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Identification of trade-offs underlying the primary strategies of plants

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ABSTRACT

Question: What are the key physiological and life-history trade-offs responsible for the evolution of different suites of plant traits (strategies) in different environments?

Experimental methods: Common-garden experiments were performed on physiologically realistic model plants, evolved in contrasting environments, in computer simulations. This allowed the identification of the trade-offs that resulted in different suites of traits (strategies). The environments considered were: resource rich, low disturbance (*competitive*); resource poor, low disturbance (*stressed*); resource rich, high disturbance (*disturbed*); and *stressed* environments containing herbivores (*grazed*).

Results: In disturbed environments, plants increased reproduction at the expense of ability to compete for light and nitrogen. In competitive environments, plants traded off reproductive output and leaf production for vertical growth. In stressed environments, plants traded off vertical growth and reproductive output for nitrogen acquisition, contradicting Grime's (2001) theory that slow-growing, competitively inferior strategies are selected in stressed environments. The contradiction is partly resolved by incorporating herbivores into the stressed environment, which selects for increased investment in defence, at the expense of competitive ability and reproduction.

Conclusion: Our explicit modelling of trade-offs produces rigorous testable explanations of observed associations between suites of traits and environments.

Keywords: evolution, life history, strategy, trade-offs.

INTRODUCTION

One key aim of plant functional ecology is to be able to predict suites of plant traits – often termed strategies or functional types – that occur in different environments (McGill *et al.*, 2006; Whitfield, 2006; Grime *et al.*, 2007). Different strategies evolve in different environments because

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trade-offs prevent the evolution of species that have superior fitness in all environments [so-called Darwinian daemons (Charlesworth, 1994; Sibly, 2002)]. Trade-offs are constraints such that improvement of one advantageous trait is only possible at the expense of another. Although a wide variety of trade-offs has been suggested (Crawley, 1997), some theories propose that just a few trade-offs are of primary importance to the evolution of plant strategies in all environments. If true, this would potentially allow the prediction of functional characteristics of species in natural plant communities from only a few environmental variables. However, contradictions between the different theories have prevented the adoption of a general theory of plant strategy evolution; the most widely publicised being between those of Tilman (Tilman, 1988) and Grime (Grime, 2001). For example, Tilman's theory predicts that superior competitiveness for the most limiting resource is the primary selective force in all environments but that different competitive strategies are selected in different environments, as a result of trait trade-offs. Grime's theory, however, predicts that superior competitiveness for a limiting resource only becomes advantageous in low-disturbance, high-resource environments (for recent discussion on the controversy, see Craine, 2005, 2007; Grime, 2007; Tilman, 2007). A resolution of their contradictory predictions has so far proved elusive (Craine, 2005, 2007; Grime, 2007; Tilman, 2007). What is needed is a rigorous methodology with which to state and analyse claims about adaptations and trade-offs, so that controversies about definitions can be avoided. Here we describe the use of such a methodology to pinpoint the trade-offs behind the evolution of plant strategies in different environments.

In Grime's CSR (Competitor, Stress tolerator, Ruderal) theory, the availability of resources and the frequency of disturbance are two key environmental variables that influence the evolution of all plants and can be used to predict strategies (Grime, 2001). At the extreme ends of the environmental spectrum exist primary strategies: *competitors* adapted to productive environments, rich in resources and without much disturbance (hereafter referred to as *competitive environments*); *stress tolerators* that are adapted to *stressed environments*, which are chronically unproductive habitats with low resource availability but also little disturbance; and *ruderals* adapted to *disturbed environments* that offer plenty of resources but are frequently disturbed (Grime, 2001). Although no analytical theory exists to explain why different strategies evolve in these different environments, Mustard *et al.* (2003) described computer simulations in which plant strategies, resembling those described by Grime, had evolved from a pool of common ancestors. These simulations used physiologically realistic model plants. The results did not allow identification of characters involved in trade-offs, because plants' strategies were only characterized in the environment in which they had evolved. Thus environmental and genetic differences between strategies were confounded. In this study, we solve this problem by comparing strategies in each of the environments of interest, using common-garden experiments.

We adopt the same terminology to identify strategies and environments as Grime. However, because of controversy as to whether herbivores are an essential component of stressed environments (Craine, 2005), we also analyse a fourth strategy, *defended plants* adapted to *grazed environments*, which are stressed environments containing herbivores. Our approach is to perform common-garden experiments with plants that have evolved in different environments. The common-garden methodology allows rigorous identification of the trade-offs responsible for the evolutionary differentiation of the plant strategies.

METHODS

Initial evolution of the primary strategies

Each model plant incorporated realistic physiological mechanisms, with 29 genetic parameters controlling its growth in response to its environment and its life history. The model is almost identical to that used by Mustard *et al.* (2003) and a general summary is given in Appendix 1. Any differences between the model of Mustard *et al.* (2003) and that used in this study are detailed below. Twenty independent populations were evolved for 2 million iterations of simulation in each of the competitive (high nitrogen/low disturbance), disturbed (high nitrogen/high disturbance), stressed (low nitrogen/low disturbance), and grazed (low nitrogen/low disturbance with herbivory) environments, using the method of Mustard *et al.* (2003). Table A1 in Appendix 1 shows the significant differences between the genetic parameters of these primary strategies.

