



Contents lists available at ScienceDirect

Biological Control

journal homepage: www.elsevier.com/locate/ybcon

Modeling the compensatory response of an invasive tree to specialist insect herbivory

Bo Zhang^{a,*}, Xin Liu^b, D.L. DeAngelis^c, Lu Zhai^{d,*}, Min B. Rayamajhi^e, Shu Ju^a

^a Department of Biology, University of Miami, Coral Gables, FL 33124, USA

^b Co-Innovation Center for Sustainable Forestry in Southern China, Nanjing Forestry University, Nanjing, Jiangsu 210037, China

^c Wetlands and Aquatic Research Center, U.S. Geological Survey, Gainesville, FL 32653, USA

^d Southeast Environmental Research Center, Florida International University, Miami, FL 33199, USA

^e USDA-ARS Aquatic Weed Research Laboratory, 3205 College Avenue, Fort Lauderdale, FL 33314, USA

ARTICLE INFO

Keywords:

Melaleuca quinquenervia

Herbivory

Biological control

Carbon and nitrogen allocation

Compensation

ABSTRACT

The severity of the effects of herbivory on plant fitness can be moderated by the ability of plants to compensate for biomass loss. Compensation is an important component of the ecological fitness in many plants, and has been shown to reduce the effects of pests on agricultural plant yields. It can also reduce the effectiveness of biocontrol through introduced herbivores in controlling weedy invasive plants. This study used a modeling approach to predict the effect of different levels of foliage herbivory by biological control agents introduced to control the invasive tree *Melaleuca quinquenervia* (melaleuca) in Florida. It is assumed in the model that melaleuca can optimally change its carbon and nitrogen allocation strategies in order to compensate for the effects of herbivory. The model includes reallocation of more resources to production and maintenance of photosynthetic tissues at the expense of roots. This compensation is shown to buffer the severity of the defoliation effect, but the model predicts a limit on the maximum herbivory that melaleuca can tolerate and survive. The model also shows that the level of available limiting nutrient (e.g., soil nitrogen) may play an important role in a melaleuca's ability to compensate for herbivory. This study has management implications for the best ways to maximize the level of damage using biological control or other means of defoliation.

1. Introduction

The effects of herbivory on plant fitness can be highly variable, as the plants are capable of exercising various compensatory responses. In this regard, McNaughton (1983) has proposed three alternative hypotheses: (1) plant fitness declines consistently as the intensity of herbivory increases; (2) plants are able to compensate for herbivory up to some level, then fitness declines with increasing herbivory; (3) plant fitness is increased by moderate levels of herbivory, then declines and becomes negative at higher levels of herbivory (herbivory optimization hypothesis, e.g., Hilbert et al. (1981)). The second hypothesis is widely reported in the literature (e.g., Kulman, 1971; Trumble et al., 1993). This is one of the important components of the ecological fitness in many plants, and is of interest to agricultural scientists in terms of crop plant yields (Southwood, 1973). It is also a matter of interest in the management of weedy invasive plants involving introduced biological control agents, such as arthropods that can inflict defoliation at different levels. For instance, Sevillano et al. (2010) reported empirical evidence of compensation for damage by biocontrol agents on the

invasive tree *Melaleuca quinquenervia* (melaleuca). The degree to which plants can compensate for herbivore damage is important to understand in planning control efforts, as it would indicate the intensity of control measures needed to suppress the plant populations to a desired level.

The purpose of this paper is to illustrate the key components of compensation in a tree and to explore the consequences for biocontrol under different resource conditions. In this study, we will use modeling to simulate the specific case of the use of biocontrol agents to suppress the population of an invasive tree *Melaleuca quinquenervia* (Cav.) Blake (hereafter referred to as “melaleuca”). This invader possesses strong invasive attributes and, from its introduction around 1900, had invaded over 200,000 ha of the ecologically sensitive freshwater ecosystems of southern Florida by the end of the century (Dray et al., 2006).

Biological control methods that deploy natural enemies such as herbivores and pathogens have been advocated as an environmentally friendly and cost effective management strategy for this noxious weed (Balcianas and Center, 1991; Bodle et al., 1994). Therefore, a melaleuca biological control program was implemented in Florida beginning in

* Corresponding authors.

E-mail addresses: bo@bio.miami.edu (B. Zhang), lzhai@fiu.edu (L. Zhai).

<https://doi.org/10.1016/j.biocontrol.2017.11.002>

Received 22 May 2017; Received in revised form 18 October 2017; Accepted 3 November 2017

1049-9644/ © 2017 Elsevier Inc. All rights reserved.

1997 with the release of *Oxyops vitiosa* Pascoe, a melaleuca weevil whose larvae and adults feed on foliage and bud tissues (Center et al., 2000). Impacts caused by this weevil to melaleuca populations began to appear in research plots during 2001. A second biological control agent, the melaleuca psyllid, *Boreioglycaspis melaleucae* (Moore), attacking foliage and inflorescences, was released during spring 2002. An unknown sooty mold, indiscriminately covering foliage and green stems, also became abundant, usually in association with heavy infestations of this scale (Rayamajhi et al., 2010). In addition, an adventive rust fungus *Puccinia psidii* G. Wint became prevalent and attacked young foliage of melaleuca trees (Rayachhetry and Elliott 1997).

Overall, the natural enemies listed above are known to inflict damage to all melaleuca life-stages, and mortality to melaleuca seedlings and saplings (Pratt et al., 2005; Center et al., 2006; Morath et al., 2006). Among biological control agents, the melaleuca weevil has been especially effective in consuming leaves, forcing melaleuca to switch resource allocation from seed production to the production of new, often unseasonal growth (Rayamajhi et al., 2008; Tipping et al., 2008). Field studies (Tipping et al., 2009) show that the melaleuca weevil attacks new leaf tissue preferentially and relentlessly, thereby contributing to continuous defoliation and re-foliation cycles. Because complete recovery of leaf tissue is rare, the usual temporary reallocation of plant assimilates to leaf production may become virtually permanent under this sustained herbivory. As a strategy for resilience, a vascular plant such as melaleuca might be assumed to reallocate its photosynthetic energy among its components (foliage, roots, and stem) in a way that compensates for damage and maximizes growth rate.

2. Components of plant compensation

The way that plants can compensate for arthropod herbivory can be highly complex, involving both the way that internal resources are allocated, and aspects of canopy architecture, leaf morphology, and phenology. Furthermore, plant compensation is also affected by extrinsic factors such as resource availability (Zhao and Chen 2012). Our model takes into account some of the key mechanisms and factors.

2.1. Compensation for defoliation

One mechanism of compensation arises naturally from defoliation. Consider a control measure such as mechanical, chemical, or biological control that reduces a tree's foliage by a certain amount. Although these measures reduce the surface area of the foliage, the decrease in the actual rate at which light is captured may be less than proportional, because the self-shading of leaves is reduced with leaf area reduction. This effect can be expressed mathematically in a simple standard representation of the relationship between leaf foliage and the growth rate, G ;

$$G = R_0(1 - e^{-k_f b_f C_f})E(v_f) \quad (1)$$

where R_0 is the maximum possible rate of growth based on photosynthesis, C_f is the leaf carbon per unit area, b_f is the leaf area per unit carbon (thus $b_f C_f = \text{Leaf Area Index, LAI}$), k_f is the rate of extinction of light per leaf layer passing through the foliage (typically between 0.3 and 0.7), and $E(v_f)$ represents the effect of the leaf nutrient to carbon ratio. The factor $(1 - e^{-k_f b_f C_f})$, the Beer-Lambert law of light extinction, represents the fraction of incident light captured as a saturating response to foliar biomass. If LAI is initially large, say about 5 or greater for many closed canopies, such that $(1 - e^{-k_f b_f C_f})$ can be close to 1, even reducing LAI by one half might not appreciably reduce the amount of light captured by the leaves. This is a compensatory mechanism, reflecting the fact that trees commonly have much foliage that is relatively shaded, which can compensate for the loss of foliage shading it by being exposed to a higher level of radiation. The above expression could represent increased efficiency of the remaining leaves in other ways as

well, such as reduced transpiration surface that improves the water status of those leaves (Ericsson et al., 1980; Perry, 1994, page 447).

