Potential of Induced Resistance as a Tool for the Management of Pathogens and Insects in Trees – an Ecological Viewpoint[†]

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Abstract

Under natural conditions, forest ecosystems are usually stable, despite the constant presence of arthropods and pathogens inherently capable of killing their tree hosts. It is likely that the phenotypic plasticity of trees, which includes inducible resistance mechanisms against attacking organisms, plays a crucial role in these interactions. Systemic induced resistance may be a common and important phenomenon in forest trees, one that allows for balanced partitioning of available resources between growth and defence. However, such physiological tradeoffs are affected by environmental variables, such as resource availability (e.g. nutrients, water, light) as well as by silvicultural activities. There is also evidence that systemic induced resistance or its counterpart, systemic induced susceptibility, may be operative concurrently in the same tree, depending on the specific organs under attack. Lastly, all these host responses can be strongly modulated by systemic cross-effects between pathogens and/or insects.

While it is established that trees possess systemically inducible defences, it is still uncertain how this knowledge might be applied to control forest pathogens and insects. This is complicated by the classic approaches used for the silvicultural control of pests, which are fundamentally centred on the assumption that plants characterised by higher vigour are also less stressed and thus more resistant to attack. In many cases, this is a fallacious premise.

Keywords: systemic induced resistance; systemic acquired resistance; plant defence theory; resistance mechanisms; cross effects.

Introduction

The management of invasive forest pathogens and insects, whether indigenous or exotic, consists of four basic sequential phases. The first is prevention, and activation of subsequent steps (eradication, mitigation, and restoration/rehabilitation) is based on defeat or success of each preceding step. The two steps where tree resistance (genetic and/or induced) appears most applicable are eradication and mitigation. Indeed, it seems plausible that any factors that contribute to extinguishing a pest population (eradication) or holding it to manageable levels (mitigation) would be advantageous to exploit. Resistance appears to fit these requirements. For example, it is theoretically possible that a founding pest population may become extinct due to demographic Allee effects (Liebhold & Tobin, 2010), if it is held below a minimum threshold size by host resistance. (Allee effects result from the often-observed correlation between population size and per capita growth rate, such that a population below a threshold size may drive itself to extinction, e.g. due to difficulty in finding suitable mating partners (Liebhold & Bascompte, 2003).) Even if such natural eradication does not occur, resistance may hold pest populations at sufficiently low levels to allow other management measures to be applied. Hopefully, these may at least lead to control or ideally eventual extinction of the pest population.

Several different kinds and definitions of resistance are recognised, depending on the basis for classification, e.g. mechanisms, phenotypes, target organisms, or other traits. Qualitative genetic resistance (vertical, single gene – Robinson, 1976) is not a viable long-term strategy in a forest environment, even when available for trees (e.g. in the case of white pine blister rust *Cronartium ribicola* J.C.Fisch. – Kinlock et al., 1970). There are two fundamental limitations to this strategy. Firstly, it is linked to specific pathogen/insect genotypes so, by definition, it is not widely applicable and secondly, it can be defeated rather quickly by rapidly evolving pest populations. A more rational approach would be to exploit quantitative (horizontal, multigenic - Robinson, 1976) resistance, because it applies to different targets at once and is usually more durable.

Fortunately, resistance in trees appears to be predominantly quantitative. This is probably due to the fact that trees need to cope with a multitude of damaging biotic agents throughout their long life spans. It is becoming increasingly apparent that a major component of this resistance is inducible, both locally and systemically. Evolutionarily, inducible resistance is a flexible solution for non-mobile organisms, such as trees, that are 'locked' into the same location sometimes for centuries or millennia. Thus, defences need only be mounted when required, insuring an optimal spatial and temporal allocation of resources (Bonello et al., 2006).

This review presents a brief summary of the state of knowledge on: (a) induced resistance in trees, particularly systemic induced resistance; and (b) the obstacles that remain in the implementation of induced resistance as a tool for the management of invasive forest pests, both indigenous and exotic. In the past 20 years or so we have learnt a great deal about the molecular, chemical, and physiological mechanisms used by trees to respond to pathogens and herbivorous insects. Unfortunately, we know considerably less about how environmental variables (e.g. nutritional or water stress) modulate such responses. If environmental effects are not taken into account, predictions on the outcomes for trees through induced resistance to pathogens and insects may be nullified.

