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Effects of *Tillandsia recurvata* Colonization on Vegetative Reserve Compounds in *Neltuma laevigata*

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ABSTRACT

Mesquite species are widely distributed across arid and semi-arid regions and provide important ecological and socioeconomic benefits, including timber, livestock forage, fuelwood, and food for human consumption. However, mesquite woodlands are threatened by several biotic factors, including insect pests, parasitic plants, and epiphytes. The abundance of the atmospheric epiphyte *Tillandsia recurvata* has been associated with the mineral characteristics of potential host-tree canopies. This study evaluated whether colonization by *T. recurvata* was associated with changes in nitrogenous compounds and carbohydrate reserves in natural stands of *Neltuma laevigata* in northern Mexico. Total soluble proteins were quantified using the Bradford method, total free amino acids using the Yemm and Cocking method, starch using a colorimetric iodine-based procedure, and total soluble sugars using the Van Handel method. Roots, stems, leaves, and fruits were compared between trees growing at a site colonized by *T. recurvata* and trees at a site where the epiphyte was absent. Total soluble protein concentrations did not differ significantly between sites in any of the evaluated organs. In contrast, significant differences in total free amino acid and starch concentrations were detected in all organs. Total soluble sugars concentrations did not differ significantly in roots or fruits, whereas significant differences were observed in stems and leaves. These findings indicate that *T. recurvata* colonization was associated with organ-specific variation in the nitrogen and carbon reserve compounds of *N. laevigata*, although total soluble protein concentrations remained unchanged.

Keywords: Atmospheric Epiphyte; Carbon Reserves; Mesquite; Nitrogenous Compounds; Starch; Total Free Amino Acids; Total Soluble Proteins; Total Soluble Sugars

1. Introduction

Mesquite (*Neltuma laevigata*) forests play a vital ecological role by establishing symbiotic associations with nitrogen-fixing bacteria and contributing substantial organic matter through litter deposition. These processes increase soil organic matter and humic substances, improve soil fertility, and facilitate the establishment and growth of neighboring plant species[1–3]. Since pre-Columbian times, mesquite (*N. laevigata*) has been one of the most valuable plant resources used by human populations inhabiting arid and semi-arid regions of the Americas. Its pods, wood, bark, leaves and gum have traditionally been used as food, fodder, fuelwood, charcoal, timber, medicine and raw materials for rural livelihoods, making this species a cornerstone of the ecological and socio-economic sustainability of dryland communities[4,5]. Among the numerous ecosystem services provided by *Neltuma laevigata*, one of the most important is its use as a renewable energy source through the production of firewood and high-quality charcoal. In addition, its durable wood is widely used for fence posts, parquet flooring, boards, planks and handicrafts, while its pods and foliage serve as livestock feed[4]. The species also provides floral resources for beekeeping, exudes gum with industrial potential, and has long been employed in traditional medicine, making it one of the most valuable multipurpose tree species in the arid and semi-arid regions of Mexico[4].

Mesquite forests are threatened by several factors, including overexploitation, land-use change, insect pests, parasitic plants such as *Psittacanthus calyculatus*, and epiphytes such as *Tillandsia recurvata*[6–8]. These biological agents can reduce host physiological performance, damage branches, affect seed production, and contribute to the deterioration of mesquite populations and associated ecosystem services[9,10]. Epiphytes are non-parasitic plants that grow on other plants, using them solely as physical support, and are predominantly found in forest canopies[11,12]. They comprise both vascular taxa, including orchids, aroids, bromeliads, peperomias, and ferns, and non-vascular groups such as lichens, mosses, and liverworts[11,13]. The genus *Tillandsia* (Bromeliaceae), commonly known as air plants, comprises more than 650 species distributed throughout the Americas[14]. Most species are epiphytes that grow on trees and shrubs, using them only as physical support without parasitizing their hosts[12]. Among the best-known epiphytic bromeliads are *Tillandsia usneoides* and *T. recurvata*[14]. Both species absorb water and nutrients directly from the atmosphere through specialized foliar trichomes rather than functional roots[15,16]. Although *T. recurvata* is not parasitic, dense infestations have become a significant management concern in some regions of Mex-

ico because they can reduce host tree vigor, impair branch physiology, and contribute to canopy decline [17].

Although epiphytic plants contribute substantially to canopy biodiversity, nutrient cycling, water retention, habitat formation, and ecosystem functioning, their ecological roles remain comparatively understudied, particularly in dry, temperate, and disturbed ecosystems [12,18,19]. Epiphytic plants contribute to forest nutrient cycling by intercepting and storing atmospheric nutrients derived from rainfall, fog, aerosols, and dry deposition [20,21]. These nutrients are subsequently transferred to the ecosystem through indirect pathways, including canopy leaching and litter decomposition, and through direct pathways, such as nutrient uptake by adventitious host roots growing within canopy soils formed by decomposing epiphytes and accumulated organic matter [22]. However, high loads of some epiphytic plants, particularly *T. recurvata*, can negatively affect certain host species by reducing leaf and shoot production, impairing hydraulic and photosynthetic performance, and increasing shoot or branch mortality [7,22,23].

The presence and abundance of *T. recurvata* are associated with host-tree identity and with canopy and bark characteristics that influence anchorage, seed establishment, microclimate, and access to atmospherically deposited nutrients [24,25]. In addition to nutrient availability, host-bark stability and chemical properties may influence the local distribution of *T. recurvata* [26]. Exfoliating bark can reduce seed anchorage, while allelochemicals released by some host species can inhibit seed germination [27]. Microclimatic factors, including light, ventilation and water availability, may also affect germination and seedling establishment within host canopies [28–30]. Within a suitable climatic range, host-tree identity, size, bark structure and bark chemistry may jointly delimit important dimensions of the local realized niche of *Tillandsia* [31].

