

Systemic acquired resistance: available information and open ecological questions

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Introduction

Systemic acquired resistance (SAR) in plants is a defence mechanism that can be induced by any one of a broad spectrum of pathogens against all of which it is then effective. The biochemical and molecular aspects of this response are rapidly becoming understood, at least for a few model organisms. The aim of this article is to draw ecologists' attention to this topic by outlining some of the ecological questions resulting from the physiological findings:

- 1 How widespread is SAR within the plant kingdom?
- 2 Does SAR fit into the framework provided by established theories on plant (anti-herbivore) defence?
- 3 What are the allocation costs and ultimately the fitness costs of SAR?
- 4 Why is SAR an inducible and not a constitutive defence?
- 5 What is the advantage of a defence induced systemically by a single pathogen, which then gives resistance against many others that are not yet causing any problems and which probably may never challenge the regarded plant?
- 6 Are there any functional or physiological relations between SAR and other biological interactions, for example mutualisms between plants and micro-organisms?
- 7 Do plants exist in nature that are older than seedlings that have not already been induced?

The many excellent reviews on the molecular aspects of SAR include those by Ryals *et al.* (1994), Hunt & Ryals (1996), Hunt *et al.* (1996), Ryals *et al.* (1996) and Schneider *et al.* (1996), and only a short overview is given here, before considering the ecological possibilities. Indeed, simply applying established ecological theories and models to the phenomenon (for example, examining SAR within the concept of fitness costs) may shed new light on this important type of plant defence.

SAR – a short synopsis

OVERVIEW

Infection by bacteria, viruses or fungi, induces many plant species to synthesize a signal at the site of infection.

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tion, which then spreads systemically throughout the plant. This leads to the expression of a broad-spectrum, long-lasting immunity in both infected and non-infected plant parts. Initially, this phenomenon was thought to be ubiquitous, and resistance was thought to be equally effective against many different pathogens (Ryals *et al.* 1994; Jackson & Taylor 1996 and literature cited therein), but more recent studies suggest intra- and interspecific variability (see later). The systemic reaction involves the production of chitinases, β -(1,3)-glucanases, lysozyme, permatins, and at least two more classes of so-called pathogenesis-related (PR) proteins (Ryals *et al.* 1996; Schneider *et al.* 1996) which may protect against further infections. Chitinases are particularly effective against several pathogenic fungi (Boller *et al.* 1983; Schlumbaum *et al.* 1986; Sahai & Manocha 1993), and the efficacy of SAR against a variety of bacteria, viruses and fungi has also been demonstrated convincingly (Boller *et al.* 1983; Hoffland *et al.* 1996; Anfoka & Buchenauer 1997; further literature cited in Schneider *et al.* 1996). A main characteristic of SAR is that the induced defence does not depend directly on the type of inducing pathogen. For example, pretreatment with bacteria (*Pseudomonas fluorescens* strain WCS417) protected radish (*Raphanus sativus*, Brassicaceae) against a fungal root pathogen as well as a bacterial and two different fungal leaf pathogens (Hoffland *et al.* 1996), and inoculation of tomato plants with tobacco necrosis virus elicited resistance against the fungus *Phytophthora infestans* (Oomyceta) (Anfoka & Buchenauer 1997).

THE SIGNALLING PATHWAY

The PR proteins produced in response to pathogens can also be induced by the plant hormone ethylene (Linthorst *et al.* 1996), or by stress, including mechanical wounding (Ignatius *et al.* 1994). SAR can also be induced experimentally by the application of certain chemicals, most notably salicylic acid (SA) and benzothiadiazole (Friedrich *et al.* 1996; Görlach *et al.* 1996; Lawton *et al.* 1996). Although the induction of chitinases and β -(1,3)-glucanases by the stress hormone ethylene has been shown in several plant species (Boller *et al.* 1983; Vierheilig *et al.* 1994 and literature cited therein), the pathway leading from a first and

locally restricted infection to the systemic response is not yet well understood. SA seems to be involved in this transduction (Malamy *et al.* 1990; Métraux *et al.* 1990; Delaney *et al.* 1994; Hunt *et al.* 1996; Thulke & Conrath 1998) but it may not be the primary transported signal (Rasmussen *et al.* 1991; Vernooij *et al.* 1994; Willits & Ryals 1998), although SA can indeed be synthesized in one leaf and translocated to the next (Shuaev *et al.* 1995; Mölders *et al.* 1996). It has also been shown to inhibit catalase activity, and elevated levels of H₂O₂ could thus function as the second messenger (Chen *et al.* 1993). However, the absence of any increase of H₂O₂ in uninfected leaves at the onset of SAR gene activation, and the phytotoxic levels needed for SAR induction (Hunt *et al.* 1996; discussed in Schneider *et al.* 1996), together with the high reactivity of H₂O₂, make it rather improbable that this component is translocated over large distances.

