Arthropod-Plant Interactions (2014) 8:205–212
DOI 10.1007/s11829-014-9305-4

ORIGINAL PAPER

Gall insects and selection on plant vigor: can susceptibility compromise success in competition?

Arthur E. Weis

Received: 28 October 2013 / Accepted: 28 March 2014 / Published online: 11 April 2014

Abstract Gall insects select vigorously growing plants and plant parts when initiating gall formation. Vigor is associated with rapid growth rate, and in turn, rapid growth confers competitiveness. Are there conditions under which the cost of vigor, in the form of increased susceptibility to attack, outweighs the benefit of competitive success? I present a simulation model to explore the interaction between susceptibility and competition on the selective advantage of increased growth rate. Assuming size-symmetric competition, the model shows that in general, vigor is favored (benefit > cost) at low to intermediate gall loads. At very high plant densities, however, plants with high gall loads may lose standing in the competitive size hierarchy from which they cannot recover. The details of this result, however, change somewhat when competition is size-asymmetric, that is, when a larger focal plant suppresses smaller neighbors, but smaller neighbors cannot exert a reciprocal effect on the focal. At low densities, the pattern of selection on growth rate is qualitatively similar to the size-symmetric case. At higher plant densities, however, fast-growing genotypes can suppress slow ones so much during the preattack phase that even at the highest gall loads they maintain their standing in the competitive hierarchy. Thus, heavy gall insect attack on vigorous plants can impose selection against high intrinsic growth rates under strong symmetric competition, but not strong asymmetric competition. While life history traits can evolve as a correlated response to selection on defensive traits that reduce susceptibility, this model reveals that susceptibility can evolve as a correlated response to selection on basic life history traits.

Keywords Gall insects · Plant vigor hypothesis · Asymmetric competition · Susceptibility · Natural selection

Introduction

Gall-inducing insects tend to choose vigorously growing plants or plant parts for gall induction (e.g., Craig et al. 1989; Kimberling et al. 1990; Vieira et al. 1996; Larson and Whitham 1997; Prado and Vieira 1999; Kopelke et al. 2003; Heard and Cox 2009; Santos and Fernandes 2010). This preference for vigorous growth has been observed at all levels of plant architecture, from individual leaves to whole plants.

In his classic work on *Pemphigus betae* (Homoptera: Aphididae) making leaf galls on *Populus*, Whitham (1978) found that the aphids strongly preferred to settle on unfolding leaves midway along newly growing shoots. These are the leaves that will grow to the largest size and therefore provide the most resources for offspring development. Similarly, the gall midge *Rhabdophaga strobiloides* (Diptera: Cecidomyiidae) more often oviposits into terminal than lateral willow shoots; the terminals grow thicker, and the galls induced there are larger and produce larger offspring (Weis and Kapelinski 1984). Preference for more vigorous shoots has been amply demonstrated by Peter Price and his associates in many species of gall-inducing sawflies (Hymenoptera: Tenthredinidae) (Price et al. 1987; Price 1991; Craig et al. 1989). In some

---

Handling Editor: John F. Tooker.

A. E. Weis (✉)
Department of Ecology and Evolutionary Biology, University of Toronto, 25 Wilcocks Street, Toronto, ON M5S 3B2, Canada
e-mail: arthur.weis@utoronto.ca

A. E. Weis
Koffler Scientific Reserve at Jokers Hill, King City, ON, Canada

populations, the galling rate on the largest size class of shoots approaches 100 %, while that on shoots at or below the average size approaches 0 %. Gall insect fitness is highest on these large stems. Sawfly preferences extend to the whole plant level as well. Fritz et al. (2000, 2003) showed that willow genotypes with higher growth rates are preferred over slower growing ones. The clear implication is that sawfly populations are not limited by the supply of host plants per se, but rather by the supply of high-quality plant shoots. This has become known as the "plant vigor hypothesis" (Price 1991).

The relationship between plant vigor and gall insect preference is not universal (De Bruyn 1995; McKinnon et al. 1999; Eliason and Potter 2000; Rehill and Schultz 2001,Santos 2010) and may be constrained by phenological mismatch (Aoyama et al. 2012). On the other hand, Cornelissen et al. 2008 found in a meta-analysis of 71 published tests that insect herbivores were on average 65 % more abundant on vigorous plants and plant parts. Notably, this study found that chewing, sucking, and mining insects, in addition to gall insects, also showed a preference toward vigorous plants and plant parts, although evidence for enhanced performance on these plants was weak. The most prominent examples of the plant vigor hypothesis include host plants in the Salicaceae, but herbivores on species in the Asteraceae (Heard and Cox 2009), Anacardiaceae (Jesus et al. 2012), Fabaceae (Grinnan et al. 2013), Fagaceae (Pires and Price 2000), Polygonaceae (Hough-Goldstein and LaCoss 2012), and Rubiaceae (Vieira et al. 1996) are also reported to follow its predictions.