Although *T. recurvata* does not obtain water or nutrients from the vascular system of its phorophytes, it can act as a structural parasite on some host species [17]. Prolonged anchorage and growth may cause anatomical damage to the bark, phloem and xylem, reduce hydraulic conductivity and, in *N. laevigata*, decrease the effective quantum yield of photosystem II [17,32]. Heavy epiphyte loads may also reduce photosynthetic performance through shading, although the magnitude and mechanism of these effects depend on the host species [17].

The production and accumulation of non-structural carbohydrate reserves, mainly total soluble sugars and starch derived from photosynthetic carbon assimilation, are essential for tree maintenance, growth, resprouting and survival during periods when current photosynthesis is insufficient [33]. Their dynamics depend on mineral nutrient availability and abiotic factors such as light, water availability and temperature [34]. Among the mineral nutrients required by plants, nitrogen (N) is generally needed in the greatest amounts and frequently constitutes a limiting factor for plant growth and development [35]. Nitrogen accumulated in vegetative tissues can be stored and subsequently remobilized to support new growth and reproductive development [36]. Nitrogen availability and chemical form can alter plant biochemical composition by modifying the accumulation and allocation of carbohydrates, nitrogen-containing compounds, and lipids [37].

Therefore, the present study aimed to evaluate the effect of *T. recurvata* on the accumulation of vegetative reserves in the form of nitrogen compounds and carbohydrates in natural stands of mesquite (*N. laevigata*) in northern Mexico.

2. Materials and Methods

2.1. Study Area

The study was conducted in two natural stands of *N. laevigata*, encompassing a total area of 1,200 ha, in the community of Emiliano Zapata, Durango, northern Mexico. To reduce environmental heterogeneity, study sites were selected based on their similarity in climatic, edaphic, and physiographic characteristics. By controlling for these biophysical variables, the study aimed to isolate the association between epiphyte colonization and vegetative carbohydrate reserves, thereby minimizing the likelihood that observed differences were attributable to site-specific environmental conditions rather than epiphyte presence. The study area is located at 24°25′53.09″ N and 103°50′41.28″ W, at an elevation of 2,020 m a.s.l., within the Mesa del Centro physiographic province. This province is characterized by extensive plains formed from alluvial deposits, interspersed with mountain ranges and isolated elevations of predominantly volcanic origin. The dominant soil types are Rendzinas and Kastanozems.

The area lies within Hydrological Region 36, specif-

ically in the Río del Peñón sub-basin, which contains El Saladillo, a permanent stream. The climate is temperate semi-arid, with cool winters and summer rainfall. Winter precipitation accounts for less than 5% of the annual total, corresponding to the BS1kw(w) climatic classification. The mean annual temperature is 16.5 ℃, and the mean annual precipitation is 526.6 mm [38].

The predominant vegetation types are natural and induced grasslands, with the tree and shrub flora largely represented by species belonging to the Fabaceae family [39].

2.2. Sample Collection

Given the logistical constraints associated with field sampling and the costs of sample preservation and processing, four spatially independent trees were sampled at each study site. This sampling effort was considered appropriate for an intensive exploratory assessment, while acknowledging the limited scope of statistical inference. Samples collected from different organs of the same tree were treated as subsamples, with each individual tree constituting the independent biological replicate.

Tree sampling was conducted in June 2019 using a random selection procedure. Four adult trees were sampled at each of two sites: the Presa Ruiz Cortines property, where trees were free of epiphytes, and Sierra de la India, where trees were colonized by *T. recurvata*. Two samples were collected from each of three organs—roots, stems, and leaves—of every selected tree. June was selected for sampling because it corresponds to a period of active physiological activity in mesquite, when leaves are fully developed and photosynthetic carbon assimilation is high. This phenological stage allows the evaluation of starch reserves after the major carbon demands associated with bud break, leaf expansion, and flowering, while preceding the substantial carbon allocation to fruit maturation and seed filling. Consequently, starch concentrations measured during this period are representative of the tree's vegetative storage status.

Stem samples were obtained as wood cores or chips using a Pressler increment borer. To collect root samples, a small trench was excavated with a conventional pickaxe until the main root was exposed, and tissue was removed at a depth of approximately 30 cm. Although mesquite develops a deep taproot capable of extending several meters to access groundwater, the majority of its fine absorptive roots, as well as a substantial proportion of the lateral structural roots that serve as storage sites for non-structural carbohydrates, are concentrated within the upper 20–40 cm of the soil profile. This shallow root distribution enables the plant to rapidly exploit pulses of soil moisture and nutrient availability following rainfall events, particularly in arid and semi-arid ecosystems.

The size and position of the branches, stems, leaves, and fruits sampled from the trees were always the same. All samples were carefully cleaned to remove soil and other adhering epiphytic material and then placed in perforated, pre-labeled aluminum bags.

Immediately after collection, the samples were frozen in liquid nitrogen to arrest biochemical and enzymatic activity. They were subsequently stored in an ultra-low-temperature freezer at −70 ℃ for one week. The samples were then freeze-dried for seven days at −40 ℃ to remove moisture and minimize further enzymatic degradation.

After lyophilization, the samples were ground to a fine powder using a blade mill. Finally, 10 mg of dry material from each sample was weighed on an analytical balance for subsequent biochemical analyses.

