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Optimal plant defence under competition for light and nutrients: an evolutionary modelling approach

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ABSTRACT

Plants compete with their neighbours for limiting resources such as light and nitrogen, which can promote competitive ability at the expense of other functions such as chemical defence against insect herbivory. This trade-off is strongly influenced by dynamic interactions with biotic and abiotic factors. Yet, understanding how these interactions influence the balance between growth and defence remains one of the key challenges in the field of plant evolutionary ecology. In this study, we investigated how resource availability, competition pressure and insect herbivore pressure drive selection on the balance between the acquisition and protection of resources. To this end, we developed a novel simulation model that combines a functional-structural plant (FSP) model of plant growth in a 3D light climate with a model of natural selection. This mechanistic modelling approach simulates plant growth, competition for above- and below-ground resources, and natural selection to investigate selection pressures on traits related to growth and defence as imposed by different levels of plant density, nitrogen availability and herbivory. The model presented in this study was able to recreate the functional equilibria predicted by principal ecological theories on the effects of resource availability and resource-driven trade-offs. This illustrates the potential of mechanistic modelling approaches such as the one presented here for future research on plant responses to dynamic and variable environments. Our results further showed a three-way interaction between plant competition for light, competition for nitrogen and herbivory that determined the optimal balance between the acquisition and protection of resources. This shows that the value of investing in the acquisition or the protection of resources is a dynamic problem that is influenced by multiple ecological interactions, trade-offs and tragedies of the commons, and therefore requires an eco-evolutionary context to be fully understood.

KEYWORDS: Competition; evolutionary ecology; functional-structural plant modelling; growth-defence trade-off; plant–herbivore interactions; plant–plant interactions; plant traits; tragedy of the commons.

1. INTRODUCTION

For many plant species, outcompeting neighbouring plants for resources such as light and nitrogen is vital to plant fitness. Therefore, plants have evolved strong plastic responses to increase their competitive ability in the presence of neighbouring plants, both above- (Ballaré and Pierik 2017) and below-ground (Mommer *et al.* 2012). These plastic responses function to optimize resource acquisition in environments that vary within and between generations (Sultan 2000). However, game-theoretical studies show that under competition for resources, natural selection on plant fitness can drive the expression of resource acquisition traits away from the population-level optimum, also referred to as a tragedy of the commons (Falster and Westoby 2003; McNickle and Dybzinski 2013). A key element to this theory is that plant fitness is not determined by the absolute value of a trait, but its relative value compared to the trait values of neighbouring plants (McNickle and Dybzinski 2013). This can lead to overexpression of traits that promote the acquisition of limiting resources, which has been demonstrated both above- (King 1990; Oksanen 1990; Zhang *et al.* 1999; Anten 2002; Falster and Westoby 2003; Dybzinski *et al.* 2011) and below-ground (Givnish 1995; Gersani *et al.* 2001; O'Brien *et al.* 2005, 2007; Dybzinski *et al.* 2011), but see (Chen *et al.* 2015).

This (over)investment in competitive ability may go at the expense of an investment in other plant functions. The balance of traits that enhance competitive ability in the presence of neighbouring plants and chemical defence against insect herbivores constitute a well-known example of such an internal resource trade-off (Züst and Agrawal 2017), which manifests as species-specific strategies or plastic responses to the environment (Herms and Mattson 1992; Züst *et al.* 2011; Ballaré 2014; Züst and Agrawal 2017). Plants use the red to far-red ratio (R:FR) in the light spectrum to detect neighbour presence (Ballaré *et al.* 1990), which elicits a range of growth-related responses that can increase the plant's competitive ability (Franklin 2008; Ballaré and Pierik 2017) as well as physiological responses that impede the plant's ability to defend itself (Herms and Mattson 1992; Ballaré 2014; Züst and Agrawal 2017). Chemical defence mechanisms are known to carry substantial metabolic costs (Gershenzon 1994; Bekaert *et al.* 2012), and their impact on plant fitness is strongly influenced by dynamic interactions with biotic and abiotic factors in the environment, such as resource availability, competition pressure and herbivore pressure (Heil and Baldwin 2002; Strauss *et al.* 2002; Cipollini *et al.* 2014; de Vries *et al.* 2017). Plants are known to optimize the costs and benefits of chemical defence by varying the defence investment to different plant parts proportional to their value, prioritizing plant parts that are important for resource acquisition (e.g. young leaves) and reproduction (e.g. flowers and seeds) (Koricheva and Barton 2012). However, these valuable plant parts are also prime targets for insect herbivores (Feeny 1976; Cates 1980; Schoonhoven *et al.* 2005) as they contain a high concentration of valuable resources such as nitrogen, which serve to maximize their potential gain to plant performance (Hirose and Werger 1987; Anten *et al.* 1995; Hikosaka *et al.* 2016) and further incentivize plants to express high levels of defence in these parts. Understanding how these interactions result in defence traits that impact plant fitness and drive selection for optimally competing and defending phenotypes, is one of the current challenges in the field of plant evolutionary ecology (Poelman 2015; Erb 2018).

