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Leaf Damage by Phytophagous Beetles alters *Terminalia catappa* Green and Senesced Leaf Chemistry

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ABSTRACT: Chemical traits of *Terminalia catappa* L. leaves were determined on the island of Guam to understand the changes caused by beetle leaf herbivory. Green leaf chemistry indicated nitrogen was the most limiting nutrient in the climate and soils of Guam. The changes in leaf chemistry following beetle damage were extensive. Senesced leaf chemistry indicated beetle damage decreased some traits that predict lower leaf litter quality, such as lignin, but also decreased some traits that predict higher leaf litter quality, such as nitrogen. The stoichiometric traits based on carbon:macronutrient and lignin:macronutrient generally predicted higher quality leaf litter following beetle herbivory. The beetles that produce this form of *T. catappa* leaf damage on Guam are non-native, and overall, the results indicate these pests will increase the rate of litter decomposition and nutrient turnover in habitats where *T. catappa* is prevalent.

KEYWORDS: Adoretus sinicus, litter quality, Phytorus lineolatus, resorption efficiency, Trigonops vulgaris

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Introduction

Terminalia catappa is one of the most abundant tree species in coastal communities in Western Pacific island nations.[1] The ability of these trees to withstand harsh coastal conditions allows it to thrive alongside other trees that protect the coastline (Figure 1A). This ability is one of the reasons for introducing the tree throughout the equatorial regions of the world, and it now grows in most tropical and subtropical countries. In addition to coastal stabilization, the species has numerous gastronomic, medicinal, and utilitarian uses.[1,2]

Several non-native beetle species on the island of Guam that feed on *T. catappa* leaves cause numerous small holes throughout the laminae, often causing a shot-hole appearance of the damaged leaves (Figure 1B). Phytorus leaf beetle (*Phytorus lineolatus* Weise; Coleoptera: Chrysomelidae), a weevil (*Trigonops vulgaris* Zimmerman; Coleoptera: Curculionidae), and the Chinese rose beetle (*Adoretus sinicus* Burmeister; Coleoptera: Scarabaeidae) are the beetles that have invaded the island of Guam to cause this damage. There are no native herbivores that damage leaves in a similar manner.

Variation of chemotypic expression of a dominant tree species that is being preferentially attacked by specialist insect herbivores can have substantial ecological consequences including changes in biogeochemical cycling.[3,4] Therefore, increased knowledge about leaf and litter quality of *T. catappa* is needed in a changing world where more invasive species exert their influence on ecological traits of the invaded communities in Western Pacific islands.

In this study, I addressed the hypothesis that *T. catappa* leaf damage by beetle herbivores will change leaf chemistry, and that these changes will persist through leaf senescence. I further determined if leaf chemical changes following beetle herbivory increased or decreased litter quality and predicted decomposition rate using established litter quality characteristics.[5]

Materials and Methods

Site traits

Ten sites throughout northern Guam were selected where shot-hole leaf damage from the non-native beetle herbivory was evident in *T. catappa* leaves. The soils for all 10 locations were formed from sediment overlying porous limestone on uplifted plateaus (Clayey, gibbsitic, nonacid, isohyperthermic Lithic Ustorthents).[6] Leaf and soil samples were collected from each site from 1 to 5 November 2017. A soil sample from 0 to 15 cm depth was collected from each site and combined into a composite sample. The pH was 7.5, and elemental content was 6.9 mg·g-1 nitrogen, 60.1 $\mu g \cdot g^{-1}$ phosphorus, 125.2 $mg \cdot g^{-1}$ carbon, 0.7 $mg \cdot g^{-1}$ potassium, 1.1 $mg \cdot g^{-1}$ magnesium, 56.9 $\mu g \cdot g^{-1}$ manganese, 14.8 $\mu g \cdot g^{-1}$ iron, 2.0 $\mu g \cdot g^{-1}$ copper, and 81.5 $\mu g \cdot g^{-1}$ zinc.