Studies on the role of plant vigor in gall insect–plant interactions have focused largely on the insect's perspective. For the plant, however, the insect's preference for vigorous growth could present an evolutionary conundrum. Fast growth rates can lead to a variety of competitive advantages for the plant, not the least of which is ability to maintain a position high in the canopy, where they have greater access to light. However, if gall insects are abundant enough, their depredations could possibly negate the competitive advantage for the fast-growing genotypes that they prefer.

The simulation model presented here explores the interplay of two selective pressures on plant growth rate—the competitive advantage afforded by fast growth versus the disadvantage of greater susceptibility to gall insects. The model explores the direction and intensity of natural selection on a gene for increased growth rate along gradients of plant and gall insect population density. It also compares the impact made by two modes of plant competition, size-symmetric versus size-asymmetric (Schwinning and Weiner 1998), on the balance between costs and benefits of increased intrinsic growth rates. The motivating question is whether there are plausible conditions in which the benefits of fast growth can be counterbalanced by the correlated increase in susceptibility? Or, is elevated attack by gall insects instead an inconsequential side effect of adaptation to other selective forces favoring vigorous growth?

The model

I constructed a spatially explicit model that follows the growth trajectories of all individuals in a population of annual plants over the course of a single generation. Half of all plants carry a gene that increases intrinsic growth rate in individual mass. Assuming that plant fecundity is directly proportional to plant mass at the end of the growing season, differences in final size translated into fitness differences. In the simulation, fast-growing plants are strongly preferred by gall insects, and so, the selective advantages to fast growth can be diminished, or even reversed, when gall insects are abundant. The model is built upon a framework developed by Weis and Hochberg (2000) that explored the impact of competition of the cost of resistance. Here, the model reflects the biology of gall insects and their hosts.

Plants were assumed to have logistic growth curves (Iwasa and Kubo 1997; Weis et al. 2001). Growth trajectories for simulated plants were determined by four factors. The first is intrinsic growth rate, which is the maximum potential mass gained per unit of current mass. Second is self-limitation on growth. As plants get larger, they cannot sustain maximum growth rates because of local resource depletion (e.g., self-shading). Further, plants must allocate more to support structures as they grow at the expense of resource-gathering structures (leaves and roots). Third, competition with neighbors will slow the growth of a given focal plant. Fourth, gall insects divert plant production away from growth and may drain resource stores.

Interactions among neighboring plants emerge from a competitive size hierarchy (Weiner 1985). The competition intensity between two neighbors at a particular time step depends on several factors. The most basic of these is the intrinsic competitive ability, which is the decrease in growth rate for a focal plant per unit mass of the neighboring plant. The full competitive impact of a neighbor is the product of (1) the focal plant's competitive ability, (2) neighbor size, and (3) the distance between the two plants. Focal plants may also exert a reciprocal competitive impact on their neighbors. When all else is equal, the larger plant "wins" the competitive contest—the larger plant suppresses the smaller one more than the smaller on suppresses the larger. This type of reciprocal competitive impact assumes size-symmetric competition. Size-asymmetric competition is discussed below.

Gall insects divert photosynthate away from plant growth during gall formation and insect maturation. This slows growth, and as a result, galled plants can lose standing in the size hierarchy. A gene that increases intrinsic growth rate may cause higher galling rates, but it will also promote *regrowth* after the galling episode, and can thus enable a galled plant to once again reach the top of the size hierarchy. The overall selective advantage of a gene for faster growth is determined by the costs of increased susceptibility against the competitive benefits of fast growth before, during, and after attack.

The following model embodies the biology outlined here. Of course, these simulations are highly simplified representations of complex biologic realities, but this exercise presents a framework for organizing our thoughts about these complexities.

Model formulation

The growth of simulated individual plants was represented by a logistic difference equation. In the absence of attack and competition, the size of an individual focal plant going into the next time unit is given by the recursion equation

$$M_{t+1} = (1+\rho)M_t\left[\frac{1}{1+\theta_F M_t}\right]$$

where M_t equals plant mass at time t, ρ is the intrinsic growth rate (mass added per unit mass), and θ_F is the self-limitation constant, that is, the suppressive effect that a focal plant exerts on itself due to allocation to support tissue, self-shading, and the like. Metabolically, ρ represents net photosynthesis of productive tissues, while θ_F reflects respiration of nonproductive tissues. This is a logistic model in that the relative growth rate, $\Delta M/M_t$, falls linearly with increasing M_t. The asymptotic plant size is reached when photosynthesis balances respiration ($M_t = \rho/\theta_F$). In a sufficiently long season, all plants reach their asymptotic size.

