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ARTICLE

Association of Environmental Factors with the Annual Dynamics of Total Soluble Sugars in Walnut

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ABSTRACT

The storage of total soluble sugars carried out by plant species is a transcendental strategy for their survival, especially in the face of adverse situations. The environment is a complex of factors that present notable variations over time. The objective of the study was to know the impact of environmental factors on the concentrations of total soluble sugars (TSS) in walnut trees in two varieties during a production cycle. TSS concentrations were determined in each sample by spectrophotometry. The environmental data were obtained from a meteorological station. The concentrations of walnut stem and root of the Wichita and Western variety were evaluated during each month of the 2016–2017 cycle and were correlated with temperature, irradiation, and relative humidity. The data were analyzed using ANOVA and regression analysis. A significant statistical difference was found for more than one factor on the variables studied. Environmental factors have an influence on the TSS reservoirs of the walnut tree and they are variable depending on the organ, the variety, and the time. Temperature was the factor with the greatest influence. One of the relevant survival

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strategies of deciduous plant species such as the pecan tree is the production, storage, and subsequent use of total soluble sugars (TSS).

Keywords: Carbohydrates; *Carya illinoinensis*; Environmental Factors; Pecan; Perennial Organs

1. Introduction

The pecan tree (*Carya illinoinensis* (Wagenh) K. Koch.) is a globally important fruit tree, although its largest production takes place in countries such as China, Iran, and the United States. Mexico ranks fourth in production, primarily in the states of Chihuahua, Coahuila, Durango, Nuevo León, and Sonora, with an annual production of over 160,000 t [1]. The Comarca Lagunera region is considered a leading pecan-producing area in Mexico, with nearly 10,000 hectares planted [2].

During a walnut production cycle, several phenological stages (bud break, leaf and flower development, flowering, fruit development and ripening) occur and may be influenced by the climatic conditions (temperature, solar radiation, rainfall, and humidity) of the growing site. In other words, the occurrence of each phenological stage can vary because environmental factors can also be highly variable, and therefore, metabolic processes (photosynthesis and respiration, which manage the capture, storage, and use of energy and carbon) may be conditioned by these factors [3]. For example, during winter, climatic conditions may trigger a state of dormancy in the walnut tree's growth and metabolism as a strategy to withstand the freezing conditions of the period. Later, as environmental conditions change, the trees' functions are reactivated, beginning with bud swelling and primordia growth. Similarly, with the change in these environmental conditions, the trees adapt and the other phenological stages begin; however, not all varieties will exhibit the same response [3].

One of the relevant survival strategies of deciduous plant species such as the pecan tree is the production, storage, and subsequent use of total soluble sugars (TSS). Without the availability of these compounds, the trees could not survive during periods when they require energy to perform their functions and photosynthetic activity is low or nonexistent [4,5]. Storage takes place mainly in perennial organs such as roots and stems, where they remain available until they are translocated to other parts of the tree when energy is required [6,7], such as in situations of drought, very low temperatures, frost, or periods of defoliation [8,9].

However, the amounts stored can vary significantly. Variation has been found between organs, phenological stages [10] and varieties [11], and environmental factors may be related to the behavior of this storage phenomenon [12].

It is well-established that living organisms develop according to their environment; however, the presence and intensity of each factor can vary greatly across the globe and over time. Consequently, the effects on organisms and their functions can also vary significantly [4,13,14]. For example, irradiation is a factor that plays a fundamental role in plant processes such as photosynthesis, photoperiod, and phototropism; that is, it influences how these species carry out their metabolic processes. Without this factor, plants would not have the energy that serves as food for them to survive and develop. In addition, irradiation also influences other environmental factors such as temperature and humidity on the planet [15].

The energy radiated from the sun flows in all directions; however, the amount that reaches the Earth's surface will vary depending on the point because its latitude differs, so the distance between these two points will be relative. On the other hand, it is considered that its intensity will vary according to the time of day or atmospheric conditions. Therefore, it is understood that the effects on plant processes will also be diverse, especially considering that over time all these aspects change and the phenological condition of each organism [15,16]; in addition to the above, it is proven that environmental factors can be altered by anthropogenic actions [16].

