CHAPTER 14

Cassava's Natural Defense against Arthropod Pests*

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Introduction

Higher plants develop physical and chemical mechanisms for their defense against pests. These defenses may be found within healthy plants or are induced through arthropod attack. They are variable in nature, and can be modified by ecological factors.

More frequently, physical mechanisms are present in healthy plants, although they are sometimes induced by pests, as in the case of callus formation. These mechanisms greatly affect the establishment of an arthropod on a plant, especially, those behaviors that prevail when the insect selects and establishes itself on a host plant.

Chemical defense is the most effective and frequent mechanism found in plants (Bell 1974), as the substances of secondary metabolism are those that exercise the most action on the environment. According to Fraenkel (1969), these substances are composed mostly for defensive functions and tend to give the plant repellent or toxic attributes, affecting insect growth.

These substances are qualified as secondary, because each family is restricted to a limited group of plants and because usually they do not appear to intervene in the basic biochemical processes of most plants. Secondary substances include alkaloids, steroids, terpenoids, phenolic compounds (e.g., flavonoids and tannins), hydrocyanic or sulfur-derived compounds (e.g., linamarin and glucosinolates), and other organic compounds whose metabolic functions within plants are not well defined (Robinson 1974; Beck and Reese 1976).

Whittaker (1970) proposed the term *allelochemical* for some secondary substances that are defined, in plant-insect interactions, as substances produced by the plant and which markedly affect the insect's growth, survival, and behavior or biology. An example of allelochemical interactions is the production of phytoalexins, which are synthesized by the plant and are induced by the presence of a foreign body, usually a microorganism. Other interactions include those that attract or repel, or are phagorepellent, inhibiting, or toxic.

Manihot esculenta Crantz (Euphorbiaceae) is reported in the literature as presenting physical and chemical mechanisms against arthropod pests (Bellotti et al. 1999). In this chapter, we present several cases that have been clearly demonstrated.

Physical Mechanisms

For cassava's resistance to thrips, *Frankliniella williamsi* (Thysanoptera, Thripidae), leaf pilosity has been clearly demonstrated as contributing to the plant's defense against these insects. Increased leaf pubescence leads to increased resistance to thrips, as the hairiness interferes with their progress in settling on the plants (Schoonhoven 1974; Bellotti and Schoonhoven 1978).

In contrast, cassava's pilosity does not disturb the cassava mealybug (*Phenacoccus manihoti* Matile-Ferrero; Sternorrhyncha: Pseudococcidae) (Calatayud and Le Rü 2006). In a study on cassava and *P. manihoti* interactions, a common and rapid reaction, also appearing in many other plant species, was

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observed: callus formation (polymer of ß(1,3)-D-glucopyranose; Figure 14-1) on contact with the mealybug's stylets (Calatayud et al. 1996). This reaction constitutes a scarring of the phloem, which thus interrupts sustained feeding by this phloemphagous insect.

Another physical mechanism of plants, which affects feeding behavior in *P. manihoti*, occurs in the plant cell wall. An analysis of the secondary compounds present in the intercellular liquids of cassava leaves has shown that phenolic acids are strongly involved in the mealybug's establishment on the plant (Calatayud et al. 1994a). These acids, precursors in the synthesis of compounds associated with cell-wall pectins, probably constitute significant factors in interactions with the insect's salivary enzymes, thus annoying the insect and changing its feeding behavior. Moreover, the level of these phenolic acids declines strongly during dry times, thus partly explaining increases in natural populations of *P. manihoti* in the field during droughts (Calatayud and Le Rü 1995).