Grazed environments

Herbivory was not incorporated into the model of Mustard *et al.* (2003) and so we include details here. Our specific interest is in how herbivory influences plant evolution in the stressed environment. It has long been theorized that herbivory is most important as a selective factor in nutrient-deficient environments (Hairston *et al.*, 1960; Fretwell, 1977; Oksanen *et al.*, 1981; Coley *et al.*, 1985). Biomass lost in these environments would take an especially long time to replace since resources are so scarce, and may not be replaced at all. Therefore, natural selection has resulted in plants in these environments that invest resources in defence at the expense of productivity (Buckland and Grime, 2000; Burt-Smith *et al.*, 2003). In contrast, in the more productive environments, there is increased selection pressure for above- and below-ground growth at the cost of defence (Fretwell, 1977; Oksanen *et al.*, 1981; Fraser and Grime, 1998; Grime, 2001). Why don't herbivores multiply in these environments to have a larger impact on plant survival? There is empirical and theoretical evidence that this is because more productive environments can support multiple trophic levels, which allows top-down control over herbivore abundance (e.g. by parasitoids and carnivores), preventing herbivores from having a major impact on plant fitness (Fretwell, 1977; Oksanen *et al.*, 1981; Fraser and Grime, 1998; Buckland and Grime, 2000).

Herbivory was simulated by removing a proportion of the above-ground biomass. The frequency of grazing per plant was a random event with a mean of one event per plant per 240 iterations. The proportion removed per grazing event was randomly selected between a maximum proportion and zero. The maximum proportion removed was a linear function of the proportion of a plant's above-ground biomass that it allocated to spines (a genetic trait), such that a plant with 100% spines would suffer 0% herbivory and a plant with 0% spines could suffer up to 100% herbivory. These modifications therefore impose a trade-off between above-ground photosynthetic biomass and defence. At the end of every time step, plant biomass removed by the herbivore was returned to a randomly chosen cell in the environment.

Experimental design for common-garden experiments

Our basic technique was a common-garden experiment, of a design used to identify physiological constraints in real plant populations (e.g. Stastny *et al.*, 2004; Langerhans *et al.*, 2005). In these

experiments, we assessed the performance of each strategy in the environment in which it evolved, and in each of the other three environments. We refer to a strategy in its own environment as 'resident', elsewhere as 'invader'. These experiments allowed us to investigate whether and why the strategies that evolved by natural selection in their own environment are more successful than alternatives. We simulated invasions by replacing newly germinated resident seedlings with invader seedlings with a probability of 0.05. This was continued until 100 invader seedlings had been introduced and subsequently died.

In each experiment, a resident population started exactly as it had finished after initial evolution, but with mutation disabled. For each of the 20 resident–invader replicates we randomly chose the invader from a different source population, but kept the same invader genotype within each invasion simulation, giving truly independent replicates. This gave 240 simulations in total (4 strategies × 3 invasion scenarios × 20 replicates).

For the simulations in which competitors invaded stress tolerators, the extremely long lifespan of the competitors meant that in some simulations, over time, the competitors could replace the stress tolerators by just persisting in the array for a long time. This result is an artefact of the parameter setting the maximum plant lifespan (also present in Mustard *et al.*, 2003), which continually increased through time in the original simulations but increased more for the competitors than the stress tolerators because of the higher reproductive rate. To address this artefact we set the maximum lifespan of all plants in these simulations equal to the maximum lifespan of the residents or invaders (whichever was larger). We discuss further the use of the 'maximum plant lifespan' parameter in the Discussion.

We recorded the average values of the ten phenotypic traits (listed in Table A2 in Appendix 2) separately for residents and invaders, for the last data output of each simulation. We also recorded the same phenotypic traits for each individual plant that died or reproduced, as well as the cause of death in the case of a mortality event, and the number of seeds produced in the case of a fecundity event. The genetic traits of residents and invaders were compared using analysis of variance (ANOVA) on normally distributed or ranked data as appropriate. For phenotypic traits we used a two-sample *t*-test or a Mann-Whitney *U*-test as appropriate.

RESULTS OF COMMON-GARDEN EXPERIMENTS

The existence of trade-offs predicts that organisms selected in one environment will lose traits that are only advantageous elsewhere. Therefore, in their home environment, residents should outcompete invaders (Sibly and Antonovics, 1992). This prediction was supported, since invaders became extinct in all but four of the 240 invasion simulations.

The fitness of a genetic strategy depends on the birth and death rates of the individuals that follow it, fitness being measured as population growth rate (Charlesworth, 1994; Sibly and Curnow, 1993), which is given, approximately, by birth rate minus death rate (Brown and Sibly, 2006). Birth rate, death rate, and fitness are plotted for each strategy in each environment in Fig. 1 and, as predicted, the resident strategies were the fittest in each environment (the results of these statistical comparisons are reported in Table A2 in Appendix 2). However, the components of fitness (i.e. birth and death rates) contrasted between strategies and environments.

