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Contrasting consequences of plant domestication for the chemical defenses of leaves and seeds in lima bean plants

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Abstract

Plant domestication is assumed to result in reduced levels of defensive compounds in crops, because this makes the plants more suitable for consumption by humans and livestock. We argue that this should mainly be reflected in the concentrations of defense compounds in the plant parts that are used for consumption and not necessarily for other parts of crop plants. We tested this hypothesis for domesticated lima bean (*Phaseolus lunatus*), by comparing its chemical defenses against a leaf herbivore, the beet armyworm *(Spodoptera exigua),* and a seed predator, the beetle *Zabrotes subfasciatus*. For seeds and leaves we determined the concentrations of cyanogenic glycosides (CNGs) in cultivated varieties and wild populations and evaluated the preference and performance of the herbivores when exposed to leaves and seeds from wild and cultivated plants. Concentrations of CNGs were significantly different between wild and cultivated plants. In the leaves the concentration of CNGs in the cultivated varieties were more than double that of the wild leaves. In contrast, seeds from cultivated plants had up to 20 times lower CNG concentration compared to seeds from the wild populations. Insect preference and performance do not parallel the chemical data. Larvae of *S. exigua* preferred wild leaves but had higher survival on cultivated leaves. The beetles, however, strongly preferred seeds from cultivated plants and females developed more quickly on these seeds. We conclude that domestication of *P. lunatus* has altered the concentration of CNGs in both the seeds and the leaves in opposite directions. This results in differential effects on the herbivores that attack these two plant structures. The contrasting effect of domestication on different plant tissues can be explained by the fact that bean plants have been specifically selected for human consumption of the seeds. Tissue-specific effects of plant domestication on plant defenses can be expected for other crops as well.

Keywords: Cyanogenic glycosides; Domestication; Seed predator; Herbivore

Introduction

Comparative studies of species interactions using plant systems in which cultivated and wild varieties coexist, provide an opportunity to examine how alterations in plant traits

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affect herbivores and their natural enemies in the same environment. Recently there has been an increasing interest in using wild and cultivated systems to study species interactions (Turcotte, Turley, & Johnson 2014; Chen, Gols, & Benrey 2015; Chen, Gols, Stratton, Brevik, & Benrey 2015; Milla, Osborne, Turcotte, & Violle 2015; Rowen & Kaplan 2016; Whitehead, Turcotte, & Poveda 2017). Artificial selection has directly or indirectly altered the defensive chemistry, architecture, and/or nutritional content of cultivated plants in a relatively short time span. Contrasting these cultivars with their wild counterparts can shed light on the way in which specific changes on plant traits can mediate species interactions.

Studies comparing cultivated and wild species have, in general, found that cultivated plants offer a better resource for herbivores (Rosenthal & Dirzo 1997; Benrey, Callejas, Rios, Oyama, & Denno 1998; Gols et al. 2008; Rodriguez-Saona et al. 2011). As a result of selective breeding, domesticated plants and their wild counterparts often differ substantially in their physical defense traits, allelochemistry, and nutrient content (Gouinguené, Degen, & Turlings 2001; Chen & Welter 2007; Wang et al. 2009; Delgado-Baquerizo, Reich, García-Palacios, & Milla 2016; Rowen & Kaplan 2016). In many cases the defensive chemistry of cultivars has been drastically reduced (Gols et al. 2008; Chacón-Fuentes et al. 2015; Whitehead et al. 2017). The pattern of reduced resistance to herbivory in domesticated crops has not been consistent across cultivated plants and their herbivores (Chen, Gols, Stratton et al. 2015; Gaillard, Glauser, Robert, & Turlings 2018; Turcotte et al. 2014), although there is evidence that changes in secondary metabolites (most often a reduction) happen to more than half of crop plants (Meyer, DuVal, & Jensen 2012). An extensive analysis of plant resistance across 29 domestication events using two generalist herbivores, the beet armyworm (*Spodoptera exigua*), and the green peach aphid (*Myzus persicae*) found that domestication significantly reduced plant resistance to attack by armyworm but did not have an effect on plant resistance to aphids (Turcotte et al. 2014). In addition, they found that different plant traits were associated with insect resistance to these two species of insects. Further, the pattern of resistance associated with domestication varies across location, history of domestication, and the form or life stage of the plant examined (Meyer et al. 2012; Chen, Shapiro, Benrey, & Cibrián-Jaramillo 2017; Whitehead et al. 2017).

