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Response of two chemotypes of *Melaleuca quinquenervia* (Myrtales: Myrtaceae) saplings to colonization by specialist herbivores

Philip W. Tipping[1,], Melissa R. Martin[2], Paul D. Pratt[3], Gregory S. Wheeler[1], and Lyn A. Gettys[4]*

Abstract

Two chemotypes of *Melaleuca quinquenervia* (Cav.) S. T. Blake (Myrtales: Myrtaceae) saplings were planted in a common garden under 2 water treatments and exposed to either restricted or unrestricted herbivory from 2 insect herbivores. Chemotypes consisted of either a predominately *E*-nerolidol terpenoid complex or one that consisted primarily of viridiflorol; both types had influenced the performance or preference of both insect herbivores in laboratory studies. The densities of the 2 specialist herbivores *Boreioglycaspis melaleucae* Moore (Hemiptera: Psyllidae) and *Oxyops vitiosa* Pascoe (Coleoptera: Curculionidae) were monitored regularly as they colonized the plantings, as were plant responses like leaf abscission and tree height. Neither the chemotype nor the water treatments influenced the densities of *B. melaleucae* and *O. vitiosa*. Trees subjected to unrestricted herbivory shed more leaf biomass than those protected by insecticides from herbivory. There was no relationship between the amount of biomass shed via abscission and the density of either herbivore despite a significant correlation with a damage rating developed for *O. vitiosa*. There was a chemotype response to herbivory whereby more leaf biomass was shed by the *E*-nerolidol chemotype than by the viridiflorol chemotype when subjected to unrestricted herbivory. Tree height was influenced by herbivory but not chemotype or water, although there were separate 2-way interactions between all factors. Thus, despite equal herbivore pressure, the response of young *M. quinquenervia* trees to abiotic and biotic forces diverged at the plant variant level.

Key Words: *Oxyops vitiosa*; *Boreioglycaspis melaleuca*; *E*-nerolidol; viridiflorol

Resumen

Dos quimiotipos de arbolitos de *Melaleuca quinquenervia* (Cav.) S.T. Blake (Myrtales: Myrtaceae) fueron plantados en un jardín común bajo 2 tratamientos de agua y fueron expuestos a la herbivoría restringida o no restringida de 2 insectos herbívoros. Los quimotipos consistían de un complejo terpenoide E-nerolidol predominantemente o uno que consistía principalmente en viridiflorol; ambas clases habían influido el rendimiento o la preferencia de ambos insectos herbívoros en los estudios de laboratorio. Las densidades de los 2 herbívoros especializados *Boreioglycaspis melaleucae* Moore (Hemiptera: Psyllidae) y *Oxyops vitiosa* Pascoe (Coleoptera: Curculionidae) fueron controlados regularmente durante su colonización de las siembras, al igual que las respuestas de las plantas como la abscisión foliar y altura de los árboles. El quimiotipo y los tratamientos de agua no influyeron la densidad de *B. melaleucae* y *O. vitiosa*. Los árboles sometidos a la herbivoría sin restricciones perdieron más biomasa foliar que los protegidos por los insecticidas de herbivoría. No hubo una relación entre la cantidad de biomasa perdida a través de la abscisión y la densidad de cualquiera de los herbívoros a pesar de una correlación significativa con una calificación de daño desarrollado para *O. vitiosa.* Hubo una respuesta quimiotipo a la herbivoría que resultó en la diminuación de más biomasa de hojas por el quimiotipo *E*-nerolidol que por el quimiotipo viridiflorol cuando fueron sometidos a la herbivoría sin restricciones. La altura del árbol fue influenciada por la herbivoría pero no por el quimiotipo o agua, aunque hubo diferentes interacciones de 2 vías entre todos los factores. Por lo tanto, a pesar de presión igual del herbívoro, la respuesta de los árboles jóvenes de *M. quinquenervia* a las fuerzas abióticas y bióticas divergieron a nivel del variante de planta.

