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Carbohydrate Dynamics in a Disturbed Forest in Mexico

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ABSTRACT

This research was carried out in three sites of temperate forest in northern Mexico in two species: *Pinus cembroides* Zucc and *Quercus grisea* L. and two phenological stages: summer and winter. Sites evaluated were: a) a site with grazing-impact (GI), b) a site with tourism-impact (TI) and a site with minimal-impact (NI). The main objective was to evaluate the concentrations (mg·g DM) of starch (STR) and total soluble sugars (TSS) in pine and oak. Carbohydrate concentrations were determined by UV-visible spectrophotometry. In the pine, the root in the GI site was the highest value in the summer stage ($\bar{X} = 45.13$ mg·g DM, $F = 33.94$, $df = 8$, $p < 0.001$). In the TSS, there was a difference in the root ($\bar{X} = 30.29$ mg·g DM, $F = 7.68$, $df = 8$, $p < 0.022$) in the summer stage. In the oak, there was a difference in the NI site: the highest concentration of STR in the leaves was present in the summer stage ($\bar{X} = 41.77$ mg·g DM, $F = 9.97$, $df = 8$, $p < 0.012$). In the TSS in the leaves, a difference was observed, as the GI site was the site with the highest concentration ($\bar{X} = 35.31$ mg·g DM), followed by the NI site ($\bar{X} = 33.97$ mg·g MS) ($F = 12.93$, $df = 8$, $p < 0.007$). The highest concentration was observed in the sites GI and MI.

Keywords: *Pinus cembroides*; *Quercus grisea*; Carbohydrates; Tourism; Grazing

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1. Introduction

Plant species store energy in the form of water reserves and compounds such as carbohydrates, proteins, amino acids and mineral salts^[1,2]. Carbohydrates are vital for plants since they provide energy; they are present in forest trees, taking part in the absorption and assimilation of nutrients^[3]. Total soluble sugars (TSS) and starch (STR) are the main compounds that provide energy within the plants. They are important for different metabolic activities and also participate in survival mechanisms when any anthropogenic threat, biotic and abiotic stress occurs in forests^[4].

Broadleaf tree species and conifers exhibit fundamental differences in the dynamics of their non-structural carbohydrates (NSCs), such as starch and soluble sugars, driven by their vascular anatomy and growth strategies^[5,6]. Furthermore, broadleaf trees show a higher proportion of axial and radial parenchyma in their wood, ranging from 10% to 40%, compared to only 5% to 10% in conifers^[7,8]. This allows broadleaf trees to maintain significantly higher carbohydrate reserves in their stems and branches. Deciduous broadleaf species show drastic fluctuations; they deplete their carbohydrate reserves in spring to rebuild their entire leaf canopy and replenish them at the end of the growing season^[9], while conifers have more limited seasonal variations in xylem carbohydrates. They often consume carbon for annual xylem growth rather than storing it in large quantities, to compensate for the lower water transport efficiency^[10,11].

Although arid and semi-arid zones cover more than 50–60% of Mexican territory, scientific research has historically focused on temperate forests and tropical rainforests^[12]. However, forests in semiarid zones require attention because they are the first line of defense against climate change and desertification^[13].

Mexico has an extensive biodiversity; there are 50 species of the Pinaceae family; the pine populations are economically important due to the pine nut and they are located in the Baja California peninsula, the Sierra Madre Occidental, the Sierra Madre Oriental, the Trans-Mexican Volcanic Belt and the southern Sierra Madre^[14,15]. Mexico is one of the two largest centers of diversity worldwide for the *Quercus* genus, due to the mountainous regions along the country^[16]. *Q. grisea* is a species endemic to Mexico^[17].

One of the activities that involves land use change in forests is grazing. This activity causes the loss and degradation of vegetation in forests, due to cattle altering soil conditions with trampling and contribution of nutrients through fecal deposition^[18]. On the other hand, tourism is an expanding activity worldwide, generating a great economic benefit for communities, rural tourism involves land use change, which results in the alteration of the ecosystem, reducing levels of nitrogen (N) and carbon (C) in the soil^[19,20]. The objective of this research was to compare the concentration of STR and TSS in root, stem and leaf in three study sites, a site with grazing-impact (GI), another with tourism-impact (TI) and a site with minimum-impact (NI) in two phenological stages: summer (S) and winter (W) in two forest tree species with different physiological processes of carbon assimilation.