2.3. Determination of Total Soluble Proteins Concentration

Total soluble proteins were extracted and quantified according to the Bradford method [40], with minor modifications. The extraction buffer consisted of 0.1 M KH_2PO_4, 0.1 M Na_2HPO_4, 5 mM dithiothreitol (DTT), 0.3% (w/v) polyethylene glycol (PEG), and 0.13% (w/v) of polyvinylpyrrolidone (PVP). 1 mL of extraction buffer was added to each microcentrifuge tube containing 10 mg of dry powdered plant material.

A stainless-steel bead was added to each tube, and the samples were homogenized for 3 min using a Maxi Mix II vortex mixer (Thermo Scientific®) to facilitate tissue disruption and protein extraction. The homogenates were then centrifuged at 10,000 rpm and 4 ℃ for 15 min using a Spectrafuge 16M centrifuge (Labnet®).

After centrifugation, 500 μL of the supernatant was transferred to a spectrophotometric cuvette and mixed with 500 μL of Quick Start™ Bradford reagent. The mixture was vortexed and incubated at room temperature for 5 min. Absorbance was subsequently measured at 595 nm using a Genesys 20 UV–Visible spectrophotometer (Thermo Scien-

tific®).

Total soluble protein concentrations were calculated from a calibration curve prepared using bovine serum albumin (BSA) as the reference standard. The resulting calibration curve had a coefficient of determination of R^2 = 0.9912.

2.4. Determination of Total Free Amino Acids

Total free amino acid concentrations were determined using the ninhydrin method described by Yemm et al.[41]. For each sample, 10 mg of dry, powdered plant material was weighed into a 2 mL microcentrifuge tube using a Pioneer analytical balance (Ohaus®). Subsequently, 650 µL of an ethanol–water extraction solution (70:30, v/v) was added, and the mixture was allowed to stand for 5 min.

The samples were centrifuged at 10,000 rpm and 4 °C for 5 min using a Spectrafuge 16M centrifuge (Labnet International®). The resulting supernatant was transferred to a clean 2 mL microcentrifuge tube. The extraction procedure was repeated twice using the remaining plant material, resulting in three sequential extracts per sample. The three supernatants were pooled in a single tube.

An 800 µL aliquot of the pooled extract was mixed with 200 µL of ninhydrin solution. The reaction mixture was heated in a boiling-water bath at 100 °C for 10 min and then allowed to cool to room temperature. Absorbance was measured at 570 nm using a spectrophotometer. Total free amino acid concentrations were calculated from a calibration curve prepared with leucine as the reference standard.

2.5. Determination of Starch

Starch concentration was determined using a colorimetric iodine method based on the procedures described by Ebell[42] and Haissig and Dickson[43]. One milliliter of distilled water was added to each microcentrifuge tube containing 10 mg of dry, powdered plant material. The samples were vortexed for 1 min using a Maxi Mix II vortex mixer (Thermo Scientific®) and subsequently heated in a boiling-water bath for 10 min to gelatinize the starch.

The samples were centrifuged at 2,500 rpm for 2 min using a Spectrafuge 16M centrifuge (Labnet®). A 300 µL aliquot of the resulting supernatant was transferred to a clean microcentrifuge tube and mixed with 900 µL of absolute ethanol. The tubes were then centrifuged at 10,000 rpm for 5 min to precipitate the starch. The supernatant was carefully decanted, and the starch-containing pellet was retained at the bottom of the tube.

The pellet was resuspended in 1 mL of distilled water by vortexing for 3 min. Subsequently, 50 µL of iodine solution was added to each tube, and absorbance was measured at 595 nm using a Genesys 20 UV–Visible spectrophotometer (Thermo Scientific®). A reagent blank containing 1 mL of distilled water and 50 µL of iodine solution was used to correct the absorbance measurements. Starch concentrations were calculated from a calibration curve prepared with rice starch (Sigma-Aldrich®) as the reference standard.

2.6. Determination of Total Soluble Sugars

Total soluble sugars concentrations were determined using the anthrone method described by van Handel[44]. For each sample, 10 mg of lyophilized, finely ground plant material was weighed into a 2 mL microcentrifuge tube (MCT-200-C Clear, Axygen Scientific®, Schwerte, Germany) using an analytical balance (PW 250, Adam®, Oxford, United States). 500 µL of a methanol–water extraction solution (70:30, v/v) was added to each tube.

The samples were homogenized for 5 min using a vortex mixer (Scilogex®, Rocky Hill, United States) and then centrifuged at 10,000 rpm and 4 °C for 15 min using a Spectrafuge 16M centrifuge (Labnet International®, Edison, United States). The resulting supernatant was transferred to a clean 2 mL microcentrifuge tube.

A 100 µL aliquot of the pooled extract was mixed with 1 mL of anthrone reagent, prepared by dissolving 150 mg of anthrone in a solution containing 76 mL of H_2SO_4 and 30 mL of distilled water. The reaction mixture was heated in a boiling-water bath for 10 min and subsequently allowed to cool to room temperature. Absorbance was then measured at 625 nm using a spectrophotometer. Total soluble sugar concentrations were calculated from a calibration curve prepared with sucrose as the reference standard.

2.7. Statistical Analysis

Data normality was assessed using the Shapiro–Wilk test at a significance level of $\alpha = 0.05$. Because the test indicated a significant departure from normality ($p < 0.05$),

differences between the two independent groups were evaluated using the nonparametric Mann–Whitney U test. All statistical analyses were performed using SPSS Statistics, version 20.