We propose that the effects of domestication may be tissue-specific and dependent on which part of the plant has been bred for consumption. A recent review by Chen, Gols & Benrey (2015) makes the same argument, but points out that as yet the evidence for this notion is scarce. Here we test this hypothesis of tissue-specific domestication effects on plant defenses by comparing chemical defenses and insect performance for leaves and seeds in wild and domesticated lima bean.

Phaseolus lunatus (lima bean), was domesticated at least twice, once in the Andean mountains of Ecuador and Northern Peru, and a second time in central-western Mexico (Motta-Aldana, Serrano-Serrano, Hernández-Torres, Castillo-Villamizar, & Debouck 2010). Once domesticated it spread throughout the Americas, and now is widely distributed in the tropics. Domestication of beans in the genus *Phaseolus* has dramatically altered morphological, chemical and nutritional traits. For cultivated beans these changes mainly involve an increase in seed and pod size, decrease in shattering, an overall decrease in toxins, and an increase in proteins and minerals (Salinas 1988; Sotelo, Sousa, & Sanchez 1995; Beebe, Gonzalez, & Rengifo 2000; Cuny, Shlichta, & Benrey 2017).

Lima bean is unique in that it is the only reported species out of approximately 52 species in the genus *Phaseolus* that contains cyanogenic glycosides (CNGs) in both the leaves and the seeds (Vetter 2000). These chemical compounds are known to be highly toxic to most living organisms (Shragg, Albertson, & Fisher 1982; Yamane et al. 2010). CNGs are toxic for some herbivores (Gleadow & Woodrow 2002; Ballhorn, Lieberei, & Ganzhorn 2005), but they act as a feeding stimulant for others (Brattsten, Samuelian, Long, Kincaid, & Evans 1983). Generalist herbivores, such as *Schistocerca gregaria* and *Spodoptera littoralis*, avoid cyanogenic glycosides (Schwarz, Wray, & Proksch 1996), but other polyphagous species, such as *Spodoptera eridania*, prefer plants with higher CNGs (Brattsten et al. 1983). Furthermore, CNGs are known to influence oviposition preferences of the Mexican leaf-bean beetle (Ballhorn & Lieberei 2006) and affect the leaf beetle's behavior and development (Ballhorn, Heil, Pietrowski, & Lieberei 2007).

In plants, CNGs are stored in the vacuoles (Vetter 2000). When plant tissue is damaged by herbivore attack, CNGs get into contact with ß-glucosidases that hydrolyze the CNGs, this causes a release of toxic hydrogen cyanide (HCN) (Zagrobelny et al. 2004). The seeds of cultivated varieties of *Phaseolus lunatus* have been shown to release less hydrogen cyanide (HCN) than their wild counterparts (Lucas & Sotelo 1984). The effect of varying CNG concentrations on the leaf consumption and feeding behavior has been assessed for leaf-feeding herbivores (Ballhorn, Kautz, Lion, & Heil 2008; Ballhorn, Kautz, & Lieberei 2010) and the performance of a seed predator on wild *P. lunatus* seeds has also been evaluated (Shlichta, Glauser, & Benrey 2014). However, little is known about the consequences of domestication of *P. lunatus* on the preference and performance of the leaf and seed herbivores. Most studies on the effects of plant domestication on susceptibility to herbivores have focused on insects that attack the same plant structure (i.e., leaves). Leaf herbivores and seed predators have different foraging strategies and feeding behaviors; therefore, there may also be differences in the effect that plant chemicals have on their behavior and performance.

In this study we examine the predicted effects of lima bean domestication on its interaction with a leaf herbivore and a seed predator. We test the hypothesis that changes in insect resistance due to breeding, are not uniform in all plant tissues,

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