2. Materials and Methods

2.1. Study Area

The study was carried out in Durango, Mexico, in three sites: grazing-impact (GI) (24°143'71.6" N) (−103°763'71.6" W), tourism-impact (TI) (24°165'20.5" N) (−103°761'66.3" W) and minimum-impact (NI) (24°164'99.1" N) (−103°762'01.5" W). The climate is temperate with average temperatures of 5 °C to 29 °C, 700 mm average rainfall and lithosol-eutric as the predominant soil.

2.2. Sample Collection

Sampling was developed in September 2022 (summer) and January 2023 (winter), 3 trees per species were sampled (50-year estimated average age), completely at random. Samples were taken from the main root, stem and leaf^[20]. Root samples were taken with a conventional pick (Truper® 14), stem samples were taken with the help of an ax (Truper® ML-4M, 36") and leaf samples were cut manually with pruning shears.

The samples were transferred to a cooler and stored in an ultra-freezer (Revco Value Plus Thermo Scientific®) at −70 °C for 1 week to avoid enzymatic activity, then they were freeze-dried (Labconco Freezone Triad Freeze Dry Systems®) for 7 days, then pulverized in a knife mill (Pulverisette 15 Fritsch®).

2.3. Determination of Total Soluble Sugars (TSS) Concentration

The concentration of TSS was determined with the anthrone methodology^[21]. 10 mg of dry matter was weighed in microtubes (Mct-200-C 2.0 mL Clear Axygen Scientific®) using an analytical balance (Adam® Pw 250 Max 250 g, d = 0.0001 g). 500 µL of an extraction solution (70% methanol/30% water) was added, then centrifuged for 10 min (Spectrafuge 16MR© Labnet International, Edison, United States) at 10,000 rpm for 5 min. 2 mL of the solution was extracted to place them in clean microtubes, and 1 mL of anthrone solution (50 mL of sulfuric acid and 100 mg of anthrone) was added. Microtubes were boiled for 10 min and left at room temperature. Absorbance was measured in a spectrophotometer (UV-Visible Thermo Scientific® Genesys 20).

2.4. Determination of Starch (STR) Concentration

To determine the starch concentration, the technique established by Ebell^[22] and Haissig and Dickson^[23] was used. 1 mL of distilled water was added to the microtubes (Mct-200-C 2.0 mL Clear Axygen Scientific®) with 10 mg of dry matter and placed in the vortex (Maxi Mix II® Thermo Scientific®) for 1 min. The tubes were boiled for 10 min to gelatinize the starch, then centrifuged at 2,500 rpm (Spectrafuge 16 m Labnet®) for 2 min. 300 µL of the supernatant was extracted and placed in clean microtubes with 900 µL of absolute ethanol and centrifuged at 10,000 rpm for 5 min to precipitate the starch.

The alcohol was emptied from the microtube, leaving the starch at the bottom. 1 mL of distilled water was added, placed again in the vortex for 3 min and 50 µL of iodine solution was added to the microtubes. Finally, the absorbance was measured in a UV-Visible spectrophotometer at 595 nm (Genesys 20® Thermo Scientific®).

2.5. Statistical Analysis

The data normality was determined with the Shapiro-Wilks test. The statistical analysis applied for this study was a factorial ANOVA and a Tukey mean comparison test was performed with a significance level of ($p \leq 0.05$) using the IBM-SPSS 20.0 statistical program.

3. Results

3.1. Site with Minimum Impact (NI)

In the pine, a significant difference was observed for STR in the stem, in summer ($\bar{x} = 47.06 \pm 3.77$ mg·g DM) and winter ($\bar{x} = 34.82 \pm 0.61$ mg·g DM) ($F = 10.26$, $df = 5$, $p = 0.03$); in root and in leaf, no significant difference was found in STR concentration. In TSS no difference was observed in root, stem and leaf. In oak in STR in the non-impact site, a difference was observed in the leaf, development ($\bar{x} = 41.77 \pm 1.37$ mg·g DM) and dormancy ($\bar{x} = 29.38 \pm 0.12$ mg·g DM) ($F = 80.91$, $df = 5$, $p = 0.001$), for root and trunk no statistical difference was observed and for TSS in stem there was observed a statistical difference in development ($\bar{x} = 32.74 \pm 0.31$ mg·g DM) and dormancy ($\bar{x} = 34.92 \pm 0.53$ mg·g DM) ($F = 12.40$, $df = 5$, $p = 0.02$) stages and in root and leaf there was no statistical difference among them (Figure 1).