The second factor in Eq. (1), $E(v_f)$, represents the effect of the nutrient to carbon ratio, N:C, in leaves; and has the form

$$E(v_f) = \frac{v_f}{v_0 + v_f} \quad (2)$$

where $v_f = N_f/C_f$, the ratio of leaf nutrient per unit area to leaf carbon per unit area, representing the fact that higher leaf N:C ratio enables higher productivity, and v_0 is a constant. $E(v_f)$ is a saturating function of v_f , an effect of diminishing returns for higher v_f . This is a potential source of compensation. If v_f is initially large, then a plant would be able to reduce nutrient uptake, by reducing fine root biomass, without resulting in a proportional reduction in primary production. The saved assimilates could be allocated to foliage.

2.2. Compensation for loss of fine root biomass

Plant nutrient uptake is another process where compensation might play a role. Although nutrient resources differ from light in that there is not the equivalent of self-shading, roots compete for nutrients, so that a decrease in fine root biomass density could decrease competition, buffering the effect of biomass loss. This has been demonstrated in models and verified with data (e.g., Caassen and Barber, 1976, Silberbush and Barber, 1983). An additional compensatory mechanism can occur when decreased root biomass leads to a decreased rate of nutrient uptake. As a tree reduces its uptake of nutrients from the soil, nutrient concentration in the vicinity of fine roots will increase due to the lower uptake rate (Rendig and Taylor, 1989), which will thus have a positive effect on the rate of uptake of the remaining roots, as described by a Michaelis-Menten function for uptake (e.g., Silberbush and Barber, 1983). While the compensatory effects of nutrient uptake properly need to be described with complex mechanistic models (e.g., Rengel, 1993, Somma et al., 1998), we can succinctly capture the two effects of fine root biomass change and soil pore nutrient concentration with a simple function for nutrient uptake, U :

$$U = \left(\frac{g_N N_{\text{pore}}}{k_N + N_{\text{pore}}} \right) (1 - e^{-k_r b_r C_r}) \quad (3)$$

The first factor is the Michaelis-Menten function for nutrient uptake as a function of soil pore nutrient concentration, N_{pore} , with half-saturation constant k_N and maximum nutrient uptake rate g_N . The second factor is a phenomenological expression analogous to light capture by foliage, in that $(1 - e^{-k_r b_r C_r})$ asymptotes to 1 for large fine root carbon, where b_r is the fine root area per unit fine root carbon and k_r is the effect of fine root density on nutrient uptake per fine root area, representing the effect of mutual competition among roots for nutrients. Therefore, a moderate reduction in fine roots from an initially high density will not reduce nutrient uptake to a proportional degree, because a compensatory effect occurs in reducing the degree of competition among the plant's roots. Although data from (Silberbush and Barber (1983), their Fig. 1) for agricultural plants show some nonlinear effect that might be due to root competition, and we can conjecture this occurs for melaleuca also, there is little information on possible parameters values, so we ignore this saturating effect here and assume a linear function of C_r instead, so that $U = g'_N C_r N_{\text{pore}} / (k_N + N_{\text{pore}})$, where $g'_N = g_N k_r b_r$; see Appendix A for details.

2.3. Compensation through changes in allocation

A tree can change the way it allocates its carbon and limiting nutrient (usually nitrogen) resources to capture not just light, but water and nutrients as well. Woody plants allocate their acquired resources, energy (or carbon) and various nutrients, to meet their several essential functions. The ability of plants to adjust carbon allocation in response

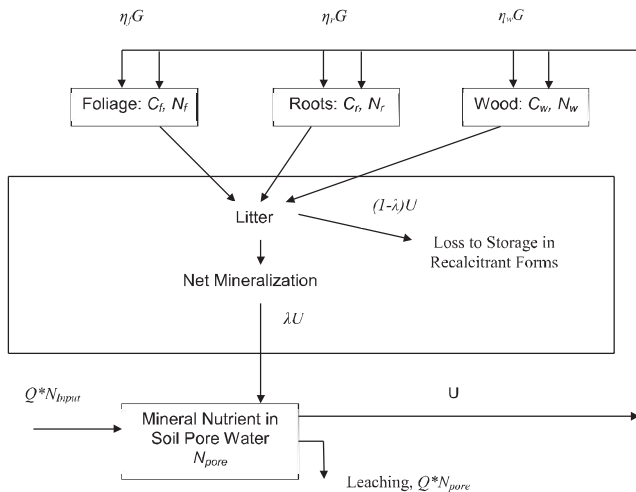


Fig. 1. Schematic of model for allocation of carbon and for nutrient cycling. The solid lines represent the flow of the limiting nutrient, while the dashed lines represent the allocation of carbon that is produced through photosynthesis. Storage outflows are not explicitly represented. Allocation ratio to foliage (η_f), to root (η_r), to wood (η_w); G : net carbon production, or growth rate; Carbon and nitrogen in the three tree components, C_f and N_f : foliage, C_r and N_r : fine roots, C_w and N_w : wood; U : uptake rate of plant-available nutrient; N_{pore} : nutrient concentration in soil-pore bound water.

to environmental conditions is widely documented (e.g., [Friend et al., 1994](#)). The trade-off in carbon investment between root and shoot (foliage) is well known and has been the subject of many studies and models (e.g., [Wilson, 1988](#); [Ingestad and Ågren, 1991](#); [Thornley, 1995](#); [Hermans et al., 2006](#)). These allocations can be adjusted to optimize growth following foliage removal. In particular, the allocation of these carbon and nutrient resources is often altered to increase resources going to foliage by reducing the amount going to roots and/or woody materials, as the leaves serve as the primary producers of photosynthesis in most woody plants ([Morath et al., 2006](#)). The reason behind the reallocation from roots to foliage in some cases may be due to a tree's initial capacity for nutrient uptake through roots being more than sufficient to balance the internal plant processes of carbon fixation to maximize growth. Just as a tree can lose some foliage without a proportional loss of total photosynthesis, under some conditions it may sometimes be able to lose some fine root area without a proportional loss of water and nutrient uptake. In that case, transfer of a greater fraction of resources from roots to foliage would not come at a high a cost to nutrient uptake. Because complete recovery of leaf tissue is rare, the usual temporary reallocation of plant assimilates to leaf production may become virtually permanent under sustained herbivory.

Each of the compensatory effects described above can be significant, so it is necessary to understand the net effect of foliage removal by considering the whole plant and soil as a system in which the plant can alter the way it allocates resources in an optimal way in response to the defoliation. This can be done through modeling both the passive effects of decreased *LAI* and the active adjustment of allocation of the tree in response to insect herbivory under its given environmental conditions.