In this study, we aim to elucidate how resource availability, competition pressure and herbivore pressure drive selection on the balance between the acquisition and protection of resources. To this end, we developed a novel modelling approach that combines a functional-structural plant (FSP) model of plant growth in a 3D light climate with an evolutionary algorithm. Analytical models of evolutionary game theory (EGT) (McNickle and Dybzinski 2013) and FSP models (Evers *et al.* 2018) have existed for decades and the merger of these two approaches has been suggested to advance our understanding of plant trait selection (Bongers *et al.* 2014). In analytical models of EGT, the adaptive value of a given strategy (trait expression) depends on how the performance level of a plant is affected by the strategy of neighbouring plants. In these analytical models, the interactions between plants through resource competition, signalling or other means are usually based on implicit assumptions. However, FSP models explicitly simulate competitive interactions by representing plants as individual entities that influence and are influenced by their environment. Examples that combine FSP modelling with EGT have become increasingly complex and dynamic, going from single root systems in a static environment (Renton and Poot 2014), to static plant canopies (Yoshinaka *et al.* 2018), to canopies of plants that grow and develop (Bongers *et al.* 2018, 2019). We expand this merger of modelling approaches to a broader ecological scale by investigating how a combination of three environmental factors (plant density, nitrogen availability and insect herbivory) affect trait selection of (i) biomass allocation patterns, (ii) chemical defence expression and (iii) the distribution of nitrogen and defence in the canopy.

2. MATERIALS AND METHODS

2.1 Model summary

The model used in this study was designed to simulate the natural selection of plant traits in a population of annual plants using a 3D FSP modelling approach (Vos *et al.* 2010). The model simulates a population of 100 individual plants, each with a distinct combination of plant traits (i.e. genotype) that determine the individuals performance and subsequent fitness under the imposed set of environmental conditions (i.e. plant density, nitrogen availability and herbivore pressure). The model simulates this population over a sequence of successive generations, allowing the population to converge to a genotype that maximizes fitness for the environmental conditions imposed (Fig. 1). Due to the computational demands of this approach, we prioritized computational efficiency at the cost of model complexity. First, in the plant growth part of the model, we included only the mechanisms that are essential to simulate internal resource trade-offs and competition between plants for both above- and below-ground resources and forwent the detail in plant growth and development that typically characterizes FSP models (de Vries *et al.* 2018; Evers *et al.* 2018). Second, we designed this model as a model of natural selection rather than a model of population dynamics, forgoing any effect that carry over multiple generations such as a seed bank, N-cycling or population growth rates (i.e. the model always simulates 100 individuals). To allow internal resource trade-offs to manifest, we applied the simple premise that a plant can only invest a given quantity of resources once, allocating it to one of three functions; the acquisition of light, the acquisition of nitrogen, or the protection against herbivory. The model uses an explicit representation of canopy structure to calculate the distribution of light interception over the individual leaves in the canopy using the Monte-Carlo path tracer embedded in GroImp (Hemmerling *et al.* 2008; Evers *et al.* 2010; de Vries *et al.* 2018) (**see Supporting Information—Methods S1** for more detail on the simulated light environment). The outcome of competition for light between individual plants in the population is thus determined by the placement of leaves relative to the leaves of neighbouring plants resulting in shading, which is in turn determined by the height of the stem the leaves are attached to. The uptake of nitrogen is assumed to be linearly related to nitrogen availability in the soil and to the plant's investment in root biomass, thereby assuming that the competition for nitrogen between plants is symmetrical (Schwinning and Weiner 1998; Cahill et al. 2000). The

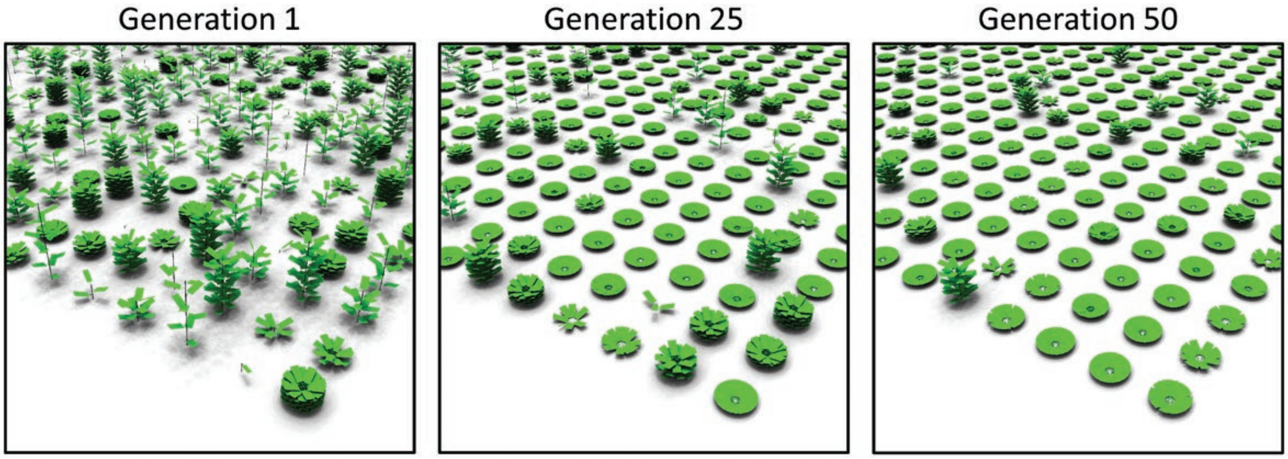

Figure 1. Changes in plant architecture through natural selection. A visual representation of initial population (generation 1) of randomly generated genotypes and the population after 25 and 50 generations of evolution in a low density, low nitrogen environment in the absence of herbivory.