3.2. Site with Grazing Impact (GI)

In STR concentrations in pine roots, a difference was observed between summer ($\bar{x} = 94.43 \pm 7.66$ mg·g MS) and winter ($\bar{x} = 47.43 \pm 2.95$ mg·g DM) ($F = 32.75$, $df = 5$, $p = 0.005$). In the stem, no difference was observed; in the leaf, a difference was observed between summer ($\bar{x} = 32.89 \pm 0.41$ mg·g DM) and winter ($\bar{x} = 30.09 \pm 0.35$ mg·g DM) ($F = 25.91$, $df = 5$, $p = 0.007$). Whereas no differences were observed in TSS in root and stem, in leaf, differences were observed between summer ($\bar{x} = 34.64$ mg·g DM) and winter ($\bar{x} = 39.34 \pm 0.54$ mg·g DM) ($F = 63.06$, $df = 5$, $p = 0.001$). In oak, the concentrations of STR were not different in any organ between summer and winter. In TSS concentration in root and stem there were no differences observed and in leaf if there was a difference between summer ($\bar{x} = 35.31 \pm 0.11$ mg·g DM) and winter ($\bar{x} = 37.95 \pm 0.33$ mg·g DM) ($F = 54.02$, $df = 5$, $p = 0.002$) (Figure 2).

3.3. Site with Tourism Impact (TI)

No difference was observed in STR and TSS concentrations in root, stem and leaves between development and winter in pine. In oak, no statistical difference was observed in root, stem and leaf in STR concentrations. TSS

concentrations showed no difference in roots and stem, summer ($\bar{x} = 24.01 \pm 2.81 \text{ mg}\cdot\text{g}^{-1} \text{ MS}$) and winter ($\bar{x} = 36.59 \pm 1.22 \text{ mg}\cdot\text{g}^{-1} \text{ DM}$) ($F = 16.78, \text{ df} = 5, p = 0.01$) (Figure 3).

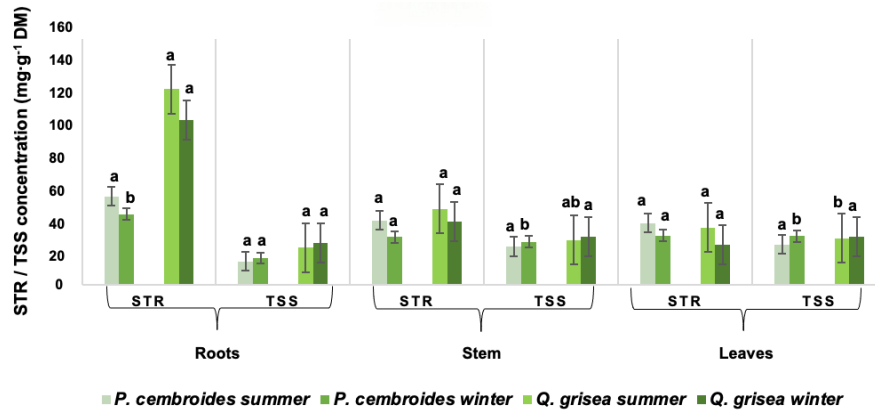


Figure 1. Concentration of starch (STR) and total soluble sugars (TSS) in the non-impact site (NI) in *P. cembroides* and *Q. grisea* in root, stem and leaf in summer and winter.

Note: Equal literals (a, b) mean that there is no significant difference between organs $p < 0.05$. Different literals (a, b) mean that there is a significant difference between organs $p < 0.05$. Vertical bars represent the standard error. n = 3. STR: starch; TSS: total soluble sugars; DM: dry matter.