3. Materials and methods: mathematical model

We used a steady state tree dynamics model with the above components to determine the allocation strategy that maximizes growth under given conditions of light, nutrient availability, and defoliation. A well-known model of tree growth and nutrient cycling is the G'DAY model ([Comins and McMurtrie, 1993](#)). This model simulates both carbon and nitrogen in tree and soil compartments. [Ju and DeAngelis \(2009, 2010\)](#) used a variation of this model in which nutrient recycling was simplified ([Fig. 1](#)). Following [Comins and McMurtrie \(1993\)](#), we used Eq. (1) for the growth rate, G , and Eq. (3) for nutrient uptake, U

But to avoid soil process complexity the explicit compartments for litter and soil in the original model were removed and nutrient (assumed nitrogen from here on) mineralization from litter was assumed to occur instantaneously, going directly to the soil-pore bound water, where it becomes available for uptake by roots, as described in Eq. (2) for U . It was also assumed that some nutrient could be lost during recycling at a rate proportional to its flux through the plant biomass.

The model simulates tree carbon (C) and nutrient (N) per unit area (m^2) in foliage, fine roots and wood components, but the tree was assumed able only to change the allocation ratio between foliage and fine roots, woody material being assumed to have a fixed allocation rate. We did not model allocation to tree reproductive biomass or the population dynamics of the herbivores that feed on the plant's foliage. The possible resource allocation by trees between leaf and foliage components in response to the different levels of herbivore inflicted defoliation was simulated. We tested three hypotheses with regard to the effects of herbivores on reducing melaleuca's growth rate: (1) Melaleuca's growth rate, biomass and nitrogen contents change when its energy allocation to the three components changes; (2) melaleuca responds optimally to higher levels of herbivory by allocating more energy to foliage and less to roots; and (3) melaleuca can tolerate higher levels of herbivory when soil nutrient level is higher. Therefore, our goal was to estimate the rate of defoliation needed to achieve a specified reduction in the growth rate under various conditions of nutrient availability to the tree and how it might change its allocations to foliage and roots in an optimal way. The full set of equations for the model is shown in [Appendix A](#). All variables and parameters are listed in [Table 1](#).

4. Application to melaleuca

This study focused on understanding the optimal carbon allocation under a range of defoliation rates by herbivory. Starting with zero herbivory, we next assumed a low herbivory level, ϕ_f of 0.25 yr^{-1} , than an intermediate level, 0.75 yr^{-1} , and finally a high value, 1.25 yr^{-1} ([Erbilgin et al., 2014](#)). All parameters are defined in [Table 1](#) for the numerical evaluation. Some key parameters were determined for melaleuca, while a few that could not be estimated were slight modifications of those in [Comins and McMurtrie \(1993\)](#). Their G'DAY model is intended to be generic. Because the feasible range on the parameters is relatively narrow, we believe the parameter values borrowed from G'DAY are sufficient for realistic model projections.

5. Results

We first simulated the change of the equilibrium values of the growth rate of total carbon per square meter (G^* , but left as G here for simplicity), along a range of the carbon allocation fractions to foliage (η_f), from 0.03 to 0.6 (the range for which $G > 0$) such that the allocation to fine roots, was $\eta_r = 1 - \eta_f - \eta_w$, for fixed $\eta_w = 0.4$ (see equations in [Appendix A](#)), for four defoliation rates (ϕ_f), for nutrient input concentration at a baseline level ($N_{input} = 0.000001 \text{ kg kg}^{-1} \text{ water}$), such that the input flux of nutrient is $N_{input} Q = 0.000001 \times 100 = 0.0001 \text{ kg m}^{-2} \text{ yr}^{-1}$, where Q is precipitation input ($\text{kg m}^{-2} \text{ yr}^{-1}$). We found that $Max(G)$ was negatively affected by increasing ϕ_f , but the tree's response, both due to the reduction of foliage self-shading and by the tree's increasing its carbon allocation to foliage, buffered the impact. When no herbivore defoliation was included in the simulation ($\phi_f = 0.0$, so that there was only a natural annual foliage loss rate, $\gamma_f = 0.25$), G reached its maximum value ($Max(G)$) when $\eta_f = 0.14$ ([Fig. 2A](#), dots), then decreased with higher η_f . When ϕ_f was increased from zero to 0.25, to simulate weak herbivory impact, $Max(G)$ occurred at $\eta_f = 0.22$, indicating that melaleuca needed to allocate a larger fraction of carbon to foliage to maximize growth rate. Importantly, the decrease in $Max(G)$ from the case of no herbivore defoliation was small, only about a 15% decrease for a doubling of the rate of foliage loss, suggesting that the compensatory effects in the model

Table 1
Variables, functions, and parameters used in the model.

Variable	Notation	Value	Reference
C_f, C_r, C_w	Carbon pool for foliage, root and wood (kg m ⁻²)		
N_f, N_r, N_w	Nitrogen for foliage, root and wood (kg m ⁻²)		
N_{pore}	Soil pore water nitrogen concentration (kg nutrient kg ⁻¹ water)		
η_f, η_r	Allocation fraction of carbon to foliage and root		
Functions	Form		
$I(C_f)$	$(1 - e^{-k_f b_f C_f})$		See text
$E(v_f)$	$\frac{v_f}{v_0 + v_f}$		See text and footnote ¹ below
$U(N_{pore}, C_r)$	$\frac{g'_N N_{pore} C_r}{k_N + N_{pore}}$		See text
Parameters	Notation	Value	Reference
R_0	Maximum possible growth rate (kg m ⁻² yr ⁻¹)	7.03	Jabowa simulation, Zhang et al. (2017)
η_w	Allocation fraction of carbon to wood	0.40	Comins and McMurtrie (1993)
ρ	Ratio of root N:C to foliage N:C ratio	0.70	Comins and McMurtrie (1993)
ν_w	N:C ratio for wood, N_w / C_w	0.0001	Comins and McMurtrie (1993)
γ_f	Senescence rate for foliage (yr ⁻¹)	0.25	Rayamajhi et al. (2010)
ϕ_f	Herbivory on foliage (yr ⁻¹)	0.5, 1 and 1.5 for low, medium, high herbivory	Rayamajhi et al. (2010)
γ_r	Senescence rate for root (yr ⁻¹)	0.60	Rayamajhi et al. (2010)
γ_w	Senescence rate for wood (yr ⁻¹)	0.005	Rayamajhi et al. (2010)
λ	Recycling ratio	0.98	Ju and DeAngelis (2009)
ν_0	Foliar N:C half-saturation constant	0.02	Rayamajhi et al., 2010
g'_N	Maximum possible steady nutrient uptake rate per ground area (kg m ⁻² yr ⁻¹)	0.15	See footnote ² below
k_N	Half-saturation coefficient for N plant uptake (kg kg ⁻¹)	0.00002	Close to value from Leadley et al. (1997)
b_f	Foliage area per unit C	10.0	Comins and McMurtrie (1993)
k_f	Radiation light extinction coefficient	0.50	Comins and McMurtrie (1993). Other references for a variety of trees closely bracket this range; e.g., Pierce and Running 1988, Cannell et al. (1987), Perry (1994, Table 15-1).
N_{input}	Input nutrient concentration (kg nutrient kg ⁻¹ water)	0.0000005, 0.000001, 0.000002 and 0.000004, four nutrient levels	See footnote ³ below
Q	Flow of water (kg m ⁻² yr ⁻¹)	100	See footnote ⁴ below

¹ The effects of nutrient to carbon ratio in foliage, $v_f = N_f / C_f$ are modeled by the function, $E(v_f) = v_f / (v_0 + v_f)$, where v_0 is the half saturation point; $v_0 = 0.02$. This is a modification of the function $E(v_f)$ in Comins and McMurtrie, where they used $E(v_f) = v_f / v_0$ for $v_f < 0.04$ and $E(v_f) = 1$ for $v_f \geq 0.04$.