3. Results

3.1. Effect of *Tillandsia recurvata* Colonization on Total Soluble Proteins Concentration in *Neltuma laevigata*

Total soluble proteins concentrations did not differ significantly between the Presa Ruiz Cortines site, where *T. recurvata* was absent, and the Sierra de la India site, where it was present, in any of the evaluated plant organs.

In roots, mean total soluble proteins concentrations were 136.40 mg g^{-1} DM at Presa Ruiz Cortines and 147.64 mg g^{-1} DM at Sierra de la India (U = 6.0, p = 0.68), and the Hodges–Lehmann estimate of the location shift was −15.22 units, with an exact nonparametric confidence interval of at least 95% ranging from −51.17 to 23.84. Similarly, no significant differences were detected in stems, with mean concentrations of 156.73 and 171.52 mg g^{-1} DM, respectively (U = 6.0, p = 0.6), and the Hodges–Lehmann estimate of the location shift was −12.30 units, with an exact nonparametric confidence interval of at least 95% ranging from −79.92 to 49.05. Leaf protein mean concentrations were 195.33 mg g^{-1} DM at Presa Ruiz Cortines and 209.37 mg g^{-1} DM at Sierra de la India (U = 6.0, p = 0.68), and the Hodges–Lehmann estimate of the location shift was −20.51 units, with an exact nonparametric confidence interval of at least 95% ranging from −63.49 to 22.16. Mean concentrations of fruit proteins also showed no significant differences between sites, with values of 166.52 and 174.37 mg g^{-1} DM, respectively (U = 7.0, p = 0.88), The Hodges–Lehmann estimate for the difference between sites was −1.39 units, with an exact conservative nonparametric confidence interval of at least 95% ranging from −32.73 to 18.34 (**Figure 1**).

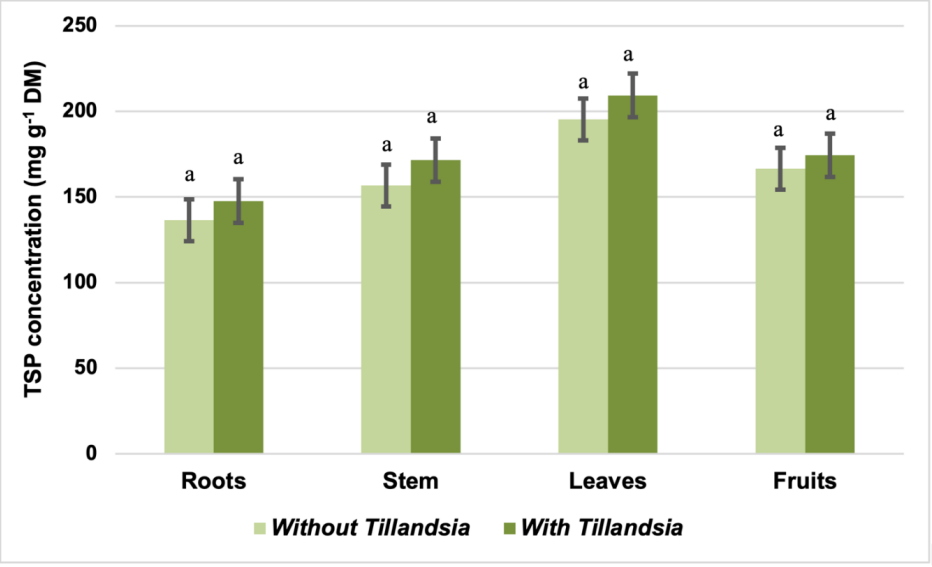

Figure 1. Total soluble proteins (TSP) concentrations in roots, stems, leaves, and fruits of *Neltuma laevigata* at sites with (dark green) and without (light green) *Tillandsia recurvata* colonization.
Note: Equal letters (a, b) mean that there is no significant difference between sites at $p < 0.05$. Vertical bars represent the standard error. n = 4. TSP: total soluble proteins; DM: dry matter.

3.2. Effect of *Tillandsia recurvata* Colonization on Total Free Amino Acids Concentration in *Neltuma laevigata*

Total free amino acid concentrations differed significantly between the Presa Ruiz Cortines site, where *T. recurvata* was absent, and the Sierra de la India site, where the epiphyte was present, in all evaluated organs. In every case, concentrations were higher at Presa Ruiz Cortines (**Figure 2**).

Root amino acid mean concentrations were 42.54 mg g^{-1} DM at Presa Ruiz Cortines and 23.87 mg g^{-1} DM at Sierra de la India (U = 0.0, p = 0.028), and the Hodges–Lehmann estimator indicated that the concentration at site

without *Tillandsia* was 36.45 units higher than the site with *Tillandsia* present, with a 95% nonparametric confidence interval ranging from 29.58 to 45.81 units. Similarly, stem means concentrations were significantly higher at Presa Ruiz Cortines than at Sierra de la India, with mean values of 69.47 and 49.25 mg g^{-1} DM, respectively (U = 0.0, p = 0.027), the Hodges–Lehmann estimator indicated that the concentration at site without *Tillandsia* was 40.07 units higher than at site with *Tillandsia* present, with a 95% nonparametric confidence interval ranging from 34.21 to 50.87 units. Leaf mean concentrations were 116.78 mg g^{-1} DM at Presa Ruiz Cortines and 90.16 mg g^{-1} DM at Sierra de la India (U = 0.0, p = 0.02), and the Hodges–Lehmann estimator indicated that the concentration at the site without *Tillandsia* was 31.88 units higher than at the site with *Tillandsia* present, with a 95% nonparametric confidence interval ranging from 27.35 to 35.22 units. The largest difference was observed in fruits, with mean concentrations of 110.95 mg g^{-1} DM at Presa Ruiz Cortines and 67.87 mg g^{-1} DM at Sierra de la India (U = 0.0, p < 0.028), the Hodges–Lehmann estimator indicated that the concentration at site without *Tillandsia* was 67.40 units higher than at site with *Tillandsia* present, with a 95% nonparametric confidence interval ranging from 61.12 to 74.05 units.