Tissue collection

The youngest fully expanded green *T. catappa* leaves are generally healthy in the presence of these beetle herbivores, and the feeding damage occurs after full expansion. Therefore, healthy youngest fully expanded leaves were used to compare with all senesced leaves (described below). The green leaves were collected from at least eight locations surrounding the canopy of the 10 sampled trees and combined into one sample. Leaves were collected from the canopy periphery at ca. half the height for each tree. Senesced leaves with no herbivory of any kind and senesced leaves with beetle shot-hole damage were harvested from the ground beneath the same experimental trees that provided the green leaf tissue. To ensure the senesced leaves were fresh litterfall, no fully desiccated leaves were included. Fresh senesced leaves of this species are red or yellow, so diagnosing fresh litterfall was unambiguous. Restricting senesced leaf collections from the ground also ensured natural

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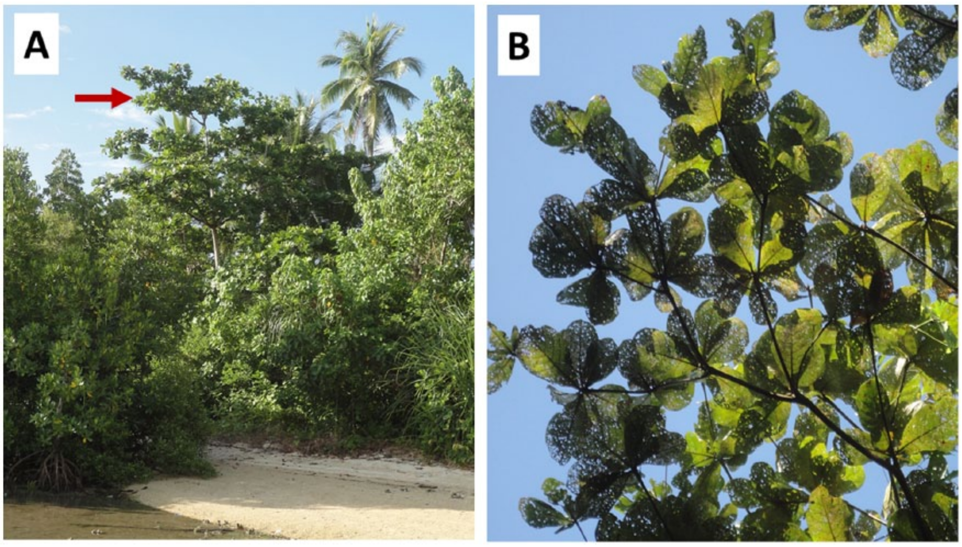

Figure 1. Healthy *Terminalia catappa* tree (red arrow) grows adjacent to a beach with mangrove trees (A). Shot-hole appearance of *T. catappa* leaves caused by beetle herbivory (B).

abscission of the litter samples. Leaf selection was restricted to leaves that appeared to have about 50% of the laminae removed. A digital photograph of each leaf was captured and ImageJ (http://imagej.nih.gov/ij/) was used to quantify the area of the holes and the total area within the outline of each leaf. These data were used to calculate how much lamina had been removed by the feeding. The height of each tree was measured.

Chemical traits

Leaf surfaces were washed with tap water, rinsed with reverse osmosis water, dried at 75°C for 24 hour, and milled to pass through 20-mesh screen. All green and senesced leaf tissue was analyzed for essential micro and macronutrients. Total nitrogen and carbon were determined by dry combustion (FLASH EA1112 CHN Analyzer, Thermo Fisher, Waltham, Mass, U.S.A.), and all other elements were determined by inductively coupled plasma optical emission spectroscopy (ICP-OES) following extraction by diethylenetriaminepentaacetic acid (Spectro Genesis; SPECTRO Analytical Instruments, Kleve, Germany).[7] Several metals were also quantified using nitric acid extraction and ICP-OES. Moreover, lignin was quantified in the senesced leaf tissue by means of the acetyl-bromide method.[8]

Statistical analyses

Resorption efficiency was calculated for nitrogen, phosphorus, and potassium as [(green concentration − senesced concentration)/green concentration]*100. For the beetle-damaged leaves, cumulative resorption included all induced chemical changes in response to the herbivory followed by all resorption behaviors during senescence. Stoichiometric traits that are relevant for litter quality were calculated with lignin or carbon as the numerator and nitrogen, phosphorus, or potassium as the denominator. The stoichiometric variables were log-transformed for analysis. Prerequisites for parametric tests were met for the remaining response variables. A paired *t*-test was used to compare beetle-damaged versus healthy leaves for all response variables.

