

Article

Interactive Effect of Copper and Herbivory on the Whole-Plant Growth of *Leucaena leucocephala*

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Abstract

This study investigated how *Leucaena leucocephala*, a dry forest plant, copes with soil copper and herbivory caused by *Schistocerca piceifrons*, crucial for understanding species adaptation in stressed environments. A 33-day factorial experiment with three copper and two herbivory treatments assessed seedling growth rates (relative growth rate of biomass—RGR_B, and leaf area—RGR_{LA}), morphology, net assimilation rate (NAR), biomass allocation, and survival. Seedlings demonstrated compensatory growth in terms of RGR_B and RGR_{LA} under high copper and herbivory. Although copper decreased overall survival, surviving individuals effectively compensated for herbivory damage. These tolerance responses, primarily driven by an increased NAR (accounting for 98% of compensation), aligned with the limiting resource model. While most morphological components remained stable, herbivory specifically increased the root–shoot ratio. These findings indicate *L. leucocephala* possesses significant resilience through physiological adjustments, like enhancing NAR, and biomass reallocation strategies, allowing it to persist despite multiple stressors common in dry forests.

Keywords: allocation mass; compensatory growth responses; morphological and physiological components; relative growth rate; *Schistocerca piceifrons*



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1. Introduction

Rapid industrial development and the incessant growth of the human population have generated serious environmental problems, including those caused by heavy metals [1]. When these metals enter the food chain, they pose a severe threat to organisms, even at low concentrations [2,3]. Copper (Cu), a widely used industrial metal, is one example of a heavy metal. It is employed in the production of enamels, pigments, tanning reagents, algacides, and agrochemicals [4], as well as being used as a growth promoter and antimicrobial agent [5,6]. Owing to its persistence (non-biodegradability), it can accumulate on surfaces and then be absorbed by plants in ionic, complex, and exchangeable cation forms [5,6]. This may lead to impaired growth and reduced biomass production [7], as well as interfere with biomass allocation, which optimizes resource use [8]. These phenomena

manifest differently in each species due to intrinsic growth factors [9]. Cu inhibits root and sprout growth by altering biochemical and physiological processes [4,9,10], resulting from reduced cell division and structural damage or death of cells in the apical meristems [11,12]. Additionally, when Cu induces lignification and cell wall stiffening, the cellular expansion process is affected, leading to reduced root and stem diameter and decreased leaf growth [4]. In addition to soil contamination by Cu, plants also face selective pressure from herbivorous insects [13]. Several studies have explored the effects of herbivory on plants [14–18], with mixed results, although some show a reduction in plant growth [17]. Different hypotheses have been proposed to explain these outcomes. One of them is the Growth Rate Model GRM [19], which suggests that plant compensatory growth would be greater in response to herbivory in resource-limited environments. This is because plants in such environments do not reach their potential maximum growth rates [20]. On the other hand, Ref. [21] introduced the Compensatory Continuum Hypothesis (CCH), proposing that plants will better compensate for herbivory damage as the availability of a specific resource (light, water, nutrients) increase. Meanwhile, Ref. [22] developed the Limiting Resource Model (LRM), which posits seven possible scenarios involving two types of resources (focal and alternate), three types of compensatory growth responses (low, neutral, and high), and environments with contrasting resource levels.

Although plant compensatory responses to herbivory have been well studied [23,24], very few studies have focused on explaining these responses through total plant growth [17,25]. In the study by Ballina-Gómez et al. [17], it was proposed that plant compensatory responses might be a function of a synergistic effect produced by the plant's total growth, rather than being expressed in isolated growth variables.

Considering that one of the most comprehensive measures of growth is the Relative Growth Rate RGR [26,27], which is influenced by both morphological and physiological components (leaf area ratio: LAR; specific leaf area: SLA; net assimilation rate: NAR), it is likely that a better understanding of plant compensatory responses to herbivory can be achieved through a combination of these components.

This study focuses on evaluating the growth responses of *Leucaena leucocephala* to the toxic effects of Cu and herbivory by the acridid *Schistocerca piceifrons* under experimental conditions. This acridid is an economically significant pest in the Yucatan Peninsula, Mexico. Four main questions were posed: (i) Are the growth and survival of *L. leucocephala* seedlings affected by Cu in the soil and herbivory by *Sch. piceifrons*?; (ii) Are the compensatory responses of *L. leucocephala* consistent with models proposed in the literature?; (iii) Which morphological and physiological components of the growth rate are involved in the compensatory response of *L. leucocephala*?; and (iv) How does biomass allocation vary under exposure to Cu in the soil and herbivory?