To address this point, a selection of previous work that deals with analyses and theories of plant defence is presented and recent contributions on systemic induced resistance in conifers from the author's own research program are reviewed. As is often the case with speculation, this document will leave the reader with more questions than answers. Hopefully this uncertainty will lead to a more critical view of forest ecosystem function and silvicultural interventions aimed at forest protection and forest biosecurity.

Systemic induced resistance and defence in conifers

Several types of systemically inducible resistance have been described in model plants (e.g. *Arabidopsis thaliana* (L.) Heynh; tobacco *Nicotiana tabacum* L.) particularly in relation to pathogenic attack, and they all basically represent forms of immunisation. For example, systemic acquired resistance (SAR) is a phenomenon in which plants become systemically more resistant to a pathogen challenge if they are first infected with the same or a different pathogen. The term SAR has specific attributes, including induction of a hypersensitive response in the host by the initial attack (usually by a biotrophic pathogen), involvement of salicylic acid as a putative mediator/signalling molecule, and the accumulation of specific pathogenesis-related (PR) proteins (Durrant & Dong, 2004). Induced systemic resistance (ISR), on the other hand, is induced by plant growth promoting rhizobacteria, is mediated by jasmonic acid and ethylene, and is also often associated with systemic accumulation of specific PR-proteins (Pieterse et al., 2001). While the induction of systemic resistance has been documented in trees, very little is known about the signaling systems in woody plants. Thus, in this paper the phrase "systemic induced resistance" (SIR) is used as a general, pathway-independent term that probably includes forms of pathway-specific systemic resistance such as SAR and ISR (Bonello et al., 2001).
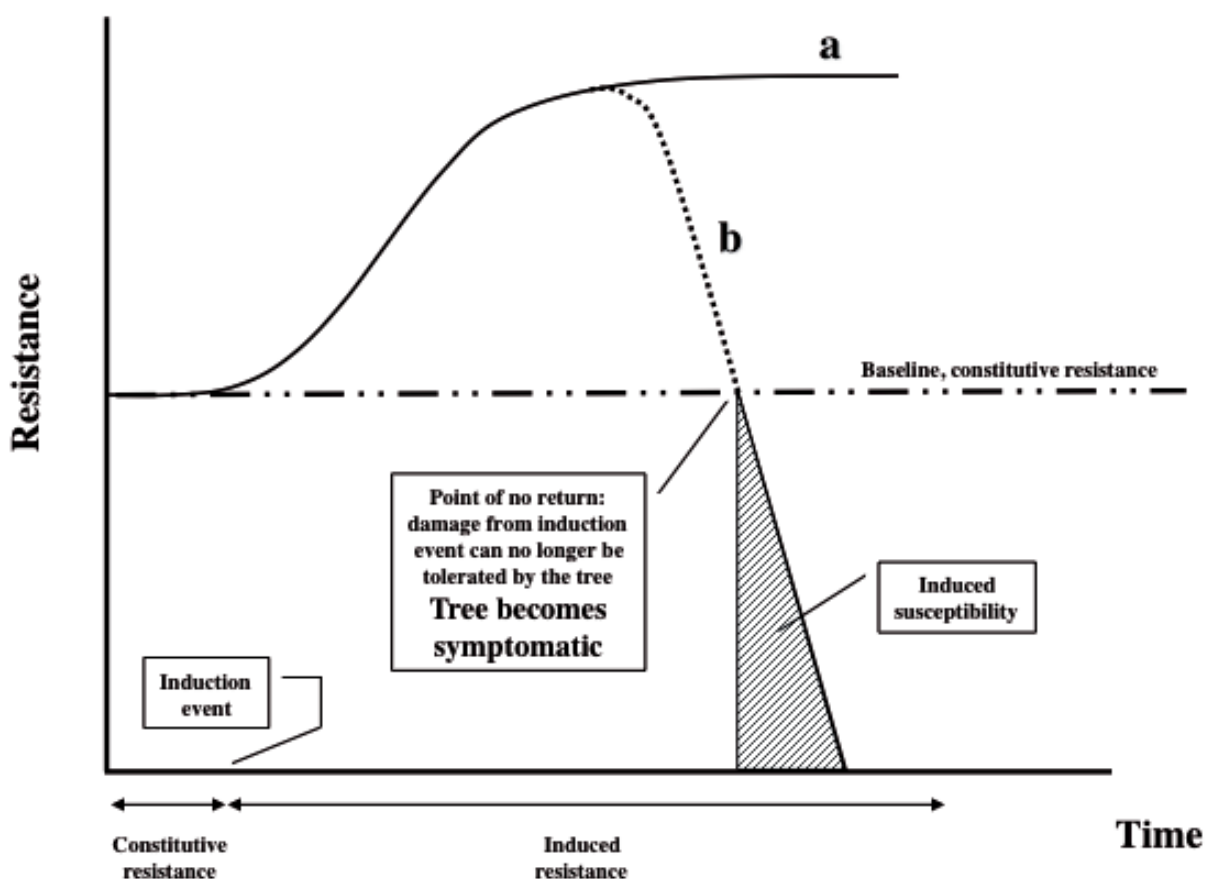
FIGURE 1: Diagram representing the Systemic Induced Resistance (SIR) hypothesis, illustrating the interplay between systemic induced resistance and induced susceptibility in trees against microbes and herbivores. A baseline level of constitutive resistance is present in all trees, but an induction event is predicted to induce SIR against both microbes and insects. SIR is predicted to remain sustained for extended periods of time (a) (e.g. Bonello et al., 2001). However, if the induction event is so severe that it causes impairment of the tree's defensive machinery, subsequent collapse of tree resistance and expression of systemic induced susceptibility (SIS) will ensue (b). An example of this would be pines infected with a root pathogen. Initially (i.e. in pre-symptomatic stages), the pines would be more resistant to bark beetle attack and infection by bark beetle-associated fungi. If the pine becomes symptomatic, then resistance begins to decline and results in the often observed increased susceptibility of symptomatic, root diseased pines to bark beetle infestation. Response scales are arbitrary. From Bonello et al. (2006). Reprinted, with permission, from *Physiological and Molecular Plant Pathology*, Volume 68, © 2006 by Elsevier, http://www.elsevier.com.