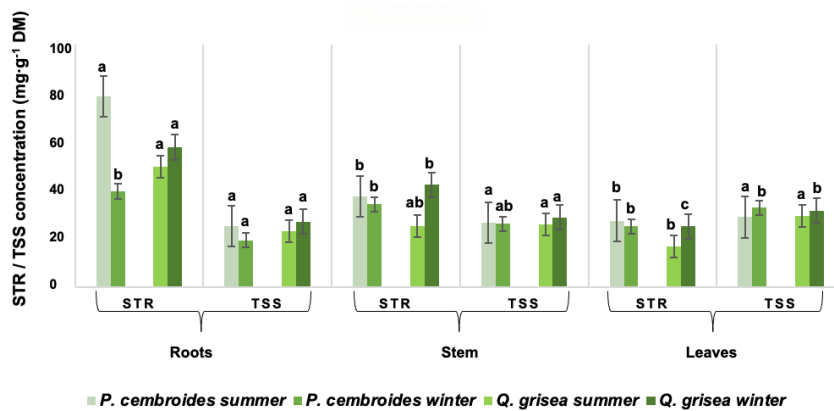


Figure 2. Concentration of starch (STR) and total soluble sugars (TSS) in the grazing-impact site (GI) in *P. cembroides* and *Q. grisea* in root, stem and leaf in summer and winter.

Note: Equal literals (a, b) mean that there is no significant difference between organs, $p < 0.05$. Different literals (a, b) mean that there is a significant difference between organs, $p < 0.05$. Vertical bars represent the standard error. n = 3. STR: starch; TSS: total soluble sugars; DM: dry matter.

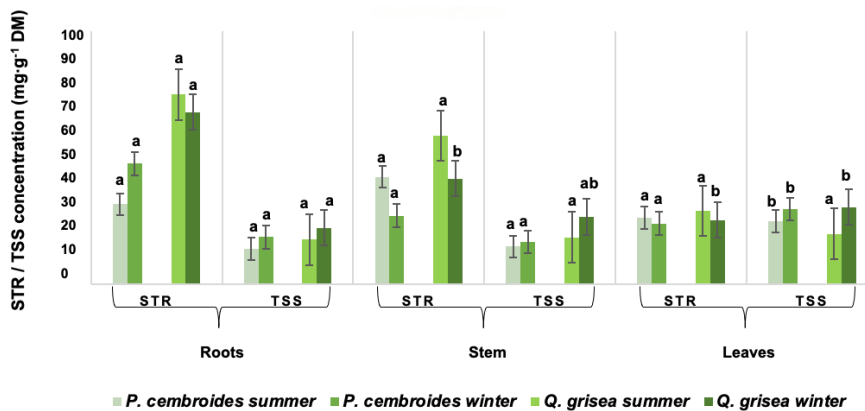


Figure 3. Concentration of starch (STR) and total soluble sugars (TSS) in the tourism-impact site (TI) in *P. cembroides* and *Q. grisea* in root, stem and leaf in late summer and winter.

Note: Equal literals (a, b) mean that there is no significant difference between organs, $p < 0.05$. Different literals (a, b) mean that there is a significant difference between organs, $p < 0.05$. Vertical bars represent the standard error. n = 3. STR: starch; TSS: total soluble sugars; DM: dry matter.

3.4. Comparison between Sites

A difference in STR concentration was observed in pine root between sites in late summer: NI ($\bar{x} = 64.85 \pm 13.16 \text{ mg}\cdot\text{g DM}$), GI ($\bar{x} = 94.43 \pm 7.66 \text{ mg}\cdot\text{g DM}$), TI ($\bar{x} = 38.05 \pm 1.26 \text{ mg}\cdot\text{g DM}$) ($F = 10.21$, $df = 8$, $p = 0.01$). In TSS concentrations difference was observed in the root in summer, NI ($\bar{x} = 16.98 \pm 2.56 \text{ mg}\cdot\text{g DM}$), GI ($\bar{x} = 30.29 \pm 3.96 \text{ mg}\cdot\text{g DM}$), TI ($\bar{x} = 16.87 \pm 0.96 \text{ mg}\cdot\text{g DM}$) ($F = 7.68$, $df = 8$, $p = 0.02$), while in oak no statistical difference was found between sites in root. A difference was observed in the summer in the stem of oak, with the highest TSS concentration in the NI site ($\bar{x} = 32.74 \pm 0.31 \text{ mg}\cdot\text{g DM}$), followed by the GI site ($\bar{x} = 31.18 \pm 3.06 \text{ mg}\cdot\text{g DM}$) and the lowest TSS concentration was observed in the IT site ($\bar{x} = 22.36 \pm 2.75 \text{ mg}\cdot\text{g DM}$).

