third instar. If the plant would be growing in isolation, this would be the best option. However, in natural environments *N. attenuata* and many other plant species that mass germinate, such as spring annuals, grow in dense cohorts, and defense induction comes with loss in competitive abilities (van Dam and Baldwin 1998, Glawe et al 2003). Thus in competitive environments, producing defense early means a loss in growth rate which can hardly be compensated for in a relatively short growth season. Both extremes, immediate induction or no induced defense at all, seem to be suboptimal strategies. Our model shows that one possible way out of this dilemma is to induce at a time that larvae are causing the most of the damage and are likely to move to neighboring plants.

During the first two instars, when larvae are small and not able to move between plants, the damage they cause is negligible, because damage scales with caterpillar size. In this stage, the effect of the 30% growth-loss when being induced is more relevant than the loss of biomass due to larval feeding.

For higher initial herbivore densities, for example when every plant receives at least one larva, slowly reacting plants will have an initial growth advantage, because they do not invest in producing defense first. In all plants, the defense maximum peaks 4-7 days after induction started (Fig. 5 top), whereas larvae stay at least 8 – 10 days on the host plant where they hatched. Therefore, if the plant defends without delay, it will be at a maximum defense level

before the larva becomes mobile, and the mobility phase will be reached even later (Fig. 5 bottom).

Under high herbivore pressure, selection by herbivore feeding as represented by our genetic algorithm leads to higher delay times. Under these conditions it is a better strategy to wait, whereas for low herbivore pressure a broad range of delay times can coexist. This is underscored by the fact that under higher herbivore pressures, variance of delay times in the population decreased more rapidly and the curve of the stationary distribution of τ values showed a sharper peak.

To test whether the resulting stationary distribution of delay times was robust, for each herbivore density we used the resulting peak values of τ to start a genetic algorithm where all plants were assigned to this same value of τ. After 300 generations, the genetic algorithm leveled out to the same resulting frequencies of the stationary distribution found for the Genetic Algorithm starting with the uniform distribution of τ (Fig. ST18 of the Supplementary Material). This means that the fitness related to delay times was always frequency-dependent, leading to a distribution of delay times rather than resulting in a single dominant time or revealing time intervals that were completely suppressed. In their natural habitat, herbivore densities change from season to season. Therefore, there will be no distinctive and constant selection pressure towards shorter or longer delay times. We therefore hypothesize that the observed variance in delay times of individual plants should be high in natural populations.

In order to test the model predictions, the variance in reaction times (kinetics) of *N. attenuata* in natural populations should be measured by damaging the plants mechanically and simultaneously adding larval saliva to the produced wound. Then, the concentrations of different defense compounds within the leaf tissue can be measured at different time points after elicitation. This outcome can then be compared with the predictions of the TIMELY model (Fig. S8 shows how the experimental corroboration could be done).

Plants can perceive attacks by herbivores as well as the strength of their local competition. Consequently, they may also phenotypically adapt their delay time to the actual level of competition. By performing experiments with different plant densities, we could show that the severity of herbivore load is the most important factor for the resulting delay times. However, without inter-plant competition, the resulting delay times would be as short as possible (Fig. S4 of the Supplement). Therefore, the evolution on optimal delay times depends on both, the number of attacking herbivores and the severity of inter-plant competition.

One more possible mechanism, which might interfere with the mechanism represented in our model, is the production of volatile organic compounds (VOCs) that are produced once larvae feed on a plant and which might induce chemical defense in neighbouring plants. However, such secondary induced defense has not been observed so far for *N. attenuata*, and therefore ignored this effect. Still, this "priming" of neighbors is included as an option in our model and thus can be explored for situations and species where such priming can be assumed to play a role (see Supplementary Material, ODD, page 29).

We designed and calibrated our model with data from *N. attenuata* as annual plant species and *M. sexta* as its main herbivore. It can, however, be easily adapted for other annual plant – insect herbivore systems. In order to do so, we tested our model for a range of settings which differ from the *N. attenuata - M. sexta* system (see Appendix and Supplementary Material). Here we found that the generally held assumption that damage done by herbivores before the defense levels are induced is always costly in terms of fitness cannot be sustained. In that sense, the model addresses a general hypothesis that now is refuted.

