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RESEARCH ARTICLE

Morphology and glucosinolate profiles of chimeric *Brassica* and the responses of *Bemisia tabaci* in host selection, oviposition and development

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Abstract

Plant structures and chemicals, which are developed from the shoot apical meristem (SAM), form the main barriers to insect feeding. A plant chimera containing cells of different genetic origins in the SAM will be morphologically and chemically different compared with the parents and thus may result in differential resistance to herbivores. In this study, we explore if particular elements of plant resistance are localized in one of the layers of SAM; the replacement of one cell layer in a chimera may be linked to change of a single resistance trait to herbivores. The morphology and glucosinolate profiles of two periclinal chimeras (labeled as TTC and TCC, respectively) and grafted parents tuber mustard (labeled as TTT) and red cabbage (labeled as CCC) were compared and the performance of whitefly (*Bemisia tabaci*) in host selection, oviposition preference and development were assessed under controlled conditions. Both chimeras possessed leaf trichomes as parent tuber mustard TTT, however, TTC had significantly more trichomes than TCC and parent TTT. Leaf wax content of both chimeras was intermediate between the two parents. Five aliphatic and two indole glucosinolates were detected in both chimeras, whereas three aliphatic glucosinolates (3-methyl-sulfinylpropyl, 4-methyl-sulfinylbutyl and 2-hydroxy-3-butenyl) were not detected in tuber mustard, and one aliphatic glucosinolate (3-butenyl) was not detected in red cabbage. Unexpectedly for a chimera, the quantities of two aliphatic glucosinolates (3-methyl-sulfinylpropyl and 4-methyl-sulfinylbutyl) in both TTC and TCC were 3- to 5-fold higher than parents. In olfactory preference assays, *B. tabaci* showed preference to CCC, followed by TCC, TTC and TTT, and number of eggs laid showed the same pattern: CCC>TCC>TTC>TTT. Interestingly, more whiteflies landed on TTT plants than the other three types in a free choice experiment and the developmental duration from egg to adult was the shortest on TTT and increased in the order TTT<TTC<TCC<CCC. Our results indicate plant defenses traits of leaf waxes, trichomes and glucosinolates are not controlled by one cell layer of SAM, but are influenced by interactions amongst cell layers. The overall findings suggest that periclinal chimera systems can be a valuable approach for the study

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of plant-insect interactions and may also be useful for future resistance breeding.

Keywords: chimera, tuber mustard, red cabbage, tobacco whitefly, behavioral response

1. Introduction

The shoot apical meristem (SAM) will develop into plant aerial parts that have characteristic structures and chemical composition. These morphological and chemical characteristics are the front line of interactions with other organisms such as herbivorous insects. In most dicotyledons, the SAM consists of three cell layers: L1, the outermost layer; L2, the middle layer and L3, the innermost layer (Meyerowitz 1997; Filippis *et al.* 2013; Frank and Chitwood 2016). Plant cell layers can be replaced under certain condition to form mosaics, and a plant chimera is such a mosaic, in which cells of different genetic origins exist in one SAM (Li *et al.* 2013). Plant chimeras can be divided into sectorial, mericlinal and periclinal. The phenotypes of sectorial and mericlinal chimera are not stable (Chen *et al.* 2006; Yan *et al.* 2014). However, a SAM of a periclinal chimera, which has at least one complete cell layer genetically different from an adjacent layer(s), forms a stable phenotype (Chen *et al.* 2006). Thus, a periclinal chimera is valuable in the study of function of cell layers, cell-cell signalling and movement, and the interaction between different cells or tissues (Kaddoura and Mantell 1991; Session *et al.* 2000; Hirata *et al.* 2001).

Essentially the replacement of cell layers as a result of grafting results in changes of biological characteristics, such as morphological characteristics and chemical composition. Clayberg (1975) grafted *Solanum pennellii*, a wild type relative of tomato (*Solanum lycopersicum*) that is resistant to greenhouse whitefly (*Trialeurodes vaporariorum*) and potato aphid (*Macrosiphum euphorbiae*), with vulnerable tomato and obtained chimeras with an epidermis of *Solanum pennellii*. The grafted plants showed resistance to the two pests. Further study showed chimeras between the two plants had similar trichome density and similar sugar ester concentration with the wild type parent, which may account for their similar resistance to aphids as the wild tomato (Goffreda *et al.* 1990). The underlying mechanism by which grafting promotes plant direct defenses remains unclear. However, previous studies showed that a graft-transmissible wound signal might play a role and the transmissible signal could be jasmonic acid or a related oxylipin (Li *et al.* 2002; Ryan and Moura 2002).

Generally, plant resistance is connected with morphology and chemistry, both of which can either be constitutive or inducible in response to a certain attack (Takabayashi and Dicke 1996; Pare and Tumlinson 1999; Dicke and Hilker 2003). Studies on morphology mainly focus on leaf color, surface wax, epidermal trichomes and cuticle, which may affect the host selection behaviour of pests (Pegadaraju *et al.* 2007; Cao *et al.* 2008; Cribb *et al.* 2010). For example, glossy leaf wax characteristics of cabbage (*Brassica oleracea*) can confer some level of resistance to diamondback moth (*Plutella xylostella*) (Eigenbrode *et al.* 1991). The red cultivars of brussels sprouts (Rubine) and cabbage (Red Acre) are much less infested with the whitefly (*Bemisia tabaci*) than green cultivars (Elsey and Farnham 1994). Brassicales produce glucosinolates, a group of secondary plant metabolites exhibiting toxic or repellent effects (Mithen 2001; Zukalova and Vasak 2002). Depending on their precursor amino acid, they are grouped into three major classes: aliphatic, indole and aromatic glucosinolates (Halkier and Gershenzon 2006). Although intact glucosinolates may provide resistance against some herbivorous insects, most of the defensive properties are caused by their hydrolysis products (Mewis *et al.* 2005). Upon plant tissue damage, e.g., by chewing or piercing of insects, glucosinolates are hydrolyzed by thioglucosidase enzymes, known as myrosinases, that are kept separate in the plant, generating a range of biologically active hydrolysis products (Bones and Rossiter 2006). These glucosinolate breakdown products can be used as feeding cues and oviposition stimulants by specialist insects (Hopkins *et al.* 2009), but mainly they are characterized by their toxicity and deterrence effects to generalist herbivorous insects (Mewis *et al.* 2005). Morphological and chemical traits of plants, however, usually intertwine in a continuum of defense against herbivores as they are present in the same plant (Schoonhoven *et al.* 2005). The interaction between these layers of defense and other trophic levels are complex (Schuman and Baldwin 2016). For example, herbivore-induced plant volatiles (HIPVs) emission and trichome production have antagonistic effects on the tritrophic interaction of tomato, leafminer and its parasitoid (Wei *et al.* 2013).

Worldwide *B. tabaci* is a major economically important pest. The Middle East-Asia Minor 1 whitefly of the species complex, also known as "B biotype", has risen to worldwide prominence as a pest in vegetable, ornamental, grain legume, and cotton production (De Barro *et al.* 2011; Liu *et al.* 2012; Sun *et al.* 2013). It can cause crop losses by direct phloem-feeding damage and indirectly by virus disease transmission (Oliveira *et al.* 2001; Navas-Castillo