Temperature is also considered a substantial factor for plants and trees, affecting their development [12,17]. As Aslam et al. [18] note, living organisms can trigger adaptation mechanisms as a survival strategy, especially in stressful situations, such as extreme temperatures (very high or very low) or significant fluctuations, like those experienced during winter. It has been reported that in trees like the walnut, temperature can significantly influence metabolic processes [19], and in the sweet cherry, it affects carbohydrate storage [20].

Relative humidity, as an environmental factor, also influences life on the planet. For plants, it requires constant adaptation because it is a highly variable factor, as it is related to air temperature. During the day, humidity may remain stable, but it can exhibit a significant gradient between morning and afternoon, as well as over longer periods such as months or years [21,22]. Water in the atmosphere, in any of its physical states, governs the climate of a place, since it is part of the complex of greenhouse gases that participate in reflecting the heat emitted by the Earth, preventing it from freezing [22].

In this context, the environment undoubtedly influences the development of living beings and each of their processes; however, information is limited regarding the influence of these factors on the behavior of TSS (sodium phosphate) in pecan trees, considering different organs, varieties, and over time. Irradiation, temperature, and relative humidity are critical for pecan production, as they determine photosynthesis rate, growth, nut quality, pests and disease risks [19]. Extreme temperatures and low humidity may cause nut cracking (50%+ loss in critical years), while high irradiation is necessary for starch synthesis. Specifically, irradiation is fundamental to photosynthetic processes. High light exposure increases starch concentration, which is essential for nut quality. Temperature influences leaf development and walnut ripening. However, very high temperatures (especially in combination with low relative humidity) following periods of precipitation cause the fruit to crack. The walnut tree requires a suitable temperature range for heat accumulation to achieve optimal development and yield. The relative humidity of the environment influences transpiration and nutrient absorption. Low relative humidity reduces growth and causes the nut to crack. Excessive humidity can affect pollination. The interaction of these three environmental variables influences the physiology of the walnut tree, allowing us to predict the behavior of the content of total soluble sugars, which are vital to the quality of the pecan nut. Proper agronomic management of these climatic variables, as well as the determination of cultivars that can tolerate variation of these variables, especially with the climate changes observed in recent years in soil and microclimate, is essential to maximize production. Therefore, the objective of this study was to determine the association of temperature, irradiation, and relative humidity with the concentration of TSS in the roots and stems of pecan trees of the Wichita and Western varieties during each month of the 2016–2017 production cycle in the Laguna Region.

2. Materials and Methods

2.1. Study Area

The study was conducted in the Laguna Region, in Torreón, Coahuila, in northern Mexico (25°33′22″ N and 103°22′ 07″ W), where a dry desert climate predominates, with average annual temperatures of 21 °C, ranging from −2 °C to a maximum of 41 °C. The average annual irradiance, precipitation, and relative humidity during the study period were 22 $MJ \cdot m^{-2}$, 18 mm, and 37.8%, respectively [23]. Plant specimens were obtained through systematic sampling. From the center of the plot, four *C. illinoinensis* trees of the Wichita variety and four of the Western variety were selected. Two root and two stem samples were taken from these trees each month during the 2016–2017 growing season. Each sample was handled identically from extraction to transport to the laboratory, including freezing, freeze-drying, and grinding [7], as well as the determination of TSS four times using the Van Handel methodology [24]. Data on temperature, irradiation, and relative humidity were obtained from the INIFAP "La Laguna" experimental field meteorological station.

2.2. Determination of Total Soluble Sugars (TSS) Concentration

The concentration of TSS was determined with the anthrone methodology [24]. 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 and 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 were extracted to place them in clean microtubes, 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 R©Genesys 20).

2.3. Environmental Data

Monthly data for average temperature (°C) and irradiation ($MJ \cdot m^{-2}$) were obtained from the National Institute of Forestry, Agricultural and Livestock Research (INIFAP, Mexico) meteorological station, located at the "La Laguna" experimental field. Units and conversion factors for solar irradiance for plants were obtained from the International System of Units and models from INRA (Institut National de la Recherche Agronomique, France).