To answer these questions, we studied the Relative Growth Rate (RGR) and its morphological (LAR, SLA) and physiological (NAR) components, as well as the biomass allocation of each plant (LWR, SWR, RWR, R). Different doses of Cu and natural herbivory were applied. Both species were selected due to their natural interaction in the lowlands of the Yucatan Peninsula. Although studies on herbivory have typically been conducted in rainforests, it has been found that damage caused by herbivorous insects is a frequent phenomenon in lowlands >40% [17,18]. Additionally, it is well known that Cu is a prevalent heavy metal in Yucatan Peninsula soils. This metal may be present in the leaves, stems, and roots of *Leucaena leucocephala*, a dominant species of the lowlands [28,29].

Based on these considerations, we hypothesize the following: (1) High concentrations of Cu in the soil and herbivory by *Sch. piceifrons* will decrease the growth (in terms of RGR_B , RGR_{AF} , and leaf production rate) and survival of *L. leucocephala*; (2) The Limiting Resource Model will best explain responses to adverse conditions such as increased Cu in the soil and

herbivory [22]; (3) Since *L. leucocephala* is classified as a fast-growing species [30], its relative growth rate (RGR_B) will likely depend on net assimilation rate (NAR) and specific leaf area SLA [31]; and (4) Biomass allocation patterns will be strongly influenced by damage to plant structures (due to Cu exposure, [32]; and herbivory, [33]).

2. Materials and Methods

2.1. Study Site and Species

This study was conducted at the Laboratory of Botany at the Instituto Tecnológico de Conkal (ITC), Yucatan, Mexico. Plant material was collected from a deciduous forest surrounding the ITC, which is located 10 m above sea level, with an average temperature ranging from 26 to 27.6 °C and annual precipitation between 728.2 and 1000 mm [34,35]. The dominant species include *Vachellia pennatula* (Fern-leaf acacia), *Caesalpinia gaumeri* (Kitim che'), *Sphinga platyloba* (Muk), *Lysiloma latisiliquum* (Wild tamarind), *Enterolobium cyclocarpum* (Guanacaste), *Mimosa bahamensis* (Sak-catzin), *Spondias mombin* (Yellow mombin), *Metopium brownie* (Chechem), *Cochlospermum vitifolium* (Buttercup tree), *Guazuma ulmifolia* (West Indian elm), *Trema micrantha* (Jamaican nettletree), *Annona reticulata* (Custard apple), *Gyrocarpus americanus* (Helicopter tree), *Piscidia piscipula* (Fish-poison tree), *Pithecellobium dulce* (Madras thorn), and *Havardia albicans* (Chucum) [36–38].

Seeds were collected from ten parental trees of *Leucaena leucocephala* (Fabaceae) ranging in height from 5 to 20 m [30] and with diameters at breast height (dbh) from 10 to 25 cm [38,39]. The seeds were sown in plastic trays containing sterile soil and placed inside the laboratory to grow experimental seedlings. Soil sterilization was performed using the vaporization method (Caldera No.-08-3095, Sioux Corporation, Bresford, SD, USA) to prevent the growth of vesicular-arbuscular fungal spores and nitrogen-fixing bacteria. The seedlings were then transplanted individually into plastic trays (15 × 10 cm). Both seeds and seedlings were irrigated every other day, and an organic fungicide (copper oxychloride 0.9 g L⁻¹ water) was applied to prevent infections by phytopathogenic fungi.

The soil type was a Leptosol with pH, 7.7; electric conductivity (1:5), 0.24 dS/m⁻¹; cation exchange capacity, 52 meq 100 g⁻¹; organic matter, 20%; N, 1.03%; P, 22.2 mg kg⁻¹; K, 2.6, Ca, 45, Mg, 2.6, and Cu, 0.32 cmol (+) kg⁻¹ as determined by Borges-Gómez et al. [40].

From the population of seedlings, 80–90 days (d) old, intermediate-sized individuals were selected, while extremes were excluded [41].