INTRA- AND INTERSPECIFIC VARIABILITY

Although parts of the signalling pathway seem to be highly conserved in evolution, and thus occur in all plant species so far investigated (e.g. in *Arabidopsis* as well as in tobacco), the type, amount and time-course of the response depends on the precise identity of both partners (Schneider & Ullrich 1994; Schneider *et al.* 1996; Botha *et al.* 1998). Thus SAR gene expression was first detected in tobacco about 6 days after inoculation (Ryals *et al.* 1994), but as early as 7 hours after a primary infection in cucumber (Schneider *et al.* 1996): in both species, patterns in the activity of the various hydrolytic enzymes depended on the inducer (Schneider & Ullrich 1994).

Variation occurs in particular with respect to the efficacy of defence. For example, *Arabidopsis thaliana* ecotypes vary in their resistance to cauliflower mosaic virus (Callaway *et al.* 1996), and *nim 1* mutants (non-inducible immunity) differ in PR-1 production, while *eds* (enhanced disease susceptibility) mutants have distinguishable phenotypes with respect to the susceptibility to pathogenic bacteria. Some lines of barley differ in their ability to produce chitinases and glucanases (Ignatius *et al.* 1994; Hunt & Ryals 1996; Hunt *et al.* 1997; Rogers & Ausubel 1997; Ryals *et al.* 1997; Shah *et al.* 1997). The various chitinases that occur within the same species may differ in location, activity, chitin-binding property and catalytic mechanism, and thus allow the plant to match many different requirements (Sahai & Manocha 1993; Iseli *et al.* 1996). β -(1,3)-glucanase, ribosome-inactivating proteins and permatins may also occur in the form of several isozymes (Darnetty *et al.* 1993).

Genes for some proteins belonging to the PR-1 subfamily may be expressed continuously, at least in shoot meristems and trichomes (Torner *et al.* 1997). As shoot meristems are especially valuable and vulnerable, whereas trichomes in most plants are involved in defence mechanisms, this finding may be

interpreted as a hint on relevant costs of SAR (see below).

SAR as a promising area for ecological research

INTERSPECIFIC VARIABILITY: HOW WIDESPREAD IS SAR?

Of 45 research articles or meeting abstracts on SAR published during 1996 and 1997, 24 were conducted using *Arabidopsis* or tobacco as the model organism, another 13 referred to cucumber, potato or tomato, and only eight presented data derived from other species; the 25 earlier papers listed by Schneider *et al.* (1996) describe a total of 17 plant species. A similarly restricted picture is apparent from the literature on chitinase (overviewed by Sahai & Manocha 1993).

The vast majority of these species are short-lived and fast-growing annuals, but known SAR markers, direct measurements of enzyme activities, or bioassays could be used to investigate the frequency of SAR in a wide range of species. So far, predominantly chitinase activity has been demonstrated for plants with other life histories, e.g. *Urtica dioica* (a chitinase of stinging nettle was characterized genetically by Lerner & Raikhel 1992), the rubber-tree *Hevea brasiliensis* (van Parijs *et al.* 1991) or poplar *Populus* sp. (Clarke *et al.* 1998). Information is needed on the time taken to establish SAR as well as the production and persistence of SAR-related mRNA and proteins after a single challenging infection. Data from a few annual species are insufficient to evaluate the adaptivity and ecological importance of SAR, or to determine whether plants with different life histories (e.g. annuals compared to long-lived trees) differ in their response.

SAR AND MUTUALISTIC INTERACTIONS

SAR is studied mainly in the context of plant-pathogen interactions, but may also be relevant to mutualistic interactions. Recent papers reported an induction of SAR by non-pathogenic root-colonizing bacteria (Pieterse *et al.* 1996; Raupach *et al.* 1996; van Wees *et al.* 1997), although the establishment of vesicular-arbuscular (VA)-mycorrhizas seems not to induce systemic reactions in host-plants (Vierheilig *et al.* 1994; Lange *et al.* 1996). SAR in cucumber and *Arabidopsis* has also been reported to be induced by compost and compost water extracts, an effect destroyed by autoclaving the compost mix and therefore most probably caused by soil-living micro-organisms (Zhang *et al.* 1998). This observation in particular leads to the question of whether any plant does exist in nature that has not already been induced by the influence of either abiotic or biotic agents.