model simulates insect herbivory as a constant rate of leaf removal that interacts with light acquisition through the consumption of leaf area and with nitrogen acquisition through the consumption of previously acquired nitrogen that is allocated to the leaves to drive photosynthesis. The distribution of herbivore damage over the leaves determined by the distribution of nitrogen and defences over the leaves (Fig. S3), assuming that the insect herbivores preferentially feed on leaves with a high nitrogen content and avoid feeding from well-defended leaves (Feeny 1976; Cates 1980; Schoonhoven *et al.* 2005; Fig. S4). The rate of herbivore damage is then directly reduced by defences (i.e. secondary metabolites) allocated to individual leaves, assuming that the reduction in herbivore damage by defences follows a saturating dose–response curve. The benefit provided by a given investment in chemical defence is a strong determinant of the adaptive value of chemical defence (de Vries *et al.* 2019) and therefore a key determinant for the outcome of selection on plant chemical defence (Cipollini *et al.* 2014). Due to the lack of empirical support for the parameterization of this relationship we relied on previous work where we explored the relation between the costs and benefits of defence and their effect on the adaptive value of plant chemical defences (de Vries *et al.* 2019). Therefore, we purposefully forgo any quantitative comparison of model results to empirical studies when discussing model results as we feel the model is not equipped to support those claims. Instead, we limit ourselves to the comparison of different treatment combinations in the model results and to qualitative comparisons to well-described ecological theories.

The simulated plants were described using a genotype characterized by four biomass allocation parameters (to roots, stem, leaves and defence (i.e. secondary metabolites that can then be distributed over the leaves)) and two parameters that describe the distribution of nitrogen and defensive compounds within the plant. The genotype of an individual plant is thus described by a given combination of values for these six parameters, together representing a genotype following a strategy in a game theoretical context. In every generation, the plants started as seedlings with a total of 5 g of biomass (e.g. carbon-based assimilates), which would be divided among roots, stem, leaves and defence according to the biomass allocation parameters of the plant's genotype. The plants accumulated more biomass over four model time steps spanning 14 days each. This number of time steps was the result of a sensitivity analysis of simulated biomass allocation to the number of time steps [**see Supporting Information—Fig. S1**].

For every generation of plants, the model took the following steps (Fig. 2):

1. An initial population was established through random generation of the values for the four allocation and two distribution parameters for 100 plants genotypes.
2. The architecture of each of these plants was constructed by distributing the total plant biomass over leaves, stem, roots and defence using the four biomass allocation parameters.
3. Nitrogen and defences were distributed over the leaves according to the two distribution parameters.
4. The distribution and severity of damage by insect herbivores was calculated based on the distribution of nitrogen and defence.
5. The reduction in leaf surface area due to herbivory was calculated, as well as the subsequent reduction in the nitrogen and defence compounds that were present in the damaged leaf as these were consumed with the leaf.
6. Plant nitrogen uptake and light interception were calculated based on the plant architecture after herbivory.
7. Light capture and the plant nitrogen content were used to simulate carbon assimilation through photosynthesis, the maximum rate of which was dependent on the photosynthetically active nitrogen in a leaf. The carbon assimilated through photosynthesis was added to the total plant biomass to conclude one time step.

Steps 2–7 were repeated for a total of four time steps for every generation.