2.2. Experimental Design

A factorial design involving three Cu treatments × two herbivory treatments (n = 6–12 individuals per treatment) was used. The Cu treatments included: a control treatment without Cu (Cu = 0), a treatment with Cu (SO₄ Cu) at a dose of 0.5 g kg⁻¹, and a treatment with duplicated Cu (SO₄ Cu) at a dose of 1.0 g kg⁻¹. The herbivory treatments consisted of a control group without exposure to herbivory and a group exposed to herbivory (with 40–60% of the area removed) which was determined by methodology of [42]. Cu was applied to the base of each seedling's stem. Thirty-one days after exposure to Cu, six seedlings from each treatment group were selected. The seedlings were placed in an air vent (40 cm in height and 60 cm in diameter), where two individuals of *Sch. piceifrons* were introduced for 24 h. Prior to the insect introduction, the acridids were deprived of food for 24 h. We recorded only seedling survival or mortality (influenced by Cu treatments) during the first 25 days of the experiment. The insects used in the study were adults, obtained from the Comité Estatal de Sanidad Vegetal de Yucatán (CESVY). The experiment lasted 33 days—25 days for plant exposure to Cu and 8 days for the evaluation of the early response to herbivory.

The traits of the seedlings evaluated at the beginning (10 seedlings per treatment) and at the end (6–12 seedlings per treatment) of the experiment included biomass growth, leaf area, and leaf number. Biomass measurements were obtained separately for leaves, stems, and roots by drying them at 55 °C for 48 h or until a constant weight was reached. Leaf area was estimated using digital photos analyzed with ImageJ software version 1.54g [43].

The environmental conditions (mean $\pm$ SD) during the experiment were as follows: temperature 25.9 ± 1.41 °C, relative humidity (RH) $81 \pm 7.74\%$ (measured using a digital thermohygrometer, model 4096, Control Company Inc., Friendswood, TX, USA), and photosynthetic photon flux density (PPFD; measured with a Li-250A, Li-Cor, Lincoln, NE, USA) 1.28 ± 0.35 (%) $\text{mol m}^{-2} \text{d}^{-1}$. Soil pH (mean $\pm$ SE; measured with a potentiometer, Oakton pH/mV/C meter, USA) for the treatments was as follows: control Cu-without herbivory = 6.5 ± 0.19 , Cu = 5.7 ± 0.18 , and Cu+ = 5.7 ± 0.2 ; control Cu-with herbivory = 6.2 ± 0.18 , Cu = 6.7 ± 0.24 , and Cu+ = 6.5 ± 0.18 .

2.3. RGR_B Estimation: Morphological and Physiological Components

Using the initial and final measurements from the experiment, the following growth indexes were calculated: relative growth rate in biomass (RGR_B ; $\text{g g}^{-1} \text{d}^{-1}$) and in leaf area (RGR_{LA} ; $\text{cm}^2 \text{cm}^{-2} \text{d}^{-1}$), leaf production rate (LPR: number of leaves), leaf area ratio (LAR: $\text{cm}^2 \text{g}^{-1}$), specific leaf area (SLA; $\text{cm}^2 \text{g}^{-1}$), leaf weight ratio (LWR; g g^{-1}), stem weight ratio (SWR; g g^{-1}), root weight ratio (RWR; g g^{-1}), root:shoot ratio (R; g g^{-1}), and net assimilation rate (NAR; $\text{mg mm}^{-2} \text{d}^{-1}$) [31].

2.4. Data Analysis

To determine the effects of Cu and herbivory on *L. leucocephala* seedling growth, generalized linear models GLM [44] were used. Plant growth for the 10 response variables was analyzed under a factorial analysis structure with two factors: inter-subject factor (three Cu treatments) and intra-subject factor (two herbivory treatments). RGR_B , RGR_{LA} , LPR, LWR, SWR, RWR, and R:S were analyzed using a Normal probabilistic model with an identity link function. While LAR, SLA and NAR were analyzed with a Gamma probabilistic model with a log link function.

