FORUM

Different strategies for studying ecological aspects of systemic acquired resistance (SAR)

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I am pleased that my original paper (Heil 1999) has prompted discussion on how the ecological aspects of responses of plants to pathogens (particularly systemic acquired resistance, SAR) should be investigated (Hatcher & Paul 2000; H & P hereafter). Our points of view differ in several aspects and further debate is to be encouraged.

H & P stress the potential interactions between SAR and other types of induced plant responses – for instance, against herbivores – and a large number of studies (including many conducted by Hatcher and co-workers, see H & P and Hatcher 1995) have indeed demonstrated important interactions between plants, herbivores and fungi. The two most important signalling pathways in induced plant defence are those mediated by salicylic acid (SA) and by jasmonic acid (JA). While some papers have suggested that there may be a positive interaction, most studies have revealed inverse relationships (Felton *et al.* 1999; Thaler *et al.* 1999). These 'trade-offs' (Thaler *et al.* 1999) may be the result of 'signal conflicts' (Bostock 1999), or even of direct inhibition. As far as I am aware, experimental evidence for a direct inhibition of SA-induced gene products by the JA signalling cascade or vice-versa is still lacking. Even if a direct inhibition could be demonstrated, the question of why this inhibition may have evolved remains unanswered. This question becomes even more pertinent given the numerous occasions on which plants growing in their natural habitat face multiple attacks by different herbivores and pathogens (Hatcher 1995).

I very much doubt that strong 'changes in conceptual frameworks' (H & P) will be needed in order to incorporate most aspects of SAR into current cost–benefit models of herbivore resistance (as outlined in Heil 1999). At least in annual species, fitness costs can be determined from reductions in seed set, whereas allocation costs (which themselves often result in fitness costs) can be measured by quantifying how limited resources are allocated. Nor do I think that an integrated approach considering all types of induced defence is required from the earliest stages of an investigation into SAR. For example, plants growing under limiting conditions require an effective defence, although they are constrained in what they are able to invest. According to the 'resource availability' hypothesis (Coley *et al.* 1985) and the 'growth-differentiation balance' hypothesis (Herms & Mattson 1992), plant species that are adapted to such conditions should invest relatively more in mobile or inducible, as compared to constitutive, forms of defence. This could be investigated by comparing the potential defence mechanisms of plant species that have different life forms and natural habitats. On the other hand, the constraints imposed when plants are actually exposed to limiting conditions will affect investment in both defence and growth, and might be the cause of the reported conflicts between different defensive pathways. Recent studies of both molecular (Longemann *et al.* 1995; Felton *et al.* 1999) and ecological (Heil *et al.* 2000) aspects, using the induction of defence in plants grown with only limited resources, have begun to provide evidence for such constraints and for an inhibition of primary metabolism. Results from studies using the cost–benefit approach are likely to suggest ecological and even evolutionary explanations for many aspects of SAR, which at the moment can only be described without any causal understanding.

Consideration of these questions becomes difficult if all the various forms of induced defence are to be included and the increasing complexity of the system may make comparative studies on different species impossible. Hatcher and co-workers choose the first of two possible approaches, whereby they concentrate on one system and try to explore all the interactions that occur. Although the entirety of the selected system can be investigated, such studies are extremely labour-intensive. Comparing different plant species is nearly impossible and it is difficult to draw conclusions concerning general mechanisms. My own approach is therefore to concentrate on more general aspects of a restricted number of

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defence mechanisms and to include the comparison of different species, which may make possible the generalization of results. For example, simply demonstrating that SAR incurs costs may suggest explanations for other, possibly general, aspects of induced defence mechanisms. Each of the two approaches has strong advantages as well as disadvantages but, in the long term, it is likely that a combination, or at least a synthesis of their results, will be needed for a real understanding of the various types of induced defence.

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References

Bostock, R.M. (1999) Signal conflicts and synergies in induced resistance to multiple attackers. *Physiological and Molecular Plant Pathology*, **55**, 99–109.

Coley, P.D., Bryant, J.P. & Chapin,F.S. III (1985) Resource availability and plant antiherbivore defense. *Science*, **230**, 895–899.

Felton, G.W., Korth, K.L., Bi, J.L., Wesley, S.V., Huhman, D.V., Mathews, M.C., Murphy, J.B., Lamb, C. & Dixon, R.A. (1999) Inverse relationship between systemic resistance of plants to microorganisms and to insect herbivory. *Current Biology*, **9**, 317–320.

Hatcher, P.E. (1995) Three-way interactions between plant pathogenic fungi, herbivorous insects and their host plants. *Biological Reviews*, **70**, 639–694.

Hatcher, P.E. & Paul, N.D. (2000) On integrating molecular and ecological studies of plant resistance: variety of mechanisms and breadth of antagonists. *Journal of Ecology*, **88**, 702–706.

Heil, M. (1999) Systemic acquired resistance: available information and open ecological questions. *Journal of Ecology*, **87**, 341–6.

Heil, M., Hilpert, A., Kaiser, W. & Linsenmair, K.E. (2000) Reduced growth and seed set following chemical induction of pathogen defence – does systemic acquired resistance (SAR) incur allocation costs? *Journal of Ecology*, **88**, 645–654.

Herms, D.A. & Mattson, W.J. (1992) The dilemma of plants: to grow or to defend. *Quarterly Review of Biology*, **67**, 283–335.

Longemann, E., Wu, S.-C., Schröder, J., Schmelzer, E., Somssich, I. & Hahlbrock, K. (1995) Gene activation by UV light, fungal elicitor or fungal infection in *Petroselium crispum* is correlated with repression of cell cycle-related genes. *Plant Journal*, **8**, 865–876.

Thaler, J.S., Fidantsef, A.L., Duffey, S.S. & Bostock, R.M. (1999) Trade-offs in plant defense against pathogens and herbivores: a field demonstration of chemical elicitors of induced resistance. *Journal of Chemical Ecology*, **25**, 1597–1609.