The most straightforward case to analyse is that of the disturbed environment, shown in Fig. 1a. Here all four strategies had similar death rates as a result of frequent environmental disturbance, but the ruderal had the highest fitness because it achieved a higher birth rate

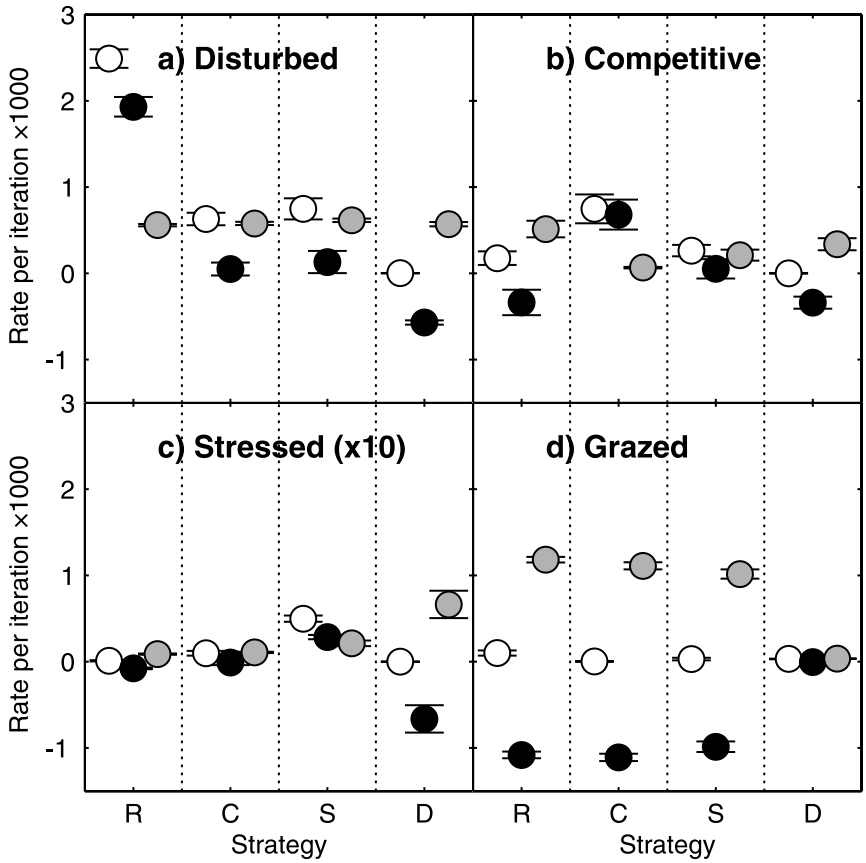

Fig. 1. Birth rates (white), death rates (grey), and fitnesses (black) of each strategy (R = ruderal, C = competitor, S = stress tolerator, D = defended) in each environment. Rates are given per 1000 iterations. Fitness is birth rate minus death rate. Birth rate was estimated as the mean average lifetime reproductive output per individual per iteration. Death rate was estimated as the slope of the log-survivorship curve in Fig. 2. In panel (c), the data have been multiplied by 10 before plotting to aid clarity. Bars indicate standard errors. Statistical comparisons are reported in Table A2 in Appendix 2.

than the other strategies. Clearly, the ruderals evolved characters that increased birth rate, but did not evolve characters that decreased death rate, in the disturbed environment.

Death rate in relation to age is conventionally displayed in log survivorship plots, as shown in Fig. 2. Death rate at any age is given by the slope of the relationship. All four strategies in the disturbed environment show linear relationships between log survivorship and age (Fig. 2a–d), implying that death rate does not change with age. This is a natural consequence of our decision to model the frequency of disturbance events as a Poisson process (identically to Mustard *et al.*, 2003). Birth rates in relation to age are shown in Fig. 3. Birth rates were significantly positively correlated with plant age in the disturbed environment for all but the defended strategy ($P < 0.05$; Fig. 3a–d). Reproduction in the disturbed environment ends at an early age when disturbance events kill the plants, so we would expect natural selection to maximize resource allocation to early reproduction. This prediction is confirmed by examination of the phenotypic characteristics of the three

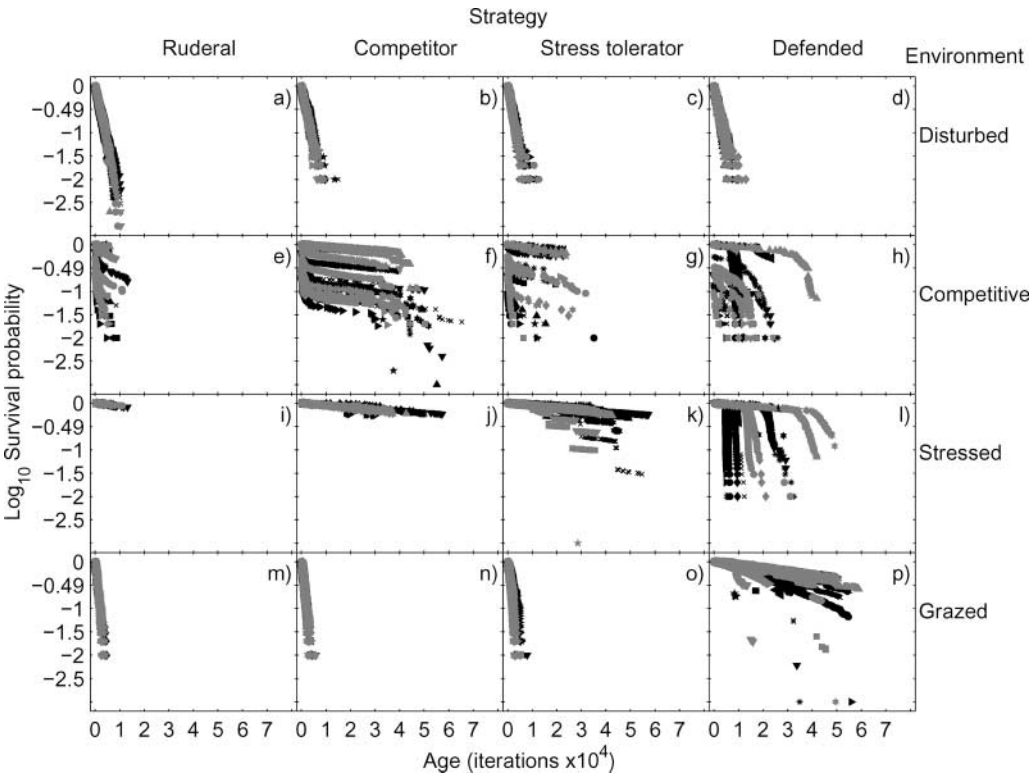

Fig. 2. Log_{10} survivorship vs. age (iterations) relationships for each strategy in each environment. Age is measured in iterations since germination from seed. Survivorship is the proportion of plants surviving to each age. Each symbol corresponds to data from one replicate, thus points from different replicates frequently overlay each other in each panel.