² The parameter g'_N is set to the value 0.15. This allows the lowest value of N_{input} to reduce the tree to near extinction.

³ Nutrient concentrations in input water was given values to produce inputs per hectare of 0.5–4 kg per year, which is within the range of literature values for forests.

⁴ Assumed to be input from 1 meter of rainfall per year and thus 100 kg per square meter per year, typical for southern Florida.

buffered the losses to herbivory (Fig. 2A x's). When herbivory became stronger ($\phi_f = 0.75$ and 1.25), $Max(G)$ occurred at still higher levels of η_f . $Max(G)$ was then substantially lower compared with zero or weak herbivory (Fig. 2A, squares and triangles, respectively). The carbon biomasses per unit area in foliage, fine roots and wood, C_f , C_r , and C_w , are linear functions of G and, like G , but C_f and C_r reach different maxima as functions of η_f , because $C_f - \eta_f G$ and $C_r - \eta_r G$. with the peak of C_f skewed to larger values of η_f (Fig. 2B) and C_r skewed toward smaller values of η_f (Fig. 2C). Only the peak in wood was identical to that of $Max(G)$ because the fraction allocated to wood did not vary (Fig. 2D). The optimal values of C_f , C_r , and C_w occur at the value of η_f where $Max(G)$ occurs.

The trends in foliar and fine root nutrients per unit area, N_f and N_r , tended to follow the trends of carbon losses both because nutrient in the leaves was lost along with carbon in the foliage and because the tree compensated for defoliation by allocating less carbon to roots, decreasing the amount of nutrient uptake and thus the values of N_f and N_r (Fig. 3A and B). As a result, the N_f / C_f ratio in foliage was relatively stable across the four levels of defoliation (Fig. 3D), due to the fact that defoliation recycled nutrient back to the nutrient pool through litterfall, for melaleuca to take up. Although for any given value of η_f , N_f / C_f increased with ϕ_f , the optimal value of η_f also increases, such that the optimal value of N_f / C_f stayed roughly the same.

An important question is whether changed levels of available nutrient change the ability of the plant to compensate, so we considered both decreased and increased values of nutrient input N_{input} . To show the effects of different values of N_{input} on maximum production, we plot the maximum value of G ($Max(G)$) over the range of ϕ_f from 0.25 to 4 for each N_{input} input concentration (0.0000005, 0.000001, 0.000004, and 0.000015). Extension of ϕ_f to 4 gives a larger range to visualize the results. First, for each level of N_{input} , $Max(G)$ decreased approximately linearly with increasing foliage loss, $\gamma_f + \phi_f$ (Fig. 4A). Second, with higher N_{input} , a higher rate of herbivory, ϕ_f , could be reached before melaleuca suffered negative growth rate ($G < 0$) and died (Fig. 4A), so that only the three lowest values of N_{input} resulted in mortality when ϕ_f exceeded some value below 4. For instance, Fig. 4A shows that the tree's growth cannot be sustained when N_{input} is only half of the baseline level, 0.0000005, and ϕ_f exceeds 0.75. This led to similar trends in carbon amount in foliage and fine roots (Fig. 4C and D). In conclusion, the same herbivory intensity had weaker impact on decreasing plant growth rate if nutrient was more available, suggesting that higher levels of herbivory was necessary for a desired limitation of melaleuca growth rate.

With increasing ϕ_f , the numerical evaluation showed that the η_f value for $Max(G)$ increased, as melaleuca increased its fraction of C allocated to foliage with increasing η_f to achieve $Max(G)$ (Fig. 4B),

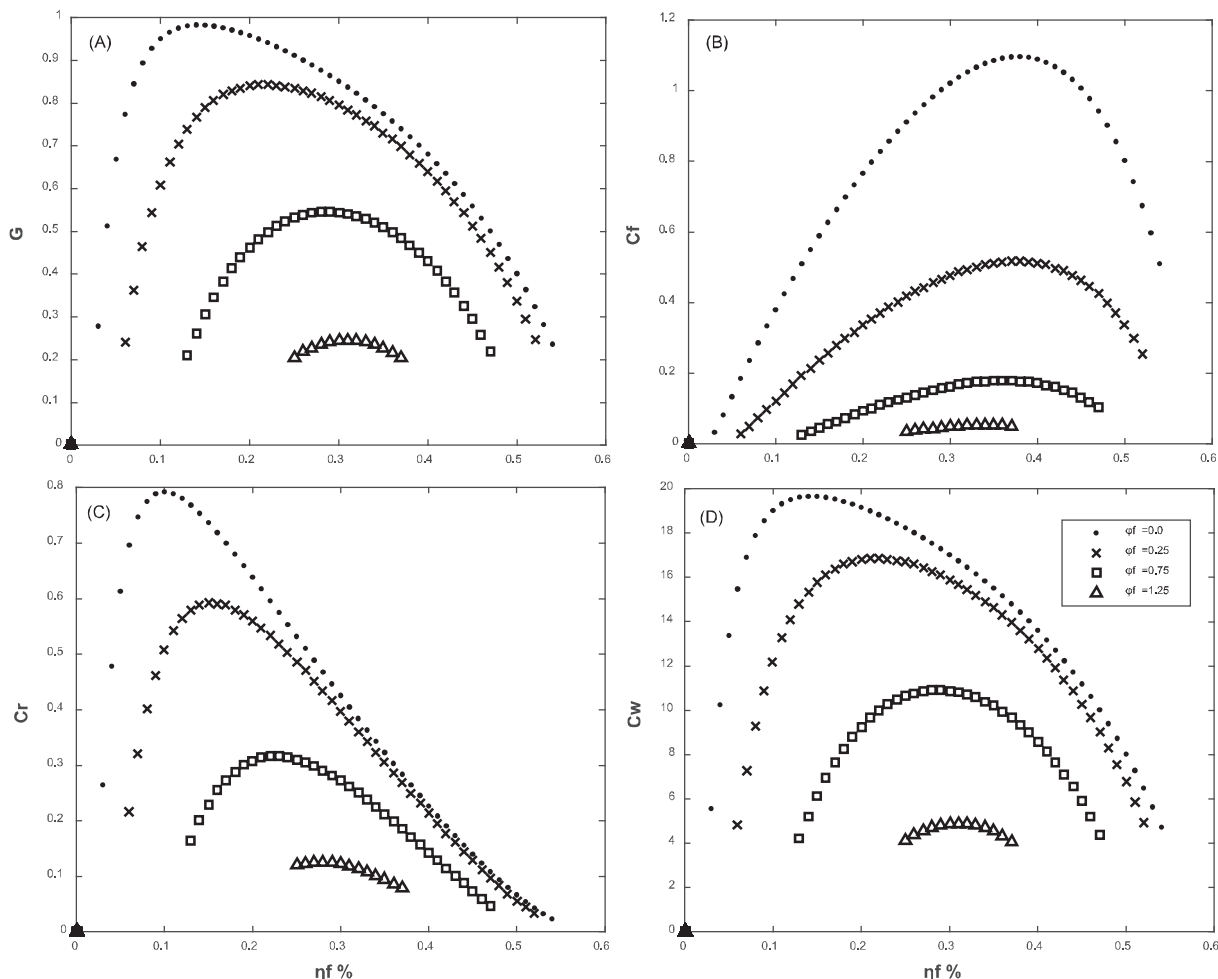


Fig. 2. Simulated relationships between carbon allocation to foliage, η_f (0–0.6) and (A) G : net carbon production, or growth rate (B) C_f : carbon amount in foliage, (C) C_r : carbon amount in fine roots and (D) C_w : carbon amount in wood, at four levels of herbivory intensity ($\phi_f = 0$; $\phi_f = 0.25$; $\phi_f = 0.75$ and $\phi_f = 1.25$). Nutrient input $N_{input} = 0.000001$, the baseline nutrient level.

although at a decreasing rate. When the five nutrient levels are compared, it is shown that, remarkably, for a given low level of defoliation, $\gamma_f + \phi_f$, the melaleuca actually allocated a smaller fraction of C to foliage, η_f , as N_{input} increased (Fig. 4B). This is counterintuitive, as it would seem that greater nutrient availability would allow the melaleuca to divert a fraction carbon initially going to roots to foliage to compensate for foliage loss. However, at these relatively low levels of defoliation, nutrient was limiting the growth rate, through the function $E(v_p)$ (see Eq. (2)), so that it was advantageous for overall plant fitness to grow more fine roots to absorb nutrient when nutrient was limiting in this parameter range. When herbivory reached a threshold ($\gamma_f + \phi_f$ greater than about 2), it became optimal for melaleuca to increase allocation of carbon to foliage when N_{input} increases.