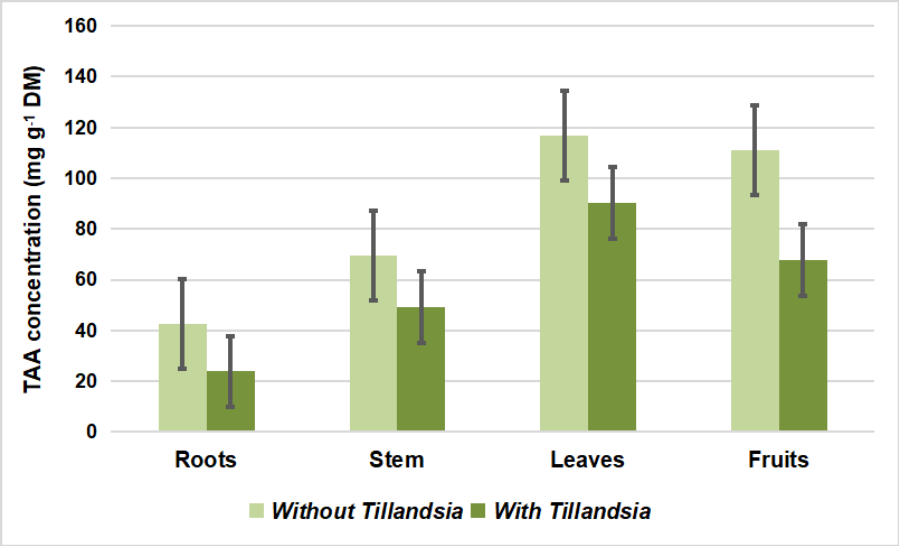

Figure 2. Total free amino acids (TAA) concentrations in roots, stems, leaves, and fruits of *Neltuma laevigata* at sites with (dark green) and without (light green) *Tillandsia recurvata* colonization.
Note: Equal letters (a, b) mean that there is no significant difference between sites at p < 0.05. Vertical bars represent the standard error. n = 4. TAA: total amino acids; DM: dry matter.

3.3. Effect of *Tillandsia recurvata* Colonization on Starch Concentration in *Neltuma laevigata*

Starch concentrations differed significantly between the Presa Ruiz Cortines site, where *T. recurvata* was absent, and the Sierra de la India site, where the epiphyte was present, in all evaluated organs. In every case, starch concentrations were higher at Presa Ruiz Cortines.

Root starch mean concentrations were 199.92 mg g^{-1} DM at Presa Ruiz Cortines and 92.36 mg g^{-1} DM at Sierra de la India (U = 16.0, p = 0.02). The estimated mean difference between groups was 211.90 units, with a 95% confidence interval ranging from 173.50 to 233.41, indicating a consistently higher starch content in the roots of trees growing at the site without *Tillandsia*. Stem mean concentrations were 110.20 and 87.34 mg g^{-1} DM, respectively (U = 16, p = 0.028), and the estimated mean difference between groups was 53.59 units, with a 95% confidence interval (CI) ranging from 48.78 to 59.19, indicating consistently greater starch reserves in the stems of trees from the site without *Tillandsia*. Similarly, leaf starch concentrations were significantly higher at Presa Ruiz Cortines than at Sierra de la India, with mean values of 67.97 and 52.87 mg g^{-1} DM, respectively (U = 16, p < 0.28), the estimated mean difference between groups was 32.68 units, with a 95% confidence interval (CI) ranging from 29.04 to 36.53, indicating consistently greater

starch accumulation in leaves at the site without *Tillandsia.* Fruit starch means concentrations were 68.39 mg g^{-1} DM at Presa Ruiz Cortines and 47.59 mg g^{-1} DM at Sierra de la India (U = 16, $p < 0.02$), the estimated mean difference between groups was 25.09 units, with a 95% confidence interval (CI) ranging from 20.92 to 28.98, indicating consistently greater starch accumulation in fruits at the site without *Thillandsia* (**Figure 3**).