Whether or not a particular plant species may benefit by delaying induction depends strongly on the characteristics of the herbivores. Delaying defenses within the plants' life time may only be profitable when the plant is attacked by an herbivore that is mobile, selective and feeds increasingly more over time (Tuomi et al. 1994; Underwood 1999; van Dam et al.

2001a). Lepidopteran larvae are good examples of such herbivores, but these criteria may also apply to other arthropod herbivores that have two discrete generations within the plants' lifetime, of which the second is more abundant (Underwood 1999). Furthermore, our model was designed to analyze the fitness effects of time-delays within one growing season, however, it could be adapted to analyze the consequences in slower growing, long-lived plants, such as trees. Trees may have delayed induced defenses that are not expressed until the next growing season after herbivore attack (Haukioja 1980; Rhoades 1983; Karban and Baldwin 1997). Such long-term delays in perennial plants may, depending on the mobility and selectivity of the herbivores, drive fluctuations in insect populations over the years (Underwood 1999) and hence the benefits of such long-term delays can only be assessed over several reproductive cycles of the plant.

To conclude, for induced defense responses in plants, "the faster the better" is not necessarily true: delays in inducible defenses can evolve to be part of the set of successful defense strategies when the plants use a small proportion of their biomass to 'rear larvae' for reducing competition from their neighbors/competitors.

Herbivore-mediated competition among plants via the evolution of delays in response timing has not been described previously and provides an intriguing an example for the adaptive behavior of plants (Meyer et al. 2014), in particular as it involves life history traits of other organisms, in this case caterpillars. The behavior of plants is no less adaptive than that of animals, but the potential for adaptation seems to be limited by their sessile nature. We have shown that plants can include insect herbivores into their fitness-maximizing strategy and thereby modify the local forces of competition to their own benefit. This indicates the high potential of merging chemical ecology and behavioral ecology via individual-based models of populations.

Appendix

Robustness analysis

We used the rationale of "robustness analysis" (Levin 1966; Grimm and Berger 2016): using unrealistic settings in terms of parameters in functions to try and "break" a model and thereby explore robustness of the main findings of a model and identify key components of a model system's organization. We therefore ran further simulations with different plant densities, mobility types of larvae and different defense investment proportions of plants to see whether they may lead to similar results, even for systems which differ from the *N. attenuata – M. sexta* system (all performed robustness experiments are listed in Tab. S2 in the Supplement)).

The robustness experiments show that for most settings the delay time, τ, remains positive (see Tab. S2 and Figs. S5, S6 and S7 (Supplementary document)).

This holds true, as long as the following prerequisites are fulfilled: herbivores must be mobile; plants must compete with one another (inter- or intraspecific); plants must share their herbivores. We therefore are convinced that our main conclusion holds: the generally held assumption that damage done by herbivores before the defense levels are induced are always costly in terms of fitness cannot be sustained. In that sense, the model addresses a general hypothesis that now is refuted.