A difference was observed in STR concentration in leaves of oak in the summer (NI $\bar{x} = 41.77 \text{ mg}\cdot\text{g MS}$), GI ($\bar{x} = 20.08 \pm 5.29 \text{ mg}\cdot\text{g MS}$), TI ($\bar{x} = 34.97 \pm 2.65 \text{ mg}\cdot\text{g DM}$) ($F = 9.97$, $df = 8$, $p = 0.01$) and TSS in the summer: NI ($\bar{x} = 33.97 \pm 0.95 \text{ mg}\cdot\text{g DM}$), GI ($\bar{x} = 35.31 \pm 0.11 \text{ mg}\cdot\text{g DM}$), TI ($\bar{x} = 24.01 \pm 2.81 \text{ mg}\cdot\text{g DM}$) ($F = 12.93$, $df = 8$, $p = 0.007$). In pine, a difference was found in STR in leaves in summer, NI ($\bar{x} = 45.13 \pm 1.92 \text{ mg}\cdot\text{g DM}$), GI ($\bar{x} = 32.89 \pm 0.41 \text{ mg}\cdot\text{g DM}$), TI ($\bar{x} = 31.61 \pm 1.02 \text{ mg}\cdot\text{g DM}$) ($F = 33.94$, $df = 8$, $p = 0.01$). Differences were observed in winter in TSS concentration in leaves, GI was the site with the highest TSS concentration, in concentration: GI ($\bar{x} = 39.34 \pm 0.54 \text{ mg}\cdot\text{g DM}$), TI ($\bar{x} = 35.78 \pm 0.37 \text{ mg}\cdot\text{g} \pm 0.62 \text{ DM}$) ($F = 35.64$, $df = 8$, $p = 0.01$).

4. Discussion

Research on vegetative reserves is essential to understand plant physiology in plants growing in adverse conditions [24-26].

In all organs evaluated in both *P. cembroides* and *Q. grisea*, it was observed that STR concentration in the root of the oak in late summer showed the highest value ($\bar{x} = 143.51 \text{ mg}\cdot\text{g DM}$). Valenzuela-Nuñez et al. [27] observed that the root is the main organ of reserve, which agrees with our research. On the other hand, Briceño-Contreras et al. [28] reported that in the summer in woody trees, a higher concentration of starch reserves occurs in roots.

Camarero et al. [29] reported a study carried out in *P.*

halepensis and *Q. ilex* in a natural forest (without anthropogenic impact), in which, in the winter, they observed a better concentration of carbohydrates in spring compared to winter.

Dettenmaier et al. [30] mention that minimum disturbance by anthropogenic activities increases the maintenance of biodiversity during the ecological processes of an area; this agrees with our results observed in the NI site.

In the site with grazing in both species (*P. cembroides* and *Q. grisea*), it was observed that the root is the organ with the highest concentration of STR in the summer. In the pine, the greatest accumulation in roots was observed in the summer, which coincides with results reported by Valenzuela-Nuñez et al., Briceño-Contreras et al., and He et al. [27,31,32]. In the summer, there was a greater accumulation of STR in pine; this can be explained by the fact that warm summer temperatures promote high rates of photosynthesis, leading to an abundance of produced carbohydrates. When these carbohydrates exceed the immediate energy demands for growth and respiration, the excess glucose is converted into starch for storage in various parts of the tree, including the roots. Roxas et al. [33] mention that it is in the winter when plant species decrease their content of energy reserves due to freezing temperatures and the assimilation of resources; therefore, in the summer, there is a greater demand for energy by forest species.

Chapin et al. [34] mention that grazing generally increases nutrient concentrations in plant tissues. In recent studies, a phenotypic plasticity response has been found in the roots of *Q. ilex*, which is reflected as a strategy to produce and consume energy as a reaction to stress [35]. It was observed that high concentrations of starch in the site with grazing are due to plants under stress conditions, such as compaction due to cattle trampling, developing capacities for efficient use of carbohydrate reserves [36].

In leaves, a higher concentration of TSS was observed in the winter in pine and oak, which indicates that in unfavorable environments, the content of energetic compounds in the leaf increases. Pan et al. [37] refer to the fact that the TSS present in the leaves of *Abies fargessi* var. *faxoniana* are related to self-protection mechanisms, so vegetative reserves serve as resistance in unfavorable environments.

In the site with tourist impact on both species, a

higher concentration of starch was observed in the stages of development and dormancy for the oak root. A higher concentration of starch was found in the root, which indicates that the root is the organ with the greatest accumulation of reserves, which agrees with Briceño-Contreras et al. ^[31] in a study carried out in *C. illinoensis*.

