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SHORT COMMUNICATION

Evolutionary consequence of indirect interactions among insect herbivores through herbivore-induced plant regrowth

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The questions of how the indirect interactions mediated by herbivore-induced plant responses influence trait evolution of herbivores have been poorly investigated. We previously demonstrated that allopatric populations of the willow leaf beetle, *Plagiodera versicolora* (Coleoptera: Chrysomelidae) could evolutionarily develop divergent preference, according to locally distinct intensity of induced plant regrowth. Our herbivore removal experiment suggested that the local intensity of herbivore-induced regrowth strongly influenced the geographic variation in the plant regrowth response. Furthermore, attack by another herbivore species could induce willow regrowth, which in turn increased the relative fitness of the beetles with strong preference for new leaves compared with the beetles with weak preference. Therefore, we conclude that the plant-utilizing trait of the leaf beetle can evolve in response to indirect effects of other herbivore species mediated by herbivore-induced plant regrowth.

Keywords: adaptive evolution; herbivore-induced plant response; preference; trait-mediated indirect interaction

Terrestrial plants show a wide range of phenotypic changes in response to biotic and abiotic damage (Ohgushi 2005). In the past two decades, ecological studies have revealed that the abundance, survival, and reproduction of herbivorous insects are indirectly influenced by other herbivore species because of herbivore-induced phenotypic changes in host plants (e.g. Utsumi and Ohgushi 2008). However, the questions of how the indirect interactions mediated by herbivore-induced plant responses influence evolution of community members have been poorly investigated. Because induced plant responses as well as genetic variation in the host plants can generate phenotypic variation within plant populations, herbivore-induced plant responses may have profound evolutionary consequences for physiology, behavior, and life history of herbivore species (Fordyce 2006; Utsumi, forthcoming).

In a willow-insect system, attack by several herbivore species induces regrowth response of willows. For example, stem-boring by a swift moth caterpillar *Endoclita excrescens* enhances new lateral shoot production in three willow species *Salix gilgiana*, *S. eriocarpa*, and *S. serissaefolia* (Utsumi and Ohgushi 2007). Because changes in foliar quality and phenology are involved in the response, herbivore-induced regrowth significantly influences densities of several herbivorous insects (Utsumi et al. 2009b; Utsumi and Ohgushi 2009). Here, we report that herbivore-induced plant regrowth

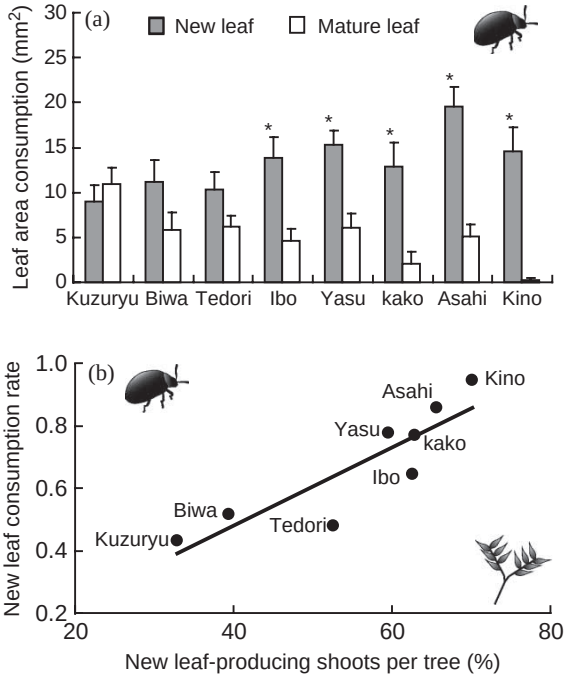

Figure 1. Among-population variation in feeding preference. (a) Consumed area of leaf disks of new and mature leaves in the choice test for the eight local populations of *P. versicolora*. An asterisk indicates significant difference between consumed area of new and mature leaves after Bonferroni correction ($P < 0.05$). (b) The relationship between the rate of new leaf consumption in the choice test and the proportion of new leaf-producing shoots per tree in the field in early summer. Reproduced with permission from Utsumi, Ando, and Ohgushi (2009a), Copyright Wiley.

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promotes a locally adaptive feeding preference of a leaf beetle, *Plagiodera versicolora*.

We found among-population variation in the strength of the feeding preference of the leaf beetle adults for leaf-age types of *S. eriocarpa* (Figure 1a). The strength of the preference was positively correlated to new leaf production of host plants across populations (Figure 1b). Our herbivore removal experiments suggest that geographic variation in the new leaf production was likely to be resulted from difference in the intensity of herbivore-induced regrowth (Utsumi et al. 2009a).

We detected a significant additive genetic variance and heritability in the preference for consuming new versus old leaves. The strength of the preference was significantly related to egg production depending on the leaf-age types (Utsumi et al. 2009a). Moreover, experimental inoculation of one of the major herbivores on willows, *Clostera anastomosis*, enhanced new lateral shoot production of *S. eriocarpa*, which in turn resulted in greater relative fitness of the leaf beetle populations with strong preference for new leaves than the populations with weak preference.

In conclusion, allopatric populations of the leaf beetle can evolutionarily develop divergent adaptive preference, according to locally distinct patterns of herbivore-induced host regrowth. In other words, the plant-utilizing trait of the leaf beetle can evolve in response to indirect effects of other herbivore species mediated by herbivore-induced plant regrowth.

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