1 ## Acknowledgements

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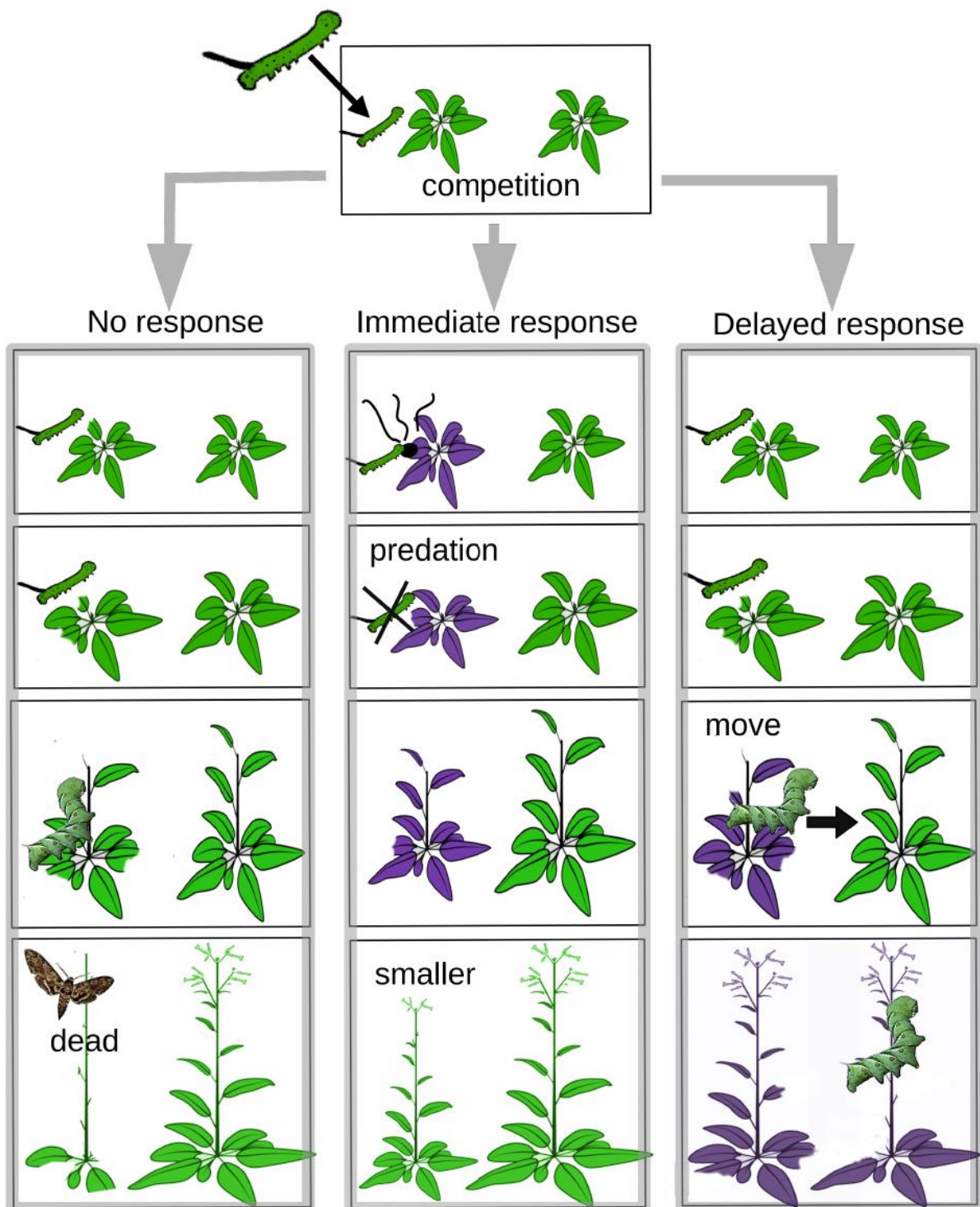
FIGURES:

Figure 1: Conceptual background of the model. Plants that have induced chemical defense are violet, green otherwise. When a plant is attacked by a larva, it has three ways to react to the attack: it does not produce defense compounds (left column), it reacts immediately by producing defense compounds (middle column), or it reacts after a certain delay time τ (right column). Possible defense actions of a plant include producing toxic substances to affect larval growth and health (violet plants) and producing volatile organic compounds to attract predators, which is most effective when the larva is small because predators or parasitoids do not attack bigger larvae (upper two panels in middle column).
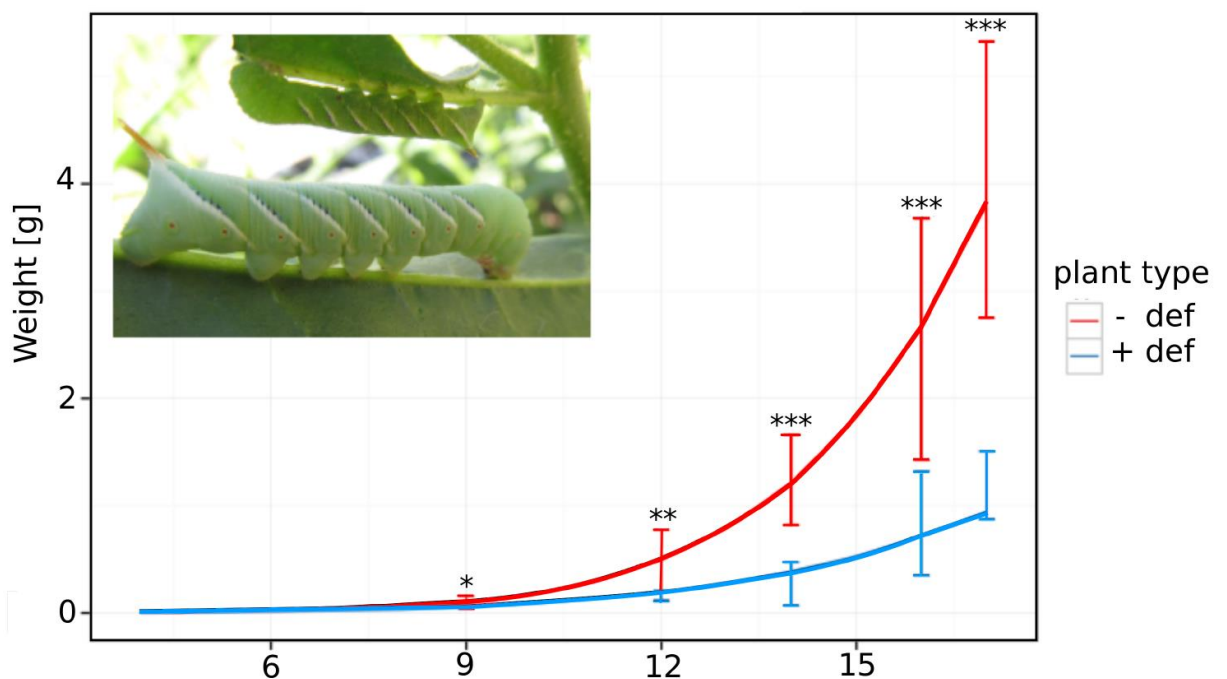

Figure 2: Growth of Manduca sexta larvae. Larvae reared on plants being unable to produce defense compounds ("- def", red line; start: N = 30, end N = 16 larvae) are compared to larvae raised on plants being maximally defended ("+ def"; start: N = 30, end N = 6 larvae). The photo shows the difference in size of a larva raised on a defenseless plant (lower larva) to one raised on a maximally defended plant (upper larva) after 14 days. Asterisks denote the p-value: three asterisks correspond to

values less than 0.001, two asterisks indicate values less than 0.01, one asterisk

means the value is less than 0.05

Parameter	Description	Default	Range tested
Number plants	Starting number plants	400	2 and 400
R_a	Resource limit. aboveground	0.15	0 - 0.6
R_b	Resource limit. belowground	0.45	0 - 0.6
τ	Delay time of the plant τ = Difference in days between first larva feeding and defense production and last larva feeding and defense production stop	random	0 - 10 d
Conversion factor	Ratio of eaten biomass converted into larva mass	0.19	0.0 - 1.0
Movement radius	Maximal distance a larva moves to another plant	5 m	0.2 - 15 m
Defense tolerance	Threshold at which mobile larvae switch plants	0.24	0.15 - 0.30

Variable	Description	Init.	Range
Ticks	A tick = 1/6 day	0	0 - 160
Biomass plant	Mass of the whole plant	60 g	10 - 500 g
Aboveground mass	Mass ot the shoot	30 g	10 - 500 g
Belowground mass	Mass ot the root	30 g	10 - 500 g
Biomass larva	Body mass of the larva	1 mg	1mg - 10 g
Defense level	Proportion of defense and plant mass	0.0	0.0 - 0.3