Palabras Clave: *Oxyops vitiosa*; *Boreioglycaspis melaleuca*; *E*-nerolidol; viridiflorol

Melaleuca quinquenervia (Cav.) S. T. Blake (Myrtales: Myrtaceae) is an ecological weed that threatens the integrity of wetlands in the greater Everglades region. This Australian tree was intentionally introduced in the late 1800s in southern Florida for use primarily as an ornamental landscape plant and for erosion control (Bodle et al. 1994). Prolific and fast growing, this tree subsequently spread into natural areas and transformed environments like sawgrass prairies into monotypic forests over vast areas (Center et al. 2012). Eventually, this plant was targeted for classical biological control using insects as part of an integrated management program (Laroche 1998). To date, this project has resulted in the release of 4 monophagous insect herbivores, 3 of which have established and are reducing the invasive capacity of this weed (Tipping et al. 2008, 2009, 2012). The first 2 insect species that were released and subsequently established widespread populations were

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Oxyops vitiosa Pascoe (Coleoptera: Curculionidae) in 1997 and *Boreioglycaspis melaleucae* Moore (Hemiptera: Psyllidae) in 2002 (Center et al. 2000, 2006). *Oxyops vitiosa* is a defoliator whose larvae feed on both leaf surfaces and consume the tissue through to the cuticle on the other side, whereas *B. melaleucae* is a phloem feeder (Purcell & Balciunas 1994; Purcell et al. 1997). Both species have unique features, like *O. vitiosa* larvae that are covered in a viscous layer of essential oils that deters predators, whereas *B. melaleucae* nymphs secret waxy filaments that form highly visible flocculent masses on leaves (Purcell et al. 1997; Wheeler et al. 2002).

Populations of *M. quinquenervia* in Florida occur in 2 distinct chemical variants that are traditionally defined as chemotypes (Desjardins 2008). One chemotype ('*E*-nerolidol') is characterized by acyclic foliar terpenes with high concentrations of the sesquiterpene *E*-nerolidol (74–95% of total oil), and the monoterpene linalool (Ireland et al. 2002; Wheeler et al. 2007). The 2nd chemotype ('viridiflorol') contains high concentrations of cyclic foliar terpenes especially the sesquiterpene viridiflorol (13–66% of total oil) and the monoterpenes 1,8-cineole and α-terpineol (Ireland et al. 2002; Wheeler et al. 2007). Chemotype profiles in Florida populations of *M. quinquenervia* matched those in Australia (Padovan et al. 2010). Both chemotypes differentially affected the preference and performance of *O. vitiosa* and *B. melaleucae* in laboratory studies. For example, Dray et al. (2004) reported that both *O. vitiosa* larval survivorship and adult weight gain were greater on *E*-nerolidol compared with viridiflorol, whereas Wheeler (2006) found greater fecundity in *O. vitiosa* adults that were fed bouquets of *E*-nerolidol leaves compared with viridiflorol leaves. Wheeler & Ordung (2005) found that although *B. melaleucae* females oviposited more than twice as many eggs on the viridiflorol than on the *E*-nerolidol chemotype, overall performance was unaffected by chemotype. Wheeler et al. (2007) suggested that this information might guide the geographic deployment of the insects to infestations that consisted primarily of the *E*-nerolidol chemotype in order to maximize insect production in the field.

The primary objective of this study was to determine if the chemotypic profile of *M. quinquenervia* influenced the field colonization of a new population of plants by the 2 specialist herbivores. A secondary objective was to quantify various plant responses as influenced by chemotype, herbivory, moisture availability, and their interactions. Two null hypotheses were proposed; the 1st was that chemotype did not influence colonization by either herbivore, and the 2nd was that the plant's response to herbivory was independent of chemotype and water availability.

Materials and Methods

Melaleuca quinquenervia saplings were propagated from cuttings of known chemotypes in a screen house and were planted into a common garden at the United States Department of Agriculture, Agricultural Research Service, Invasive Plant Research Laboratory in Ft. Lauderdale, Florida, on 4 Apr 2003, when they were 0.5 m tall. Plant chemotypes were determined by gas chromatography–mass spectrometry analysis of ethanol extracts from leaves as described previously (Wheeler 2006). The prevailing soil type at the field was a Margate fine sand, siliceous hyperthermic Mollic Psammaquent, with less than a 1% slope. The experimental design was a complete 2 × 2 × 2 × 6 factorial randomized block with 2 herbivore treatments, 2 chemotype treatments (*E*-nerolidol or viridiflorol), 2 irrigation treatments, and 6 blocks, with the tree as the experimental unit located in the center of each square 56.25 m^2 plot. Each sapling was planted in the center of a 1 m^2 plastic mat which served to suppress weeds and catch leaves that were shed by the plant.

