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Impact of Crop Domestication on Tri-trophic Interaction in Insect Pests

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Abstract

Crop domestication is the process of artificially selecting plants to increase their suitability to human tastes and cultivated growing conditions. There is increasing evidence that crop domestication can profoundly alter interactions among plants, herbivores, and their natural enemies. However, there are few generalizable predictions on how insect herbivores and natural enemies should respond to artificial selection of specific plant traits. We reviewed the article to determine how different insect herbivore feeding guilds and natural enemy groups (parasitoids and predators) respond to existing variation in wild and cultivated plant populations for plant traits typically targeted by domestication. Our goal was to look for broad patterns in Tri trophic interactions to generate support for a range of potential outcomes from human-mediated selection. Overall, we found that herbivores benefit from directional selection on traits that have been targeted by domestication, but the effects on natural enemies were less studied and less consistent. In general, herbivores appear to mirror human preferences for higher nutritional content and larger plant structures. In contrast, the general effect of lowered plant secondary metabolites did not always influence herbivores consistently. Given that crop domestication appears to be a transformative process that fundamentally alters insect–plant interactions, we believe that a more detailed understanding of the community-wide effects of crop domestication is needed to simultaneously stimulate both biological control and plant breeding efforts to enhance sustainable pest control.

Key words: Crop domestication, herbivores, biological control, Tri trophic interactions, natural enemies

Introduction

Crop domestication is the process of artificially selecting plants to increase their suitability to human requirements: taste, yield, storage, and cultivation practices. There is increasing evidence that crop domestication can profoundly alter interactions among plants, herbivores, and their natural enemies. In general, domesticated crop plants tend to possess more exaggerated physical traits, simpler morphologies, altered nutritional content, and reduced plant defences compared with their wild ancestors. Therefore, phytophagous insects and their natural enemies evolved with wild crop ancestors for hundreds of millions of years prior to all domestication events. Given that the traits of domesticated crops have arisen from artificial selection rather than natural selection, domesticated crop phenotypes are likely to be ecologically novel with respect to species within higher trophic levels. We discuss the consequences of crop domestication on the ecology and evolution of the interactions between plants, herbivorous insects, and their natural enemies.

Terminologies

1. Crop domestication: - Crop domestication is the process of artificially selecting plants to increase their suitability to human requirements: taste, yield, storage, and cultivation practices.

2. Tri trophic interaction: - Interactions among plants, herbivores, and their natural enemies.

3. Consequences: - The effect, result, or outcome of something occurring earlier.

4. Domestication syndrome: - Many domesticated crops possess a suite of selected characteristics, which have collectively been called the domestication syndrome. This syndrome includes the following major traits: Reduction or loss of means of dispersal, Brittle rachis, Reduced grain shattering, Reduction or loss of dormancy, More compact growth habit etc.

5. Secondary plant metabolites: - Secondary metabolites are chemicals produced by plants for which no role has yet been found in growth, photosynthesis, reproduction, or other "primary" functions. e.g., glycosides, phenols, tannins, alkaloids, terpenoids and saponins. Many secondary metabolites are toxic or repellent to herbivores and microbes and help defend plants producing them. Production increases when a plant is attacked by herbivores or pathogens.

6. Herbivore-Induced Plant Volatiles: - HIPVs are Semio-chemicals (natural signal chemicals mediating changes in behaviour and development) plants produce after insect damage occurs which act to repel pests and attract their natural enemies.

Effects of crop domestication on tri-trophic interactions

A. Morphological traits

1. **Enlargement of plant structures: -** The enlargement of specific plant structures is the most widely emphasized of all of the changes that arise from domestication. Examples of gigantism can be found by comparing crops such as tomato, maize, beans, artichokes, sunflower, and squash with their wild ancestors.

The plant vigour hypothesis proposed by Price predicts that insect herbivores will tend to oviposit on plant organs that grow faster and larger. Example: In domesticated sunflower, increased flower size from domestication is positively correlated with landing and egg laying effort of female sunflower moths, *Homoeosoma electellum*, but increased seed size is negatively associated with parasitoid accessibility to *H. electellum* larvae.