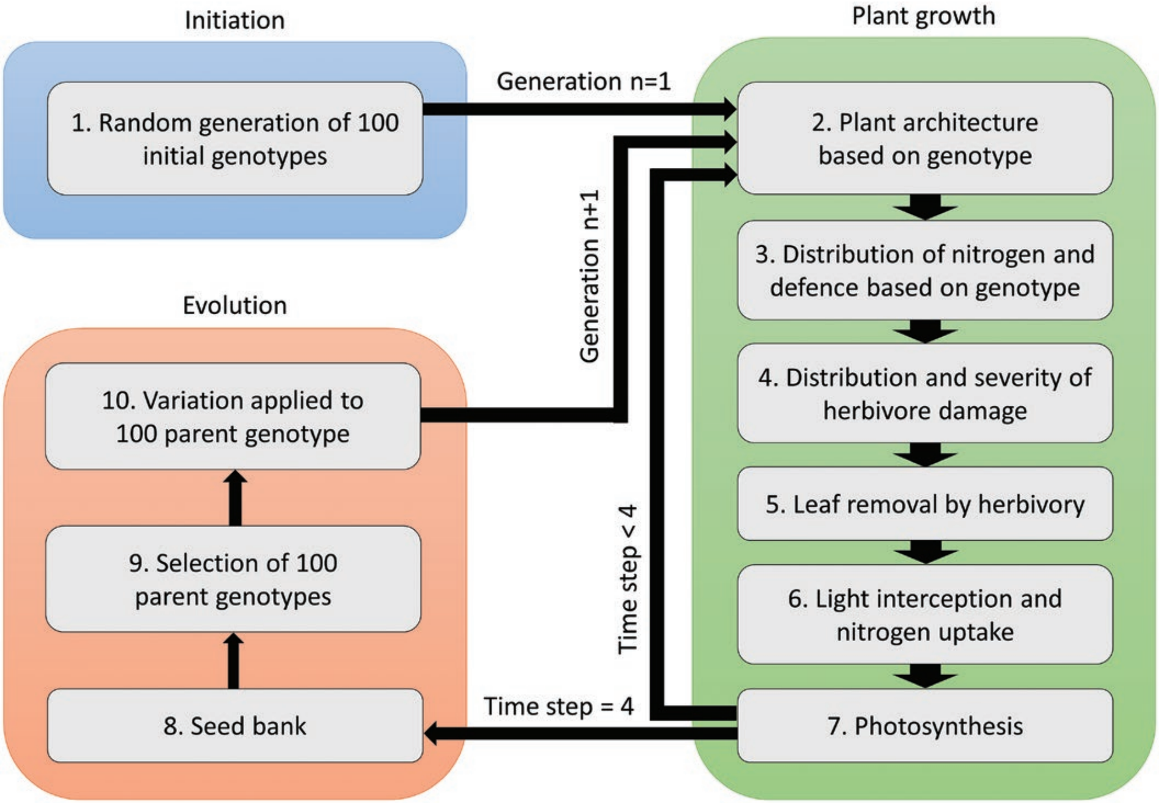

Figure 2. Model flow chart. Flow chart of the model showing the steps involved in the initiation (blue) of the first population of 100 random genotypes (1), the plant growth part of the model (green) that eventually determines plant fitness (2–7) and the evolutionary part of the model (red) that determines how plant fitness translates to the next generation (8–10).

8. The plants allocated the assimilates produced during the final time step to seed production, which determined the probability for its genotype to be represented in the next generation.
9. A new population of genotypes was constructed by randomly drawing 100 genotypes from the plants in the previous generation, with the chance for a genotype to be drawn being proportionate to its seed production, representing its fitness.
10. This next generation of plants inherit the genotypes randomly drawn from the previous generation with a fixed range of variation applied to all parameters that make up those genotypes.

A sensitivity analysis showed that 75 generations per replication was sufficient for evolution to converge on stable parameter values [**see Supporting Information—Fig. S2**]. Ten replications per treatment combination were performed to account for model stochasticity. The components of the plant growth and evolutionary parts of the model are explained in detail in the supporting information [**see Supporting Information—Methods S1**], and parameter values used in the model can be found in **Supporting Information—Table S1**.

2.2 Simulations

The model was used to simulate two levels of competition for light, represented by two population densities (1 plant per m^2, 16 plants per m^2), a range of potential herbivore damage levels (0–0.3 with steps of 0.05, fraction of leaf area) and four or five levels of soil nitrogen availability for each plant density (see Table 1). Some key results are presented by comparing an environment where plants experience weak competition for both light and nitrogen (i.e. low plant density and high nitrogen availability; 1 plant per m^2 and 2 g N per plant) with scenario's where plants experience strong competition for light and weak competition for nitrogen (i.e. high plant density and high nitrogen availability; 16 plants per m^2 and 2 g N per plant) or where plant experience strong competition for both light and nitrogen (i.e. high density and low nitrogen availability; 16 plants per m^2 and 0.125 g N per plant).

2.3 Model output

Results are reported using the average trait values of the population after 75 generations of selection. We report carbon allocation to stems, leaves, roots and defence, leaf level allocation of defence in per gram of leaf biomass, as well as plant level distributions of defence and nitrogen across leaves. Model output was tested for significance by conducting an analysis of variance (ANOVA) at the 5 % probability level, and all reported differences were highly significant ($P < 0.001$) unless stated otherwise.

Table 1. Soil nitrogen availability per plant and per m^2 used in the analysis.

Plant density	g N per plant	g N m^{-2}	Plant density	g N per plant	g N m^{-2}
1 plant per m^2	0.5	0.5	16 plants per m^2	0.125	2
	1	1		0.25	4
	2	2		0.5	8
	4	4		1	16
				2	32

3. RESULTS

3.1 Carbon allocation to stems, leaves and roots

The population level average trait values show that a high plant density selected for taller plants (i.e. a higher allocation of biomass to stems) than a low plant density (Fig. 3C and D). These taller plants also invested less biomass in roots (Fig. 3E and F) to accommodate the increased allocation to stems, which resulted in high-density plants having considerably lower root-shoot ratios than low-density plants. Plants invested less in roots with an increase in nitrogen availability (Fig. 3E and F), which led to an increased allocation to leaves and stems (Fig. 3A–D). These carbon allocation patterns were mostly independent of the herbivore pressure faced by the plants (Fig. 3).