The survival probability of *L. leucocephala* seedlings was estimated 25 days after the start of the experiment, using control levels as a reference. A logistic regression model was applied, with survival as the response variable and Cu treatment (categorical) and time (covariate) as independent variables. The model coefficients were estimated, and the Wald χ^2 statistic was used under the maximum likelihood method to test the effects of Cu and time factors on survival. These analyses were conducted in SPSS 22 [45]. Path analyses were performed to examine the potential direct and indirect relationships between RGR_B (endogenous variable), morphological components LAR, SLA, and LWR, and the physiological component NAR (exogenous variables). The model was adjusted using χ^2 analysis ($p > 0.05$) and AIC values [46]. This analysis was performed in Amos 4.0 (Amos Development Corporation, Crawfordville, FL, USA).

3. Results

3.1. Effects of Cu and Herbivory on the Growth and Survival of *L. leucocephala* Seedlings

No factor significantly influenced RGR_B (Figure 1A). However, the Cu $\times$ herbivory interaction was significant for RGR_{LA} , while the factors did not differ as independent effects (Figure 1B; Table 1). Leaf production rate (LPR) was significantly affected only by herbivory, with higher rates in the control treatment (Figure 1C).

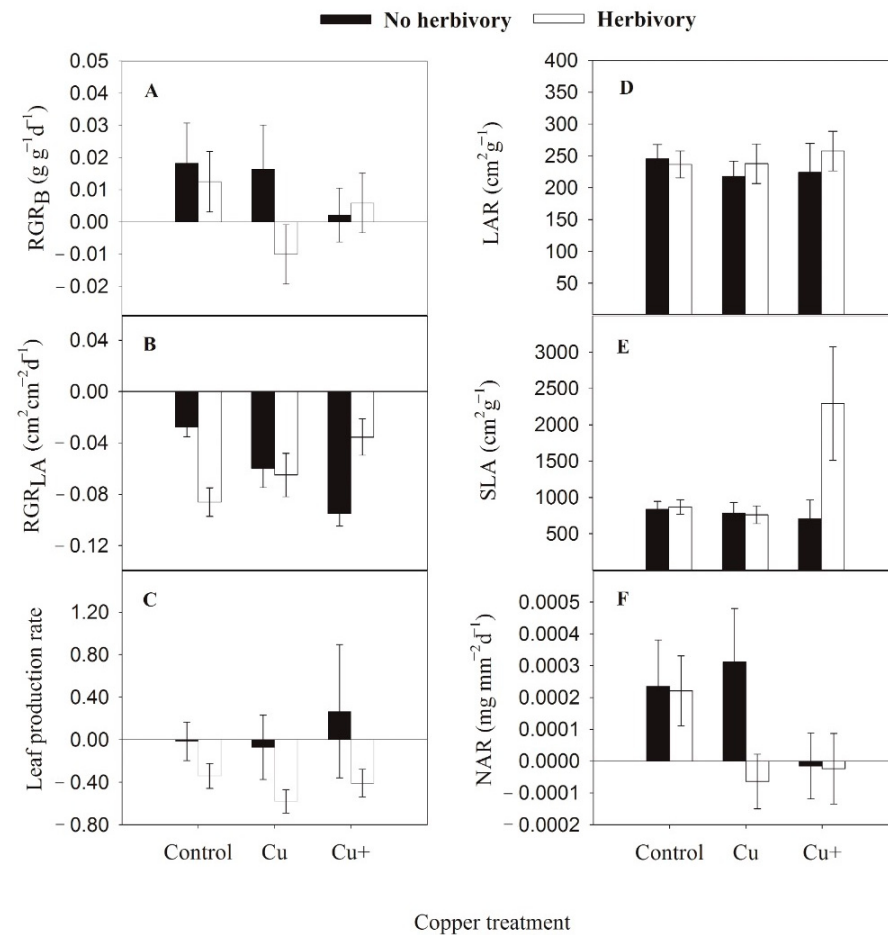


Figure 1. Effect of copper and herbivory of locust (*Sch. piceifrons*) on the growth, morphological and physiological components of RGR_B in *L. leucocephala* seedlings. (A) RGR_B, (B) RGR_{LA}, (C) Leaf production rate, (D) LAR, (E) SLA and (F) NAR.

Table 1. Effect of copper and herbivory on plant growth and morphological components of the RGR_B (mean ± SE) in *L. leucocephala* seedlings.