Similarly, Miranda et al. ^[38], in a study carried out in *Pinus canariensis* under disturbance effects, observed that the high carbohydrate content is a C reservoir for future physiological activities, such as the regeneration of the crown and needles in the formation of new photoassimilates, repairing possible damage to the stem, recycling the reserves where nutrients are stored and then resuming cell growth and development activities.

In forest species, to improve photosynthesis and make the mobility of vegetative reserves more efficient for different metabolic activities, it is important to evaluate the different dynamics of forest species affected by constant changes in ecosystems due to climate change ^[38], in this case ecotourism is commonly a friendly pastime, but poorly managed or in excess it can negatively impact the diversity and structure of natural ecosystems, with processes such as soil compaction, erosion, habitat alteration, among others, generating land use change in forest areas ^[39].

If compared, the root in the three sites, differences were found, the highest concentration of carbohydrates was observed in the site GI in the summer in pine for both STR and TSS, the SI site was the lowest in concentration in the summer for both STR and TSS compounds, this agrees with Valenzuela-Núñez et al., Briceño-Contreras et al., and He et al. ^[27,31,32], who reported that it is in the summer and in the root where there is the greatest concentration of vegetative reserves.

However, Chapin et al. ^[34] mention that grazing generally increases nutrient concentrations in plant tissues. This is because grazing for plant species becomes a stress situation, generating compaction due to trampling by livestock, and generating greater use of carbohydrate reserves ^[36] in the root, which is the main organ of energy reserves.

In the stem, there were differences in the summer for oak; the SI site was the site with the highest concentration of TSS, whereas the IT site showed the lowest concentration, agreeing with Dettenmaier et al. ^[30]. These authors report that minimum disturbance due to anthropogenic ac-

tivity results in greater preservation of biodiversity during the different biological processes of the ecosystem.

However, Fermaniuk et al. ^[40], in a research carried out on the species *Betula papyrifera* in two seasonal samplings, taking into account different stress conditions due to biotic and climatic activities, did not find a significant difference in carbohydrates. It is important to mention that the stem is the organ through which carbohydrates and nutrients are transported to support the different physiological activities of plant species ^[38,41].

The leaves showed a higher STR concentration in the summer in the pine in the SI site, while in the winter, differences were found in TSS in pine, the highest concentration was observed in the IP site, this agrees with what was reported by Dettenmaier et al. ^[30], who mention that the less alteration due to anthropogenic activities in a site, the greater the conservation of ecosystems in a given area, which agrees with our data.

However, in the site with GI there was a difference in TSS in the winter, which is related to the results mentioned by Chapin et al. ^[34], who refer to the high concentrations of vegetative reserves in plant tissues, due to grazing since trampling leads to soil compaction and with this a demand for reserves in this case in the leaves, so the TSS mobilize at any time in the face of any anthropogenic activity participating in metabolic activities ^[41], these variations observed are due to the differences between ecosystems in this case forests, since currently there is a lot of variation in different ecosystems due to climate change and plant species respond differently to different biotic and abiotic variations ^[42-44].

5. Conclusions

Studies based on carbohydrates, particularly on TSS and STR reserves, are currently of great relevance in the forestry field in order to understand the behavior and physiology of forest tree species in Mexico, in this case *P. cembroides* and *Q. grisea*.

Actually the forests are immersed in different disturbances by human activity and land use change, combining climatic variations influencing the behavior of forest trees.

The largest energy reserve was found in the site with grazing impact and minimum impact in the root, showing

higher concentrations than the stem and leaf, it is suggested to continue with studies of this type by adding the carbon analysis, adding the climatic variables to relate how they influence the concentration of carbohydrates.

Author Contributions

Project design, E.A.B.-C. and L.M.V.-N.; sampling, E.A.B.-C., J.G.M.-Z., L.M.V.-N., E.C.-A. and E.M.-C.; statistical analysis, E.A.B.-C., J.G.M.-Z., D.I.C.-M. and V.C.-V.; writing, E.A.B.-C., J.G.M.-Z., L.M.V.-N., D.I.C.-M., V.C.-V., E.C.-A. and E.M.-C.; translation, V.C.-V. All authors have read and agreed to the published version of the manuscript.

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Data are unavailable due to privacy.

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Conflicts of Interest

The authors declare no conflict of interest.

AI Use Statement

The authors declare that no artificial intelligence (AI) tools were used in the preparation of this manuscript.

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