Herbivore treatments consisted of an herbivore control where herbivory by *B. melaleucae* and *O. vitiosa* was either restricted by regular applications of an insecticide or not restricted by applications of water. The insecticide was acephate (O,S-dimethyl acetylphosphoramidothioate) applied with a hand pressurized backpack sprayer at a concentration of 0.367% ai (v/v) until runoff. This systemic insecticide was applied as needed (every 3–6 wk) to prevent the insect populations from establishing on the plants. The insecticide concentration and application frequency neither inhibited nor stimulated plant growth (Tipping & Center 2002). Water availability was controlled with treatments that consisted of either natural rainfall or natural rainfall plus continuous irrigation using drippers that provided a mean flow rate of approximately 7.5 L h^{-1} applied to a spot on the soil directly next to the trunk, resulting in continually saturated soils under the dripline of the tree.

Every 2 to 3 d, the plastic mat around each tree was checked for abscised leaves, which were counted, weighed for fresh weight biomass, and then dried to a constant weight to obtain dry weight biomass. The tall height of the surrounding grass around the border of the plastic mat helped to prevent the abscised leaves from being blown off the mat. Every 30 d, the following measurements were taken: plant height, the numbers of small (instars 1–3) and large larvae (instars 4–5) and adults of *O. vitiosa*, the number of colonies of *B. melaleucae* as indicated by discrete flocculent masses, and a damage rating based on the percentage of leaves that showed *O. vitiosa* larval feeding, ranked as (0) no damage, (1) up to 25%, (2) 26–50%, (3) 51–75%, (4) 76–99%, and (5) 100% damaged. The duration of the experiment was from 30 May to 11 Aug 2003.

Repeated measures analysis of variance was used to examine the influence of the herbivory, chemotype, and water treatments and their interactions on plant and insect parameters. Variables like the number of insects per cm of tree height were calculated to take into account changes in tree growth. Two-sample *t*-tests were used to separate selected means post-hoc. All statistical analyses were conducting using SAS v 9.1 (SAS Institute 2004).

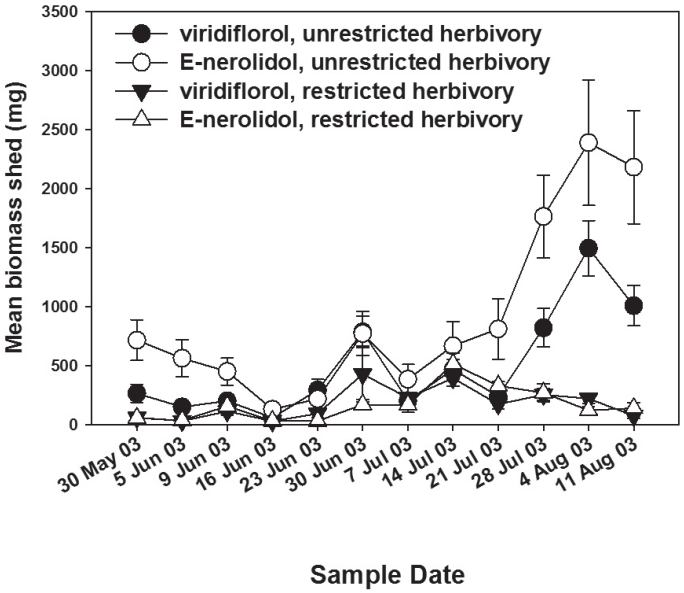


Fig. 1. Mean (± SE) dry weight biomass of leaves shed via abscission by saplings of 2 *Melaleuca quinquenervia* chemotypes subjected to 2 levels of herbivory by *Oxyops vitiosa* and *Boreioglycaspis melaleucae*.

