LETTER TO THE EDITOR

FITNESS COSTS OF CHEMICALLY-INDUCED RESISTANCE: DOUBLE EDGED SWORD OR (UN)STABLE EQUILIBRIUM?

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Plant fitness costs are referred to as the trade off between resources allocated for growth and reproduction and disease resistance. Nevertheless, plants have coevolved with their enemies, thus relying on the sustainability of costs involved in defence response under natural conditions. At the cultivar level, the gap left by insufficient pre-infectional barriers is filled by a set of reactions that follow pathogen recognition and lead to systemic acquired resistance (SAR).

In this view, inducible defence mechanisms may have been favoured by natural selection whenever their efficacy could be coupled with minimized costs. By adopting induced resistance as a facultative trait, plants have acquired some benefits over a constitutive defence strategy. They avoided the diversion of essential available resources from growth and breeding and the accumulation of auto-toxic secondary metabolites, when not under pathogen pressure (Heil, 2002). The emergence of agriculture, around 10,000 years ago, inevitably altered this scenario, unbalancing the equilibrium between constitutive and inducible defence systems. Crops selection, mainly addressed to quality and yield traits, has inadvertently led to the loss of defence alleles.

Recently, a novel class of chemicals, known as resistance inducers or plant activators, have been introduced for crop protection. They act by priming the plant for a long-lasting, broad-spectrum and systemic immunity, the same as, or similar to, that triggered by pathogen-associated molecular elicitors. Apparently they mimic the matching between genes for host resistance (*R*) and those for pathogen avirulence (*avr*), giving rise to SAR (Gozzo, 2003). The immunized plant acquires enhanced competence in activating a rapid and strong defence system that does not become evident until it is challenged by the pathogen, when an effective defence response actually occurs (Conrath *et al*., 2001). Accordingly, the plant does not necessarily incur appreciable fitness costs, even though a feeling to the contrary is sometimes perceived, as emerged during the recent Symposium on "Induction of Resistance in Plants", organized by the Italian Society for Plant Pathology at the VII National Meeting of the Italian Federation for Life Sciences (FISV, Riva del Garda, September 2005).

At present, data reported on fitness costs in enemy-free systems are contradictory, depending on plant, elicitor, micrometeorological and environmental conditions, plant nutritional and growth status (Heil *et al*., 2000; Iriti and Faoro, 2003). As a matter of fact, fitness costs of chemically-induced resistance become evident only when defences are elicited under conditions in which processes involved in plant growth are forced to compete with those required by SAR. In other words, the fitness cost of chemically-induced resistance remains under a detectable threshold as long as sufficient resources are available. Last, but not least, enhancement of plant growth and yield, as well as improvement of foodstuff quality and plant cross tolerance to insect diseases and abiotic stresses have been frequently reported after SAR induction (Inbar *et al.* 1998; Reddy *et al*., 1999; Bittelli *et al.,* 2001; Ait Barka *et al*., 2003; Iriti *et al*., 2003; Cooper *et al*., 2004; Kim *et al*., 2005). Moreover, chemical activators can improve the efficacy of other plant defence strategies, such as induced systemic resistance (ISR) by plant growth promoting rhizobacteria (PGRP) (Zehnder *et al*., 2001).

Thus, in spite of the criticism, and the obvious complexity of evaluating fitness costs, due to the variability of systems, research progress in this area would be greatly welcome. The recent finding that chemical elicitation can increase the nutraceutical content of plant products adds a further stimulus (Verpoorte *et al*., 2002). Up to now only observed in cell suspension culture systems, this approach should be exploited *in planta*, in view of the number of benefits for human health expected by a regular consumption of enriched plant foods (Poulev *et al*., 2003; Iriti *et al*., 2004, 2005). Finally, a crop protection strategy based on chemically induced resistance appears to be safer for the environment than the use of residual pesticide. Besides preserving plant biodiversity, it is less prone to incur selection of fungicide-resistant pathogen strains by virtue of the multigene complex regulated by resistance inducers.

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