For example, Bonello et al. (2001) demonstrated SIR in *Pinus radiata* D.Don (Monterey or radiata pine) by the pitch canker pathogen *Fusarium circinatum* Nirenberg O'Donnell by using artificial inoculations of this ascomycete in the field (4- to 6-year-old, up to approx. 6-m-tall trees), and in the greenhouse (4-year-old, approx. 1.5-m-tall potted ramets). Systemic induced resistance is also likely to occur naturally. Large, mature *P. radiata* growing in long-term monitoring plots on the Monterey peninsula in California were found to be severely affected by pitch canker in 1996. Yet by 1999, the same trees were shown to be free of disease, despite continuing high pathogen pressure in those areas (Gordon, Storer, & Wood, 2001). Trees in remission were also more resistant to the pathogen in artificial test inoculations. The idea that SIR occurred

in *P. radiata* is further supported by other circumstantial evidence. In particular, *P. radiata* trees growing in natural and semi-natural areas with a long history of disease incidence were shown to be significantly more resistant to artificial inoculations than trees in areas where the disease was found more recently (Gordon, 2006). This result suggests that exposure of *P. radiata* populations to the pathogen resulted in enhanced disease resistance over large temporal and spatial scales.

Blodgett et al. (2007) showed that SIR also occurs in young (5-year-old) Austrian pine (*Pinus nigra* Arnold) when induced with canker pathogens such as *Diplodia pinea* (Desm.) Kickx and *D. scrobiculata* de Wet, Slippers & Wingfield under controlled greenhouse conditions. Interestingly, the induction signal moved

bidirectionally, eliciting SIR both acropetally and basipetally (Blodgett et al., 2007). Anatomical and biochemical responses in the stems and branches of *P. nigra* were associated with those phenotypes that demonstrate SIR. In particular, SIR may be linked to an integrated host defense response that includes enhanced lignin deposition (Blodgett et al., 2007; Bonello & Blodgett, 2003), accumulation of soluble phenolics and specific proteins (Blodgett et al., 2007; Bonello & Blodgett, 2003; Wallis et al., 2008; Wang et al., Eyles et al., 2006), higher activity of specific defensive enzymes (Barto et al., 2008), and induction of traumatic resin ducts and resin flow (Luchi et al., 2005).

