Trade-Offs Between Induced and Constitutive Resistance in Two Pine Species: Secondary Chemistry, Effective Antiherbivore-Resistance, and Effect of Nutrient Availability

Luis Sampedro,[1] Xoaquín Moreira,[2] and Rafael Zas[2]

Abstract

Constitutive chemical defenses, always expressed in the plants, and plastic defensive responses, those mobilized in response to plant injury or other cues or herbivory risk, differ in their benefits in terms of fitness for long-lived plants. Induced defenses are considered to be less expensive than constitutive preformed defenses since the cost is realized only when required. Plant defense theory predicts that, as secondary metabolism is costly for the plant, presenting effective levels of constitutive defenses and the ability of expressing efficient inducible defenses by a plant are two resource-related attributes that are not likely to be maximized at the same time. Furthermore, selective pressure favoring the expression of induced responses is likely to be lower in those lineages well defended constitutively, as they would be less subjected to herbivore attacks. A negative, non-spurious genetic correlation between constitutive and inducible defenses illustrates this classical trade-off. The existence of these evolutionary conflicts has been suggested often in the literature and sometimes reported for angiosperms, but rarely in conifers and not yet in pine trees. Besides, the emergence of this genetic constraint could be hidden by environmental factors affecting growth potential, such as nutrient availability.

In this paper we present the results from three independent experiments aimed to explore the existence of this trade-off in 2-year-old seedlings of Maritime pine (*Pinus pinaster* Aiton) and Monterey pine (P. *radiata* D. Don), native from similar climate regions in Europe and North America. We used 22 mM methyl-jasmonate (MJ), a fitohormone involved in the biosynthetic pathways of chemical defenses, to induce pine defensive responses. In the first experiment, we analyzed the secondary chemistry of constitutive (control) and MJ-induced *P. pinaster* seedlings belonging to 18 half-sib families from the Atlantic population of Galicia (northwest Spain). One month after induction, we performed an *in vivo* feeding bioassay with a generalist insect herbivore (the large pine weevil, *Hylobius abietis*) to check how the expressed defenses reflected the ability to resist the attack. In the second experiment, we reproduced the same design with 34 half-sib families belonging to *P. radiata*. In the third experiment, we analyzed this trade-off in a wider collection of *P. pinaster* genetic entries (33 half-sib families) grown either in low- or in high-phosphorus availability, to test if this trade-off could be dependent on environmental context. We explored the existence of trade-offs regressing the difference in mean resistance levels between experimentally MJ-induced individuals and control individuals from a given family (induced-control) against the family means of control treatment. Correlations were checked not to be spurious by means of Monte-Carlo analysis.

We identified, in both species, strong negative genetic correlations between induced and constitutive concentrations of total polyphenolics, resin content, and effective resistance against weevil and caterpillar damage, with R^2 ranging from 0.38 to 0.80 (all relationships significant at $P < 0.001$). Negative genetic correlations observed under complete fertilization in *P. pinaster* appeared to be likely spurious, providing evidence that this trade-off is context dependent.

[1]Centro de Investigación Forestal de Lourizán – UA MBG-CSIC, Apdo 127, 36080 Pontevedra, Galicia, Spain.
[2]Misión Biológica de Galicia, MBG-CSIC, Apdo. 28, 36080 Pontevedra, Galicia, Spain.
Corresponding author: lsampe@uvigo.es.