strategies. Figure 4 shows that the period between reproductive events was shorter in the ruderal strategy ($P < 0.05$). This allowed the ruderals to produce more seeds than the invaders within their lifespan ($P < 0.05$), and therefore to leave more offspring before being destroyed by a disturbance event.

In the competitive environment (Fig. 1b), the competitor strategy obtained its advantage largely through increased birth rates ($P < 0.05$), but competitor death rates also were lower than those of invaders ($P < 0.05$). The competitor survivorship curves are non-linear, with initially high death rates for young plants, low death rates for most of the plants' lifespan, and a final downturn near the end of life when plants reached their maximum lifespans or died due to insufficient nitrogen (Fig. 2f) [plants died if the ratio of nitrogen to carbon in their tissue became less than 0.005, as in Mustard *et al.* (2003)]. The death rates of invaders were higher than those of competitors in all stages of their lives ($P < 0.05$; Fig. 2e–h). Further investigation revealed that the high death rates of young plants were largely due to the young being starved of carbon through lack of light. Competitors survived this initial period by allocating resources to growth instead of reproduction, and so on average grew larger than invaders in terms of height and leaf area ($P < 0.05$; Fig. 4b–d). Invaders were thereby outcompeted for light, and so had higher death rates throughout their lives.

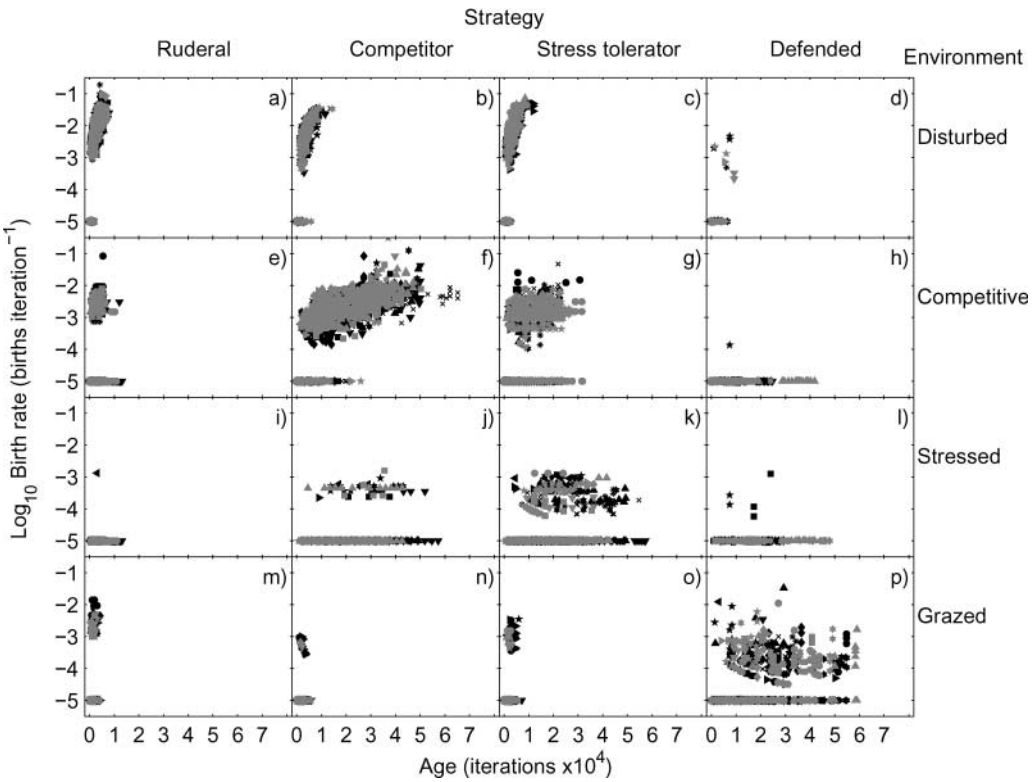

Fig. 3. Log_{10} birth rate vs. age (iterations) relationships for each strategy in each environment. Birth rate is the number of seeds produced at a reproductive event divided by the length of time since the last reproductive event, or by age if this is first reproduction. Conventions as in Fig. 2. Birth rates of zero are shown as $\log_{10}$ birth rate = −5.

Competitors also invested more biomass below ground as roots ($P < 0.05$; Fig. 4e) to increase nitrogen uptake in the face of local nitrogen depletion by themselves and their neighbours. Because competitors allocated resources to growth instead of reproduction, their allocation to seeds was depleted ($P < 0.05$; Fig. 4b). This is a direct result of the resource allocation trade-off: competitors traded-off reproduction for increased growth. As competitors grew larger, the number of seeds produced per reproductive event increased, resulting in a significant positive correlation between birth rate and plant age ($P < 0.05$; Fig. 3f).