Specific resistance induced by pathogens can also be expressed against insects, and *vice versa*. For example, SIR induced by the root and butt rot pathogen, *Heterobasidion annosum* (Fr.) Bref. was demonstrated in 30-year-old ponderosa pine (*P. ponderosa* Dougl. ex Laws.) growing in an experimental plantation. In that study, logs taken from artificially inoculated trees were challenged with a bark beetle, the California five-spined ips, *Ips paraconfusus* Lanier. Beetles feeding on logs from infected trees ingested significantly less phloem tissue than beetles feeding on logs from control trees (McNee et al., 2003).

A second case of cross-induction of systemic resistance between a pathogen (*D. pinea*) and an insect pest, the European pine sawfly (*Neodiprion sertifer* (Geoffroy)) was demonstrated in a highly replicated, two-year experiment. Cross-induction in 4-year-old potted *P. nigra* was found to be both asymmetric within a single year and variable between years (Eyles et al., 2007). That is, prior induction with the insect induced systemic resistance in the plants to subsequent fungal challenge in 2006 — but not in 2005. In 2005, fungal infection elicited induced systemic resistance against the insect. In both years, prior infection by the fungus induced systemic resistance against the same fungus. This was the first report in any tree of whole-plant induced systemic resistance against a defoliating insect induced by a fungal pathogen and *vice versa*.

At least with conifers, these studies have shown that SIR can be induced in trees ranging in size from small, 4-year-old potted saplings to large, naturally occurring or planted, field grown mature trees. Based on this evidence and that of others (e.g. Hatcher et al., 2004; Lappalainen & Helander, 1997; Raps & Vidal, 1998), the SIR hypothesis has been proposed, which predicts a dynamic interplay between trees, microbes, and herbivores (Bonello et al., 2006). This interplay can be either sustained or transiently expressed, depending on the damage level resulting from the induction event (Figure 1) (Bonello et al., 2006). If SIR is to be used as a management tool in forest protection and biosecurity, it must be fine-tuned so that a sufficient level of resistance is sustained without transitioning into what is defined as systemic induced susceptibility (SIS)

(Figure 1) (Bonello et al., 2006). It is hypothesised that it is the initial level of induction damage that determines whether SIR or SIS is induced and maintained in a tree (Figure 1). The induction of SIR or SIS also appears to be organ-dependent (Blodgett et al., 2007; Bonello et al., 2008). With such high levels of system-specific variability, the feasibility of implementing SIR in forest protection is likely to depend on the specific pathogen- or herbivore-system under scrutiny at a given place and time.

Even with such limitations, it is now indisputable that trees both possess and deploy inducible defence systems systemically and that these are mediated by signalling molecules that remain unknown at present. Knowledge of SIR elicitors (see, for example, Bonello & Blodgett, 2003; Hubbes, 1999) and signalling pathways in trees will be critical to the future deployment of practical forest pest management strategies. This is analogous to the recent development of products (such as the salicylic acid analogue acibenzolar-*S*-methyl; synonym BTH, trade name Actigard or BION) that induce natural resistance in crop plants (Vallad & Goodman, 2004). The best known example of a defence elicitor in trees is methyl jasmonate. This compound is a phytohormone that is well known to induce both molecular responses and resistance not only to necrotrophic pathogens but also chewing insects, at least in conifers (e.g. Erbilgin et al., 2006; Faldt et al., 2003; Hudgins & Franceschi, 2004; Krokene et al., 2008; Martin et al., 2002).