3.2 Allocation to defence

Under low levels of herbivore damage and high levels of soil nitrogen availability, the model selected for plants that did not invest in defence (Fig. 3G and H). The plant defence investment increased with an increase in herbivore damage and a decrease in the availability of nitrogen (Fig. 3G and H). Strong competition for light, but not for nitrogen, selected for plants that invested less in defence compared to plants that experience weak competition for both light and nitrogen (Fig. 4). Conversely, strong competition for both light and nitrogen selected for a higher defence investment compared to plant that experience weak competition for both light and nitrogen (Fig. 4).

3.3 Distribution of defence

In the absence of herbivore damage, the plant did not invest any carbon into defence and thus the model showed no selection for a given distribution of defence in the canopy (Fig. 5A). The distribution of defence in the plant was not under selection by the level of herbivore damage ($F = 1.5$, $P = 0.21$), but was under strong selection by plant density (Fig. 5B). In the low plant density, the model selected for a light skew in the distribution of defence towards young leaves, indicated by a peak in the frequency distribution around 0.4 (Fig. 5B, green). An increase in plant density that affected competition for both light and nitrogen selected for a stronger skew in the distribution of defence towards young leaves (Fig. 5B, yellow). However, the absence of a distinct peak in the frequency distribution suggests that this treatment combination either exerted weak selection pressure or selected for two different optimal trait values. An increase in plant density that affected only competition for light selected for a defence distribution that was heavily skewed towards young leaves, indicated by a clear peak in the frequency distribution below 0.1 (Fig. 5B, blue). However, these pants no longer invested in defence (see Fig. 4), which leads us to conclude that this strong skew in the distribution of defence co-evolved with a decrease in the allocation of biomass to defence to allocate an increasingly limited pool of defensive compounds to the youngest leaves.

3.4 Distribution of nitrogen

The distribution of nitrogen in the canopy was not affected by herbivore damage, showing the same pattern with no herbivore damage (Fig. 5C) as with high herbivore damage (Fig. 5D). When plants experience weak competition for both light and nitrogen, the model selected for a light skew in the distribution of nitrogen towards young leaves (indicated by a peak in the frequency distribution between 0.3 and 0.5, Fig. 5C and D, green). An increase in the competition for light, but not for nitrogen, exerted a stronger selection pressure on the nitrogen distribution (indicated by a higher and narrower peak in the frequency distribution), selecting for a distribution skewed towards young leaves (indicated by a peak in the frequency distribution around 0.35, Fig. 5C and D, blue). An increase in the level of competition for both light and nitrogen selected for a further skew in the distribution of nitrogen towards young leaves (indicated by a peak in the frequency distribution around 0.125, Fig. 5C and D, yellow).

4. DISCUSSION

4.1 Biomass allocation patterns

Principal ecological theories postulate that resource limitation is expected to increase biomass allocation towards plant parts that acquire that resource (Thornley 1972; Bloom *et al.* 1985; Tilman 1988), and that plants in nutrient poor environments are expected to express higher levels of defence due to the reduced capacity for regrowth in these environments (Coley *et al.* 1985; Cipollini *et al.* 2014). These theories are widely supported by empirical studies, exemplified by extensive meta-analyses showing that light and nutrient availability are the predominant determinants of biomass allocation patterns (Poorter *et al.* 2012), that plant defences are more beneficial to plant performance in nutrient poor environments (Koricheva 2002) and that plants in nutrient poor environments express higher levels of defence (Endara and Coley 2011). Our results are in line with the predictions made by these ecological theories, showing that from the evolutionary FSP model emerge the functional equilibria related to resource availability and resource driven trade-offs. Another principal ecological concept that emerged from the model was the inherent asymmetry of height-driven competition for light (Weiner 1990), which makes it the quintessential example of a tragedy of the commons (Falster and Westoby 2003; McNickle and Dybzinski 2013). This tragedy emerged in the model results, showing an increased investment in stem growth under strong competition for light.