In the stressed environment, stress tolerators experienced higher death rates than the ruderals and competitors ($P < 0.05$ and $P = 0.058$, respectively; Fig. 1c), but this was more than compensated by their higher birth rates ($P < 0.05$). To understand the underlying mechanism, it is helpful first to look at the survivorship curves of ruderals and competitors (Fig. 2i, j). Their death rates were constant with age, and non-reproductive mortality proved to be predominantly due to disturbance events. For stress tolerators, however, periods of constant death rate were interspersed with brief periods of high death rate associated with reproduction, producing a series of downward steps in their survivorship curves (Fig. 2k). Further investigation revealed that these periods of high mortality were caused by seed

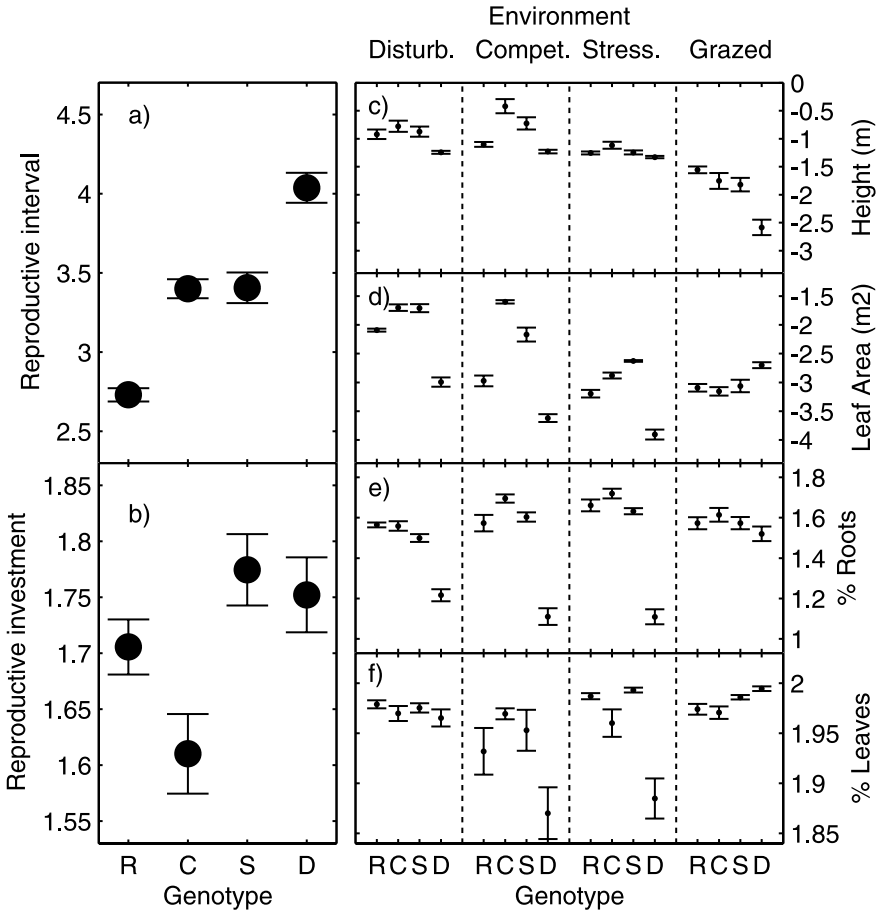

Fig. 4. Genetic (a, b) and phenotypic (c–f) traits of the four evolved plant strategies (R = ruderal, C = competitor, S = stress tolerator, D = defended). All traits are $\log_{10}$-transformed means, interval bars are standard errors. (a) Interval (iterations) between reproductive events; (b) percentage of above-ground resources that a plant allocates to seeds per reproductive event; (c) height; (d) leaf area; (e) root weight as % plant weight; (f) leaf weight as % (leaf + stem weight). Note that, in contrast to (c–f), the parameters in (a) and (b) are 100% heritable, so there is no difference in performance between environments. Another six characters are shown in Fig. A1 in Appendix 2. Statistical comparisons are reported in Table A2 in Appendix 2.

production, which rendered some plants physiologically unviable. Between reproductive attempts, the stress tolerators invested predominantly in resource acquisition, having a larger leaf area and a larger proportion of their above-ground biomass invested in leaves ($P < 0.05$; Fig. 4d–f). They also waited longer between reproductive events than the ruderals, and when they did reproduce they allocated a relatively large proportion of their resources to seed production (Fig. 4a, b). We conclude that stress tolerators took extra risks to reproduce, but that this was an advantageous trade-off in the stressed environment, since, in contrast, the competitors only achieved very limited reproduction, and the ruderal and defended strategies almost none (Fig. 3i–l).

In the grazed environment, the residents' key advantage was a lower death rate than invaders ($P < 0.05$; Fig. 1d). This was achieved by investing in spines, which represented a significant proportion of their above-ground biomass (55%, standard error = 1.2%). Since the invaders were not defended, they were heavily grazed and so lived for only a short period (Fig. 2m–p). The cost to defended plants of their investment in spines was that their birth rates were generally lower than those of invaders (Fig. 1d, Fig. 3m–p). To achieve any reproduction at all, defended plants waited significantly longer between reproductive events (Fig. 4a), and when they did reproduce they invested more in reproduction than did competitors or ruderals (Fig. 4b). Furthermore, since plants were generally small and competition for light was less important, most above-ground biomass was invested in leaves rather than stems (Fig. 4f).