In summary, systemic resistance can be induced in trees under controlled and field conditions, and the effects have been described in some detail. However, the outcome of SIR may not always be predictable, in part because the genetic background of the individual trees or local populations may affect the amplitude or quality of the host response to induction. In this respect, screening individual lines or families for their inducibility may or may not be advisable/useful once an invasion is recognised in the field. Second, SIR could also be negated altogether by overriding effects from environmental variables, whose impacts on SIR we do not yet fully understand. Examples include lack of water due to drought, and either deficiency or excess of nutrients, all of which may be encountered even under the controlled silvicultural conditions found in plantations or urban environments.

Evidence of plant growth rate and nutrient availability effects on induced resistance

In many cases, it has been accepted that the way to increase the natural defences of trees has been to promote so-called "vigour" by reducing stress. Vigour is a rather subjective measure of "well being" that has almost always been equated to high growth rate or a good overall appearance of the crown. For example, increased vigour through fertilisation is one of the most
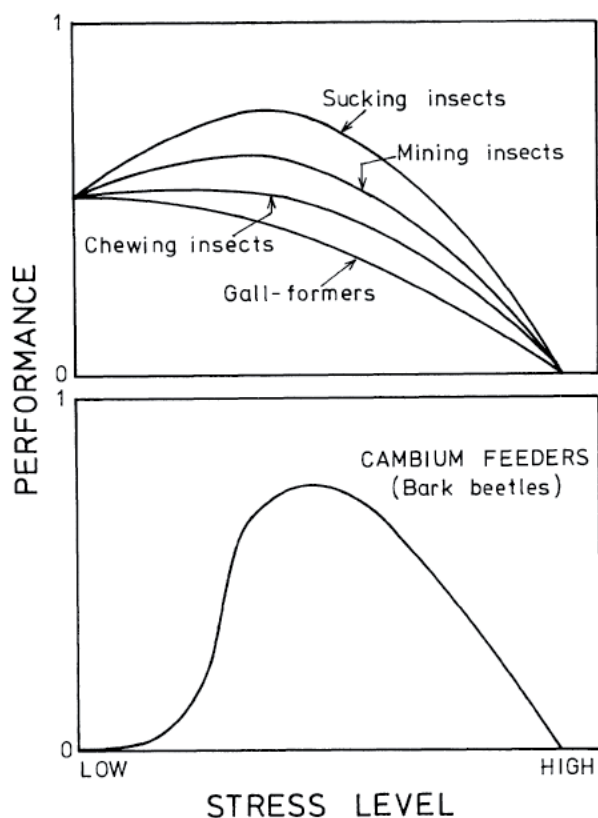
FIGURE 2: Hypothetical representation of insect performance in relation to host-tree stress level for different insect feeding guilds. From Larsson (1989): Reprinted, with permission, from *Oikos*, Volume 56, © 1989 by Wiley-Blackwell, http://www.wiley.com/.

common recommendations to increase the resistance of trees in controlled environments. In fact, vigour and pest resistance are often conflicting states for a plant.

A major review of 70 different studies by Koricheva, Larsson, & Haukioja (1998) illustrates the disconnect between stress and resistance in the case of insect pests. In the so-called 'plant stress hypothesis', plants under conditions of stress are presumed to be more susceptible to insect attack because the tissues become either more nourishing or concentrations of phenols are reduced. This hypothesis has almost become the standard model but, in reality, a large part of the evidence supporting the plant stress hypothesis is somewhat circumstantial. In their analysis, Koricheva, Larsson, & Haukioja (1998) showed that, in general, there is no relationship between abiotic stresses, such as water/nutrient deficiency or air pollution, and growth rate, fecundity, survival or density of colonisation by harmful insects belonging to a number of different functional groups, (sucking, leaf-mining, gall-forming, defoliating (chewing), and wood-boring guilds). These authors also noted a large variability in results associated mainly with the different guilds. The

performance of sucking and/or wood-boring insects is generally higher on stressed plants than healthy ones. In contrast, defoliating and/or gall-forming insects are disadvantaged. Ultimately, this analytical study/review confirmed the hypothesis of Larsson (1989) that the various guilds are favoured by a host under stress in the following order: wood-boring (such as cambium feeders) > sucking > mining > chewing > gall-forming insects (Figure 2).