Effect	RGR _B (g g ⁻¹ d ⁻¹)	χ ²	RGR _{LA} (cm ² cm ⁻² d ⁻¹)	χ ²	LPR (no.)	χ ²	LAR (cm ² g ⁻¹)	χ ²	SLA (cm ² g ⁻¹)	χ ²
Inter-subjects										
Copper treatment		1.67 ns		0.44 ns		1.35 ns		0.27 ns		7.37 *
Control	0.0157 ± 0.0079 a		-0.0534 ± 0.0097 a		-0.1585 ± 0.1184 a		241.48 ± 15.15 a		848.96 ± 74.01 a	
Low copper	0.0042 ± 0.0090 a		-0.0623 ± 0.0107 a		-0.3063 ± 0.1803 a		227.05 ± 18.67 a		772.51 ± 93.94 a	
High copper	0.0048 ± 0.0069 a		-0.0518 ± 0.0133 a		-0.2243 ± 0.1979 a		248.48 ± 24.92 a		1859.2 ± 605.3 b	
Intra-subjects										
Herbivory treatment		1.03 ns		0.015 ns		8.49 **		0.36 ns		7.4 *
Control	0.0150 ± 0.0077 a		-0.0503 ± 0.0085 a		0.0081 ± 0.1610 a		231.90 ± 14.89 a		794.97 ± 81.11 a	
Herbivory	0.0035 ± 0.0055 a		-0.0609 ± 0.0091 a		-0.4357 ± 0.0703 b		244.88 ± 15.68 a		1379.6 ± 331.2 b	
Copper × Herbivory		1.77 ns		20.24 ***		0.68 ns		0.52 ns		9.48 *

Note. Different letters indicate significant differences (Bonferroni < 0.05). * $p < 0.05$. ** $p < 0.01$. *** $p < 0.001$. ns, not significant.

The survival of *L. leucocephala* seedlings exposed to Cu treatments differed significantly among the treatments (Table 2). During the first 10 days, seedling survival was higher with intermediate Cu application. However, after the 11th day, survival began to decline in the Cu treatments. By the 25th day, survival had decreased to 30% and 45% in both the Cu and Cu+ treatments (Figure 2).

Table 2. Results of a logistic regression to predict survival of seedlings of *Leucaena leucocephala*.

Factor	Exp (β)	β	Standard Error	Confidence Intervals 95%		χ^2 Wald	df	p Value
				Lower	Upper			
Copper treatment						86.3	2	<0.0001
Cu	0.543	−0.610	0.132	0.420	0.703	21.5	1	<0.0001
Cu+	0.288	−1.244	0.181	0.222	0.375	86.1	1	<0.0001
Time (Days)	0.849	−0.163	0.009	0.835	0.864	349.6	1	<0.0001

Note. We included time and copper treatments as continuous and categorical variables. In each variable we showed beta parameters estimates ($\beta \pm$ standard error), significance level (χ^2 Wald), Exp (β), confidence intervals (95%), and its degrees of freedom (df).

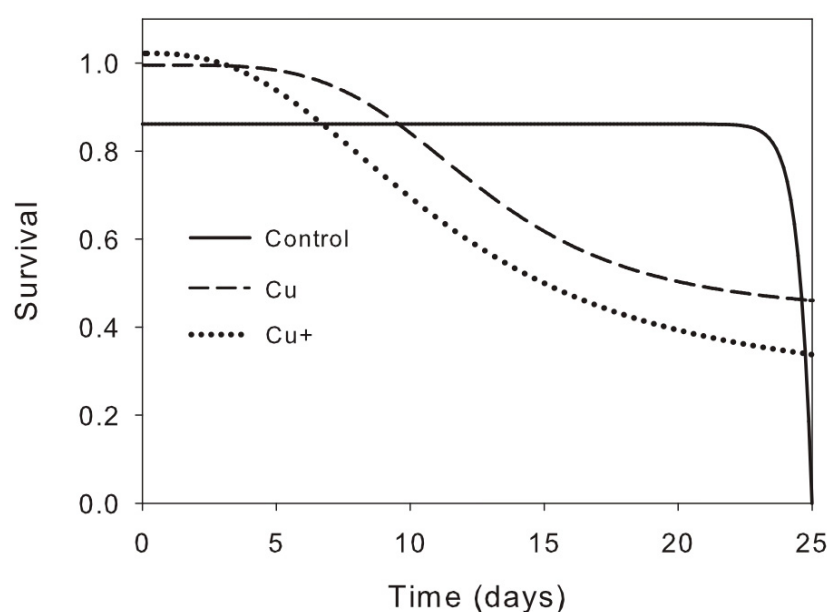


Figure 2. Logistic regression to estimate survival probability as a Cu treatment function and time in seedlings of *L. leucocephala* for 25 days.