DISCUSSION

Mustard *et al.* (2003) demonstrated an association between environments, characterized by nitrogen availability and disturbance frequency, and the plant strategies that evolve within them, in simulation models. Here we use common-garden experiments to reveal why these strategies evolved. This methodology allows us to make rigorous links between underlying trade-offs and evolved functional traits in each environment. By being completely specific about the physiological model and the archetypal environments analysed, no doubt is left as to whether particular traits are adaptive in specified environments, and whether or not particular traits are involved in trade-offs.

In the disturbed environment, the best strategy is: live fast, die young. This is a recognized characteristic of species exploiting highly disturbed environments. By allocating a large proportion of their resources to reproduction, ruderals paid costs in other environments, being too short in the competitive environment and accumulating insufficient resources for seed production in the stressed environment. In the competitive environment, the key physiological trade-off is between allocating resources to somatic growth and allocating them to reproduction. By allocating resources to growth instead of reproduction, competitors grew taller than invaders and outcompeted them for resources. In other environments, competitors were at a disadvantage because they allocated resources to growth that would more profitably have been allocated to reproduction. Contrastingly, in the stressed environment, it was nitrogen that was limiting and the problem was to acquire resources to be able to reproduce at all. Only the stress tolerators acquired sufficient resources to reproduce. They did this by investing in resource acquisition, having a larger leaf area and a larger ratio of leaf to shoot biomass, and waiting longer between reproductive events, and when they did reproduce they allocated more resources to seed production. The key adaptation of the stress tolerators was that they were better at acquiring the limiting resource from their environment.

Superior competitiveness for a limiting resource is thus characteristic of both competitor and stress-tolerator strategies, as predicted by Tilman (1982, 1988), with investment in height over leaf biomass being the key physiological distinction between the two strategies. This appears to rule out the association of slow growing, competitively inferior strategies with nutrient stressed environments suggested by Grime and others (Grime *et al.*, 2007). The contradiction is resolved by considering the defended strategy. Survival in the grazed environment, identical to the stressed environment other than the presence of herbivores, requires investment in defence, at the expense of somatic growth and reproduction.

A significant investment in plant defences against herbivory is characteristic of stress tolerators in nature (Coley *et al.*, 1985; Grime, 2001). Higher growth rates in plants tend to be positively associated with palatability (Coley *et al.*, 1985; Grime, 2001) and theory predicts that well-defended plants have sub-optimal growth rates because they invest more biomass in non-photosynthetic defensive compounds (Coley *et al.*, 1985; Grime, 2001). Our results support these findings. Investment in non-photosynthetic spines may appear disadvantageous in the short term because biomass production is reduced, but is adaptive overall because defended plants survive longer.

Our analysis provides a rigorous explanation of why plants from environments differing in terms of resource availability and disturbance frequency may have evolved to resemble Grime's CSR pattern of strategy variation, and points towards a resolution of the controversy about the importance of competition for limiting resources. Our evolved plants do not match all features of Grime's CSR pattern, and there are numerous traits, trade-offs, and environments that are not incorporated in the existing model. A mutable 'maximum lifespan parameter' was incorporated in this model (and that of Mustard *et al.*, 2003) to allow sufficient evolution to occur in the scenarios with low disturbance rates. Disabling this parameter meant that, in low disturbance environments, some plants would live for a long time without sufficient turnover of generations to allow the evolution of distinct strategies. Relaxing this assumption and incorporating more realistic mortality scenarios (such as through wind-throw events) is a natural area for future study. It also is likely that the simplistic way in which we have modelled the below- and above-ground environment will affect plants' resource foraging, and so shape plant trait evolution. In particular, our simplified representation of roots and leaves does not allow the realistic development of extensive resource heterogeneity in either environment (for studies of plant adaptations to above- and below-ground resource heterogeneity, see Drew, 1975; Pearcy *et al.*, 1985; Grime *et al.*, 1986; Campbell and Grime, 1989; Jackson and Caldwell, 1989; Rincon and Grime, 1989; Campbell *et al.*, 1991; Robinson and Van Vuuren, 1998; Grime, 2001). This may be why our competitors did not evolve highly dynamic foraging strategies for above- and below-ground resources as predicted by plant strategy theories (Grime, 2001), and by theoretical models that take into account the spatial location of different plant parts and resource depletion zones (e.g. Colasanti *et al.*, 2001). Allocation to defence and the simulation of herbivory in the grazed environments (admittedly in a very simplistic way) were the only modifications to the model of Mustard *et al.* (2003) that we explored. Given the major effects of these modifications, future studies should explore in more detail the effects of incorporating selection pressures of herbivory in a range of environments, and of simulating more realistic plant–herbivore interactions

We believe we have captured here the essential differences between the primary strategies in our model and revealed the trade-offs that ultimately are responsible for their evolution (Grime, 2006; McGill *et al.*, 2006; Grime *et al.*, 2007). We hope this will lead towards a new paradigm as broad as those originally proposed by Grime and Tilman, as called for by Craine (2007).

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APPENDIX 1: MODEL DESCRIPTION AND STRATEGY EVOLUTION

The plant model is described in full in Mustard *et al.* (2003), of which the following is a summary. The model is an iterative, spatially explicit, individual-based simulation model of plant evolution, with iteration steps corresponding to one hour in real time. It is best thought of as two parts, the environment in which the plants grow and interact, and the plants themselves. The model was developed to study the interdependent evolution of multiple biologically relevant traits in different environments. We therefore incorporated abstract representations of several functional traits of plants while making other simplifying assumptions about the environment to avoid the model becoming too complicated for simulation and analysis. As a result, we do not expect every trait to match reality. Instead, we focus on understanding why the different strategies evolved, whether there are any similarities with real plants, and thus whether any insights can be made into the evolution of real plants from how our model plants evolved.