In experiments where different levels of stress are examined, it is often noted that the performance of insects increases with stress up to a threshold level, but then decreases in a more or less quadratic function (Figure 2). This unintuitive observation means that moderately stressed plants are more susceptible than more severely stressed plants. This is a general observation but is especially found with cambium feeders, like bark beetles. The situation is further complicated by interactions between the environment, the genotype of the host plant, and the genetic background of the particular insect pest population. In each case, including defoliation, a very interesting result of the review by Koricheva, Larsson, & Haukioja (1998) was that insects may be more favoured by stress on fast growing (i.e. more vigorous) than on slow growing plants, at least in terms of survival (Figure 3). This suggests that alleviating stress by promoting plant growth (e.g. *via* fertilisation) may be counterproductive in the context of pest management.

It is essential to understand how plants respond physiologically to nutrient availability in order to predict the responses of insects to various situations of stress for the host. This understanding is particularly important for nitrogen, as this element is generally the most limiting) to plant growth in more or less natural settings. Various hypotheses have been proposed to model plant responses to variable availability of nitrogen. Almost all hypotheses involve a trade-off between conditions that favour plant growth (e.g. high nitrogen fertility) and accumulation of defensive compounds against insects and pathogens (mainly secondary metabolites) (Koricheva, Larsson, Haukioja, & Keinanen, 1998). Of the creditable plant defence hypotheses, perhaps the most mature (Stamp, 2003) is the 'growth-differentiation balance hypothesis' (GDBH) (Herms & Mattson, 1992). In situations where the net rate of assimilation (photosynthesis) reaches stable levels (saturation), the GDBH provides for compensation of carbon used for primary metabolism (basically, relative growth rate) with that used for incorporation into secondary metabolism (Figure 4). Herms (2002) showed that nitrogen fertilisation had either a zero or negative effect on the resistance of trees to pests in almost all cases in which it was studied. Cases in which higher vigour leads to increased susceptibility to insects have also been documented in situations of natural gradients of soil fertility (Herms, 2002). Work in our group has shown that high nitrogen fertility causes
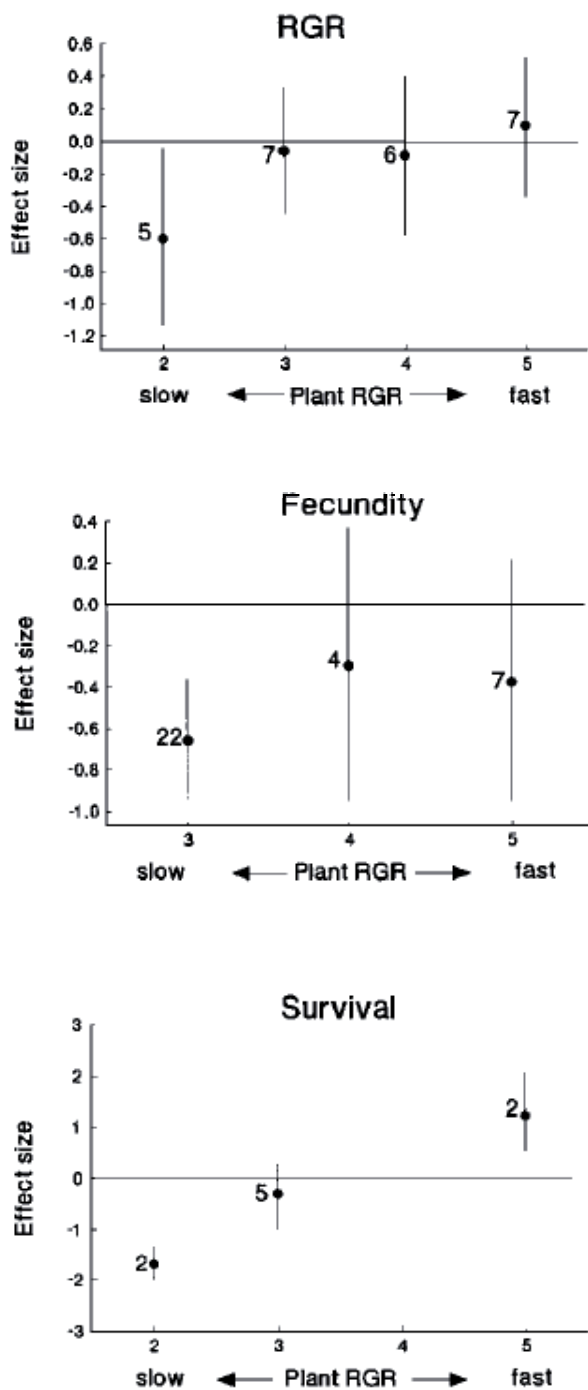
FIGURE 3: Mean effect sizes of stress treatments on the performance of chewing insects on plants with different relative growth rates (RGRs). Chart titles refer to insect traits. *Numbers adjacent to symbols* show the sample size; *vertical bars* indicate the 95% confidence interval (CI). Only survival was significantly affected by plant growth rate (*p* = 0.010). However, a tendency can be observed for all three traits toward a reduction on slow-growing plants. From Koricheva, Larsson, & Haukioja (1998). Reprinted, with permission of the author and the *Annual Review of Entomology,* Volume 43, © 1998 by Annual Reviews, http://www.annualreviews.org.