The goal was to evaluate the selective advantage of a gene that increases growth rate. Thus, the simulations included mixtures of fast and slow-growing genotypes. In any one run, the basic growth equations for the two genotypes differed only for ρ.

Competition is modeled by adding terms to depict suppression by neighboring plants:

$$M_{t+1} = (1+\rho)M_t\left[\frac{1}{(1+\theta_F M_t)\,(1+\sum\delta^{-1}\theta_N M_{N,t})}\right]$$

where $M_{N,t}$ is the mass of an immediate neighbor N at time t, δ is distance between neighbor and focal plant, and θ_N is the competition coefficient, that is, the suppressing effect of one unit of neighbor mass on focal plant growth. When plants are evenly spaced, δ^{-1} is proportional to plant density. The parameter values used here are basically the same as used by Weis and Hochberg (2000) and reflect a modest genotypic difference in growth rate. The simulated growing season had 34 time intervals, which gave ungalled plants time to approach their size plateau.

The model assumes that during gall growth, a proportion of current production, G, is diverted from plant growth. During the time intervals of gall growth, the intrinsic growth rate, ρ, is reduced by a factor of 1-G. It also makes the strong assumption that gall insects attack all plants of the fast-growing genotype and ignore the slow-growing genotypes. This extreme assumption recalls well-studied natural systems where the fastest-growing plant parts were consistently galled, whereas average or below average parts were virtually gall free (Whitham 1978; Price et al. 1987; Craig et al. 1989).

Spatial layout and timing of attack

Each plant occupied a cell in an evenly spaced 16 × 16 hexagonal grid, with all cells occupied. Genotypes were assigned randomly to cells. Each plant competed with its six immediate neighbors. No direct interactions with more distant neighbors were included in the growth equations, but indirect interactions emerge from the spatial structure. For instance, a particularly large neighbor two cells away from the focal plant could suppress the intervening neighbor and thus benefit the focal plant. To avoid an edge effect, the model assumed that the plants along one edge were the immediate neighbors of those along the opposite edge, thus pulling the grid into a virtual torus.

Competition intensity was varied by changing interplant distance, δ. At large values of δ, neighbors had little effect on one another. When $\delta = 1$, the suppressing effect of a neighbor on the focal plant was as large as the focal plant's own self-limitation.

I varied the time at which attacks were initiated and the length of the gall/gall insect growth period. Variation in timing did not lead to qualitative differences in model outcome, except at the limit where very late attack left no time for regrowth—a situation that does not match the biology of gall insect–plant interactions. In the simulation runs presented here, attack and gall growth start during time interval 14 (of 34), when plants approach their highest absolute growth rate ($\delta M/t$). Gall insects mature and cease to divert plant resources at interval 19.

Competition symmetry

The model considered both size-symmetric and size-asymmetric competition (Schwinning and Weiner 1998). Competition is symmetric when a neighboring plant exerts a suppressing effect on the focal plant in proportion to its size, i.e., $\theta_N M_{N,t}$, and the focal plant exerts a reciprocal effect on the neighbor proportional to its own size. Gross competitive impacts are not equal—a larger plant will have