2.4. Statistical Analysis

Homoscedasticity and normality of the data were checked (Levene, Shapiro-Wilk, respectively), logarithmic transformation of the data was performed; descriptive statistics were obtained, comparison of means was performed, factorial ANOVA test (variety, month, and interaction) and curvilinear regression analysis ($p < 0.05$) with the SPSS Version 18.0 program [25]. Pearson correlation and multiple regression analyses were performed. The relationship that offered the best fit was considered to determine the relationship between TSS concentration in each compartment (root and trunk) and environmental factors (temperature, irradiation, and relative humidity); residual analyses were performed for each test.

3. Results and Discussion

3.1. Correlation between Temperature and TSS Concentration in Walnut Root of the Wichita and Western Varieties

The results of the regression analysis regarding the relationship between temperature (°C) and TSS concentration in the root of *C. illinoinensis* of the Wichita variety indicated a significant cubic correlation ($F = 6.792$, d.f. = 2.9; $p = 0.016$; $R^2 = 0.602$) (**Figure 1**); that is, temperature predicts TSS concentrations in this organ and walnut variety by 60%. The equation was:

$$\text{TSS concentration in Wichita root} = 37.114 + 0.000(T) + 0.007(T)^2 + 0.0002(T)^3.$$

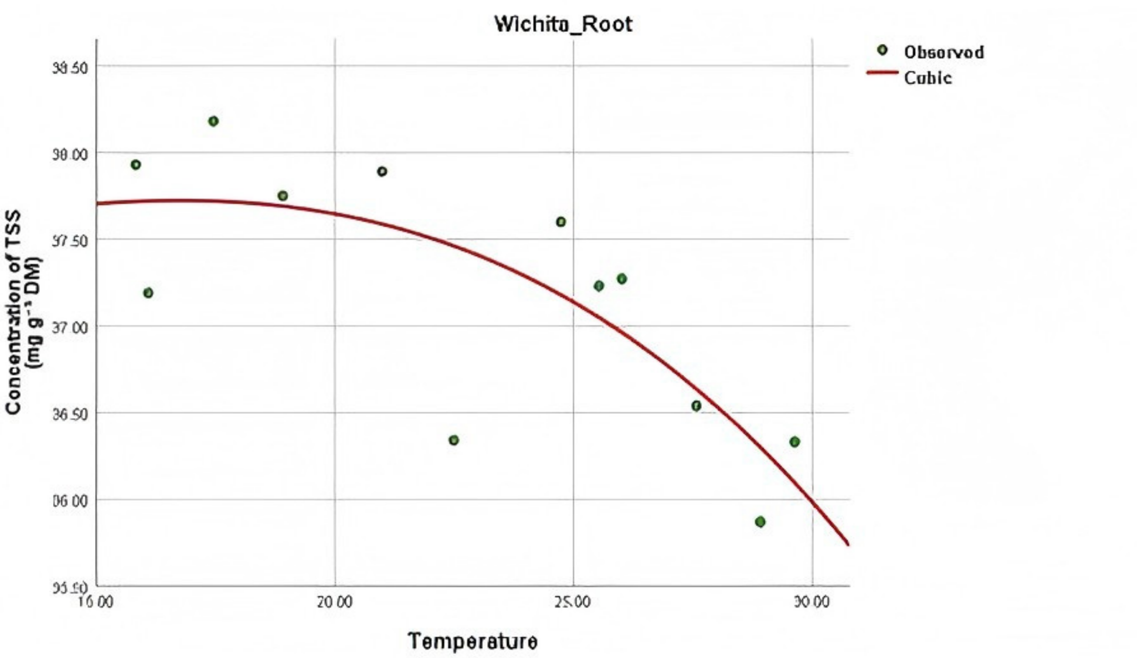

Figure 1. Correlation between temperature and total soluble sugars concentration in walnut root of the Wichita variety.