Table 1: Parameters and variables of the individual-based model. Default and initial

values of parameters and variables, respectively, are given as well as possible ranges
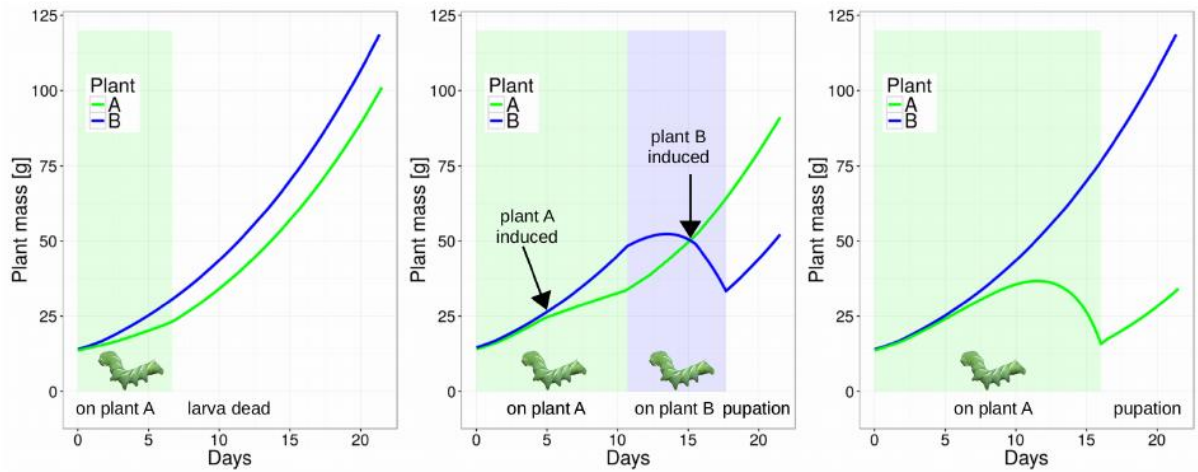
and, if applicable, units.