2. Alteration of glumes and spines: - The grains of most wild cereals are enclosed by glumes, lemmas, and pleas, which protect them from damage by seed feeders, in particular birds. Example: Across five lineages of wheat within the genus has selected for larger seed size and greater free-threshing, meaning that the seeds easily separate from the glume. This trait strongly affects susceptibility to herbivore attack. For instance, female wheat midges, *Sitodiplosis mosellana*, lay their eggs on the glumes, and the larvae crawl in between the glume and seed to feed on the seed. By selecting for a looser glume attachment to the seed, wheat domestication has increased plant susceptibility to the wheat midge.

3. Decreased branching and tillering: -

- Crop domestication has frequently selected for a simplification of plant architecture, with reduced branching.
- The greater tillering ability of wild ancestors appears to be an important strategy to tolerate herbivory, giving plants more opportunities and nodal points to compensate for the damage to the apical meristem. Therefore, reduced branching and tillering associated with domestication can dramatically reduce crop tolerance to herbivory.

- For example, wild rice produces more tillers that are less erect than those of domesticated rice, resulting in greater habitat diversity and higher densities of lycosid spiders, a keystone predator.

4. Change in trichome density: -

- Hairs or glandular outgrowths on the surfaces of plants.
- Strongly reduced during the domestication process.
- With few exceptions, reduced trichomes are positively correlated with an increase in herbivore damage, growth, and higher oviposition for most herbivore guilds.
- In some plant genera (e.g., Solanum) trichomes also produce chemicals (glandular trichomes) that entrap or are toxic to insect herbivores and their natural enemies.
- Reductions in trichomes tend to have a negative effect on predatory mites, but a mixed effect on predation levels by coccinellid beetles and other larger predators.

5. Greater phenological uniformity: -

- To increase the efficiency of harvests and reduce multiple harvesting trips, humans have selected for greater synchronization of flowering and maturation within the plant and within the population.
- When flowering occurs uniformly, all tillers may be susceptible at the same time to boring insects, and a single female can cause proportionally greater damage to domesticated plants than to the more heterogeneously flowering wild relatives.

6. Other morphological traits: -

- Domestication has decreased tissue toughness, and increased tissue palatability in most crop plants; all of these changes facilitate herbivore access to plant structures and may allow insect herbivores to develop faster.
- For example, a decline in leaf toughness in maize associated with domestication is associated with higher ovipositional preference by the specialist corn leafhopper, *Dalbulus maidis*. Also, the long-horned borer *Dectes texanus* can chew more easily on the leaf petiole of domesticated sunflowers than on the leaf petiole of wild sunflowers, enabling it to oviposit more frequently and more easily into leaf holes on the former. In addition, wild sunflowers exude more resinous substance than do domesticated sunflowers, which helps to protect wild plants from *D. texanus*.

B. Plant Resistance Metabolites:

- Secondary metabolites play an important role in insect-plant interactions.
- Secondary metabolites may stimulate oviposition and feeding by specialist insect herbivores, whereas they may deter or physiologically hamper more polyphagous herbivores.
- Studies that compare chemical resistance traits in wild and cultivated systems are increasing in number, and their outcomes are very consistent: Domesticated plants provide a better food resource for herbivores than their more toxic wild progenitors.

Performance of herbivores and their natural enemies mediated by secondary metabolites:

- One of the most important consequences of plant domestication on species interactions is the loss or reduction of plant metabolites that are toxic for herbivores.
- For example, performance of bruchid beetles (*A. obtectus*, *Z. subfasciatus*) has repeatedly been shown to be better on several varieties of domesticated beans of the genus Phaseolus than on wild beans. Compared with wild beans, domesticated beans contain lower concentrations of phenolics and cyanogenic glycosides, but they are also larger, softer, and more nutritious. Example: - Glucosinolates in crucifers are known to serve as ovipositional stimulants and larval food plant attractants for many specialist insects. A reduction in the concentration of these compounds in cultivars may increase their

susceptibility to insect pests, or make them difficult to be located, not only by the herbivores, but also by the natural enemies of these herbivores.