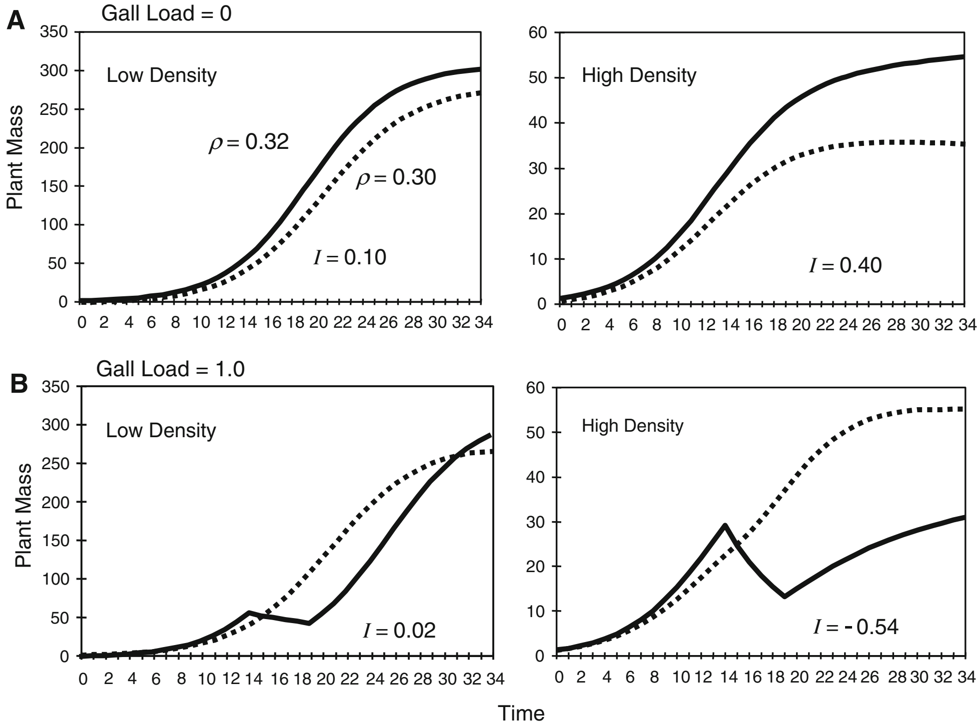

Fig. 1 Mean growth trajectories for two plant genotypes, one fast- and the other slow-growing, at low densities and at high densities, with zero gall load ($G = 0$) and maximum gall load (all fast growers attacked, and all resources assimilated during the attack period allocated to gall/gall insect growth, $G = 1$). Attack begins on day 14, and gall growth is completed on day 19. Competition is size-symmetric. Note the differences in scale for plant mass at the two densities. **a** In the absence of gall insects, intense competition at high plant density amplifies the inherent advantage of rapid growth; fast growers quickly reach the top of the size hierarchy and remain there. **b** When attacked, individuals with the fast-growth genotype can regain their size advantage before the end of the season if plant density is low, but intense competition at high density prevents regrowth; attack sends fast growers to the bottom of the size hierarchy, from where they are unable to recover. Model parameter values used were $\theta_F = 0.001$, $\theta_N = 0.001$, at low density, $\delta^{-1} = 0.01$, and at high density, $\delta^{-1} = 1.0$

a greater effect on a smaller one than vice versa—but, competition is symmetric on a *per unit biomass* basis. Competition for soil resources may typically be symmetric, with light competition typically being asymmetric. The model used the formulation of Law et al. (1997) for the asymmetric competition coefficient:

$$\theta_{\text{asym}} = \theta_N \left[1 + \frac{1}{1 + e^{M_F - M_N}} \right],$$

where M_F and M_N are the sizes of the focal and neighbor plants at the beginning of the time interval. When the focal plant is much smaller than the neighbor, $\theta_{\text{asym}} \cong \theta_N$, whereas $\theta_{\text{asym}} \cong 0$ in the reverse situation. With asymmetric competition, the effect of a neighbor plant on a focal plant was thus determined by both neighbor size and by the size difference (i.e., $\theta_{\text{asym}} \times M_{N,t}$).

Selection intensity

To assess the relative fitness of the two genotypes over a broad array of gall loads and plant densities, selection intensity was quantified as

$$I = \frac{M_f - M_s}{\overline{M}},$$

where M_f and M_s are the mean final biomasses for the fast- and slow-growing genotypes, respectively, and $\overline{M}$ is the population mean final biomass. Assuming fitness is proportional to size, the slow genotype is favored when I is negative while the fast is favored when I is positive.

Results

Basic effects of gall load and competition on selection growth rate

Gall insect attack diminished the advantages of fast growth. When both plant and gall insect densities are high, the *slower*-growing plant genotypes had the fitness advantage. Simulation results given in Fig. 1 illustrate the interplay of gall load and competition on plant fitness at four extremes of galling rate and plant density. The panels in these figures depict average growth curves for fast and slow plant genotypes ($\rho = 0.32$ vs. 0.30, a 6.7 % difference) under size-symmetric competition.

Figure 1*a* shows that in the absence of attack ($G = 0$), the 6.7 % increase in growth rate led to a 10 % size advantage at low plant density ($\delta^{-1} = 0.01$), but a 40 % advantage at higher density ($\delta^{-1} = 1.0$). Faster plants reached a substantial size earlier in the season, thereafter suppressing slower-growing neighbors. This suppression was intensified at higher density.

Gall insect attack diminishes the benefits of faster growth at low plant density and reverses the benefits at high density (Fig. 1b). At the heaviest galling rate ($G = 1$), plants decreased in size (as they would when stored resources are drawn down, or plant modules die), over the gall growth period. This sent galled plants to the bottom of the size hierarchy. At low density, regrowth by galled plants was mildly hindered by competition, but given their higher intrinsic growth rate, they ended with a 2 % size advantage. At higher density, however, the suppressive impact of the size advantage enjoyed by ungalled neighbors is amplified by their close proximity. This led to a 54 % *disadvantage* for fast growth.

Growth trajectories under size-asymmetric competition were qualitatively similar, but quantitatively more divergent, with the faster-growing plant gaining a larger size advantage in the absence of gall insects. The effects of gall load on size differences are detailed below.

Density-dependent reversals in selection

The simulation was run under a broader range of plant densities and gall loads to more fully explore patterns of density-dependent change in the intensity and direction of selection on growth rate. This exploration was repeated for both the size-symmetric and size-asymmetric modes of competition.