Environment

The environment is modelled as a 10×10 square cell toroidal array, in which only one germinated plant can occupy a cell at a time (although a cell can be empty). Above-canopy

light is assumed to be continuous through time and uniform. Total nitrogen in the environment is also constant. Nitrogen is modelled in two forms: organic nitrogen derived from dead plant tissue and inorganic nitrogen derived from decomposed organic nitrogen. These are assumed to be uniformly distributed within each cell. At the beginning of each simulation, the designated total amount of nitrogen is uniformly distributed among the 100 cells in the environment as inorganic nitrogen. Organic nitrogen builds up in the cells as plant tissue or whole plants die and decompose into inorganic nitrogen as a function of the carbon : nitrogen ratio. A slow rate of inorganic nitrogen diffusion between adjacent cells is also modelled. Competitive and disturbed environments were high in nitrogen (2 kg $N \cdot m^{-3}$); the other environments were low in nitrogen (0.1 kg $N \cdot m^{-3}$).

A disturbance event is assumed to kill immediately all of the plants in the cells it affects. To simulate a disturbance event, a cell in the array is randomly chosen to be the locus of the disturbance and a randomly chosen area (between 1 and 100 cells) is selected around that cell, within which all of the plants are killed. The probability of a disturbance event per iteration in the disturbed environment was 0.005 and in the other environments was 0.0001.

Plant parameters

Twenty-nine genetic parameters (30 for the defended strategy) control the allocation of carbon and nitrogen among the different plant parts, the maximum plant lifespan, and some aspects of the plant's investment in seed production (for a complete description, see Table 1 and Figures 1 and 2 of Mustard *et al.*, 2003). Phenotypic characters depended not only on genotype but also on environment. Note that none of the trade-offs identified in our results are explicitly programmed into the model; rather, the trade-offs are emergent features of the model that we were only able to identify by the experimentation described in the main text. Furthermore, a mutable maximum plant lifespan parameter was assumed because of time restrictions rather than because of biological reality (for an example, see Harper, 1977). Future studies could investigate the effect of relaxing this assumption and only allowing mortality for physiological reasons.

Plant structure

Each model plant has a stem, leaves, and nine roots. Defended plants also have aboveground defence. Leaves are assumed to be evenly distributed within a cylinder, with the height set by the stem height and the horizontal projection of the leaves on the ground determined by a simple scaling relationship with plant weight. This horizontal projection is restricted to the outer boundary of the neighbouring cells. Similarly, the plant roots are in different cells in the local neighbourhood, with one root being in the plant's own cell and one in each of the eight neighbouring cells.

Carbon and nitrogen uptake

Plants fix carbon as a function of the incident light, their leaf area, and their leaf nitrogen content. Incident light is an exponential decay function of the overlapping leaf area from neighbouring plants. Fixed carbon is then allocated among the different plant organs according to a series of allocation steps. For the defended plants, a genetic parameter

controls the proportion of carbon that is already allocated above ground that subsequently is allocated to above-ground defence, as opposed to leaves and stems. Nitrogen uptake by each root is a function of the root biomass, the inorganic nitrogen content, and a nitrogen uptake scalar that is regulated by the plant nitrogen content. Nitrogen not allocated to storage is assumed to be homogeneously distributed throughout the plant such that all plant tissues have the same ratio of carbon to nitrogen.

Plant death

The mortality rates of plant parts are modelled as linear functions of the plant nitrogen content. Whole plants die if their nitrogen concentration goes unrealistically low, their respiratory costs exceed their carbon gains through photosynthesis, they reach a maximum 'lifespan' parameter, or they experience a disturbance event. The total biomass of the dead plant is added to the organic matter pool in the cell of the plant locus.

Seeds

Seeds are asexually produced at constant intervals in a plant's lifetime and at plant death (except when a plant dies due to disturbance). Seed size is assumed to be constant. The number of seeds produced per reproductive event is a function of the above-ground nitrogen content of the plant and a parameter controlling the proportion of those resources it allocates to seed production. Seeds inherit the parameters of their parents. Seeds are randomly dispersed after production. All of the seeds that land in a cell since the last germination event are recorded. Seeds in this seed pool die at a low mortality rate. When a cell becomes empty, one seed – out of all of the seeds in the cell – is randomly selected to germinate, and the rest are assumed to die.

Table A1. Significant differences ($P < 0.05$) between the genetic traits of the three primary strategies*

Genetic traits	Competitor	Ruderal	Stress tolerator	Defended
Proportion above-ground nitrogen allocated to seeds	Low	Medium	High	High
Interval between seed production events	Medium	Low	Medium	High
Maximum lifespan (iterations)	High	Low	Medium	High
Potential variation in above-ground : below-ground biomass	High	Low	High	Low
Root foraging ability	Low	High	High	Medium
Potential variation in leaf area : leaf weight	High	Low	High	Low
Internal plant [N] at which roots stop absorbing nitrogen	High	Low	High	High
Potential variation in leaf : stem biomass	Medium	High	Medium	Low

* Determined using ANOVA with $df_1 = 3$, $df_2 = 19$. Some genetically determined traits involved more than one parameter (see Mustard *et al.*, 2003, for further detail). We have omitted the actual parameter values for brevity and instead state 'High' or 'Low' if a strategy has a mean parameter value that is significantly larger or smaller, respectively, than one or more of the others. Traits denoted 'Medium' have parameter values that are significantly different, and between, the other parameter values or not significantly different from either 'High' or 'Low' parameter values.