In the same way, a statistically significant cubic correlation was also observed in the Western variety (F = 5.06, d.f. = 2.9; $p = 0.034$; $R^2 = 0.526$) (**Figure 2**), meaning that temperature has a 52.6% effect on the TSS content in the root of the Western walnut variety. The equation was:

$$\text{TSS concentration in Western root} = 49.960 - 1.020(T) + 0.000(T)^2 + 0.001(T)^3.$$

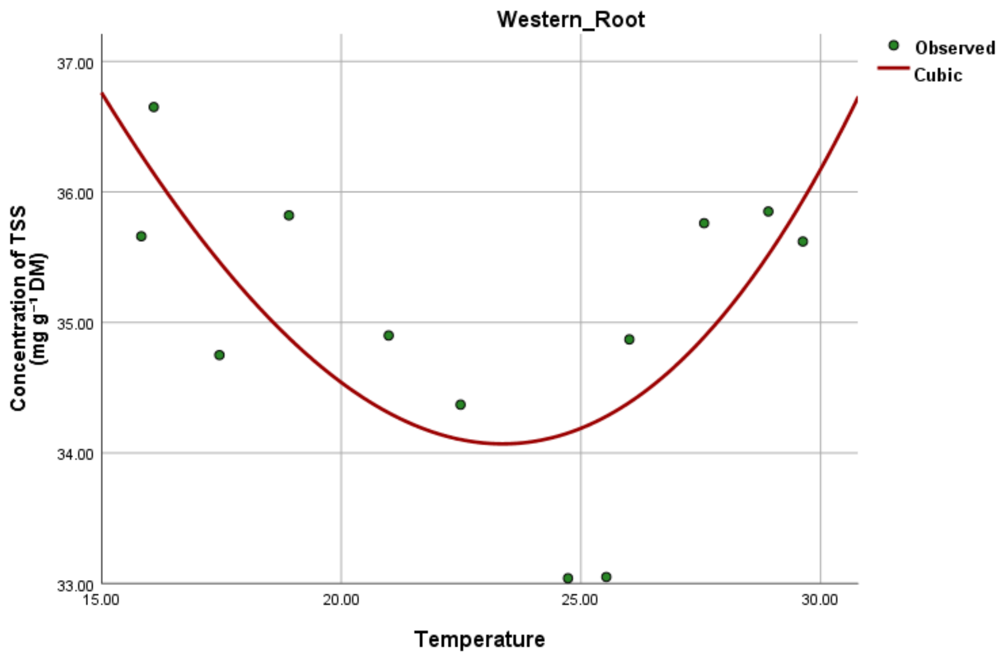

Figure 2. Correlation between temperature and total soluble sugars concentration in walnut root of the Western variety.

According to Aslam et al. [18] and Jung et al. [26], living beings can trigger adaptation and survival mechanisms under stress caused by extreme temperatures or when significant temperature fluctuations occur, such as during the winter period, where temperatures can vary considerably. This aligns with the findings of Wang et al. [10], where Wichita and Western walnut trees showed a high capacity to store carbohydrates, primarily during the coldest months of the year, which is consistent with the results reported here.

In this same sense, they agree with what was reported by Beppu et al. [20], who recorded changes in carbohydrate concentrations in sweet cherry trees associated with the temperature conditions of a region of Japan, finding that when temperatures were low, carbohydrate concentrations were significantly higher than when temperatures increased.

Furthermore, they agree with Asseng et al. [27] who indicated that there is a significant relationship between plant production and temperature conditions, since, when higher temperature conditions were present, production decreased, probably because during high temperatures other metabolic processes are activated that require energy in other sites of the organism, distributing it and reducing its availability. In addition, they mention that the effect may vary according to the cultivar of the species and the phenological stage in which it is found.

Likewise, our results correspond to those reported by Pan et al. [28], who found a higher concentration of non-structural carbohydrates in the root and stem organs, also observing variability between different varieties, presenting the lowest values during the period when growth begins and reserves are mobilized to new shoots; which in the case of walnut takes place in the months with the highest temperatures.

3.2. Correlation between Temperature and TSS Concentration in Walnut Stems of the Western and Wichita Varieties

The relationship between temperature (°C) and the concentration of total soluble sugars in the stem of *C. illinoinensis* of the Western variety was significant of the cubic type (F = 24.648, d.f. = 2.9; p = 0.000; R^2 = 0.846) (**Figure 3**), with the equation:

$$\text{TSS concentration of stem in Western} = 33.573 + 0.316(T) - 0.025(T)^2 + 0.000(T)^3,$$

that is, temperature predicts 84.6% of the TSS concentrations in the stems of walnut of this variety, where T = monthly average temperature, while for the Wichita variety this variable did not show a statistically significant correlation with temperature (F = 0.343, d.f. = 2.9; p = 0.151). This is why no figure alluding to this correlation is presented.