Figure 3: Plant biomass in one two-plants-simulation. Three different τ values are shown: left: $\tau = 0$, middle: $\tau = 5$ days, right: $\tau > 10$ days. In all cases, plant A (green line) starts with a freshly hatched larva. In the left panel, it defends immediately and eventually kills the larva at day 7, in the right panel, it reacts so slowly that the larva completes its full life cycle on the plant. Therefore, the plant suffers considerable damage. Panel in the middle: the plant reacts after a certain delay. The larva survives, reaches 3rd instar and becomes thus mobile. It is send to the competing plant and plant A can recover. The plant B receives more damage in this scenario than the formerly infested plant.
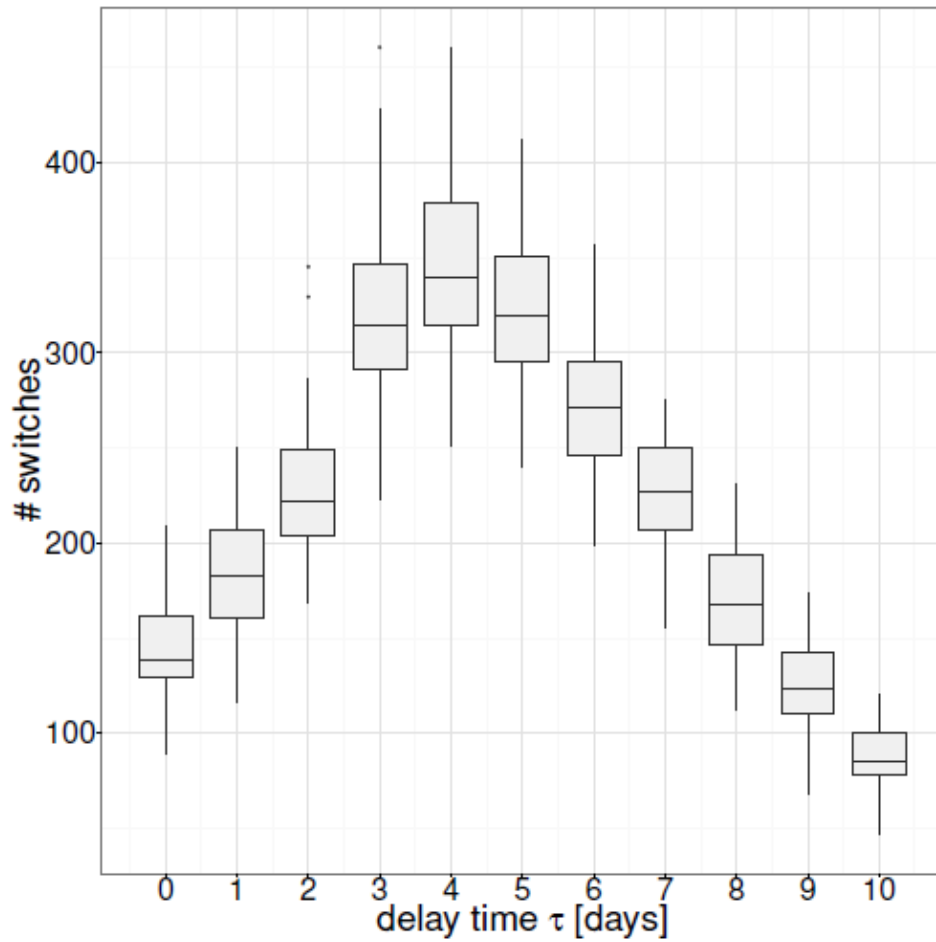
Figure 4: Number of plant switches, i.e. larvae changing their host plant caused by a plants chemical defense or its death, per simulation with three hundred caterpillars. All plants have the same indicated delay time τ ; larvae can switch plants more than once.