Chemical Mechanisms

An important characteristic of cassava biochemistry is the presence of cyanogenic compounds in leaves,
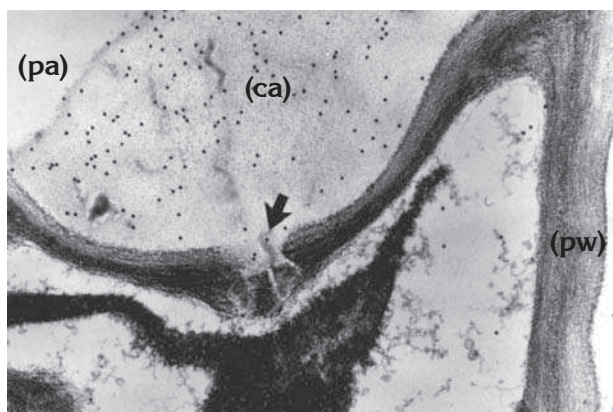

Figure 14-1. Microphotograph of a cross-section of cassava leaf tissue infested by mealybug *Phenacoccus manihoti*. The section, which shows a phloem cell, was treated with the polyclonal antibody specific against the substance ß(1,3)-D-glucopyranose, a constituent of the callus (ca). This reaction makes visible the gold particles carrying the antibody (black points in the callus). The callus results from the cell responding to the perforation (black arrow) that the insect made in the primary cell wall (pw). The callus covers the hole and thus prevents the plasmalemma (pa) from draining and causing cell death. These elements (callus, perforation, plasmalemma) are found within the insect's feeding area. (Calatayud and Múnera 2000; adapted from Calatayud et al. 1996.)

stems, and roots. In plant tissues, the cyano (CN)[3] group links with D-glucose to form cyanogenic glucosides (Conn 1980), mostly linamarin (Figure 14-2) (Butler et al. 1965).

When wounded, cassava tissues excrete hydrocyanic acid (HCN). This property, known as cyanogenesis, results specifically from the action of an endogenous enzyme (ß-glucosidase) on linamarase (Figure 14-2; Conn 1980). The cyanogenesis releases a toxic molecule, thus protecting cassava against pests. However, such protection has yet to be clearly demonstrated (Hruska 1988).

In roots, cyanogenesis can constitute a defense against the subterranean burrower bug, *Cyrtomenus bergi* Froeschner (Hemiptera: Cydnidae). The HCN released through an attack from this insect on roots was demonstrated to play a repellent role. Cassava varieties with low HCN levels are usually attacked more severely than those with high HCN levels (Castaño et al. 1985; Bellotti and Riis 1994; Riis 1997; Bellotti et al. 1999). Furthermore, high levels of HCN in artificial diets (with levels similar to those found in bitter cassava varieties) were clearly demonstrated to be toxic to the burrower bug (Cortés et al. 2003), indicating that cassava varieties with high levels of HCN are also toxic to *C. bergi*.

However, for several reasons, cyanogenesis in cassava does not constitute a defense mechanism against the mealybug. Linamarin itself is not toxic to *P. manihoti* and seems more like a phagostimulant (Calatayud et al. 1994a, 1994b; Calatayud 2000).

Under natural conditions, the insect has an enzymatic complex capable of hydrolyzing linamarin (Calatayud et al. 1995). However, the linamarase of *P. manihoti* does not seem to come from the insect itself, but from bacteria contained in its digestive tract (Calatayud 2000). The HCN levels found within their digestive tract are not toxic to the insect, as it possesses an effective system of excretion or detoxification (Calatayud et al. 1994b).

Furthermore, the location of linamarase in plant tissues differs from that of its substrate, linamarin (Pancoro and Hughes 1992). This, and the fact that *P. manihoti* stylets, on penetrating, causes almost no