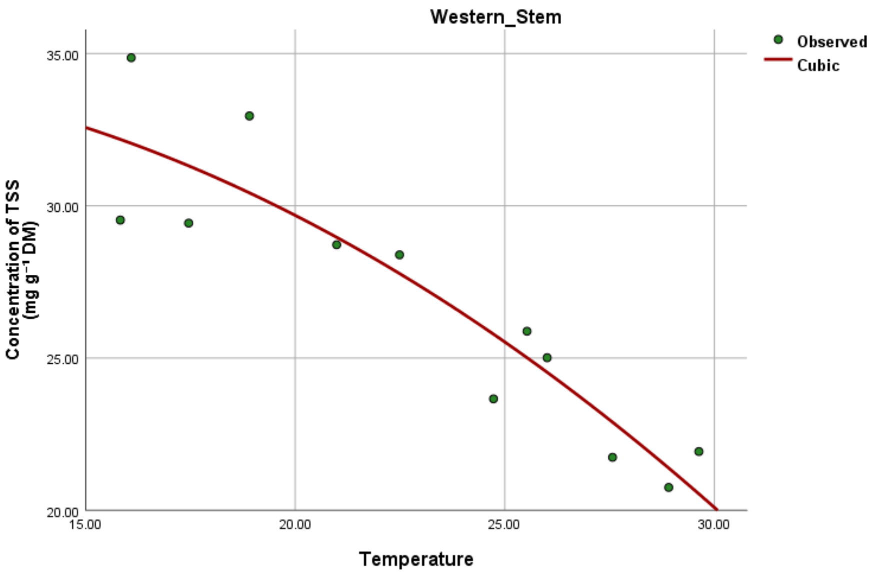

Figure 3. Correlation between temperature and total soluble sugars concentration in walnut stem of the Western variety.

The above results show similarity to those reported by Vanderschuren and Agusti [7], who reported high concentrations of these compounds in walnut stems during the winter months, when temperatures were lower and began to decrease at the end of the dormancy stage, when temperatures tend to increase gradually. They observed that during the dormancy stage (freezing period), the concentrations found in the stems of Western walnut trees were at a rate of 41.86 Mg/g DM, while during the increase in temperatures at the beginning of the phenological production stage, these concentrations decreased considerably to 17.32 Mg/g DM. This is probably because the temperatures promote new shoots and growth, which demand energy to carry them out, and because there is no photosynthetic production, the trees mobilize and use non-structural carbohydrates such as TSS stored in roots and stems, causing their decrease.

On the other hand, they agree with the findings of Kannenberg et al. [29], who stated that tree stems are organs that accumulate a large portion of non-structural carbohydrates as a reserve, and that these reserves can vary over time and among different species. They observed different amounts of carbohydrates in poplar and white oak trees in response to the same environmental factors, noting that environmental factors are paramount in plant processes. In this sense, it can be said that each variety of the same species could behave differently under the same temperature conditions.

Likewise, the results reported here are consistent with those indicated by Aguiló-Nicolau et al. [30], regarding the crucial role of temperature in carbohydrate production processes such as photosynthesis, and that these processes are generally also related to situations such as water restriction or high light intensity caused by summer conditions, or irrigation conditions where evaporation exceeds the capacity to maintain a high and constant water potential throughout the day. The difference in the influence of temperature on TSS concentration in both varieties could be due to their different adaptive capacities to the effects of temperature, as shown in the root organ; although they showed statistical differences, the numerical values were also different.

3.3. Correlation between Irradiation and TSS Concentration in Walnut Root of the Wichita and Western Varieties

The relationship between irradiation and the concentration of total soluble sugars in the root of *Carya illinoinensis* of the Wichita variety was significant of the cubic type (F = 4.336, d.f. = 2.9; $p = 0.048$, $R^2 = 0.491$) with the following equation:

TSS concentration of Wichita root =

$$36.961 + 0.000(I) + 0.007(I)^2 + 0.0002(I)^3,$$

that is, the TSS concentrations in the stems of walnut trees of this variety could be influenced by 49% by the effect of irradiation (**Figure 4**).