Size-symmetric competition

When competition is symmetric on a per unit mass basis, increasing plant density amplifies the selective impact of gall insects on growth rate, as shown in Fig. 2. Density-load combinations that favored the fast-growth genotype are white, and those that disfavored it are shaded. The border between the white and shaded areas of the surface is the “payback contour,” that is, where the selective advantage equals the selective disadvantage.

At low plant density, the fast-growth genotype is favored regardless of gall load (left edge of surface, Fig. 2). At high plant density, fast growth is highly favored in the absence of gall insects, but highly disfavored when gall loads are large (the right edge of surface, Fig. 2). As plant density increases, the payback point occurs at progressively lower gall loads. For instance, in this simulation at a gall load of $G = 0.8$, the fast genotype has a small net advantage at the lowest plant density ($\delta^{-1} = 0.01$), but when density is at the highest end ($\delta^{-1} = 2.54$), the situation reverses, and the fast genotype suffers a ~50 % disadvantage. Given $G = 0.8$, fast and slow genotypes are equally fit at intermediate plant density (e.g., $\delta^{-1} = 0.10$). Thus, as plant population densities fluctuate, the direction of selection on growth rate could likewise fluctuate.

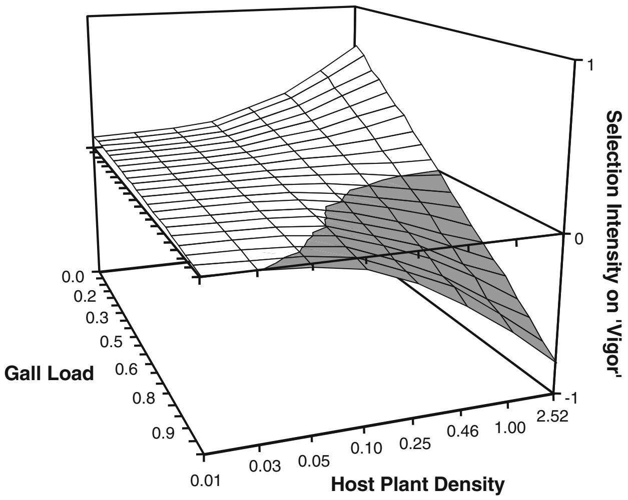

Fig. 2 Selection intensity acting on plant “vigor” (intrinsic growth rate, ρ) at various combinations of gall load, G, and plant density, δ^{-1}. Competition is size-symmetric. Selection favors fast growth at low gall insect densities and/or at low plant density (*unshaded region*) but turns against rapid growth when both density and gall load are high (*shaded region*). The four corners of the surface roughly correspond to the four growth trajectory scenarios depicted in Fig. 1. Competition is size-symmetric. Parameter values used were $\rho = 0.32$ and 0.30, $\theta_F = 0.001$, and $\theta_N = 0.001$

Size-asymmetric competition

The pattern of density-dependent reversals in selection is more complex when competition is asymmetric. In this case, the larger plant suppresses the smaller, but the smaller is unable to exert any reciprocal suppressing effect. Figure 3 shows the net selection intensity on growth rate at the same density and gall load values as for Fig. 2. All parameters are the same, except that the symmetric competition coefficient, θ_N, is replaced by its asymmetric counterpart, θ_{asym}.

Several important differences to the size-symmetric case are apparent. First, even at low plant density, selection turns against fast growth at high gall loads. This is evident as the left edge of the surface in Fig. 3 dips below zero at $G \approx 0.9$ (c.f. Fig. 2). Second, the payback contour is no longer monotonic; at higher gall loads (e.g., $G = 0.8$), selection favors fast growth at low and high densities, but

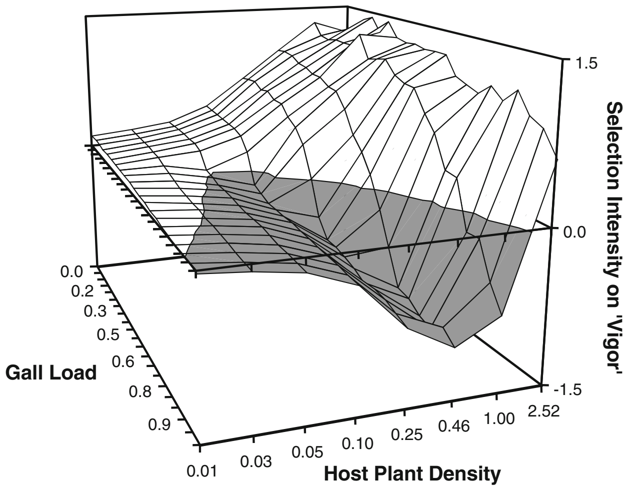

Fig. 3 Selection intensity acting on plant "vigor" (intrinsic growth rate, ρ) at various combinations of gall load, *G*, and plant density, δ^{-1}. Competition is size-*asymmetric*. Larger individuals suppress their smaller neighbors, but smaller individuals exert no reciprocal effect on larger neighbors, and this intensifies the competitive size hierarchy. At low densities, selection turns against rapid growth at lower gall loads (unshaded region) than under size-symmetric competition because intensified competition in the postattack period lowers re-growth potential. At higher densities, higher gall loads are required to turn selection against fast growth (*shaded region*); this is because intensified competition in the preattack period gives fast growers a size advantage so large that only extreme gall loads can reverse it. The same as in Fig. 2, except θ_N was modified to θ_{asym}, as described in text