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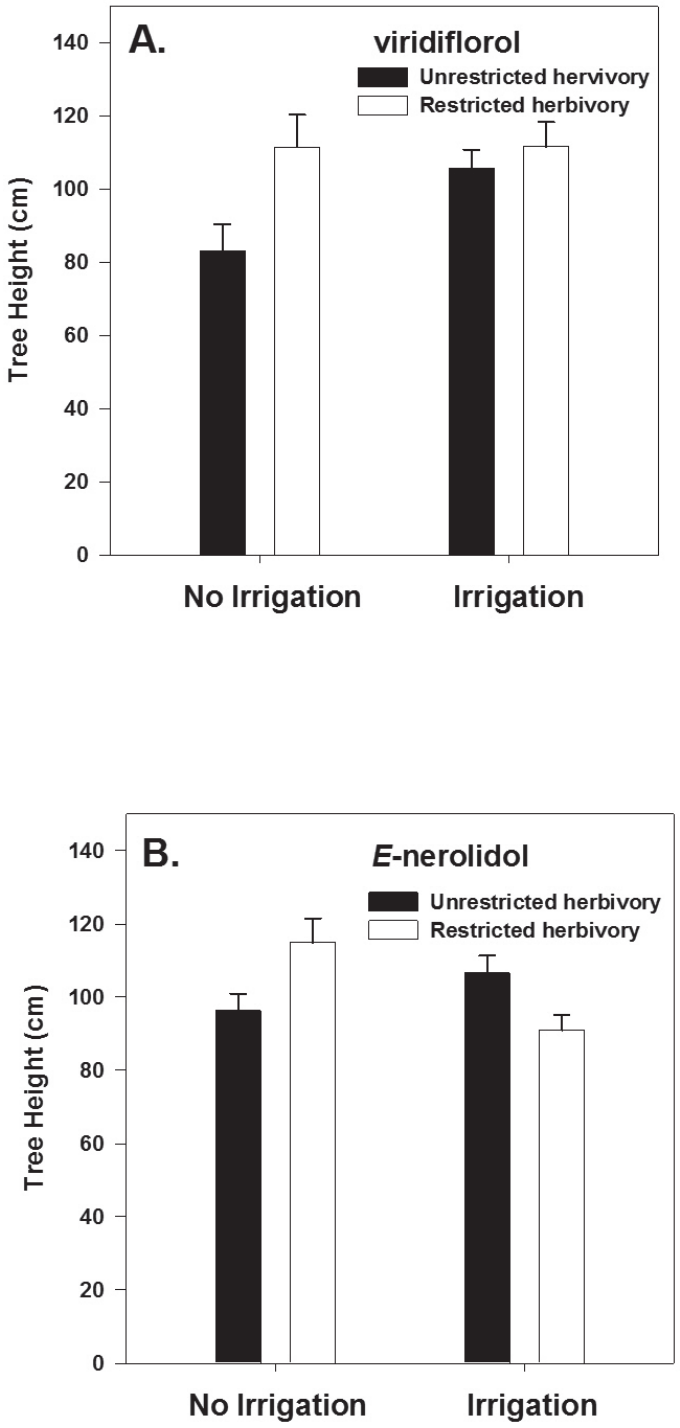


Fig. 2. Final mean (± SE) height of *Melaleuca quinquenervia* saplings of 2 chemotypes (A: viridiflorol; B: *E*-nerolidol) after exposure to 2 levels of insect herbivory and 2 water treatments.

Results

Plant chemotype did not influence the densities of either colonizing insect species or the damage ratings, thus supporting the 1st null hypothesis (Table 1). The 2nd null hypothesis was not supported because the amount of leaf biomass shed from trees via abscission was influenced by chemotype ($F_{1, 35}$ = 9.3, P = 0.004), albeit to a lesser degree compared with herbivory, with an herbivory × chemotype interaction whereby most leaf biomass was shed from the *E*-nerolidol chemotype when subjected to unrestricted herbivory (T = 2.04; df = 41; P = 0.04) (Fig. 1). Chemotype also indirectly influenced tree height through interactions with both herbivory and water (Table 1). For example, the chemotype × herbivory interaction was caused by a change in magnitude whereby trees with the viridiflorol chemotype grew taller when herbivory was restricted compared with unrestricted (T = 2.30; df = 65; P = 0.02), whereas tree height for the *E*-nerolidol chemotype was unaffected by herbivory (T = 0.19; df = 61; P = 0.85) (Fig. 2). The chemotype × water interaction with tree height was caused by a minor change in magnitude whereby trees with the viridiflorol chemotype responded more to irrigation than those with the *E*-nerolidol chemotype (T = 1.70; df = 67; P = 0.09) (Fig. 2).