3.2. Effects of Cu and Herbivory on Morphological and Physiological Components of RGR_B

Only SLA was significantly influenced by both the Cu $\times$ herbivory interaction and by the individual factors (Figure 1E). LAR and NAR showed no significant changes due to either factor or their interaction (Figure 1D,F).

The behavior of the morphological and physiological components across herbivory and Cu treatments did not show substantial variation; therefore, samples were combined without considering treatment differences, and a cause–effect model was developed. The physiological component NAR had a significant positive influence on RGR_B (98%). Although other morphological components like SLA and LWR also showed some influence, these were not significant (Figure 3). Similarly, the negative paired correlations among components such as NAR, SLA, and LWR were not significant (Figure 3).

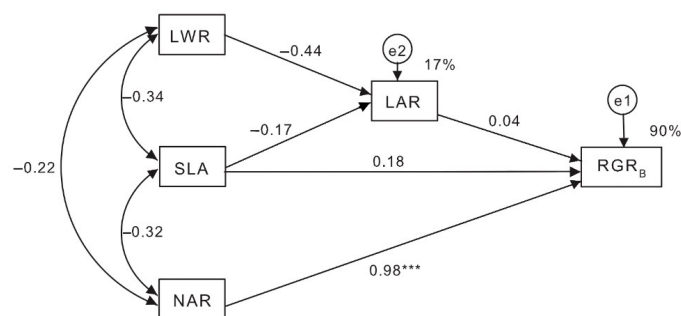


Figure 3. Path analysis of causal influences of morphological (LAR, SLA, and LWR) and physiological (NAR) components on RGR_B of *L. leucocephala* seedlings. Numbers on arrows are standardized path coefficients (equivalent to correlation coefficients). *** Indicate significant standardized path coefficients ($p > 0.0001$). Circles indicate error terms (e1–e2). Model fitted the data: $\chi^2 = 0.300$, probability level = 0.861, AIC = 36.300.

3.3. Effect of Cu and Herbivory on Mass Allocation in Seedlings of *L. leucocephala*

In R:S, only the Cu $\times$ herbivory interaction was significant, and herbivory alone significantly influenced this interaction (Figure 4D). Herbivory also had a significant effect on LWR, which was higher in the control seedling group (Figure 4A). Stem and root allocation (SWR and RWR, respectively) did not vary with Cu or herbivory treatments (Figure 4B,C).

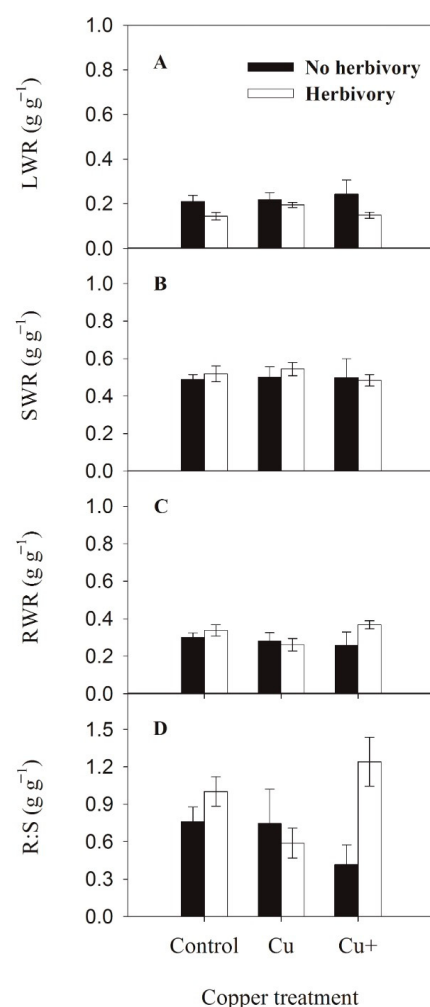


Figure 4. Effect of copper and herbivory of locust (*Sch. piceifrons*) on the mass allocation to (A) leaves (LWR), (B) stems (SWR), (C) roots (RWR) and (D) ratio root:shoot (R:S) in *L. leucocephala* seedlings.