disfavors it at intermediate densities. At the highest plant densities, asymmetric competition favors the fast-growth genotype even when gall loads are at their maximum (the right edge of the surface, Fig. 3). These differences from the symmetric case emerge from the fact that very small size differences between neighbors are quickly amplified by asymmetric competition.

Here is the cause of the nonmonotonic payback contour. At low plant density and very high gall load, asymmetric competition turns selection against fast growth. Even though low density makes competition weak, the size loss inflicted on heavily galled plants leaves them vulnerable to suppression by slightly larger, ungalled neighbors. Asymmetric competition renders these galled plants incapable of exerting a counter-balancing suppressive effect. Consequentially, galled plants are prevented from regaining the size advantage despite their higher intrinsic growth rate. This pattern intensifies at intermediate densities.

At the highest densities, however, fast-growth genotypes gain an insurmountable advantage early in the season. By the time of gall insect attack, the size difference between the fast and slow genotypes is so great that even a load of $G = 1$ cannot close the gap. Thus, the fast genotype suppresses the slow throughout the entire season without a reciprocal impact of slow on fast.

Discussion

The simulation model asks if gall insect preference for vigorous plants can affect selection on plant growth rate. One cost of high gall loads associated with plant vigor is the loss of competitiveness. The results suggest that both the benefits and the costs of faster growth are amplified when high plant population density intensifies competition. Under extreme gall loads, where most of production is lost to the plant during gall formation and development, increased intrinsic plant growth rate is insufficient to overcome strong competition by ungalled neighbors.

Additional runs of the model tested genotypes with smaller differences in grow rates than shown here. When the growth rate advantage is small, selection turns against the faster genotype at lower gall loads and lower densities. However, if the genotypes show scant differences in vigor, and thus scant differences in quality, one would not expect gall insects to show strong preferences. In runs where the difference between the fast and slow types is very large, the fast one is always favored.

Returning to the original question—are there plausible conditions in which the benefits of fast growth can be counterbalanced by the correlated increase in susceptibility to gall insect?—model results suggest the answer is most frequently no. The infestation rates required to turn selection against fast growth appear to be higher than those seen over the long term in plant-gall insect systems. Although Price and his colleagues (Price et al. 1987; Price 1991; Craig et al. 1989) found that nearly 100 % of highly vigorous shoots are galled, over the entire plant individual, there are many less vigorous shoots that are not, which limits plant allocation to the gall. From the plant's perspective, the increase in gall insect attack that comes with increased vigor is more likely an inconsequential side effect of adaptation to other selective forces favoring rapid growth. Nevertheless, there is interesting biology behind this negative finding, including the variety of outcomes when plants are subjected to both herbivory and competition, and the place of plant growth rate per se as a trait conferring susceptibility to attack.

Competitive symmetry of the costs and benefit of plant vigor

The symmetry of competitive impact changes the potential outcome of selection at high density. Interactions between neighboring plants are thought typically to be size-symmetric when they compete for soil resources, while light competition is thought to be size-asymmetric (Weiner 1990; Casper and Jackson 1997). A plant with a larger root mass may take up more nutrients from the three-dimensional soil matrix, but no more than proportional to its size.

The smaller plant still has access to the remaining nutrients and can extract these before their neighbors do. By contrast, light enters the habitat along one dimension. A taller plant intercepts and reflects photons that will never reach shorter plants lower in the canopy. It is impossible for shorter neighbor to deprive a taller neighbor of light. In a review of long-term forestry experiments, Pretzsch and Biber (2010) found evidence for asymmetric competition on rich soils, where light is the limiting factor, but symmetric competition in poorer soils, where it is not.

In the model, symmetric competition caused the costs of fast growth, in the form of susceptibility to greater gall insect attack, to increase more with plant density than the benefits. The situation is more complex with asymmetric competition, where the highest plant densities can cause benefits to increase more than costs. These contrasting patterns arise because at high density, asymmetric competition can give fast-growing plants an insurmountable advantage before attack occurs. A plant that gains an early size advantage can suppress its neighbors so much that its position atop the size hierarchy is not relinquished, even under the heaviest attack. This type relationship between early growth and competitive success in the face of herbivory has been seen among seedling of silver birch (Prittinen et al. 2003). There, taller plants were more heavily damaged by insect herbivores, but nonetheless grew more in the postattack period, presumable because their height allowed them to dominate the upper canopy, depriving the less-damaged, slower-growing seedlings of light.