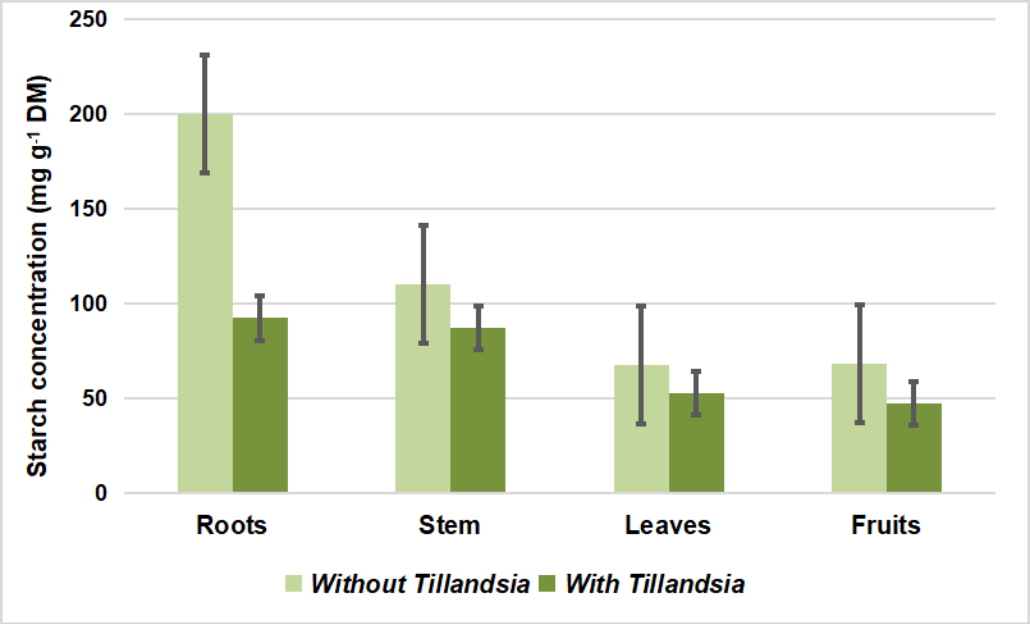

Figure 3. Starch concentrations in roots, stems, leaves, and fruits of *Neltuma laevigata* at sites with (dark green) and without (light green) *Tillandsia recurvata* colonization.

Note: Equal letters (a, b) mean that there is no significant difference between sites at $p < 0.05$. Vertical bars represent the standard error. n = 4; DM: dry matter.

3.4. Effect of *Tillandsia recurvata* Colonization on Total Soluble Sugars Concentration in *Neltuma laevigata*

Total mean concentrations of soluble sugars varied among plant organs in their response to site conditions. No significant differences were detected between the Presa Ruiz Cortines site, where *T. recurvata* was absent, and the Sierra de la India site, where the epiphyte was present, in roots or fruits. In contrast, significant differences were observed in stems and leaves, with higher concentrations at Presa Ruiz Cortines.

Root total mean concentrations of soluble sugars were 20.08 mg g^{-1} DM at Presa Ruiz Cortines and 18.24 mg g^{-1} DM at Sierra de la India (Mann–Whitney U = 8.0, $p = 0.100$), and the Hodges–Lehmann estimator indicated a difference of 0.09 units between sites, with a 95% nonparametric confidence interval ranging from −4.73 to 2.66 units. Stem means concentrations were significantly higher at Presa Ruiz Cortines than at Sierra de la India, with values of 29.12 and 23.92 mg g^{-1} DM, respectively (U = 0.0, $p = 0.02$), the Hodges–Lehmann estimator indicated that the concentration at site without *Tillandsia* was 9.24 units higher than at site with *Tillandsia* present, with a 95% nonparametric confidence interval ranging from 5.11 to 13.16 units. Similarly, leaf mean concentrations were 24.33 mg g^{-1} DM at Presa Ruiz Cortines and 20.84 mg g^{-1} DM at Sierra de la India (U = 0.0, $p = 0.028$); the Hodges–Lehmann estimator indicated that the concentration at the site without *Tillandsia* was 8.52 units higher than at site with *Tillandsia* present, with a 95% nonparametric confidence interval ranging from 5.36 to 14.87 units. Fruit means concentrations did not differ significantly between sites, with values of 29.59 mg g^{-1} DM at Presa Ruiz Cortines and 24.84 mg g^{-1} DM at Sierra de la India (U = 0.0, $p = 0.2$), the Hodges–Lehmann estimator indicated that the concentration at site without *Tillandsia* was 4.92 units higher than at site with *Tillandsia* present, with a 95% nonparametric confidence interval ranging from 0.39 to 7.55 units (**Figure 4**).

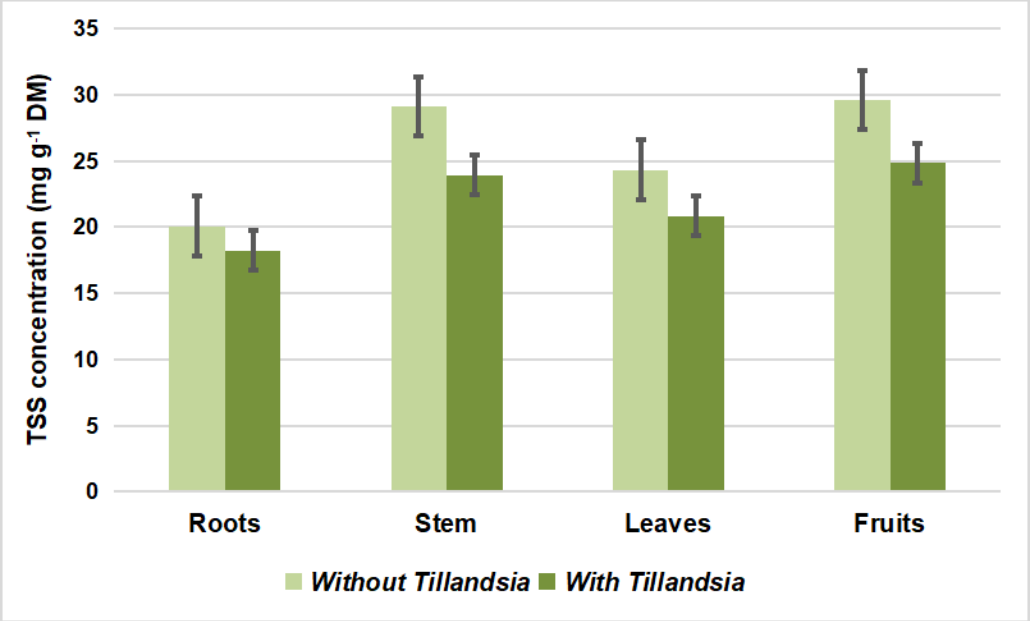

Figure 4. Concentration of total soluble sugars (TSS) in *N. laevigata* in root, stem, leaf and fruits in a site with (dark green) and without (light green) *Tillandsia recurvata*.
Note: Equal letters (a, b) mean that there is no significant difference between sites at $p < 0.05$. Vertical bars represent the standard error. n = 4. TSS: total soluble sugars; DM: dry matter.