6. Discussion

This study provides results of a model showing the possible compensatory response of trees, melaleuca in this case, to increased defoliation. We are not aware of prior theoretical studies that have examined the influence of herbivory on the resource allocation and compensation in woody perennials with the explicit aim of estimating the possible way that plant compensation alters the effects of defoliation on an invasive plant, although relevant empirical work has been done (Holland et al., 1996; Pratt et al., 2005; Rayamajhi et al., 2008; Tipping et al., 2008). In our study compensatory mechanisms include the fact that there is substantial self-shading of leaves of trees ($LAI \approx 10$

in the absence of herbivory), so that loss is somewhat compensated for by the greater light-capturing efficiency of the remaining foliage. A second compensatory mechanism that a plant has is to increase its allocation to the component, in this case foliage, that suffers damage. A third component is greater nutrient uptake efficiency of individual fine roots as fine root biomass decreases due to greater relative allocation of carbon to foliage.

Melaleuca's optimization of growth resulted in a shift in allocation to foliage in the model. The response of G to energy allocation to foliage (η_f) was unimodal, reaching a maximum and then decreasing. Biomass and nitrogen contents follow a similar trend to growth rate. Such unimodal distribution indicated that there is an optimal allocation ratio among foliage and fine roots to obtain the maximum growth rate (Iwasa and Roughgarden, 1984; Poorter et al., 2012).

The net effect of the compensation was to greatly buffer the negative effect of defoliation. Comparing the three herbivory levels (low, medium and high), we found that growth rates consistently decreased with higher rates of defoliation, as observed empirically by (Rayamajhi et al., 2010), and the maximum growth rates appeared at higher foliage allocation ratios when defoliation increased. Besides growth rate, foliage carbon and nitrogen contents all decreased with stronger herbivory, which agrees with Rayamajhi et al. (2010), that nitrogen and carbon are both removed from affected leaf tissues. In addition, by comparing foliage N:C ratios across the values of $\gamma_f + \phi_f$ from low to high, it is observed that there is relatively little difference in these ratios, although there is an apparent slight increase for the highest value.

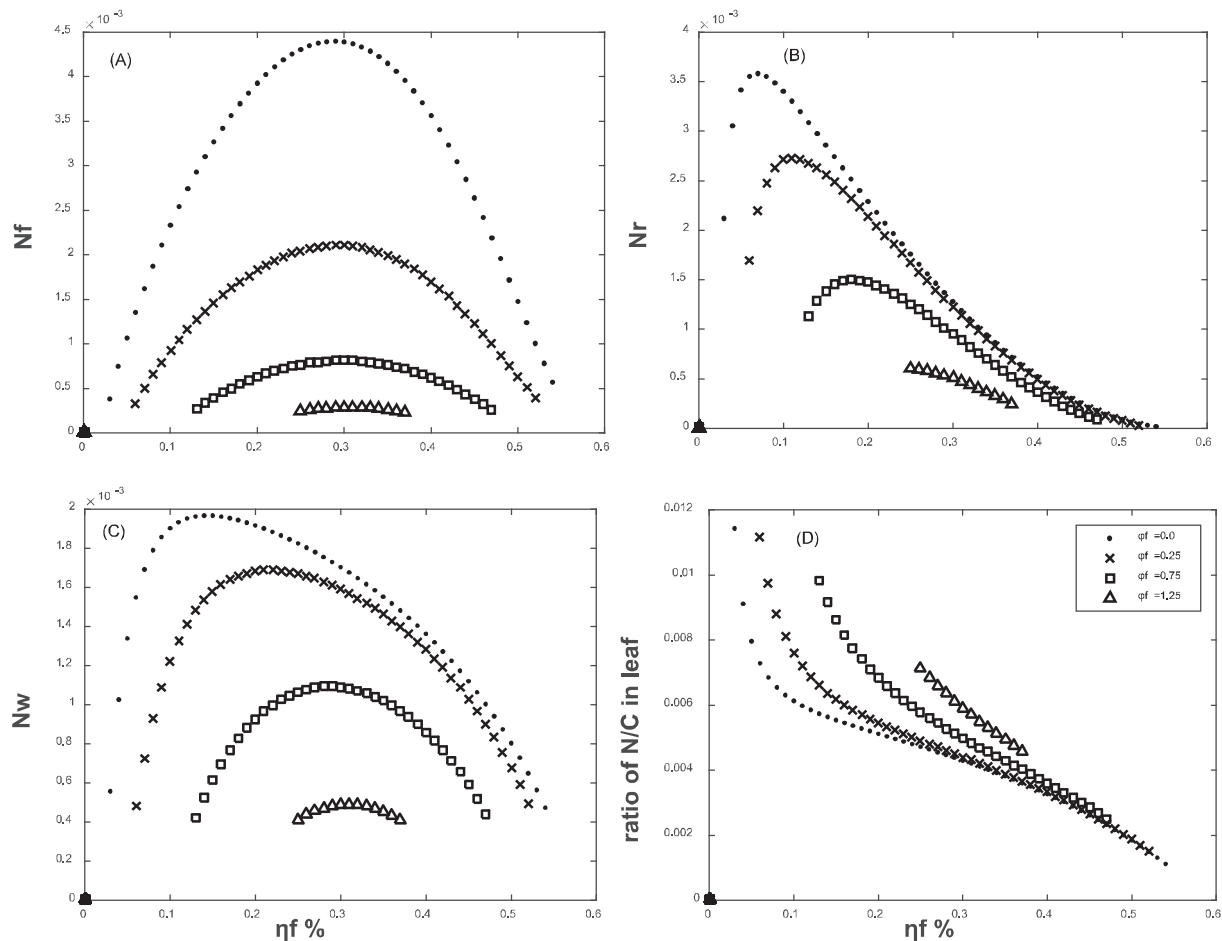


Fig. 3. Simulated relationship between carbon allocation to foliage, η_f (0–0.6) and (A) N_f : nutrient content in foliage, (B) N_r : nutrient content in fine roots, (C) N_w : nutrient content in wood and (D) nutrient/carbon ratio in foliage, at four herbivory intensities ($\phi_f = 0.0$; $\phi_f = 0.25$; $\phi_f = 0.75$ and $\phi_f = 1.25$). Nutrient input $N_{input} = 0.000001$, the baseline nutrient level.

The model predicts that melaleuca growth rate declines linearly with increases in ϕ_f , although, as noted above, the plant's compensatory mechanisms result in the slope of the growth rate decline versus herbivory being small. Therefore, the model does not show a 'threshold' behavior in which increasing herbivory leads to a sudden drop in the growth rate, which might have been expected.