Susceptibility as a correlated trait

A superficial reading of the literature on plant–herbivore interactions could give the impression that herbivores choose their hosts to avoid the "bad stuff." But surely, selection will favor herbivores with behaviors that lead them to the "good stuff"—the energy and nutrients needed for growth and reproduction. Price's "plant vigor" hypothesis (Price 1991) states that many herbivorous insects choose to feed on the most vigorous plants or plant parts because these provide superior nutrition. White (2009) argued that this pattern would especially apply to herbivores dependent on newly formed plant tissues, such as gall insects (Weis et al. 1988). Many gall insects preferentially attack more vigorous individuals or plant modules (Craig et al. 1989; Kimberling et al. 1990; Larson and Whitham 1997; Prado and Vieira 1999; Kopelke et al. 2003; Heard and Cox 2009; Santos and Fernandes 2010), often resulting in improved gall insect performance. This pattern has been seen in other herbivore guilds as well (Spiegel and Price 1996; Inbar et al. 2001; Cornelissen et al. 2008; Grinnan et al. 2013). Choice of vigorous plant parts does no ensure high performance for herbivores (McKinnon et al. 1999; Kopelke et al. 2003; Fritz et al. 2003; Cornelissen et al. 2008), but regardless of the consequences for the insect, preference for vigorous plants means that genes regulating plant growth and development can directly affect both herbivore load and herbivory tolerance (Fig. 2; see also Weis et al. 2001).

Coley et al. (1985) made a case for a connection between plant growth rate and herbivore attack. Their argument was based on the shifts in the costs and benefits of defensive chemicals between resource-poor and resource-rich environments. Basically, they argued that in resource-rich environments, plants evolve high intrinsic growth rates. High growth rate, in turn, allows fast replacement of eaten tissues, and so, the optimal allocation to defense is small. The difficulty of replacing eaten tissue in poor environments favors high defense investment. This logic, which is based on the costs and benefits of resistance, is congruent with the argument put forth here. Herbivores may prefer fast-growing plants either because they are poorly defended (i.e., fast growth due to low defense costs) or because they provide a superior diet (i.e., have greater concentrations of water, protein, and other nutrients relative to cellulose and lignin). In either case, a gene that increases plant growth rate also increases susceptibility. In one case, the gene directly accelerates basic growth mechanisms while in the other, it affects growth indirectly by reducing the allocation of resources to resistance factors. Thus, not only will life history traits evolve as a correlated response to selection on defensive traits that reduce susceptibility, susceptibility can evolve as a correlated response to selection on basic life history traits.

Acknowledgments Thanks go to Michael Hochberg for helpful discussions and guidance in model development. Helpful comments from B. Campitelli and S. Wadgymar improved the manuscript. Financial support was provided by a Discovery Grant from the National Scientific and Engineering Council (Canada).

References

Aoyama T, Akimoto SI, Hasegawa E (2012) Gall distribution as a compromise between the optimal gall-site selection and the synchrony to host-plant phenology in the aphid *Kaltenbachiella japonica*. Arthropod-Plant Interact 6:461–469

Casper BB, Jackson RB (1997) Plant competition underground. Annu Rev Ecol Syst 28:545–570

Coley PD, Bryant JP, Chapin FS (1985) Resource availability and plant antiherbivore defense. Science 230:895–899

Cornelissen T, Fernandes WG, Vasconcellos-Neto J (2008) Size does matter: variation in herbivory between and within plants and the plant vigor hypothesis. Oikos 117:1121–1130

Craig TP, Itami JK, Price PW (1989) A strong relationship between oviposition preference and larval performance in a shoot-galling sawfly. Ecology 70:1691–1699

De Bruyn L (1995) Plant stress and larval performance of a dipterous gall former. Oecologia 101:461–466

Eliason EA, Potter DA (2000) Budburst phenology, plant vigor, and host genotype effects on the leaf-galling generation of *Callirhytis cornigera* (Hymenoptera: Cynipidae) on pin oak. Environ Entomol 29:1199–1207

Fritz RS, Crabb BA, Hochwender CG (2000) Preference and performance of a gall-inducing sawfly: a test of the plant vigor hypothesis. Oikos 89:555–563

Fritz RS, Crabb BA, Hochwender CG (2003) Preference and performance of a gall-inducing sawfly: Plant vigor, sex, gall traits and phenology. Oikos 102:601–613

Grinnan R, Carter TE, Johnson MT (2013) The effects of drought and herbivory on plant–herbivore interactions across 16 soybean genotypes in a field experiment. Ecolo Entomol 38:290–302