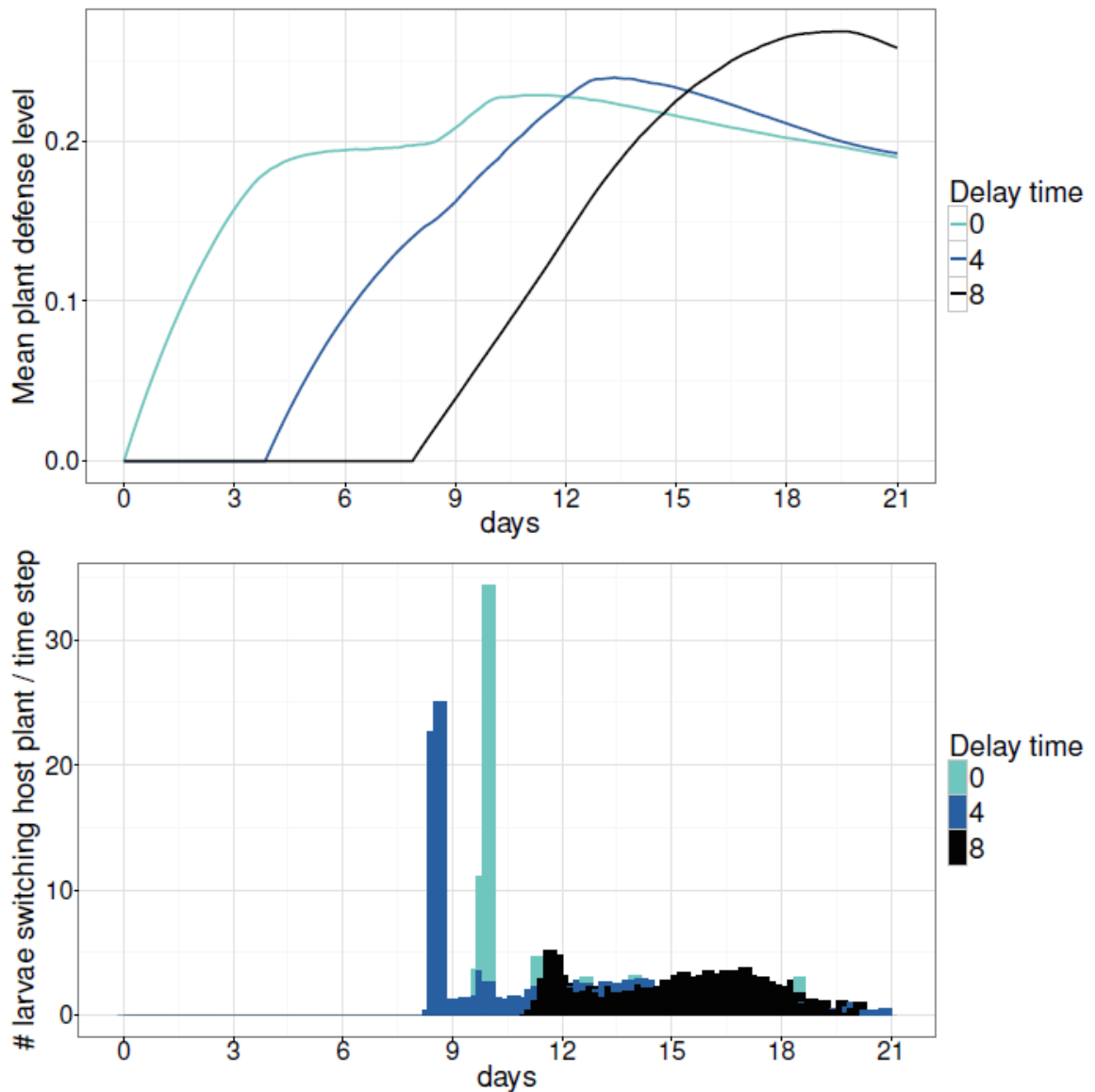
Figure 5: Mean plant defense level of all plants in the simulation (upper panel) and number of larvae switching plants per day due to chemical defense (lower panel). Simulations started with three hundred larvae, 50 simulations were run per delay time, all plants in a simulation had the same delay time, which is indicated by different colors. Note that the sequence of the timing of plant (upper panel) and larvae responses (lower panel) for delay times of 0 and 4 days is reversed.
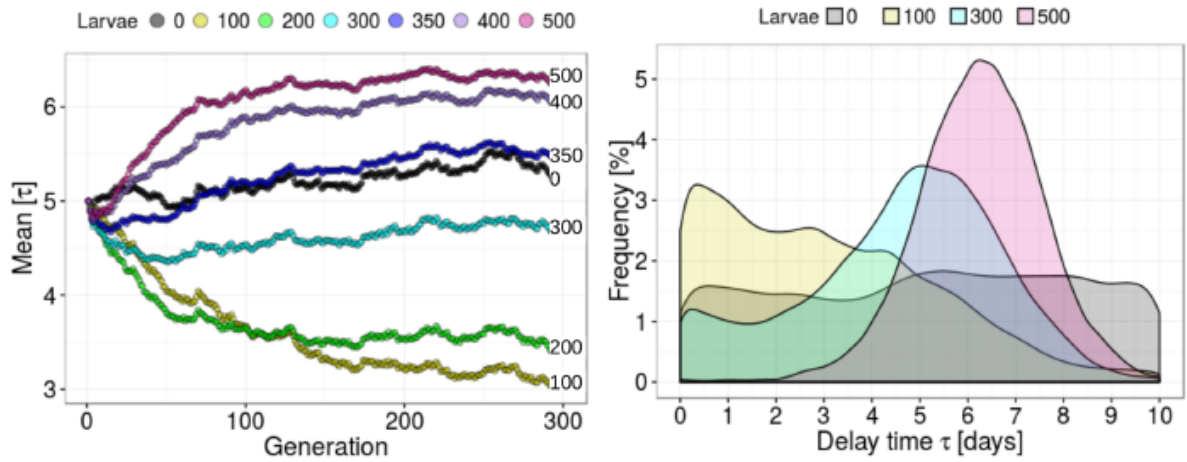
Figure 6: Evolving means (left panel) and final frequencies (right panel) of delay times τ for different initial numbers of larvae. The genetic algorithm started with randomly assigned delay times (τ ∈ [0, 10] days) in the first generation and ran for three hundred generations.