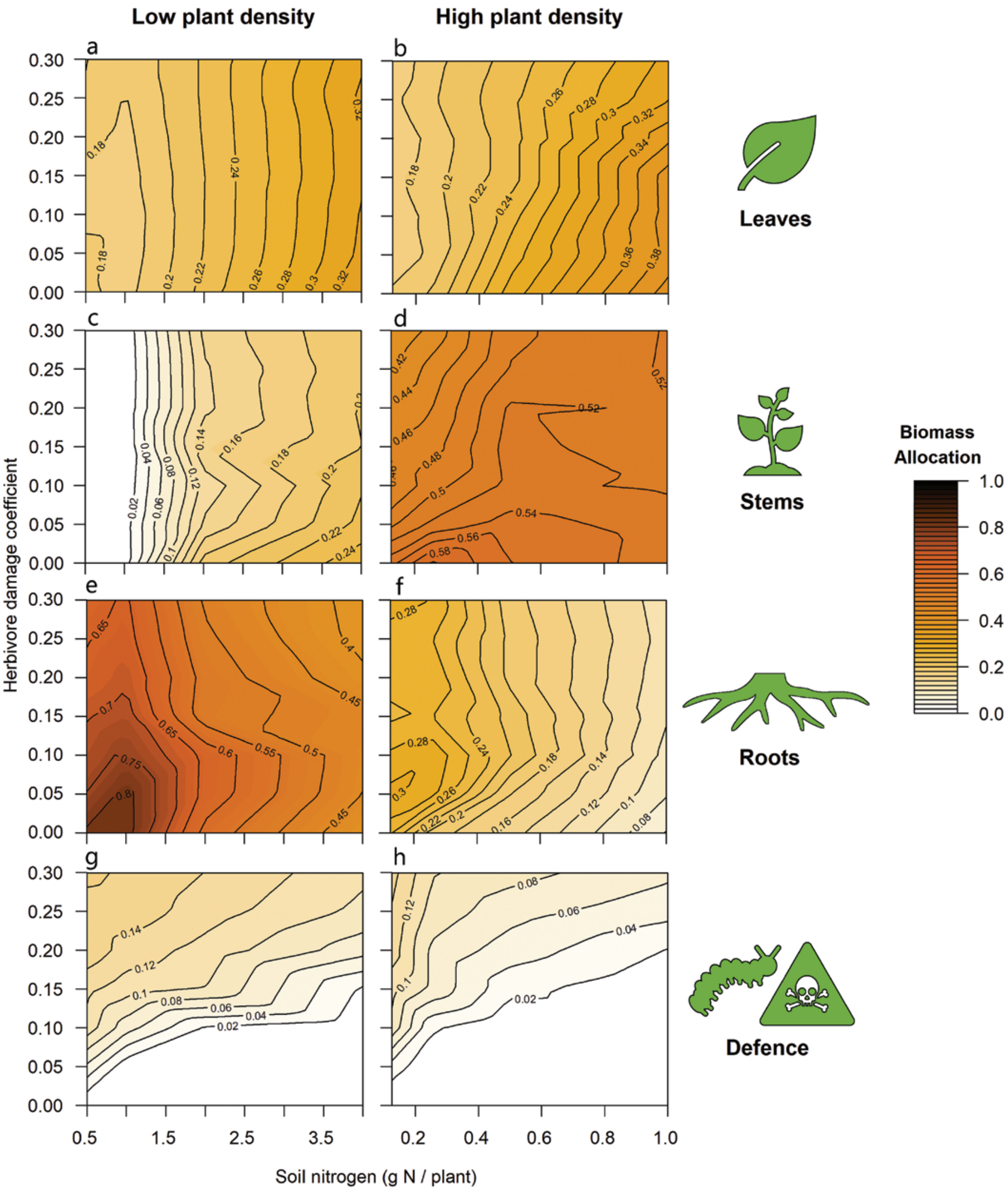

Figure 3. Biomass allocation as a function of soil nitrogen, herbivore damage and plant density. Smoothed allocation parameter landscapes as a function of soil nitrogen content (*x*-axis, g N per plant), herbivore damage (*y*-axis, *h* in eq. S15), and plant density (low: 1 plant per m^2; high: 16 plants per m^2). These biomass allocation traits are the result of 75 generations of selection and represent the partitioning of biomass to leaves (A, B), stems (C, D), roots (E, F) and defence (G, H). White areas represent a biomass allocation of zero, and black areas represent a biomass allocation of one. Note that the values of these four biomass allocation parameters add up to one.

4.2 The effect of nitrogen availability and plant density on defence

Our results further show that an increase in plant density selected for lower levels of chemical defence expression if plant density only affected competition for light, but not competition for nitrogen. These results are in line with our current understanding of the linkage between plant density and plant defence through R:FR signalling, which mediates a decrease in plant defence expression in high plant densities (Ballaré 2014; Ballaré and Pierik 2017). However, little direct experimental evidence exists to inform us about the effect of competitive interactions between plants on the relationship between nutrients and defence. Research on the R:FR driven trade-off between chemical defence and competitive ability has focussed on above-ground interactions rather than a combined effect of above- and below-ground interactions. However, in natural systems, an increase in plant density can be expected to reduce the nitrogen availability per plant, thereby increasing competition for both light and nitrogen. In this scenario, our results show that an increase in plant density selected for a higher defence investment, which suggests that R:FR mediation of defence might only be beneficial to plant fitness under high nitrogen conditions, but not when plants strongly compete for nitrogen. This leads us to hypothesize that the linkage between R:FR and defence might be weaker in low nitrogen environments. While the effect of nitrogen on the R:FR mediation of defence has yet to be investigated experimentally, we do know of nitrogen affecting other R:FR responses. The impact of nitrogen on the R:FR mediation of tillering has been shown in rice (Zhong *et al.* 2002) and wheat (Sparkes *et al.* 2006), where low nitrogen availability increased the sensitivity of tiller death to R:FR. This shows that the availability of, and competition for nitrogen can play an important role in determining the adaptive value of light responses in a competitive environment, and we advocate that this needs to be more clearly addressed in research on phenotypic plasticity in relation to competition and defence.