Heard SB, Cox GH (2009) Plant module size and attack by the goldenrod spindle-gall moth. Can Entomol 141:406–414

Hough-Goldstein J, LaCoss SJ (2012) Interactive effects of light environment and herbivory on growth and productivity of an invasive annual vine, *Persicaria perfoliata*. Arthropod-Plant Interact 6:103–112

Inbar M, Doostdar H, Mayer RT (2001) Suitability of stressed and vigorous plants to various insect herbivores. Oikos 94:228–235

Iwasa Y, Kubo T (1997) Optimal size of storage for recovery after unpredictable disturbances. Evol Ecol 11:41–65

Jesus FM, Silva JO, Fagundes M, Fernandes GW (2012) Differential female attack and larval performance of a galling Cecidomyiidae on the host, *Astronium fraxinifolium* (Anacardiaceae), in contrasting habitats. Entomol News 122(1):10–21

Kimberling DN, Scott ER, Price PW (1990) Testing a new hypothesis: plant vigor and *Phylloxera* distribution on wild grape in Arizona. Oecologia 84:1–8

Kopelke JP, Amendt J, Schönrogge K (2003) Patterns of interspecific associations of stem gallers on willows. Divers Distrib 9:443–453

Larson KC, Whitham TG (1997) Competition between gall aphids and natural plant sinks: plant architecture affects resistance to galling. Oecologia 109:575–582

Law R, Marrow P, Dieckmann U (1997) On evolution under asymmetric competition. -. Evol Ecol 11:485–501

McKinnon ML, Quiring DT, Bauce E (1999) Influence of tree growth rate, shoot size and foliar chemistry on the abundance and performance of a galling adelgid. Funct Ecol 13:859–867

Pires CS, Price PW (2000) Patterns of host plant growth and attack and establishment of gall-inducing wasp (Hymenoptera: Cynipidae). Environ Entomol 29:49–54

Prado PIKL, Vieira EM (1999) The interplay between plant traits and herbivore attack: a study of a stem galling midge in the neotropics. Ecol Entomol 24:80–88

Pretzsch H, Biber P (2010) Size-symmetric versus size-asymmetric competition and growth partitioning among trees in forest stands along an ecological gradient in central Europe. Can J For Res 40:370–384

Price PW (1991) The plant vigor hypothesis and herbivore attack. Oikos 62:244–251

Price PW, Roininen H, Tahvanainen J (1987) Why does the bud-galling sawfly, *Euura mucronata*, attack long shoots? Oecologia 74:1–6

Prittinen K, Pusenius J, Koivunoro K, Roininen H (2003) Genotypic variation in growth and resistance to insect herbivory in silver birch (*Betula pendula*) seedlings. Oecologia 137:572–577

Rehill BJ, Schultz JC (2001) *Hormaphis hamamelidis* and gall size: a test of the plant vigor hypothesis. Oikos 95:94–104

Santos J (2010) Pattern of attack of a galling insect reveals an unexpected preference-performance linkage on medium-sized resources. Revista brasileira de entomologia 54:96–103

Santos JC, Fernandes GW (2010) Mediation of herbivore attack and induced resistance by plant vigor and ontogeny. Acta Oecologica 36(6):617–625

Schwinning S, Weiner J (1998) Mechanisms determining the degree of size asymmetry in competition among plants. Oecologia 113:447–455

Spiegel LH, Price PW (1996) Plant aging and the distribution of *Rhyacionia neomexicana* (Lepidoptera: Tortricidae). Environ Entomol 25:359–365

Vieira EM, Andrade I, Price PW (1996) Fire effects of a *Palicourea rigida* (Rubiaceae) gall midge: a test of the plant vigor hypothesis. Biotropica 28:210–217

Weiner J (1985) Size hierarchies in experimental populations of annual plants. Ecology 66:743–752

Weiner J (1990) Asymmetric competition in plant populations. Trends Ecol Evol 5:360–364

Weis AE, Hochberg ME (2000) The diverse effects of intra-specific competition on selection for resistance: a model and its predictions. Am Nat 156:276–292

Weis AE, Kapelinski AD (1984) Manipulation of host plant development by the gall midge *Rhabdophaga strobiloides*. Ecol Entomol 9(457):469

Weis AE, Walton R, Crego CL (1988) Reactive plant tissue sites and the population biology of gall makers. Annu Rev Entomol 33(467):486

Weis AE, Simms EL, Hochberg ME (2001) Will plant vigor and tolerance be genetically correlated? Effects of intrinsic growth rate and self-limitation on re-growth. Evol Ecol 14:331–352

White TCR (2009) Plant vigor versus plant stress: a false dichotomy. Oikos 118:807–808

Whitham TG (1978) Habitat selection by Pemphigus aphids in response to response limitation and competition. Ecology 59:1164–1176