Allocation to reproduction was not included in the model. But the plant's compensatory allocation of carbon and nitrogen to foliage would come at a significant cost to reproduction. As a result, the resulting loss in reproductive capacity should ultimately lead to decline in melaleuca populations (Pratt et al., 2005). This finding has significant management implications, in particular that the degree of biocontrol herbivory to reduce the plants growth to a desirable level will depend on the environmental conditions in which the plant is growing; this suggests that selection and integration of control strategies should carefully consider the environmental context in which management is required (Shea et al., 2005; Sevillano et al., 2010; Shea et al., 2010; Raghu et al., 2014). Because a tree may respond at a less than proportional decrease in growth rate to herbivore defoliation, due to compensation, this effect must be taken into consideration in both the design of biocontrol and evaluation of its effects.

Our study corroborates the findings in other plant systems in which nutrient conditions played an important role in their ability to defend against herbivory through compensation (Dickson, 1989). In this study, we simulated five levels of nutrient input and we found that growth rate and carbon production were lower under lower nutrient conditions, consistent with photosynthetic rate and biomass production being lower with lower nutrient inputs (Goolsby et al., 2004; Stevens et al.,

2008). We found that when herbivory was weak, an increase in nutrient input concentration, N_{input} , led to lower optimal carbon allocation ratio to foliage, and more to fine roots, as nutrient limitation exceeded carbon limitation in that case. However, at high levels of herbivory, higher N_{input} led to greater allocation to foliage to compensate for the loss in carbon. As a result, this study showed that high soil nutrient level ameliorates the impact of herbivory and increases tolerance.

Our findings support the report by Tipping et al. (2008) that the impact of herbivory can lead to a decline of melaleuca growth rate and further limit its invasion potential, but that plant compensation mechanisms can reduce the effect of herbivory. Moreover, the effect of defoliation on growth seems to follow McNaughton's first alternative hypothesis, that plant growth (or fitness) declines consistently with the level of herbivory. Our model does not show any sign of herbivory optimization of the plant, i.e., increase in growth rate for low levels of herbivory (McNaughton's Hypothesis 3).

We should note some limitations of the way the model has been constructed that may need to be modified in the future work. For instance: the model does not have a carbon storage component that can be utilized for short-term response to herbivore. Also, the lack of soil processes in our model could cause some of the effects of rapid defoliation on litter and soil dynamics to be ignored, which may be important to the plant's function (Bardgett et al., 1998). Better parameter values for melaleuca are also needed. For example, we chose the value of light extinction, $k = 0.5$, based on Comins and McMurtrie (1993). Lower values of k will lead to less ability for compensation. However, nearly all literature that we can find support values in the range $0.3 < k < 0.7$. Further studies with the model will attempt to correct

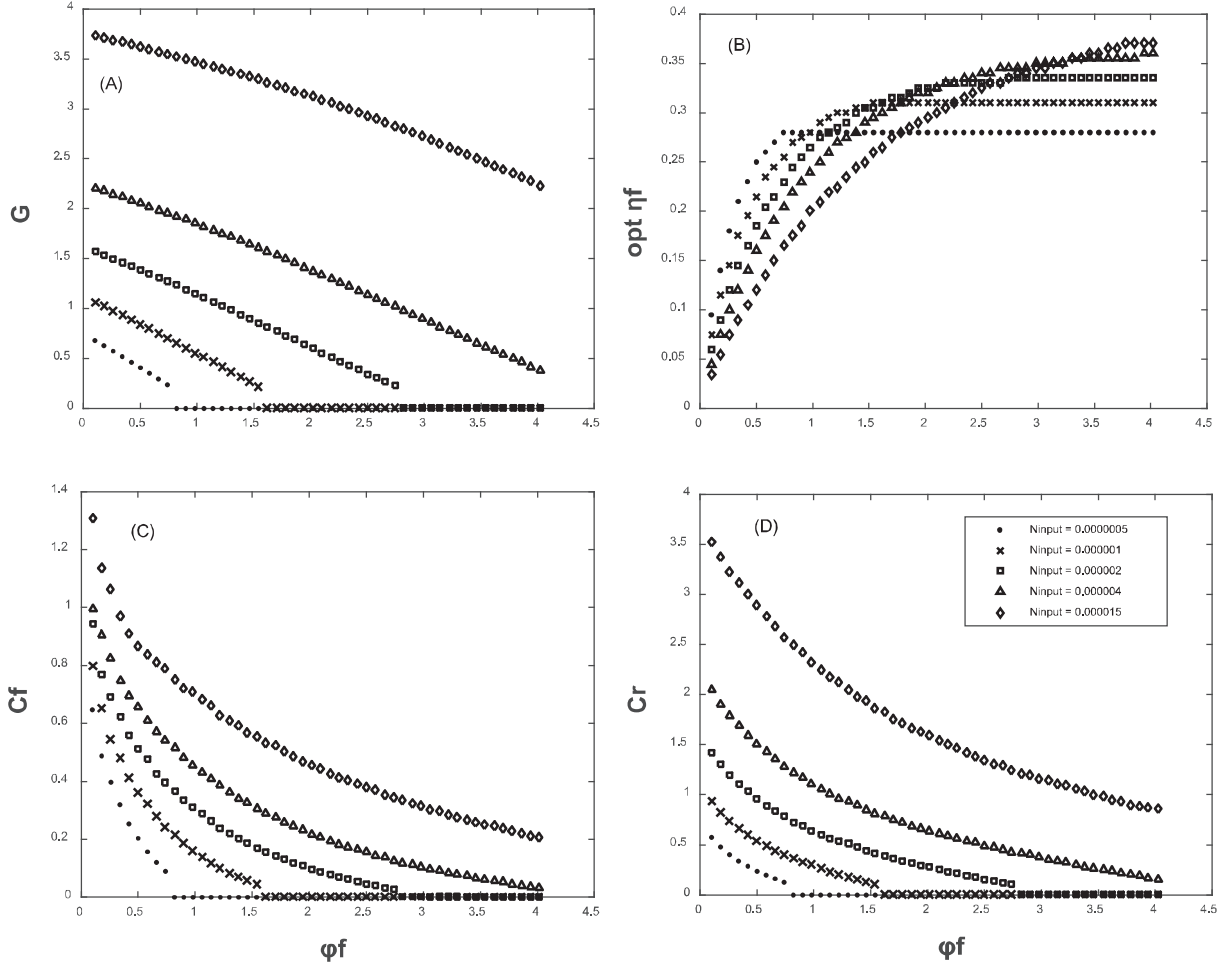


Fig. 4. Simulated relationship between defoliation ratio (0.1–4) and (A) $Max(G)$: maximum growth rate, (B) C_f : carbon amount in foliage, (C) C_r : carbon amount in root and (D) C_w : carbon amount in wood, at four soil nutrient inputs ($N_{input} = 0.0000005$; $N_{input} = 0.000001$; $N_{input} = 0.000002$; $N_{input} = 0.000004$, $N_{input} = 0.000015$).

these limitations.

Acknowledgments

We are thankful to the USGS’s Greater Everglades Priority Ecosystem Science for supporting Bo Zhang, Lu Zhai and Donald L.