4. Discussion

The organic matter cycle is vitally important because it maintains the fertility of the soil surrounding the tree. Although *T. recurvata* can contribute organic matter and nutrients to soils beneath mesquite canopies, high epiphyte loads may reduce host vigor, impair hydraulic and photosynthetic functioning, and increase shoot and branch mortality. Under drought or other environmental stress conditions, extensive infestations may contribute to stand-level forest decline and ecosystem degradation [45].

Heavy epiphyte loads can alter canopy nutrient cycling by intercepting and temporarily retaining atmospheric and litter-derived nutrients, including inorganic nitrogen. In some epiphyte–host systems, these changes, together with shading, mechanical interference or allelopathic effects, may reduce shoot production, branch vigor and host fitness. However, evidence that epiphytes cause persistent soil nitrogen infertility and eventual whole-tree depletion remains limited and system-dependent [46]. This hypothesis is consistent with the findings of the present study, which showed lower total amino acid concentrations at the Sierra de la India site, where samples were collected from trees colonized by epiphytic plants.

Furthermore, leaf litter was observed accumulating within the *Tillandsia* biomass. This observation is consistent with evidence that epiphytic bromeliads can intercept and retain leaf litter and other particulate organic material, forming temporary canopy pools of carbon and nutrients and modifying their subsequent transfer to the soil through litterfall and throughfall [47,48]. The accumulation of leaf litter within *Tillandsia* plants may temporarily delay the transfer of organic matter and nitrogen to the soil surrounding *N. laevigata*, potentially modifying the spatial and temporal availability of nutrients in the substrate [45,49]. A reduction in plant-available soil nitrogen may have contributed to the lower total amino acid concentrations observed in the host trees by limiting nitrogen uptake and assimilation [50,51]. However, this mechanism should be confirmed through measurements of soil ammonium and nitrate, tissue nitrogen, nitrogen-assimilation enzyme activity, and biological nitrogen fixation.

T. recurvata may negatively affect the early development of its host through allelochemical activity, as methanolic and dichloromethane extracts of the epiphyte have been shown to reduce radicle elongation in *N. laevigata* seedlings. Furthermore, branches with more than 50% *T. recurvata* cover exhibited significantly fewer live shoots and a greater number of dead shoots than paired branches with less than 50% epiphyte cover [17,22,45].

In a study conducted in a Mexican scrubland, the au-

thors evaluated the effects of *T. recurvata* infestation on *Parkinsonia praecox* and reported that a higher abundance of *T. recurvata* on *P. praecox* was associated with an increased number of dead shoots, likely as a consequence of reduced photosynthetic activity caused by shading from the epiphyte[52,53]. The findings of the present study support this observation, as carbohydrate reserves, including total soluble sugars and starch, exhibited lower concentrations at the site affected by *T. recurvata* than those reported in other studies[17,45].

The results of the present study are consistent with previous reports indicating that epiphytic plants may negatively affect host performance by reducing carbohydrate reserves and increasing shoot and branch mortality[45]. Although *T. recurvata* does not extract water or nutrients directly from the host vascular system, its presence on branches may reduce light interception and photosynthetic activity through physical coverage and shading[17]. This reduction in photosynthetic capacity could limit carbohydrate synthesis and accumulation, thereby explaining the lower concentrations of carbohydrates observed in the present study.

The results of the present study suggest that epiphytic plants may induce structural damage and physiological stress in mesquite trees through multiple mechanisms, including increased mechanical load on branches, spatial restriction of developing shoots, potential allelopathic effects, interception of water and nutrients, accumulation of atmospheric pollutants, and shading of host tissues[17,45,51]. These stress factors may limit photosynthetic activity and reduce carbohydrate accumulation, ultimately affecting the growth, vigor, and long-term vitality of the host tree[17,45,51].

These processes remain insufficiently studied, and recent evidence suggests that the association between deteriorated branches and high epiphyte loads may partly reflect branch age and within-crown shading rather than a strictly causal effect of epiphytes. Older branches, especially those located in lower or inner canopy positions, may experience reduced light availability and natural decline, while their longer persistence also increases the probability of epiphyte colonization and accumulation. Thus, high epiphyte loads on deteriorated branches may result from both epiphyte-induced stress and the greater susceptibility of older, shaded branches to colonization and senescence[45,54].

It is important to emphasize that the physiological and ecological mechanisms potentially underlying the observed differences were not directly evaluated in this study. Although nitrogen limitation, reduced photosynthetic performance associated with epiphyte-induced shading, and changes in nutrient cycling may provide biologically plausible explanations for some of the observed patterns, these mechanisms should be regarded as hypotheses rather than demonstrated causal processes. Soil nitrogen availability, plant nitrogen status, photosynthetic parameters, and enzyme activities involved in carbon and nitrogen metabolism were not directly measured. Therefore, the present results provide evidence of variation in vegetative reserve components under the evaluated conditions but do not allow the specific physiological mechanisms responsible for such variation to be established. Future studies combining measurements of carbon and nitrogen reserves with photosynthetic performance, nutrient availability, and metabolic or enzymatic indicators would help determine whether these proposed mechanisms contribute to the responses associated with *Tillandsia recurvata* colonization.