Results

The beetle-damaged senesced leaves contained holes that represented 44% of the lamina area. The mean tree height was 4.2 m. Macronutrient concentrations of green *T. catappa* leaves were within expected ranges and followed the order nitrogen > potassium > calcium > phosphorus > magnesium > sulfur (Table 1). Micronutrient concentrations were also as expected and followed the order manganese > iron > zinc > boron = copper > nickel. Of the metals, lead and selenium were detected but cadmium, cobalt, and chromium were not detected. Nitrogen:phosphorus was 4.8 ± 0.3, nitrogen:potassium was 1.2 ± 0.1, and potassium:phosphorus was 4.0 ± 0.1.

Beetle herbivory exerted a marked influence on leaf chemistry of senesced leaves (Table 2). Lignin was reduced 39% and nitrogen was reduced 22% in beetle-damaged leaves in comparison to healthy leaves. Other nutrients that were reduced by beetle herbivory were calcium, magnesium, manganese, and boron. In contrast, the potassium content of beetle-damaged leaves was 45% higher than the potassium levels in healthy leaves. Nickel content of beetle-damaged leaves was 300% higher than the nickel levels in healthy leaves. Carbon, phosphorus, sulfur, iron, zinc, and copper were nutrients that were unaffected by beetle herbivory. Of the metals, cadmium and chromium were reduced by beetle herbivory, but cobalt, lead, and selenium were not influenced by beetle herbivory.

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Table 1. Chemical traits from the youngest fully expanded green *Terminalia catappa* leaves (n = 10).

TRAIT	MEAN + SE	TRAIT	MEAN + SE
Nitrogen (mg·g^{-1})	12.9 ± 1.2	Copper (µg·g^{-1})	15.5 ± 0.7
Phosphorus (mg·g^{-1})	2.7 ± 0.1	Boron (µg·g^{-1})	16.8 ± 2.5
Potassium (mg·g^{-1})	10.8 ± 0.2	Cadmium (µg·g^{-1})	ND
Calcium (mg·g^{-1})	9.3 ± 2.8	Cobalt (µg·g^{-1})	ND
Magnesium (mg·g^{-1})	2.1 ± 0.2	Chromium (µg·g^{-1})	ND
Sulfur (mg·g^{-1})	1.7 ± 0.1	Nickel (µg·g^{-1})	1.1 ± 0.3
Iron (µg·g^{-1})	32.2 ± 3.8	Lead (µg·g^{-1})	0.4 ± 0.3
Manganese (µg·g^{-1})	41.2 ± 3.9	Selenium (µg·g^{-1})	7.6 ± 0.2
Zinc (µg·g^{-1})	26.3 ± 2.5		

ND: not detected.

Table 2. Chemical traits from senesced *Terminalia catappa* leaves as influenced by beetle herbivory. Mean ± SE (n = 10).