4. Discussion

4.1. Compensatory Growth and Survival of *L. leucocephala* in Response to Cu Effects

The present study demonstrates the ability of *L. leucocephala* to compensate for its growth, in terms of RGR_B and RGR_{LA} , in response to high concentrations of Cu in the soil—even over a short response time—as demonstrated by Ballina-Gómez et al. [17] with another woody tropical species. Although other studies have reported growth compensation in *L. leucocephala* due to the presence of Cu in the soil [28,29,47–49], few studies have tested the effects of herbivory [50,51]. For that reason, this study focuses strongly on how seedlings specifically respond to these stressors. Similarly, Nanthavong and Sampanpanish [52] showed that *Mimosa pudica* (Fabaceae) plants exposed to arsenic contamination were able to offset their growth, as estimated by RGR_B . In contrast, Marozzi et al. [53] found that *Pistia stratiotes* (Araceae) did not alter its growth in the presence of lead (Pb).

It is important to consider the low doses of Cu, as such doses may stimulate growth, unlike high doses, which can be toxic [28]. On the other hand, although the decrease in seedling growth (in terms of RGR_B) was not significant in the Cu treatments, lower values were observed. This is understandable, as the accumulation of heavy metals in plant tissues leads to lower biomass allocation, since energy is primarily used for adaptation mechanisms in response to high concentrations of the metal [47,54].

While the survival of *L. leucocephala* was affected as the dose of Cu increased, it was observed that surviving plants managed to compensate for herbivory damage, as proposed by Freeman et al. [55], who obtained similar results with *Brassica juncea* and *Stanleya pinnata*. They related these results to the elemental defense hypothesis, which posits that hyper-accumulation has evolved as a protection against herbivores or infections. The similarity in results may suggest the effectiveness of *L. leucocephala* as a hyper-accumulator species when tolerating Cu and herbivory, rather than just as a useful species for bioremediation [28].

We considered three models proposed to explain the relationship between resource availability and compensatory growth responses to herbivory. By comparing the three models of RGR_B , RGR_{LA} , and LPR growth responses, we found that the most useful model to explain these responses was the LRM. This model could explain all the responses when considering the differences in resource availability, Cu, and herbivory. Our results align with those reported by [17,56], who identified LRM as the best model for explaining plant tolerance to herbivory.

When analyzing the CCH, which posits that in high-resource-availability environments, plants may have a greater ability to respond to herbivory than in low-resource-availability environments [21], we found our results similar to those of a meta-analysis examining 11 responses of compensatory growth. In that analysis, no support was found for the GRM, but 10 studies supported the CCH [57]. However, the heterogeneous results obtained among the compensatory models may indicate a more complex relationship between tolerance and the levels of Cu used, unless the genetic stock of the species is known [58].

The LRM is particularly useful for understanding various stress tolerance scenarios, especially in limited resource environments [59]. Our results suggest that only the RGR_{LA} of *L. leucocephala* supported the CCH. However, this finding was consistent with the LRM scenario, suggesting that herbivory increased Cu acquisition in the soil, resulting in overcompensatory growth in environments with high Cu availability [57,60]. The growth stimulation in *L. leucocephala* at low concentrations of Cu (20 mg kg^{-1}) has been reported previously [28]; however, in our study, these effects were observed at high concentrations ($>200 \text{ mg kg}^{-1}$). This demonstrates the potential of this species as a tolerant plant to Cu in the soil.