high susceptibility of *Pinus resinosa* Aiton (red pine) to *D. pinea.* This relationship is also directly associated with declines in the concentrations of both lignin and soluble phenolics (Blodgett, Herms, & Bonello, 2005).

Inducing resistance in trees through the accumulation of secondary metabolites is energetically expensive. Such resistance can only be supported by photosynthate translocated to the site of biosynthesis (Berryman, 1988; Miller & Berryman, 1985) and involves tradeoffs with growth and/or reproduction (e.g. Heijari et al., 2005; Heil & Baldwin, 2002; Moore et al., 2003). Thus, intense or extended stress that impairs a tree's ability to support defensive processes can lead to situations modelled by the leftmost side of Figure 4. For example, drought stress reduces induced secondary metabolite production in conifers and consequently lowers resistance (Croisé & Lieutier, 1993; Lewinsohn et al., 1993; Lombardero et al., 2000). Frischknecht, Bättig, & Baumann (1987) observed that wound-induced alkaloid accumulation (another form of secondary metabolite-based defence) was substantially decreased in drought stressed plants. These studies suggest that limitations in photosynthetic function (whether it is due to nitrogen limitation, drought stress, or even root disease) may lead to severe carbon stress. In turn, carbon stress may constrain biosynthesis of not only induced defences but also constitutive defences (leftmost side of Figure 4). Such constraints are likely to limit the effectiveness of any SIR programmes we may want to deploy.

Implications for applicability of systemic induced resistance to forest protection and biosecurity

The rapidly evolving field of SIR in trees holds great potential for pest control, as long as we remain aware of the limitations imposed by common environmental constraints. The above synthesis of existing literature on the responses of trees to forest pests is designed to caution the reader about the allure of a potential 'magic bullet' solution to pest control. In reality, no such solution currently exists for large natural or semi-natural forest areas.