TRAIT	HEALTHY	BEETLE-DAMAGED	*T*-VALUE	*P*
Lignin (mg·g^{-1})	227.4 ± 10.0	137.7 ± 8.7	8.93	<.0001
Carbon (mg·g^{-1})	452.1 ± 7.5	444.7 ± 8.1	0.74	.4802
Nitrogen (mg·g^{-1})	8.7 ± 0.5	6.8 ± 0.4	4.14	.0025
Phosphorus (mg·g^{-1})	1.0 ± 0.1	0.9 ± 0.2	0.68	.2515
Potassium (mg·g^{-1})	1.1 ± 0.1	1.6 ± 0.2	3.63	.0055
Calcium (mg·g^{-1})	38.9 ± 2.6	30.4 ± 2.0	3.16	.0116
Magnesium (mg·g^{-1})	3.6 ± 0.2	3.2 ± 0.1	2.57	.0303
Sulfur (mg·g^{-1})	0.6 ± 0.01	0.6 ± 0.01	1.76	.1120
Iron (µg·g^{-1})	54.3 ± 3.8	56.6 ± 3.1	0.60	.5631
Manganese (µg·g^{-1})	270.0 ± 29.6	142.3 ± 22.6	4.31	.0020
Zinc (µg·g^{-1})	33.8 ± 1.8	35.4 ± 2.5	0.64	.5384
Copper (µg·g^{-1})	7.9 ± 0.5	9.5 ± 0.8	2.08	.0677
Boron (µg·g^{-1})	41.3 ± 2.5	33.6 ± 1.8	3.07	.0134
Cadmium (µg·g^{-1})	0.4 ± 0.03	0.3 ± 0.02	3.85	.0039
Cobalt (µg·g^{-1})	0.2 ± 0.02	0.2 ± 0.01	0.85	.4171
Chromium (µg·g^{-1})	1.0 ± 0.2	0.5 ± 0.03	2.91	.0174
Nickel (µg·g^{-1})	0.3 ± 0.04	1.2 ± 0.3	3.48	.0070
Lead (µg·g^{-1})	1.7 ± 0.5	1.0 ± 0.4	1.36	.2057
Selenium (µg·g^{-1})	2.5 ± 0.3	2.1 ± 0.2	1.60	.1449

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Table 3. Stoichiometry and resorption traits of senesced *Terminalia catappa* leaves as influenced by beetle herbivory. Mean ± SE (n = 10).

TRAIT	HEALTHY	BEETLE-DAMAGED	*T*-VALUE, LOG-TRANSFORMED	*P*
Lignin:nitrogen	27.6 ± 2.6	20.3 ± 2.4	2.40	.0272
Lignin:phosphorus	234.0 ± 20.0	158.1 ± 14.1	3.63	.0019
Lignin:potassium	214.9 ± 18.0	94.8 ± 13.2	5.96	<.0001
Carbon:nitrogen	53.4 ± 2.8	65.4 ± 2.7	3.29	.0041
Carbon:phosphorus	466.0 ± 28.4	502.3 ± 40.2	0.66	.5176
Carbon:potassium	424.9 ± 33.5	297.1 ± 23.7	3.75	.0015
Nitrogen resorption (%)	32.8 ± 3.1	47.0 ± 3.4	4.13	.0025
Phosphorus resorption (%)	64.2 ± 2.2	66.2 ± 2.3	0.64	.5359
Potassium resorption (%)	90.0 ± 1.4	84.8 ± 1.0	3.81	.0041

The derived stoichiometry traits that define litter quality and leaf senescence dynamics were varied in the direction of change in response to beetle herbivory (Table 3). Lignin:nitrogen, lignin:phosphorus, lignin:potassium, and carbon:potassium of beetle-damaged leaves were greatly reduced when compared to healthy leaves (range of 26%–56% reduction). In contrast, carbon:phosphorus was not affected and carbon:nitrogen was increased 22% by beetle herbivory. Nitrogen resorption was increased 43%, potassium resorption was decreased 6%, and phosphorus resorption was unaffected by beetle herbivory.

Discussion

No native herbivore is known to damage *T. catappa* leaves with the shot-hole appearance, so attributing the changes that were measured to the three non-native beetles that produce this form of damage is unambiguous. This first look at how non-native beetle damage to *T. catappa* leaves altered leaf chemistry indicated the changes were substantial. The results provide an example of the need to consider all direct and indirect plant responses to non-native insect herbivory as a means of understanding chemical ecology changes as a component of invasion biology.[9–11]

Lignin, nitrogen, calcium, magnesium, and manganese were among the chemical constituents that were significantly reduced by beetle herbivory. This response could be due to preferential consumption of these constituents in relation to the other leaf constituents, or it could be due to stimulation of increased resorption during senescence following the herbivory.