DeAngelis’s research by providing necessary funds. We also appreciate collaborative efforts of researchers from USDA-ARS Aquatic Weed Research Laboratory in Fort Lauderdale, FL. We are grateful for review comments from Jacoby Carter and one anonymous reviewer. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Appendix A. Appendix Mathematical model

With the modifications made the on the original G’DAY model (Comins and McMurtrie, 1993), it reduces to six equations for carbon and nitrogen in the three tree components, foliage (C_f and N_f), fine roots (C_r and N_r), and wood (C_w and N_w);

$$\frac{dC_f}{dt} = \eta_f G - \gamma_f C_f - \phi_f C_f \tag{A1a}$$

$$\frac{dC_r}{dt} = \eta_r G - \gamma_r C_r \tag{A1b}$$

$$\frac{dC_w}{dt} = \eta_w G - \gamma_w C_w \tag{A1c}$$

$$\frac{dN_f}{dt} = (U - \eta_w \nu_w G) \frac{\eta_f}{\eta_f + \rho \eta_r} - \gamma_f N_f - \phi_f N_f \tag{A1d}$$

$$\frac{dN_r}{dt} = (U - \eta_w \nu_w G) \frac{\rho \eta_r}{\eta_f + \rho \eta_r} - \gamma_r N_r \tag{A1e}$$

$$\frac{dN_w}{dt} = \eta_w \nu_w G - \gamma_w \nu_w C_w \tag{A1f}$$

plus a seventh equation for the nutrient concentration (N_{pore}) in soil-pore bound water;

$$\frac{dN_{pore}}{dt} = Q(N_{input} - N_{pore}) - U + \lambda(\gamma_f N_f + \phi_f N_f + \gamma_r N_r + \gamma_w v_w C_w) \quad (A1g)$$

N_{pore} is the equivalent of R of the simple model. Separate equations for carbon and a limiting nutrient allow the $N:C$ ratio in foliage, fine roots, and wood to be variable.

In the above equations, the function G represents net carbon production, or growth rate. In particular,

G = net carbon production, or growth per unit time ($\text{kg m}^{-2} \text{yr}^{-1}$)

$$= R_0 I(C_f) E(v_f) \quad (A2)$$

$I(C_f)$ = light interception factor

$$= 1 - e^{-k_f b_f C_f} \quad (A3)$$

$E(v_f)$ = rate-limiting effect of leaf $N:C$ ratio on growth, where

v_f = $N:C$ ratio in foliage = N_f / C_f

$$E(v_f) = \frac{v_f}{v_0 + v_f} \quad (A4)$$

The parameter R_0 is the maximum possible primary production, b_f is the foliage per unit carbon, and k_f is the light extinction factor. The factor $E(v_f)$ represents the assumption that the photosynthetic efficiency of foliage is dependent on the $N_f:C_f$ ratio. The three parameters γ_f , γ_r , and γ_w are the loss rates, through litterfall, of foliage, fine roots, and wood, while ϕ_f is the loss rate of foliage through herbivory. The three parameters, η_f , η_r and η_w , govern the allocation of energy between foliage, fine root biomass, and wood, respectively, where $\eta_f + \eta_r + \eta_w = 1$. For convenience, we assume here that η_w is fixed; that is, whatever the relative allocations to foliage and roots, the fraction allocated to wood stays the same. The constants γ_f , γ_r , and γ_w are senescence (i.e., litterfall) rates. The constant ϕ_f represents additional loss rate of foliage due to herbivory. It is assumed that a fixed ratio, v_w , of N to C , is first allocated to wood, and then the rest of the nutrient is allocated to foliage and fine roots in the proportions $\eta_f / (\eta_f + \rho\eta_r)$ and $\rho\eta_r / (\eta_f + \rho\eta_r)$, respectively.

The function U represents nutrient uptake,

U = uptake rate of plant-available nutrient ($\text{kg m}^{-2} \text{yr}^{-1}$),

where

$$U = \left(\frac{g'_N N_{pore}}{k_N + N_{pore}} \right), \quad (A5)$$

where the parameter g'_N is the maximum possible nutrient uptake rate and k_N is the half saturation constant. In Eq. (1) g ,

Q = flow of water through the soil ($\text{kg m}^{-2} \text{yr}^{-1}$)

N_{input} = nutrient concentration in external input water ($\text{kg nutrient kg}^{-1}$ water)

λ = fraction of nutrient recycled; the remainder is assumed tied up in recalcitrant forms or, if nitrogen, also lost to gaseous forms.

If some loss of available nutrient to recalcitrant forms or to the atmosphere potentially occurs during decomposition of litter, then $0 \leq \lambda \leq 1$. The model does not assume any carbon or nutrient storage within the plant.

The mathematical analysis of the model to find the equilibrium value of G , as a function of parameters, is presented in Ju and DeAngelis (2010) and also in our On-line Supplementary Material Appendix B. The analysis produces an implicit equation for the plant production as a function of herbivory, nutrient availability and other factors, and was evaluated numerically.

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocontrol.2017.11.002>.

References

- Balcianas, J.K., Center, T.D., 1991. Biological control of *Melaleuca quinquenervia*: Prospects and conflicts. In T.D. Center, R.F. Doren, R.L. Hofstetter, R.L. Myers, L.D. Whiteaker, Proceedings of the Symposium on Exotic Pest Plants, November 2–4, 1988, Miami, Florida 1–22. Tech. Rep. NPS/NREVER/NRTR-91/06 Washington, DC: U.S. Department of the Interior, National Park Service.
- Bardgett, R.D., Wardle, D.A., Yeates, G.W., 1998. Linking above-ground and below-ground interactions: how plant responses to foliar herbivory influence soil organisms. *Soil. Biol. Biochem.* 30, 1867–1878.
- Bodley, Michael J., Ferriter, Amy P., Thayer, Daniel D., 1994. The Biology, Distribution, and Ecological Consequences of *Melaleuca Quinquenervia* in the Everglades. The Ecosystem and its Restoration, Everglades, pp. 341–355.
- Caassen, N., Barber, S.A., 1976. Simulation model for nutrient uptake from soil by a growing plant root system. *Agron. J.* 68, 961–964.
- Cannell, M.G.R., Milne, R., Sheppard, L.J., Unsworth, M.H., 1987. Radiation interception and productivity in willow. *J. Appl. Ecol.* 24, 261–278.
- Center, T.D., Pratt, P.D., Tipping, P.W., Rayamajhi, M.B., Van, T.K., Wineriter, S.A., et al., 2006. Field colonization, population growth, and dispersal of *Boreioglycaspis melaleucae* Moore, a biological control agent of the invasive tree *Melaleuca quinquenervia* (Cav.) Blake. *Biol. Control.* 39, 363–374.
- Center, T.D., Van, T.K., Rayachhetry, M., Buckingham, G.R., Dray, F.A., Wineriter, S.A., et al., 2000. Field colonization of the melaleuca snout beetle (*Oxyops vitiosa*) in south Florida. *Biol. Control.* 19, 112–123.
- Comins, H.N., Mcmurtrie, R.E., 1993. Long-term response of nutrient-limited forests to CO₂ enrichment – equilibrium behavior of plant-soil models. *Ecol. Appl.* 3, 666–681.
- Dickson, R.E., 1989. Carbon and nitrogen allocation in trees. *Ann. Sci. Forest.* 46, S631–S647.
- Dray, F.A., Bennett, B.C., Center, T.D., 2006. Invasion history of *Melaleuca quinquenervia* (Cav.) S.T. Blake in Florida. *Castanea* 71, 210–225.
- Erbilgin, N., Galvez, D.A., Zhang, B., Najjar, A., 2014. Resource availability and repeated defoliation mediate compensatory growth in trembling aspen (*Populus tremuloides*) seedlings. *PeerJ* 2.
- Ericsson, A., Hellkvist, J., Hillerdal, H., Xf mer, K., Larsson, S., et al., 1980. Consumption and pine growth: hypotheses on effects on growth processes by needle-eating insects. *Ecol. Bull.* 32, 537–545.
- Friend, A.L., Coleman, M.D., Isebrands, J.G., 1994. Carbon allocation to root and shoot systems of woody-plants. *Basic Life Sci.* 62, 245–273.
- Goolsby, O.A., Zonneveld, R., Bourne, A., 2004. Prerelease assessment of impact on biomass production of an invasive weed, *Lygodium microphyllum* (Lygodiaceae: Pteridophyta), by a potential biological control agent, *Floracarus perrepae* (Acariformes: Eriophyidae). *Environ. Entomol.* 33, 997–1002.
- Hermans, C., Hammond, J.P., White, P.J., Verbruggen, N., 2006. How do plants respond to nutrient shortage by biomass allocation? *Trends Plant. Sci.* 11, 610–617.
- Hilbert, D.W., Swift, D.M., Detling, J.K., Dyer, M.I., 1981. Relative growth-rates and the grazing optimization hypothesis. *Oecologia* 51, 14–18.
- Holland, J.N., Cheng, W.X., Crossley, D.A., 1996. Herbivore-induced changes in plant