Behaviour of herbivores and natural enemies mediated by info chemicals:

- Secondary metabolites also play an important role in host location behaviour of both the herbivores and their natural enemies.
- Info chemical-mediated foraging is better studied for natural enemies of the insect herbivores than for the herbivores themselves.
- Consequently, changes in total emission rates of volatile secondary metabolites in domesticated versus wild plants may have limited value in predicting the effect on volatile-mediated foraging on an herbivore and its natural enemies. These quantitative comparisons that plant domestication has led to lowered volatile emissions.
- In maize, the range of quantitative variation in volatile emissions was substantial but similar among maize varieties and teosinte, whereas the composition of the blend appears to be preserved.
- In contrast, American maize varieties did not emit the terpene (E)-β-caryophyllene, which mediated the attraction of a parasitic wasp and an entomopathogenic nematode in laboratory studies conducted in Europe.
- Although there seems to be a general pattern of reduced attraction of natural enemies to info chemicals emitted by domesticated crops compared with wild ancestors.

Nutrition:

- Humans have deliberately selected for changes in nutritional content within crops, such as sugar (sugar beet or sugarcane), oil (sunflower, canola), protein (maize, various crops), or mineral content.
- It has also been demonstrated that artificial selection can dramatically alter plant nutritional composition. Domestication can also alter plant mineral nutrition, even if it is not explicitly targeted by artificial selection.
- For example, phosphorous levels are higher in bean landraces than in wild genotypes, whereas iron and zinc levels are lower in domesticated than in wild beans.
- Plant quality is a strong determinant of insect herbivore performance, fecundity, and ultimately population growth.

Increased sugar content:

- Some crops such as maize, sugar beet, and sugarcane, have been targeted by domestication for higher sugar content.
- However, unnaturally high sugar content could negatively affect herbivores.
- Example, an upper threshold of sugar content in dates, beyond which populations of the spider mite *Oligonychus afrasiaticus* (McGregor) decline.
- In a frugivorous tephritid fly, *Bactrocera cucurbitae*, where increased sugar in the bitter gourd decreased larval density.

Increased protein content:

- Protein is required for insect growth, but it is generally present in plants at much lower levels than in animals.
- Higher levels in plant nitrogen in domesticated plants increase performance, fecundity, and ovipositional preference of insect herbivores, especially piercing-sucking, leaf mining, and chewing herbivores. Although chewing herbivores showed a trend of increased performance on plants with higher nitrogen levels, the effect was more variable.
- The effects of increased nitrogen on parasitoids and predators are most likely to be indirect and tied to the performance of their prey or host.
- However, when plant nitrogen is increased, natural enemy populations may not be able to increase at the same rate as herbivore populations, thereby limiting their effectiveness in regulating herbivore populations.