Mutual symbioses with endophytic fungi that have evolved in several grasses and trees participate in the plants' anti-herbivore defence by providing secondary

metabolites, especially neurotoxic alkaloids (Clay 1990). However, little is known about the interactions between the defence mechanisms established during SAR and mutualistic endosymbionts, but it is likely that the considerable indirect cost of SAR will result from its antagonistic effects on mutualistic organisms.

SAR and theories on plant defence

Can intra- and interspecific patterns in type, extent and time-course of SAR be accounted for by existing theories of chemical defence in plants, which in most cases are formulated as an anti-herbivore response?

INDUCIBLE VS. CONSTITUTIVE DEFENCE

In contrast to the human immune system in which specific antibodies are produced as a reaction to each distinct antigen, SAR – once induced by a single pathogen – provides protection against a range of different pathogenic organisms. It is difficult to understand, given the evidence for continuous PR gene expression (Tornero *et al.* 1997), why a first – and probably severe – infection is required rather than systemic resistance being constitutive. A model proposed by Karban *et al.* (1997) points out that induced chemical defence may be more effective against herbivores than constitutive resistance. Small amounts of toxin may hardly reduce the herbivore's benefit from feeding on plant tissue, but increasing toxin levels may cause a progressively greater decrease in benefit at higher levels. The authors demonstrated mathematically that, in this case, variable toxin levels will lead to a lower benefit for the herbivore than the continuous presence of the corresponding mean level. Plants differ in their level of constitutive and inducible defence against pathogens (Keen 1992), and the applicability of this model to SAR could therefore be tested by quantifying the effects on the fitness of both plants and pathogens for host-plant species with different levels of inducible defence.

ALLOCATION AND FITNESS COSTS

Most theories on plant defence, however, assume that there will be a cost to fitness resulting from the production of defence chemicals or structures, which at least must be balanced by the resulting benefit. Inducible defence may thus reduce the overall costs by producing chemicals only when their function is actually required. Ecological costs should ideally be measured as reduction in fitness, i.e. fewer offspring will be produced because of the operation of the trait considered (Simms & Rausher 1987; Marquis 1991; Sagers & Coley 1995). Although, at least in long-lived species, fitness costs are hard to quantify directly (Chapin 1989), several studies have demonstrated that fitness costs may be estimated by measuring reduction in growth rates (Coley 1986; Sagers & Coley 1995;

Steinberg 1995 for empirical studies; Skogsmyr & Fagerström 1992 for a theoretical model). Because resources invested in one distinct trait are no longer available for other functions such as reproduction, fitness costs may be estimated in terms of allocation costs, for example by calculating energy and construction costs (Penning de Vries *et al.* 1974; Gulmon & Mooney 1986; Skogsmyr & Fagerström 1992; Gershenson 1994; Griffin 1994; Simms & Triplett 1994) or simply by quantifying the allocation of limited resources such as nitrogen (Evans & Black 1993).

To my knowledge, only three studies have so far been published that attempt to quantify the costs of resistance against pathogens, and their results do not allow any generalization about the possible costs of SAR. Simms & Triplett (1994) were not able to detect fitness costs of resistance of *Ipomoea* spp. to anthracnose, nor could Simms & Vision (1995) prove direct allocation costs of localized resistance of young *Ipomoea* plants. In an attempt to use reduction in germination success to quantify the costs of anti-fungal resistance to different *Avena fatua* lines, Burdon & Müller (1987) obtained contradictory results from their greenhouse and field studies. However, SAR can be induced chemically in wheat by application of BION[®] (benzo (1,2,3) thiadiazole-7-thio-carbonic acid S-methyl ester; NOVARTIS, Basel, Switzerland) (Friedrich *et al.* 1996; Görlach *et al.* 1996; Lawton *et al.* 1996), and preliminary results from field studies (M. Heil, personal observations) show that treatment of plants with BION reduced the number of seeds produced. Data from several *Macaranga* species, which have evolved obligate or facultative mutualisms with ants to protect them continuously and very effectively against herbivory and secondary infections (Fiala *et al.* 1989, 1994), offer similar hints as to the costs of SAR. Chitinase activities were lower in three *Macaranga* species than in species from other genera that show no mutualistic interactions with ants. *Macaranga* plants thus seem to have a remarkably low ability to produce at least one class of PR proteins, and no costs are incurred by the production of compounds that are not required in these plants due to the effective anti-herbivore and anti-fungal defence provided by the ants (Heil *et al.* 1999).