4.2. Contribution of Morphological and Physiological Components to the RGR_B of *L. leucocephala*

Several studies have demonstrated the predominant role of morphological and physiological components in the growth of plant species, mostly focusing on the effects of variation among species [61], salinity stress [62], light availability [63], herbivory [17,64,65], mycorrhizal fungi [66], and water availability [67]. However, few studies have addressed the effects of heavy metals, with notable examples being Gandhi et al. [68] and Ali et al. [69]. In this study, we present empirical evidence to explain the role of morphological and physiological components of RGR_B in the growth responses of *L. leucocephala* to a heavy metal (Cu). Generally, the morphological component of greatest importance for RGR_B is the SLA [70–74], which is contrary to our results; in this study, the component with the most significant influence was NAR (98%). This suggests a modification in the efficiency of the photosynthetic apparatus, stimulated by Cu [75]. Such modification may reduce the quantity of chlorophyll and carotenoids, negatively affecting photosynthetic efficiency [76–78]. Additionally, the internal mechanisms of the plant may activate its ability to avoid and/or tolerate Cu stress, thereby preventing metal translocation to the aerial parts of the plant [47,79].

On the other hand, herbivory by *Sch. piceifrons* did not produce any variation in the morphological and physiological components of RGR_B . These findings contrast with those of Camargo et al. [24] regarding *Datura stramonium*, which reported an increase in NAR after a simulated herbivory event. Similarly, Ballina-Gómez et al. [17] Carrillo-Herrera et al. [65] found an increase in NAR after simulated herbivory in *Brosimum alicastrum* and *Vitis tiliifolia*, but a decrease in leaf area (LAR).

4.3. Mass Allocation in *L. leucocephala*

As a general pattern, we found that biomass allocation decreased in the following order: SWR, RWR, and LWR. In certain tropical forests, it has been documented that plant species exhibit patterns similar to those observed in our study [80]. When analyzing biomass allocation in plant structures, only the LWR varied significantly due to the effects of herbivory, while SWR and RWR were not affected. These findings are similar to those reported by Huu Thanh et al. [81], who evaluated growth in four species (*Bidens pilosa*, *Ludwigia adscendens*, *Ludwigia octovalvis*, and *Ipomoea aquatica*). The decrease in LWR in seedlings that experienced herbivory and were in environments with high Cu concentrations suggests a structural reallocation [8,82] of biomass from stems (SWR) to leaves (LWR). This result was confirmed by the high biomass proportion allocated to roots and stems (R:S) in plants affected by herbivory [31]. Additionally, Hackett et al. [83] found that herbivory caused by the aphid *Macrosiphum euphorbiae* on potato plants significantly altered biomass allocation, leading to an increase in stem biomass. Although minor, the effects of copper on the increase in mass allocation from roots to leaves have also been reported in *Leucanthemum vulgare* [8].

Overall, the biomass allocation in leaves (LWR), stems (SWR), and roots (RWR) of *L. leucocephala* supports the idea that seedling responses to herbivory are a function of a synergistic response among different plant structures [16,23]. Furthermore, the total growth responses (RGR_B) were based on NAR, a physiological component closely related to the photosynthetic rate [84,85], rather than on the deployment of leaf area (SLA and LWR).

L. leucocephala seedlings exhibited compensatory growth in terms of RGR_B and RGR_{AF} in the presence of high levels of Cu and herbivory damage. These tolerance responses were best explained by the limiting resource model (LMR). Seedling survival decreased as a result of Cu in the soil; however, the seedlings demonstrated compensatory responses following herbivore damage. The contamination of *L. leucocephala* by Cu and herbivory damage did not significantly impact the morphological and physiological components;

nevertheless, the net assimilation rate (NAR) drove the compensatory growth responses through RGR_B . The mass allocation was only affected in terms of R:S, which increased when seedlings were subjected to herbivory damage.

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Abbreviations

The following abbreviations are used in this manuscript:

RGR	Growth Rate
RGR_B	Relative Growth Rate in Biomass
RGR_{LA}	Relative Growth Rate in Leaf Area
LAR	Leaf Area Ratio
SLA	Specific Leaf Area
NAR	Net Assimilation Rate
LWR	Leaf Weight Ratio
SWR	Stem Weight Ratio
RWR	Root Weight Ratio
R:S	Root:Shoot Ratio
GRM	Growth Rate Model
CCH	Compensatory Continuum Hypothesis
LRM	Limiting Resource Model
DBH	Diameter at Breast Height
ITC	Instituto Tecnológico de Conkal.
CESVY	Comité Estatal de Sanidad Vegetal de Yucatán.
SE	Standard Error
GLM	Generalized Linear Models
ANOVA	Analysis of Variance
AIC	Akaike Information Criterion
RH	Relative Humidity
PPFD	Photosynthetic Photon Flux Density

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