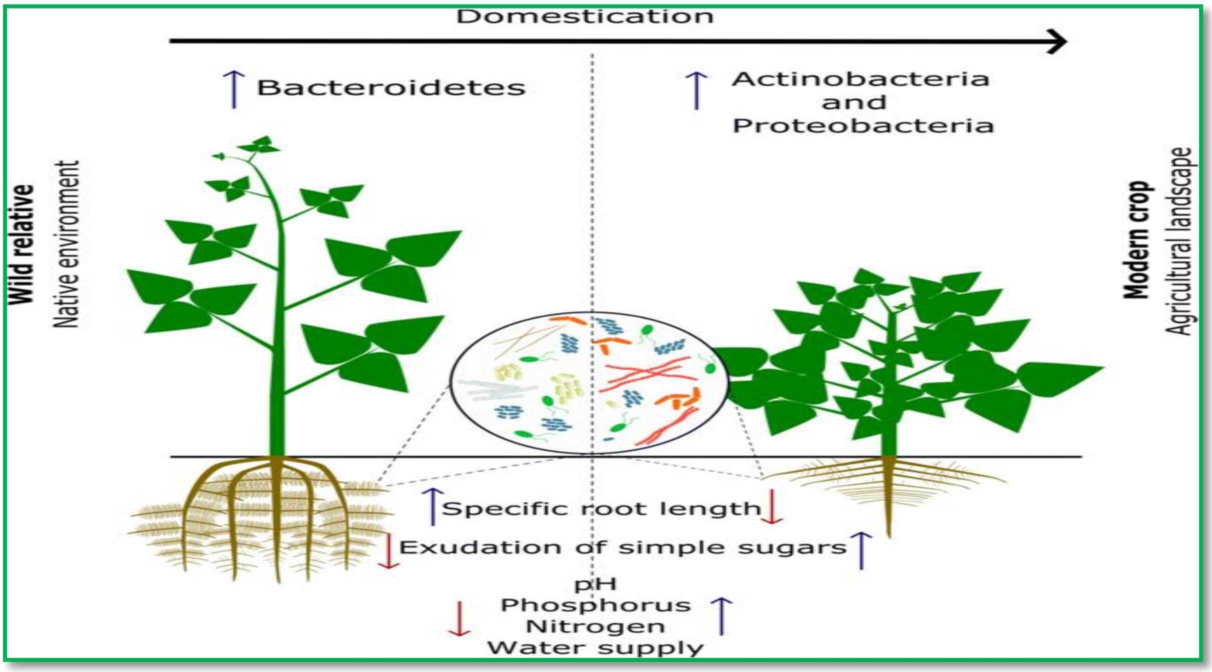

Fig. Impact of domestication on soil management, plant phenotype, plant physiology, and rhizobacterial diversity

Potential outcomes

- An increase in the size of the plant structure or organ used by herbivores will result in increased abundance and performance of herbivores and herbivores may benefit from an adverse effect on natural enemy accessibility.
- Seed predators, fruit burrowers, gall feeders, and in general herbivores that feed on internal and protected plant structures will be mostly affected by the size and accessibility (e.g., stem toughness, seed coat thickness) of this structure.
- A reduction in physical defences (e.g., trichomes and latex) in crop plants will positively affect both herbivores and natural enemies.
- An increase in the nutrient content of crop plants or plant structures will result in increased herbivore and natural enemy performance.
- Plant traits will indirectly affect natural enemies via the changes in the density and quality of the herbivorous host or prey. Increased densities of herbivores due to enlargement of organs/structure and their performance due to decreased toxicity will increase the availability of hosts/prey quality to support parasitoid development.
- On the other hand, increased herbivore performance on crop plants due to higher nutrient content may negatively affect natural enemies due to faster herbivore development and increased ability to encapsulate parasitoid eggs ('slow growth-high mortality' hypothesis).
- For all of the above outcomes, we would expect that: the performance of herbivores and natural enemies that are associated with the tissues targeted by domestication will be altered more than the performance of herbivores and natural enemies associated with tissues that are not targeted by domestication.
- Altered plant traits in crop plants will differentially affect generalist and specialist herbivores. For example, generalist herbivores will benefit from a reduction in plant secondary metabolites than specialists, which are adapted to the plant's chemical defences.

- Selection on plant traits will differentially affect generalists and specialist parasitoids. For example, plant volatiles may have been reduced in crop plants rendering them less attractive or harder to find for generalists than for specialist parasitoids.
- The previous potential outcomes mostly refer to single plant traits. Correlated plant traits will most likely have non-additive but interactive effects on herbivores and natural enemies. For example, an increase in seed size may be accompanied by a decrease in the thickness of the seed coat. Seed predators and their parasitoids may improve their performance on these seeds because of the greater ease in chewing through or ovipositing through a thinner seed coat. Therefore, increased herbivore and natural enemy performance may result from greater access to seed resources due to the thinner seed coat rather than greater overall resources from an increased seed size.

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