Herbivory increased the amount of leaf abscission with a greater than 4-fold difference in biomass shed between restricted and unrestricted herbivory treatments (Fig. 3). Although there was a positive relationship between the damage caused by *O. vitiosa* and the amount of leaf biomass shed via abscission (r = 0.32, P = 0.0002), there were no correlations between the densities of *O. vitiosa* (r = −0.001; P = 0.98) or *B. melaleucae* (r = −0.06; P = 0.45) and the amount of leaf biomass that was shed. Water treatments had no effect on leaf abscission and there were no interactions with herbivory ($F_{1, 35}$ = 0.29; P = 0.59) or chemotype ($F_{1, 35}$ = 0.13; P = 0.72) (Table 1). Tree height was influenced primarily by herbivory but not directly by chemotype or water, although there were interactions between all 3 factors as mentioned above with chemotype (Table 1). The herbivory × water interaction was explained by a change in magnitude whereby non-irrigated trees were shorter when subjected to unrestricted herbivory compared with restricted herbivory (T = 3.37; df = 59; P = 0.001), whereas the mean height of irrigated trees was the same regardless of herbivory (T = 0.72; df = 67; P = 0.47). The chemotype × water interaction is explained in the above paragraph.

Discussion

The evidence for differential herbivore preference or utilization of chemotypes in the field is limited with results that frequently contrast with one another (Macel & Klinkhamer 2010). This may be a function of the temporal flux of the characteristic constituent compounds of

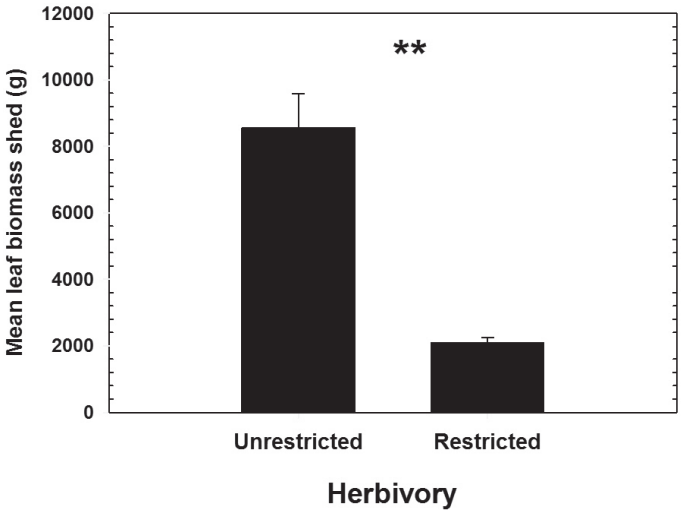


Fig. 3. Total mean (± SE) leaf biomass shed via abscission by *Melaleuca quinquenervia* saplings subjected to unrestricted or restricted herbivory by *Oxyops vitiosa* and *Boreioglycaspis melaleucae*. **: P = 0.01.

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Table 1. Results of ANOVA for *Melaleuca quinquenervia* parameters with chemotype, herbivory, and water as main factors. The measurements of *Oxyops vitiosa* and *Boreioglycapsis melaleucae* are based on the number of individuals per cm of tree height.