SAR AND THEORIES ON ANTI-HERBIVORE DEFENCE

The 'optimal defence' hypothesis (Rhoades 1979) assumes that defence is most important and thus should be most intensive in those parts that are most valuable to the plant, such as young leaves and shoot meristems. In contrast, the 'growth-differentiation balance' hypothesis (Herms & Mattson 1992) assumes a metabolic competition between processes involved in plant growth and 'differentiation' processes necessary for, for example, the synthesis of defence chemicals. This competition should reduce the resources

available to defend still growing tissues, and young leaves and shoot meristems should therefore be the least defended parts of a plant. The production of SAR-related proteins instead of proteins that are relevant for growth, the diversion of products of the shikimic acid pathway (Schneider & Ullrich 1994) to synthesize anti-bacterial phenolic compounds rather than aromatic amino acids, and enhanced lignification as reported by Hammerschmidt & Kuc (1982) and Barber *et al.* (1989), suggest that SAR may incur costs in terms of competition for limited resources.

The clear set of physiological data given by Herbers *et al.* (1996) allows the two theories to be evaluated. The induction of PR protein transcripts in tobacco leaf discs floated on solutions of different sugars depended strongly on leaf developmental stage. Older leaves were highly inducible, while the same concentration of sugars failed to elicit a clear response in leaves that were not yet fully unfolded. It is difficult to use source-sink relationships to explain why only those leaves that produce high amounts of sugars by photosynthesis should be able to use these sugars as signal molecules, but according to the hypothesis of Herms & Mattson (1992) young, still growing, leaves may just be unable to produce PR proteins simply because their whole metabolic apparatus is needed for the biosynthesis of growth-relevant proteins. At least for this example, the 'optimal defence' hypothesis, which would predict high defence levels especially in the young leaves, can be discounted. Further studies using different inducers and comparing their efficacy in dependence on leaf age and developmental stage are needed, however.

PHYSIOLOGICAL RELATIONS BETWEEN SAR AND ANTI-HERBIVORE DEFENCE

Unlike SAR, studies on chemical anti-herbivore defence have so far mainly focused on ecological problems and cost-benefit models rather than signalling pathways and resulting gene activities (Hammerschmidt 1993). However, the signalling pathway of SAR, and the octadecanoid pathway (Doares *et al.* 1995) which is involved in induced resistance against herbivores, may interact. Jasmonic acid, a central signal of the octadecanoid pathway, is produced within a few minutes after insect feeding (Blechert *et al.* 1995) and leads to an activation of several defence genes (Doares *et al.* 1995). The application of jasmonic acid also induces the production of PR proteins and therefore resistance against phytopathogens (Cohen *et al.* 1993; Schweizer *et al.* 1993). Although salicylic acid can lead to enhanced resistance of cotton to both insects and phytopathogens (Khoshkhoo *et al.* 1993), Bi *et al.* (1997) failed to identify SA as a signal in the anti-herbivore defence of this species, and Korth & Dixon (1997) also demonstrated that pathways leading to anti-herbivore defence are not activated by abiotic damage.

In this case, an ecological point of view can again provide a framework for understanding the physiological findings. In nature, herbivore attack or mechanical wounding often leads to secondary pathogen attack, and using primary wounding as a signal for the induction of SAR enables the plant to be prepared for probable secondary pathogen attacks. On the other hand, herbivores seldom use heavily infected plant parts as a food source, and induction of anti-herbivore defence by signals derived from pathogen attack would therefore probably lead to the synthesis of superfluous defence molecules.

Progress in ecology essentially needs testable theories as well as pluralism and diversity in new approaches (Weiner 1995). The application of specialized theories to a broader spectrum of findings often paves the way for rapid scientific developments, and the combination of formerly separated scientific disciplines can also result in new insights. Integration of SAR into ecological field research should thus provide the possibility for successful further research.

Acknowledgements

I wish to thank my supervisor, K.E. Linsenmair, University of Würzburg, for allowing the time necessary to spend on the literature search and on conducting the field studies on SAR. Many thanks also to K.E. Linsenmair, B. Fiala, W. Kaiser, R. Riedel, C. Merell and two anonymous referees for helpful comments on earlier versions of the manuscript. Finally I would like to thank the managing editor of this journal, Dr L. Haddon, for kindly improving my English.

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