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3. For an explanation of this and other abbreviations and acronyms, see *Appendix 1: Acronyms, Abbreviations, and Technical Terminology*, this volume.
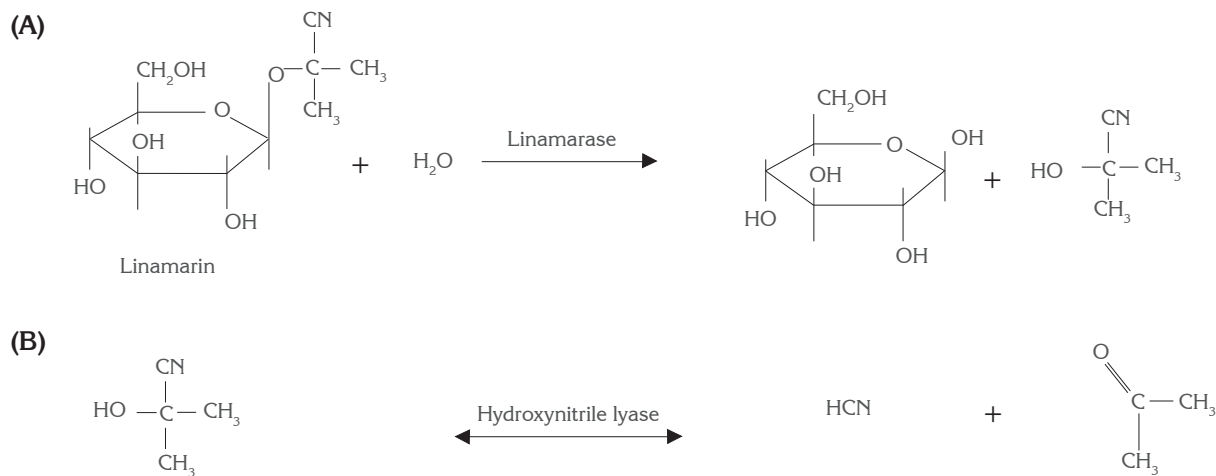
(A)

(B)

Figure 14-2. The chemical formula for linamarin, and cyanogenesis flow chart illustrates the release of HCN through the actions of linamarase **(A)** and hydroxynitrile lyase **(B)** (Calatayud and Múnera 2000).

wounding (Calatayud et al. 1994a), suggests that cassava–mealybug interactions are unlikely to initiate cyanogenesis.

Although no alkaloids were evident in cassava, some glycosylated flavonoids were detected (Calatayud et al. 1994b), including rutin (Figure 14-3), the absence of which, in plants, is more significant than its presence (Harborne and Williams 1975). They were demonstrated as affecting *P. manihoti* growth and development (Calatayud et al. 1994b; Calatayud 2000).

One defensive response that cassava displays against *P. manihoti* appears to be an increase in rutin levels. Such an increase varies with season and is less pronounced during dry times. This partly explains increases in natural populations of *P. manihoti* in the field during drought (Calatayud et al. 1994c). However, the negative effect of rutin on *P. manihoti* growth and development does not seem to result from a toxic action on the insect but more from being phagorepellent in nature (Calatayud 2000).

Conclusions

In *M. esculenta*, the natural defenses against arthropod pests described in the literature seem to affect in particular the establishment or sustained feeding (through phagorepellence) of the pest in the plant. The mechanisms used are physical (pilosity and callus formation) or chemical (HCN and rutin).

No example from the literature has clearly shown a cassava variety having a toxic effect on pests or as
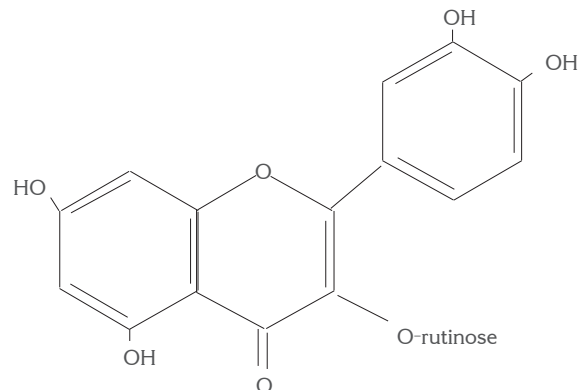
Rutin = quercetin (3,3', 4', 5,7-pentahydroxyflavone) + rutinose
Rutinose = rhamnose + glucose

Figure 14-3. Chemical formula for rutin (Calatayud and Múnera 2000).

possessing a toxic molecule that works against the pests' development and growth. This is partly evidenced by the almost total lack of development of varietal resistance to control the several arthropod pests of cassava (Bellotti and Schoonhoven 1978; Bellotti et al. 1999).

However, a variety of cassava (M Ecu 72) and a wild *Manihot* species (*M. flabellifolia* Pohl [Euphorbiaceae]) demonstrated resistance, and may therefore be promising for isolating genes for resistance to whitefly, *Aleurotrachelus socialis* Bondar (Hemiptera: Aleyrodidae) (Bellotti et al. 1999; Carabalí et al. 2010). The mechanisms of resistance to this whitefly are yet to be described, although physical factors appear probable.

Acknowledgments

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