	Chemotype (C)		Herbivory (H)		Water (W)		H × C		H × W		C × W	
Variable	df	TSS (%)	df	TSS (%)	df	TSS (%)	df	TSS (%)	df	TSS (%)	df	TSS (%)
Biomass shed (g)	1	3.7*	1	17.6**	1	0.09	1	3.7*	1	0.04	1	0.003
Tree height (cm)	1	0.02	1	3.1*	1	0.19	1	2.2	1	7.3**	1	3.0*
O. vitiosa cm ht^{-1}	1	0.1	1	6.1**	1	0.2	1	1.6	1	0.3	1	0.03
B. melaleucae cm ht^{-1}	1	0.01	1	15.5**	1	0.12	1	0.2	1	0.03	1	0.1
Damage rating	1	0.1	1	15.3**	1	1.1	1	0.1	1	0.4	1	0.02

Presented are the degrees of freedom (df) and the rounded percentage of variance explained by a factor (TSS) calculated using the formula: TSS = 100 × (factor SS / total SS). There were no significant H × C × W interactions. Asterisks indicate significance levels, *: $P = 0.05$, **: $P = 0.01$.

chemotypes in response to climatic, edaphic, and biotic factors, as well as their interactions, which may moderate their influence (Perry et al. 1999; Pecetti et al. 2006; Szakiel et al. 2011). Laboratory studies that eliminate natural biotic and abiotic factors are likely to produce exaggerated results because the differences in insect fecundity, longevity, or preference evident in controlled laboratory settings may not translate to variable field population parameters like density (Zvereva et al. 2010). In a greenhouse study, Morath et al. (2006) also found no chemotype differences in the optical density of chlorophyll in *M. quinquenervia* leaves following feeding by *B. melaleucae*.

Although both chemotypes were colonized equally by 2 specialist herbivores, the chemotypes reacted differentially with the *E*-nerolidol chemotype dropping more leaf biomass in response to herbivory than the viridiflorol chemotype. Premature abscission of leaves in response to herbivory is a common general response of woody plants (Zvereva & Kozlov 2014) and can be related to the rate of photosynthesis occurring in a leaf; once it drops below a certain level, abscission may occur in order to prevent a drain on water and nutrients from outweighing the contribution of fixed carbon (Hensel et al. 1993). This outcome may exacerbate defoliation to where it exceeds actual amount of biomass directly consumed (Mazía et al. 2012). In general, premature leaf abscission in response to herbivory is a tolerance rather than a resistance strategy to reduce the negative effects of localized damage to the whole plant (Zvereva & Kozlov 2014). Fast growing trees like *M. quinquenervia* are generally argued to invest less in chemical defense and instead opt for tolerance to herbivory (Coley et al. 1985; Strauss & Agrawal 1999). In this case, leaf abscission patterns may diverge even at the plant variant level as evidenced by the *E*-nerolidol saplings that grew to the same height regardless of herbivory, whereas the saplings with viridiflorol chemotype, found to be less suitable for *O. vitiosa* in laboratory studies, grew taller when herbivory was restricted. This may signal a different sensitivity of a more preferred variant like the *E*-nerolidol chemotype to herbivory, which is manifested by a more rapid abscission response before metabolic costs negatively influence other growth parameters such as vertical growth rate. Saplings in many habitats that grow tall fast may gain an advantage by reaching critical light resources before competitors, including conspecifics (King 1994). The results of this study suggest that differential *M. quinquenervia* responses to herbivory exist at the plant variant or chemotype level during early phases of growth.

These data also have particular relevance to the patterns of herbivore colonization. There is a paucity of data in the scientific literature that quantifies host plant selection at the earliest stage of patch colonization. Our findings indicate that selection of host plants by colonizing *O. vitiosa* and *B. melaleucae* adults and their resulting offspring are not influenced by chemotype or water availability. Colonization patterns among the tested treatments suggested that herbivory by the biological control agents is uniform, with no saplings escaping attack due to variation in preference. One limitation of this experimental design is the short duration that colonization can be measured. Dispersal of herbivores into a new habitat or host patch is inherently ephemeral, but is critical to understanding the realized host use patterns of intentionally introduced natural enemies.

The disparate results from laboratory, greenhouse, and field studies obscure a wider understanding of the role of chemotypes in *M. quinquenervia* insect–plant interactions. Longer-term studies may provide additional insight by assessing how more mature trees of different chemotypes allocate internal resources while subjected to different and more extended levels of herbivory and resource availability.

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