APPENDIX 2: ADDITIONAL RESULTS

Four of the phenotypic characters are shown for each strategy in each environment in Fig. 4. The remaining six phenotypic characters are shown in Fig. A1. The results of the statistical analysis of the differences between invaders and residents in each environment are summarized in Table A2.

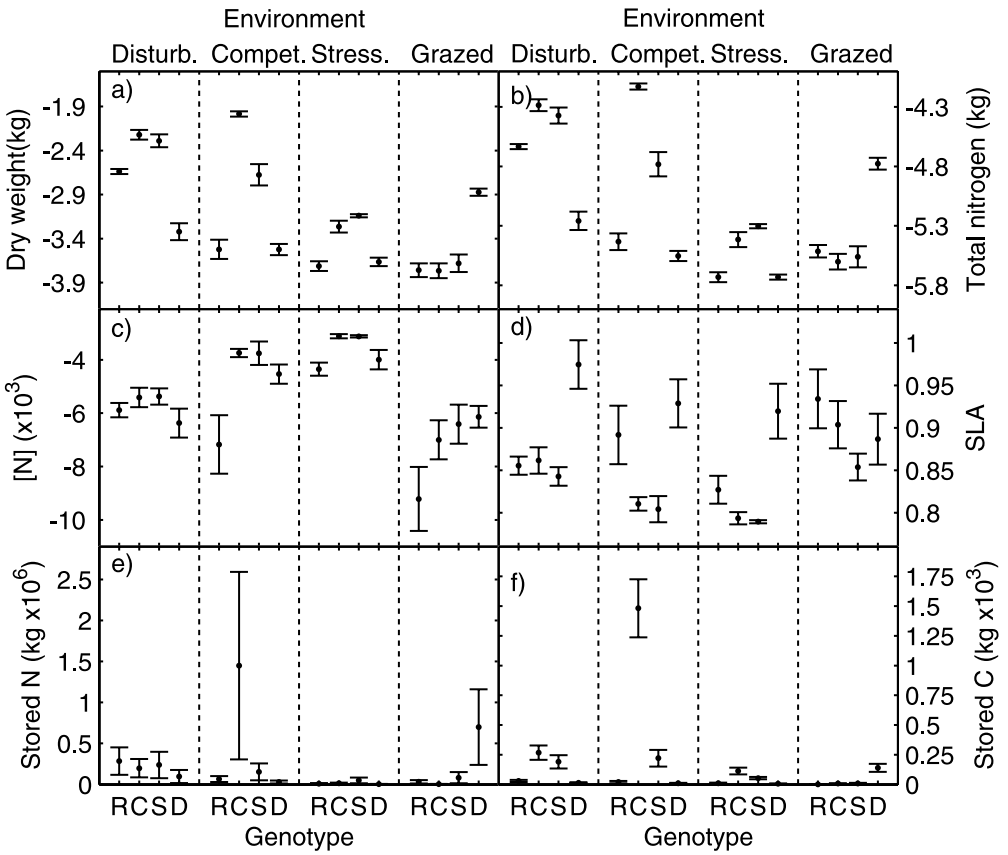

Fig. A1. Log mean and standard errors (interval bars) of the phenotypic characters of each invader and resident strategy in each environment. Four further characters are shown in Fig. 4. [N] is plant nitrogen concentration (kg N : kg C), SLA is the ratio of leaf area to leaf weight.

Table A2. Statistical comparisons of the phenotypic characters shown in Fig. 4 and Fig. A1

Environment:	Disturbed			Competitive			Stressed			Grazed		
Invader strategy:	C	S	D	R	S	D	R	C	D	R	C	S
Phenotypic character												
Death rate (deaths per iteration)	NS	**	NS	***	*	***	**	NS	*	***	***	***
Birth rate (births per iteration)	***	***	***	***	***	***	***	***	***	*	***	NS
Fitness (birth rate – death rate)	***	***	***	***	***	***	***	***	***	***	***	***
Lifetime seed production	***	***	***	***	**	***	***	***	***	***	***	***
Plant height (m)	NS	NS	NS	***	NS	**	NS	NS	NS	***	***	***
Total leaf area (m^2)	***	**	***	***	*	***	***	***	***	*	**	NS
Prop. biomass below ground	NS	**	***	*	**	***	NS	*	***	NS	*	NS
Leaf weight : above-ground weight	NS	NS	*	NS	NS	***	NS	*	***	**	***	**
Plant weight (kg)	***	***	***	***	***	***	***	*	***	***	***	
Total plant nitrogen (kg)	***	**	***	***	***	***	***	NS	***	***	***	***
Plant nitrogen concentration (kg N : kg C)	NS	**	NS	**	NS	NS	***	NS	*	*	NS	NS
Leaf area : leaf weight	NS	NS	***	NS	*	***	NS	NS	***	NS	NS	NS
Plant stored nitrogen (kg)	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Plant stored carbon (kg)	***	**	NS	***	***	***	**	NS	**	***	**	**

Note: Each cell reports the results of a two-sample *t*-test, or a Mann-Whitney *U*-test comparing one invader strategy with the resident in the specified environment. $N = 20$ in each sample. $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$. *Invader strategy*: C = competitor, S = stress tolerator, R = ruderal, D = defended.