- carbon allocation: assessment of below-ground C fluxes using carbon-14. *Oecologia* 107, 87–94.
- Ingestad, T., Ågren, G.I., 1991. The influence of plant nutrition on biomass allocation. *Ecol. Appl.* 1, 168–174.
- Iwasa, Y., Roughgarden, J., 1984. Shoot root balance of plants - optimal-growth of a system with many vegetative organs. *Theor. Popul. Biol.* 25, 78–105.
- Ju, S., DeAngelis, D.L., 2009. The R* rule and energy flux in a plant-nutrient ecosystem. *J. Theor. Biol.* 256, 326–332.
- Ju, S., DeAngelis, D.L., 2010. Nutrient fluxes at the landscape level and the R* rule. *Ecol. Model.* 221, 141–146.
- Kulman, H.M., 1971. Effects of insect defoliation on growth and mortality of trees. *Ann. Rev. Entomol.* 16, 289–315.
- Leadley, P.W., Reynolds, J.F., Chapin III, F.S., 1997. A model of nitrogen uptake by *Eriophorum vaginatum* roots in the field: ecological implications. *Ecol. Monogr.* 67, 1–22.
- McNaughton, S.J., 1983. Compensatory plant-growth as a response to herbivory. *Oikos* 40, 329–336.
- Morath, S.U., Pratt, P.D., Silvers, C.S., Center, T.D., 2006. Herbivory by *Boreioglycaspis melaleucae* (Hemiptera: Psyllidae) accelerates foliar senescence and abscission in the invasive tree *Melaleuca quinquenervia*. *Environ. Entomol.* 35, 1372–1378.
- Poorter, H., Niklas, K.J., Reich, P.B., Oleksyn, J., Poot, P., Mommer, L., 2012. Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytol.* 193, 30–50.
- Perry, D.A., 1994. *Forest Ecology*. Johns Hopkins Press, Baltimore.
- Pierce, L.L., Running, S.W., 1988. Rapid estimation of coniferous forest leaf area index using a portable integrating radiometer. *Ecology* 69, 1762–1767.
- Pratt, P.D., Rayamajhi, M.B., Van, T.K., Center, T.D., Tipping, P.W., 2005. Herbivory alters resource allocation and compensation in the invasive tree *Melaleuca quinquenervia*. *Ecol. Entomol.* 30, 316–326.
- Raghu, S., Osunkoya, O.O., Perrett, C., Pichancourt, J.B., 2014. Historical demography of *Lantana camara* L. reveals clues about the influence of land use and weather in the management of this widespread invasive species. *Basic Appl. Ecol.* 15, 565–572.
- Rayachhetry, M.B., Elliott, M.L., 1997. Evaluation of fungus-chemical compatibility for *Melaleuca quinquenervia* control. *Weed Technol.* 11, 64–69.
- Rayamajhi, M.B., Pratt, P.D., Center, T.D., Tipping, P.W., Van, T.K., 2008. Aboveground biomass of an invasive tree *Melaleuca quinquenervia* before and after herbivory by adventive and introduced natural enemies: a temporal case study in Florida. *Weed Sci.* 56, 451–456.
- Rayamajhi, M.B., Pratt, P.D., Center, T.D., Van, T.K., 2010. Insects and a pathogen suppress *Melaleuca quinquenervia* cut-stump regrowth in Florida. *Biol. Control.* 53, 1–8.
- Rendig, V.V., Taylor, H.M., 1989. *Principles of Soil-Plant Interrelationships*. McGraw-Hill Publishing Company, New York.
- Rengel, Z., 1993. Mechanistic simulation models of nutrient uptake: a review. *Plant Soil* 152, 161–173.
- Sevillano, L., Horvitz, C.C., Pratt, P.D., 2010. Natural enemy density and soil type influence growth and survival of *Melaleuca quinquenervia* seedlings. *Biol. Control.* 53, 168–177.
- Shea, K., Jongejans, E., Skarpaas, O., Kelly, D., Sheppard, A.W., 2010. Optimal management strategies to control local population growth or population spread may not be the same. *Ecol. Appl.* 20, 1148–1161.
- Shea, K., Kelly, D., Sheppard, A.W., Woodburn, T.L., 2005. Context-dependent biological control of an invasive thistle. *Ecology* 86, 3174–3181.
- Silberbush, M., Barber, S.A., 1983. Sensitivity of simulated phosphorus uptake to parameters used by a mechanistic-mathematical model. *Plant Soil* 74, 93–100.
- Somma, F., Hopmans, J.W., Clausnitzer, V., 1998. Transient three-dimensional modeling of soil water and solute transport with simultaneous root growth, root water and nutrient uptake. *Plant Soil* 202, 281–293.
- Southwood, T.R.E.A.N., G. A., 1973. Economic aspects of pest management strategies and decisions. *Ecol. Soc. Aust. Mem.* 1, 168–184.
- Stevens, M.T., Kruger, E.L., Lindroth, R.L., 2008. Variation in tolerance to herbivory is mediated by differences in biomass allocation in aspen. *Funct. Ecol.* 22, 40–47.
- Thornley, J.H.M., 1995. Shoot-root allocation with respect to C, N and P – an investigation and comparison of resistance and teleonomic Models. *Ann. Bot-London* 75, 391–405.
- Tipping, P.W., Martin, M.R., Nimmo, K.R., Pierce, R.M., Smart, M.D., White, E., et al., 2009. Invasion of a west everglades wetland by *Melaleuca quinquenervia* countered by classical biological control. *Biol. Control.* 48, 73–78.
- Tipping, P.W., Martin, M.R., Pratt, P.D., Center, T.D., Rayamajhi, M.B., 2008. Suppression of growth and reproduction of an exotic invasive tree by two introduced insects. *Biol. Control.* 44, 235–241.
- Trumble, J.T., Kolodnyhirsch, D.M., Ting, I.P., 1993. Plant compensation for arthropod herbivory. *Ann. Rev. Entomol.* 38, 93–119.
- Wilson, J.B., 1988. A review of evidence on the control of shoot-root ratio, in relation to models. *Ann. Bot-London* 61, 433–449.
- Zhang, B., DeAngelis, D.L., Rayamajhi, M.B., Botkin, D., 2017. Modeling the long-term effects of introduced herbivores on the spread of an invasive tree. *Landscape Ecol.* 32, 1147–1161.
- Zhao, J., Chen, J., 2012. Interspecific variation in compensatory regrowth to herbivory associated with soil nutrients in three *Ficus* (Moraceae) saplings. *PLoS One* 7.