In cases where a founding invasive pest population, whether exotic or indigenous, can be exactly circumscribed to a spatially limited location, and the pathogen/pest is not highly mobile (as is the case with a flying insect or a profusely sporulating fungus vectored by insects or dispersed by air currents), one can assume that induction of resistance might aid in the extinction or mitigation of that founding population. In such instances, we may elect to treat the host trees with currently known signalling molecules, such as acibenzolar-*S*-methyl or methyl jasmonate, to enhance resistance. It is also conceivable that biotic agents, or inactivated forms of biotic agents or their components (Bonello & Blodgett, 2003), could be used as elicitors.
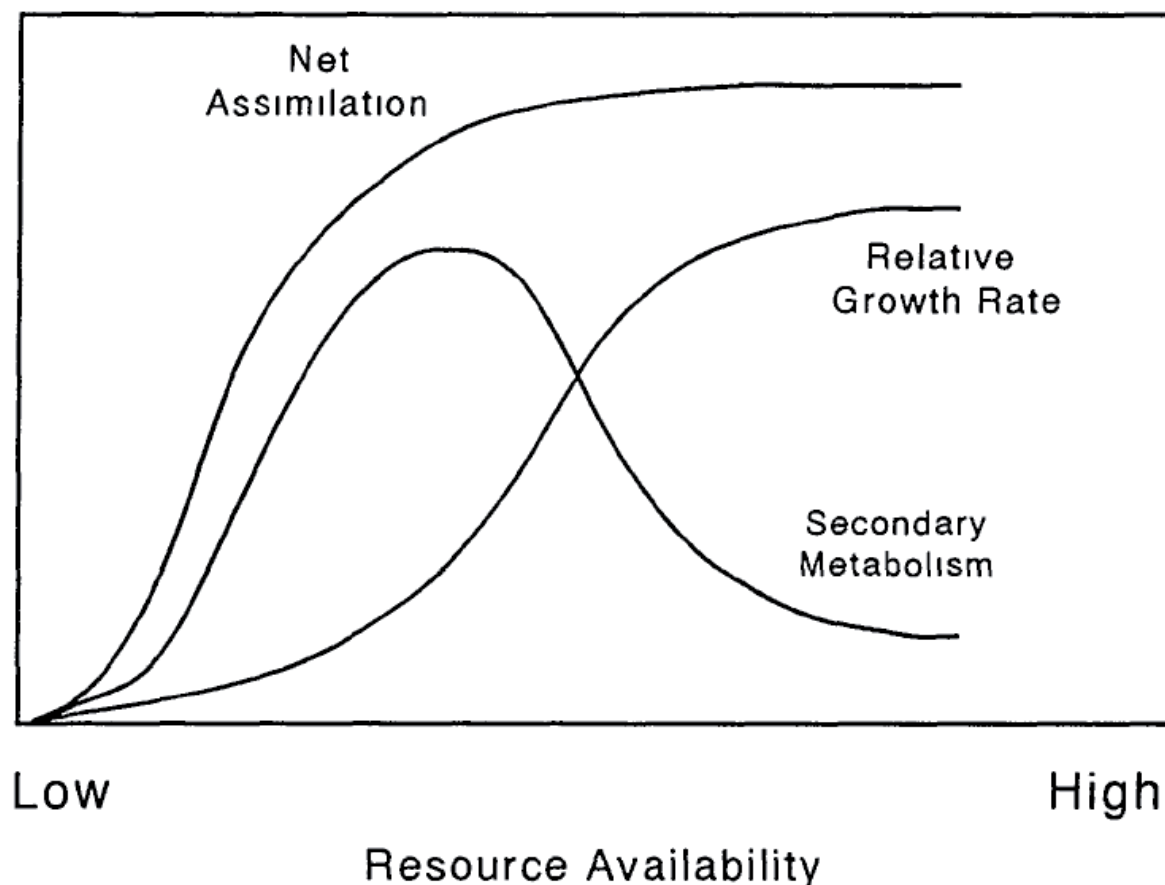
FIGURE 4: Norms of reaction for plant net assimilation rate, relative growth rate, and secondary metabolism in response to changing resource availability. Response scales are arbitrary. From Herms and Mattson (1992). Reprinted, with permission, from the *Quarterly Review of Biology*, Volume 67, © 1992 by University of Chicago Press, http://www.journals.uchicago.edu/.

Either of these approaches would require extensive testing to ensure the safety of the products and the avoidance of unintended consequences, including non-target effects, particularly if these approaches are considered for relatively large areas. Induction of resistance may also have negative tradeoffs with growth (Gould et al., 2008; Heijari et al., 2005), but the greater good of extinguishing a pest population may override such concerns, even in production forestry.

Although the limitations expressed above appear to be insurmountable at present, the use of induced resistance in forest protection and biosecurity should not be discounted. Other current approaches to affected forests stands involve either pesticides or sanitation by clear cutting and removal (e.g. by burning - Withgott, 2004). Induced resistance offers tremendous potential as a more benign approach, environmentally, than either of these. Ultimately, the question of whether SIR becomes a practical approach for forest protection and biosecurity (either alone or in combination with other management tools in integrated management programs) can only be addressed by conducting rigorous, in depth research to improve our understanding of the mechanisms that cause resistance, both within trees and at the stand level. This will only be possible if the stakeholders involved (government, academia, foresters, concerned citizen groups, etc.) make a concerted effort to secure the financial resources that are necessary to achieve this goal.

Acknowledgements

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