Similarly, for the Western variety, a statistically significant cubic correlation was observed (F = 6.204, d.f. = 2.9; $p = 0.020$, $R^2 = 0.580$) with the following equation:

TSS concentration of Western root =

$$45.678 - 0.760(I) + 0.000(I)^2 + 0.0004(I)^3,$$

which indicates that for this variety, these concentrations could be influenced by 58% by the irradiation conditions (**Figure 5**).

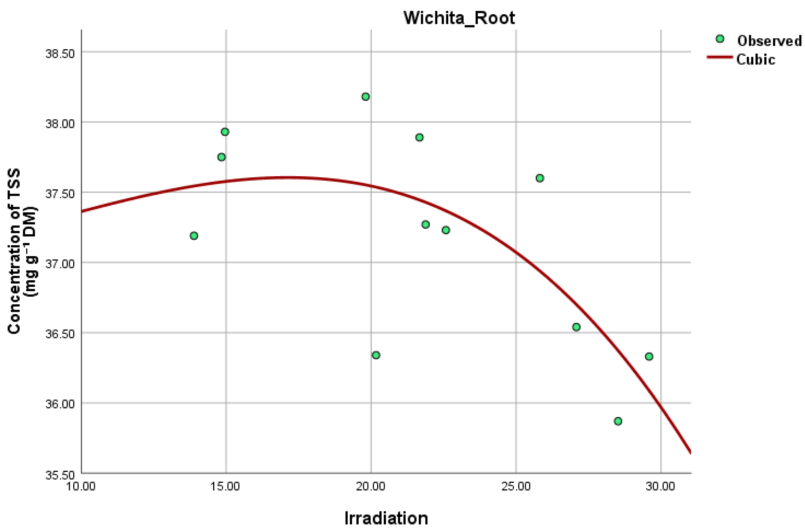

Figure 4. Correlation between irradiation and TSS concentration in walnut root of the Wichita variety.

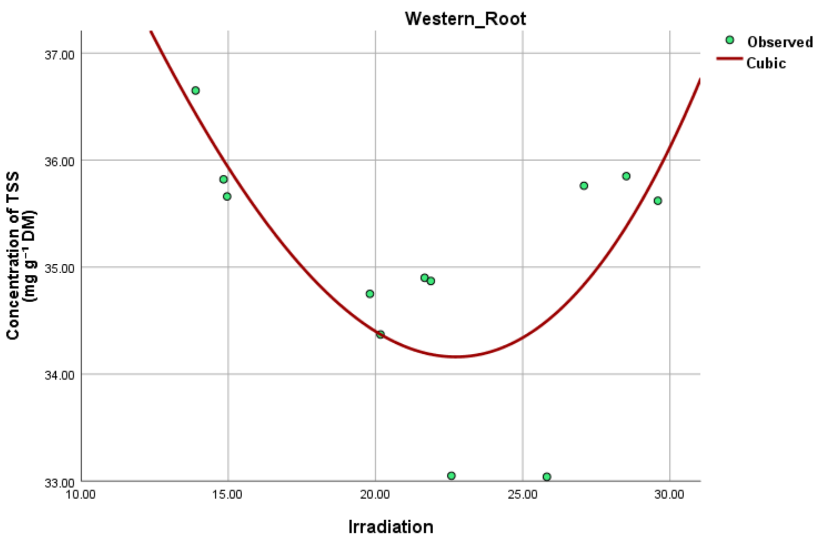

Figure 5. Correlation between irradiation and TSS concentration in walnut root of the Western variety.

Without the energy from radiation, the production of carbohydrates needed by plants to survive could not take place, as it plays a fundamental role in the processes of carbohydrate synthesis, respiration, and CO_2 release. The light energy emitted is vital in the photochemical phase of photosynthesis (the light-dependent reactions). Radiation is a source of energy for plants during photosynthesis, and the efficiency with which plants utilize it depends on the wavelength. Radiation above 700 nm does not favor plant photosynthesis; on the contrary, it accumulates heat.

In Wang et al. [10], it was also found that the root is the organ that accumulates the most carbohydrates, however, they presented slightly higher amounts of TSS in the months where there is less frequency of cloudiness, in the flowering stage that covers the months of greater solar radiation.