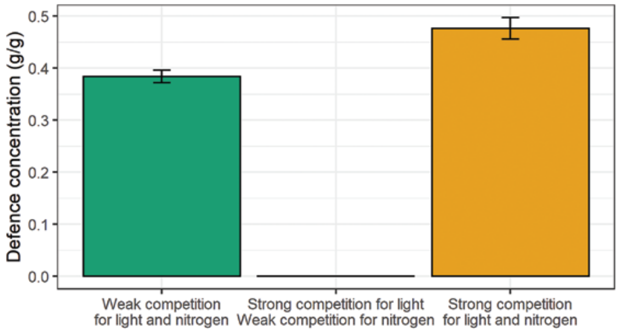

Figure 4. The effect of competition for resources on leaf defence investment. Average leaf defence investment (grams of defence/grams of leaf mass) after 75 generations of selection by heavy herbivore damage ($h = 0.3$ in eq. S15) under weak competition for both light and nitrogen (1 plant per m^2 and 2 g N per plant, green), strong competition for light and weak competition for nitrogen (16 plants per m^2 and 2 g N per plant, blue) or strong competition for both light and nitrogen (16 plants per m^2 and 0.125 g N per plant, yellow).

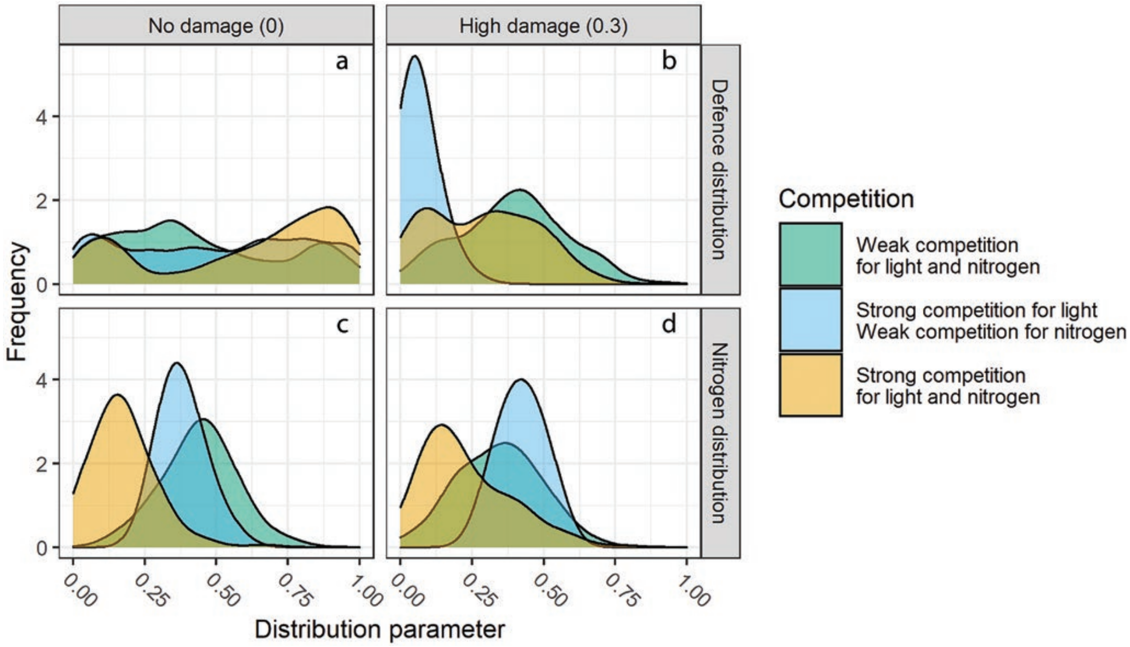

Figure 5. The effect of competition for resources and herbivory on the distribution of nitrogen and defence. Frequency of nitrogen and defence distributions after 75 generations of selection by no herbivore damage (A, C; $h = 0$ in eq. S15) or heavy herbivore damage (B, D; $h = 0.3$ in eq. S15) under weak competition for both light and nitrogen (1 plant per m^2 and 2 g N per plant, green), strong competition for light and weak competition for nitrogen (16 plants per m^2 and 2 g N per plant, blue) or strong competition for both light and nitrogen (16 plants per m^2 and 0.125 g N per plant, yellow). The *y*-axis shows the frequency that a given distribution parameter value (*x*-axis) occurred. A distribution parameter value below 0.5 represents an increased allocation of nitrogen/defence towards top leaves and values above 0.5 the opposite.

4.3 Distribution of defence and nitrogen

A second hypothesized benefit of the light mediation of plant defence is the optimization of defence distribution in the canopy to protect the most valuable plant parts in terms of current resource allocation and future resource acquisition (Ballaré 2014). Because the model simulates a plant architecture that grows vertically from an apical meristem, the youngest leaves are generally also the leaves that are most favourably positioned relative to the light gradient. This led the model to select for a distribution of nitrogen that follows the light gradient, allocating more nitrogen towards young leaves in all treatment combinations. This selection pressure was stronger in denser canopies, indicated by taller and narrower peaks in the frequency distributions at high plant densities and low levels of herbivore damage. These observations are in line with our understanding of the optimal distribution of nitrogen in the canopy, which is predicted and observed to favour leaves that capture more light (Hirose and Werger 1987; Hirose *et al.* 1987; Hirose 2005; Hikosaka *et al.* 2016), which is more pronounced in dense canopies (Anten *et al.* 1995). The distribution of defence generally followed the distribution of nitrogen, favouring defence allocation to young leaves. This preferential allocation of defence to young leaves was especially apparent in plants that invested little biomass in defence, where young leaves were more defended than the nitrogen distribution would suggest. At higher levels of defence investment, the selection pressure on the distribution of defence was lower than the selection pressure on the distribution of nitrogen, indicated by a broader distribution of values in the frequency distribution (Fig. 5B). This suggests that young leaves are the first and most important leaves to allocate defences to, increasing defence allocation to older leaves as the total defence investment increases.