Several published reports of *T. catappa* leaf chemistry allow direct comparisons to my results. Analyses of metal content of *T. catappa* leaves was reported in India to more fully understand how leaves used for herbal remedies may pose a human health risk.[12] The relative ranking of manganese, zinc, iron, and lead contents were similar to the results herein. Copper and zinc concentrations reported herein were within the range of *T. catappa* leaves from various contaminated sites in India, but my cadmium and lead concentrations were below the range from these same sites.[13] In Philippine sites containing excessive cadmium or chromium, cadmium was accumulated in *T. catappa* roots and chromium was accumulated in stems, but neither revealed appreciable concentration in leaves.[14] Unfortunately, none of these reports included adequate detail about leaf age in the methods, and only two included the date of collection, so meaningful comparisons among the studies are not readily enabled. Numerous minerals were quantified in *T. catappa* tissues in Brazil,[15] but because total content rather than concentration was reported, there is no approach to compare their results with the literature. Element mass expressed on leaf mass or leaf area basis is accepted for use so experimental results can be contributory to the worldwide leaf economic spectrum literature on green[16,17] or senesced[18] leaf traits.

Green leaf stoichiometry indicated these *T. catappa* trees were nitrogen-limited by using nitrogen:phosphorus or nitrogen:potassium as the diagnostic.[19–23] The potassium:phosphorus quotient revealed phosphorus was more limiting of *T. catappa* in these Guam habitats than was potassium.[19]

Climate,[24,25] soil chemical and biological traits,[26] and litter quality[27,28] are the main drivers of decomposition rate. In an insular setting where climate and soils are similar, the chemical and structural traits of the individual components of leaf litter exert the greatest influence on leaf litter decomposition. Therefore, stoichiometric traits of senesced leaf tissue allow a prediction of litter decomposition speed. The direction and extent of changes to litter quality caused by insect herbivory are not universal. Following herbivory, litter quality and speed of litter decomposition can be increased or decreased depending on the host-herbivore combination.[29-31]

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The use of senesced *T. catappa* leaf stoichiometry to predict litter decomposition speed revealed contrasting results. All three quotients derived with lignin as the numerator indicated beetle herbivory would increase *T. catappa* litter decomposition speed, as the quotients were reduced by herbivory. However, the three quotients derived with carbon as the numerator were erratic with regard to decomposition predictions. Carbon:potassium predicted increased, carbon:nitrogen predicted decreased, and carbon:phosphorus predicted no change in litter decomposition speed following beetle herbivory. As a group, the absolute lignin and carbon content and the stoichiometric traits indicate beetle herbivory increased litter quality of senesced *T. catappa* leaves.[5]

Recent invasions of Guam by specialist herbivore insects of *Cycas micronesica*[32] and *Cocos nucifera*[33] generated similar leaf chemical responses to the feeding damage. Universally, senesced leaf litter quality was increased by the damage caused by the non-native insects. The combined results from multiple host tree species in Guam indicate that the patterns of nutrient sequestration in the litter layer may be disrupted by the invasive pests such that the rate of nutrient release will be substantially increased. This will shorten the timespan in which carbon is sequestered in the litter layer of Guam and therefore exert relevance to the ongoing debate of how anthropogenic activities are influencing the carbon cycle.

Author Contributions

TEM contributed all aspects of conceptualization, methodology, analysis, and writing.

Disclosures and Ethics

As a requirement of publication the author has provided to the publisher signed confirmation of compliance with legal and ethical obligations including but not limited to the following: authorship and contributorship, conflicts of interest, privacy and confidentiality and (where applicable) protection of human and animal research subjects. The authors have read and confirmed their agreement with the ICMJE authorship and conflict of interest criteria. The authors have also confirmed that this article is unique and not under consideration or published in any other publication, and that they have permission from rights holders to reproduce any copyrighted material. Any disclosures are made in this section. The external blind peer reviewers report no conflicts of interest.

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