These results are also consistent with the report by Deng et al. [31], who concluded that when there is less light, photosynthetic activity decreases considerably, affecting the production of non-structural carbohydrates such as TSS. This indicates that irradiation is a factor that greatly influences the production and storage of these carbohydrates, since they found that under shade and drought treatments, these compounds in the roots of trees of a pine species had increases of 5.1%. They mentioned that the stress to which the trees are subjected can lead to different carbon partitioning mechanisms.

3.4. Correlation between Irradiation and TSS Concentration in Walnut Stem of the Wichita and Western Varieties

The relationship between irradiation and the concentration of total soluble sugars in the stem of *C. illinoinensis* of the Wichita variety (**Figure 6**) was significant of the cubic type (F = 5.895, d.f. = 2.9; p = 0.023, R^2 = 0.567) with the following equation:

$$\text{TSS concentration of Wichita stem} = 34.326 + 0.356(I) - 0.022(I)^2 + 0.000(I)^3.$$

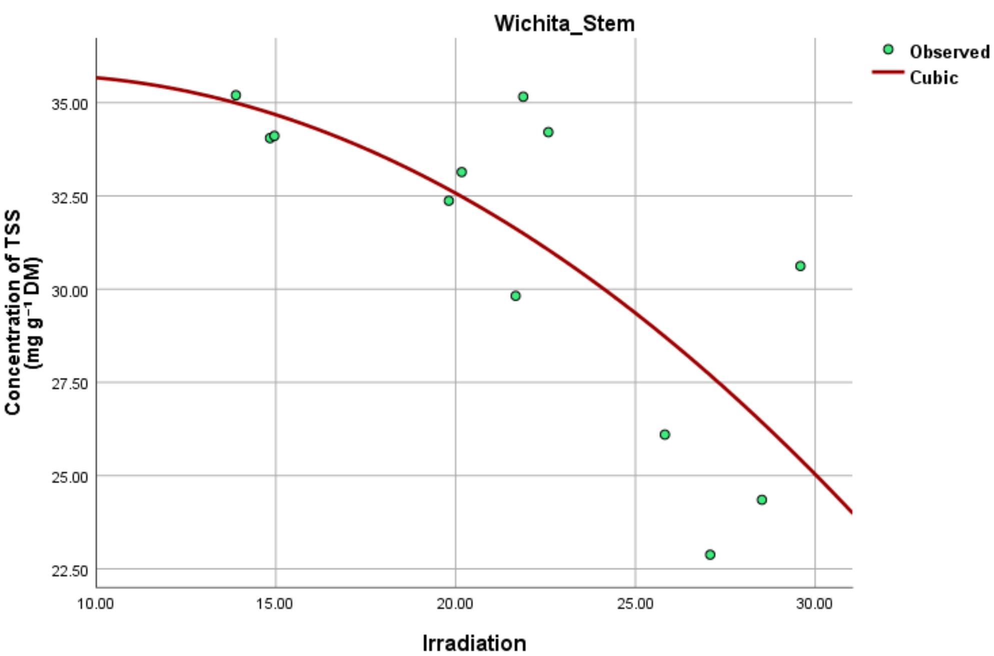

Figure 6. Correlation between irradiation and TSS concentration in walnut stem of the Wichita variety.

The relationship between irradiation and the concentration of total soluble sugars in the stem of *Carya illinoinensis* of the Western variety was significant of the cubic type (F = 42.764, d.f. = 2.9; p = 0.000, R^2 = 0.905, **Figure 7**) with the following equation:

$$\text{TSS concentration of Western stem} = 45.565 - 0.895(I) + 0.000(I)^2 + 0.000(I)^3.$$