4.4 Herbivore community dynamics and plant–herbivore interactions

Our model assumes the herbivore damage on a plant to be independent from other plants, while insect herbivores are known to select their host based on chemical defence expression (Schoonhoven *et al.* 2005; Viswanathan *et al.* 2005; Poelman *et al.* 2008). Therefore, plant chemical defence can be seen to function not only to reduce herbivore damage and to distribute it within the plant, but to deflect it to neighbouring plants. This function of defence makes the herbivore damage experienced by a plant dependent on the level of defence expression of its neighbours, and theoretically results in a tragedy of the commons where defence levels exceed their optimal value (McNickle and Dybzinski 2013). Accounting for the dynamics within a herbivore community and how it interacts with the plant community is a logical next step in the analysis of optimal defence (de Vries *et al.* 2017). However, this analysis becomes exceedingly challenging due to the complexity of herbivore communities and specificity of plant–insect interactions (Stam *et al.* 2014), the cross-talk between different systems of defence (Pieterse *et al.* 2012), and the occurrence of keystone herbivores in the insect community that by their presence affect likelihood of colonisation of the plant by other insect herbivores (Poelman and Kessler 2016). Future advancements in the field of insect community ecology might see the development of agent-based models of insect behaviour that can be combined with FSP models of plant growth and development.

4.5 Plant architecture and plant plasticity

The plant phenotype used in this study allowed us to investigate the effect of competition for above- and below-ground resources on the trade-off between their acquisition and protection. A model with a more realistic representation of plant phenotypic plasticity potentially allows for more interaction between plant traits, the emergence of more distinct strategies and potential co-existence of different functional strategies in a single simulated population. Many of assumptions made in our model to increase the model's computational efficiency are related to traits that are known to be highly sensitive to changes in the light environment and nitrogen availability, such as branching (Domagalska and Leyser 2011) or leaf senescence (Lim *et al.* 2007). These morphological responses generally allow for better post-herbivory regrowth potential in low plant densities, potentially reducing the need for direct defences in favour of tolerating herbivore damage, especially in the absence of competition (McNickle and Evans 2018).

In this study, the environmental conditions that drive natural selection in the model were assumed to remain constant both within and over generations. However, plants growing under natural conditions face highly dynamic environmental conditions that change within and over generations. Plants have evolved plastic responses to express the multiple phenotypes in various environments, allowing plants to maximize their fitness over multiple generations (Bradshaw *et al.* 1965; Sultan 2000). FSP modelling has shown that subtle variation in the sensitivity of a plastic response can have profound consequences for plant fitness (Bongers *et al.* 2018) and can therefore be a strong driver of evolution. Future development of our evolutionary FSP model can shed light on the optimal response of one or more plastic traits to an environmental condition that is set to vary within and between generations, such as plant density or herbivore pressure.

4.6 Conclusions

Using simple rules to describe plant growth, competition for above- and below-ground resources, and natural selection, the model presented in this study was able to recreate the functional equilibria predicted by principal ecological theories on the effects of resource availability and resource-driven trade-offs. This emergent nature makes this modelling approach a highly promising tool for future research on plant responses to dynamic and variable environments. The model also showed a three-way interaction between plant competition for light, competition for nitrogen and herbivory that determined the optimal balance between the acquisition and protection of resources. This highlights that the value of investing in the acquisition or the protection of resources is a dynamic problem that is influenced by multiple ecological interactions, trade-offs and tragedies of the commons, and is therefore only relevant within an eco-evolutionary context.

SUPPORTING INFORMATION

The following additional information is available in the online version of this article—

Methods S1. Detailed model description.

Figure S1. Sensitivity of biomass allocation patterns to the number of model time steps.

Figure S2. The change in population average trait values over generations.

Figure S3. Relative distribution weight as a function of relative leaf rank.

Figure S4. Relative herbivore damage as a function of relative leaf rank.

Table S1. Model parameters describing plant architecture and resource acquisition.

SOURCE OF FUNDING

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CONTRIBUTIONS BY THE AUTHORS

J.d.V. designed and coded the model, conducted simulations and analysed the data. J.d.V., J.B.E., E.H.P. and N.P.R.A. interpreted the data and wrote the manuscript.

CONFLICT OF INTEREST

None declared.

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DATA AVAILABILITY

The model code and data generated by the model are publicly available in the dryad repository at https://doi.org/10.5061/dryad.bnzs7h474.

LITERATURE CITED

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