An important limitation of the present study is the relatively small number of biological replicates (n = 4 per site). Although the use of non-parametric statistical procedures and the reporting of confidence intervals provide a suitable framework for analyzing the available data, the limited sample size reduces statistical power and constrains the generalization of the observed patterns. Therefore, the differences and trends identified in vegetative reserve concentrations should be interpreted cautiously and primarily within the context of the populations and environmental conditions evaluated in this study. Increasing biological replication and including additional populations across different environmental conditions would be necessary to determine whether the observed patterns are consistent and broadly representative of the response of *N. laevigata* to *T. recurvata* colonization.

The hypothesis proposed by Benzing and Seemann[46] provides a useful framework for interpreting the results of this study, since clear differences were observed between the plot composed of trees colonized by *T. recurvata* (Sierra de la India) and the plot without apparent epiphyte colonization (Presa Ruiz Cortines). These differences may be associated, at least in part, with the structural load imposed by *T. recurvata* on mesquite branches[45]. Previous studies have shown that high epiphyte loads can affect branch vitality, reduce

shoot production, modify bark, xylem and phloem anatomy, and decrease photosynthetic performance in phorophytes [17]. Therefore, rather than representing only a mechanical burden, the presence of *T. recurvata* may alter resource allocation, hydraulic functioning and carbon balance, which could be reflected in changes in nitrogenous compounds and total soluble sugars within the physiology of mesquite trees [55].

Although the presence of epiphytes did not significantly affect total soluble protein content, it significantly reduced total amino acid concentration in tissues colonized by *T. recurvata*. Amino acid pools are among the most responsive components of plant metabolism under stress conditions, often changing before detectable alterations in total protein content [56]. Moreover, increasing evidence indicates that heavy infestations of *T. recurvata* can negatively affect host performance through structural and physiological mechanisms, while plant–plant interactions involving parasitic or epiphytic species can trigger metabolic and defense responses in the host [57].

Nitrogen deficiency is one of the major physiological constraints limiting tree growth [58]. Reduced nitrogen availability restricts the biosynthesis of amino acids, particularly glutamine and glutamate, which are central to nitrogen assimilation, storage, and transport [59]. Consequently, nitrogen limitation impairs protein synthesis, reduces shoot formation and leaf development, and ultimately decreases tree growth and biomass accumulation [58].

5. Conclusions

The present study demonstrates that *T. recurvata* colonization is associated with significant reductions in total free amino acids and carbohydrate reserves (starch and, in some organs, total soluble sugars) in *N. laevigata*, whereas total soluble protein concentrations remain unaffected.

These findings suggest that epiphyte colonization is linked to alterations in carbon and nitrogen metabolism without causing detectable changes in overall protein content. Although the underlying mechanisms were not directly evaluated, the observed metabolic pattern is consistent with reduced photosynthetic performance and altered nitrogen availability previously reported for heavily colonized trees.

Although the present results provide evidence of differences in some components of vegetative reserves between the evaluated sites, these findings should be interpreted with caution because of the limited biological replication (n = 4 per site). Consequently, the results should not be considered conclusive evidence of a generalized effect of *T. recurvata* colonization on *N. laevigata*. Further studies with greater biological replication, additional populations, and experimental designs that allow environmental and site-related effects to be separated from epiphyte colonization effects are required to confirm these patterns and establish their broader ecological significance.

Consequently, dense *T. recurvata* infestations may compromise host physiological vigor by decreasing metabolic reserves required for growth, maintenance, and reproduction. From an ecological perspective, the observed variation in vegetative reserves may be relevant to the conservation and management of mesquite ecosystems experiencing heavy *T. recurvata* colonization. Because stored carbon and nitrogen compounds contribute to growth, tissue maintenance, resprouting, and recovery from environmental stress, persistent changes in these reserves could potentially influence the resilience of mesquite trees, particularly under the water- and nutrient-limited conditions characteristic of arid and semi-arid environments. However, given the observational nature and limited biological replication of the present study, these ecological implications should be considered as hypotheses requiring further evaluation. Long-term monitoring of epiphyte colonization together with physiological indicators of host condition could help identify trees or populations potentially at risk and provide.

Author Contributions

Writing, J.L.E.-D.L., L.M.V.-N., C.G.-D.l.P., Q.K.S.-R., E.A.B.-C., G.R.-B., J.C.R.-S., J.A.H.-H., C.N.-M., J.V.-A. and R.A.C.-J.; sampling, J.L.E.-D.L., L.M.V.-N., C.G.-D.l.P., E.A.B.-C., G.R.-B., J.C.R.-S., J.A.H.-H., C.N.-M. and R.A.C.-J.; lab work, J.L.E.-D.L.; statistical analysis, J.L.E.-D.L., L.M.V.-N., C.G.-D.l.P., Q.K.S.-R., E.A.B.-C. and J.V.-A.; project design, L.M.V.-N. All authors have read and agreed to the published version of the manuscript.

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Data are unavailable due to privacy. Contact the corresponding author if interested in collaborative work.

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Conflicts of Interest

The authors declare no conflict of interest.

AI Use Statement

No AI tools were used for data analysis, interpretation, or generation of scientific content. All outputs were critically reviewed and edited by the authors. The authors take full responsibility for the integrity and accuracy of the work.

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