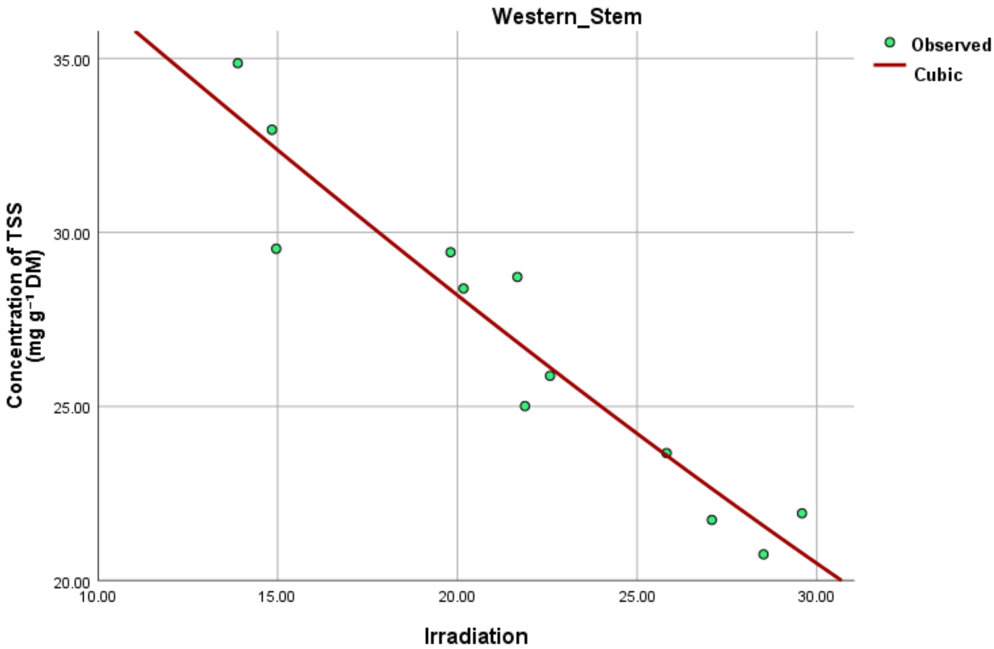

Figure 7. Correlation between irradiation and TSS concentration in walnut stem of the Western variety.

It can be observed that the storage of TSS in walnut stems shows greater susceptibility to irradiation in the Western variety than in the Wichita variety. Higher values were recorded during the months with more irradiation, which agrees with what was reported by Liu et al. [19] regarding the possible different behavior in the storage of a compound in the stem of walnut trees, depending on the variety, in response to the influence of an environmental factor such as irradiation. These authors found that the storage of protein nitrogen in the stem of walnut trees behaved differently under the effects of irradiation, arguing that the compounds can fluctuate in terms of hours or days due to the capacity of plants to adapt to variations in environmental factors. Furthermore, there is variation between different varieties, concluding that it may be due to the fact that the size of the stems influences the accuracy of the measurement of the compounds.

Similarly, Aguiló-Nicolau et al. [30] mention that, although the influence of environmental factors on the reaction mechanisms of plant species is not exclusive and total, it has an important influence, and that irradiation intervenes in the processes of carbohydrate production, such as photosynthesis. On the other hand, they mention that its influence on this aspect could be related to factors such as the position of their photosynthetic organs, such as the leaves, depending on the species and variety, they may present different angles with respect to the position of their leaves, therefore, have differences in the micromoles of light captured per square meter per second during a day.

On the other hand, our results coincide with those mentioned by Ramesh et al. [32], who stated that irradiated energy in trees of a mulberry variety showed changes in growth parameters, new shoots, roots, height, leaf area, fertility, among others. This suggests that this factor, by influencing these parameters, could be reflected in the capacity for carbohydrate production due to greater photosynthetic capacity and a larger area for capturing irradiated energy. The results of Vanderschuren and Agusti [7] also align with the findings regarding TSS concentrations in the stems of walnut trees of both varieties, as they also found statistically significant differences during the different months encompassing the phenological stages studied. During these months, radiation conditions were variable, with higher concentrations in the stems compared to the roots, affected by the variable photoperiod in the study area during that cycle.

3.5. Correlation between Relative Humidity and TSS Concentration in Walnut Stems of the Wichita and Western Varieties

The relationship between relative humidity and the concentration of total soluble sugars in the stem of *Carya illinoinensis* of the Wichita variety was significant (F = 11.110, d.f. = 1.10; p = 0.008; R^2 = 0.526, **Figure 8**) with the following equation:

TSS concentration of Wichita stem = 0.031 + 0.940 * RH.

That is, the TSS concentrations in the stem of the Wichita variety walnut can be predicted by the behavior of the relative humidity present at the site. At slightly above 50%, it was observed that when the relative humidity increased, TSS concentrations were partially increased in the stems of the walnut trees.

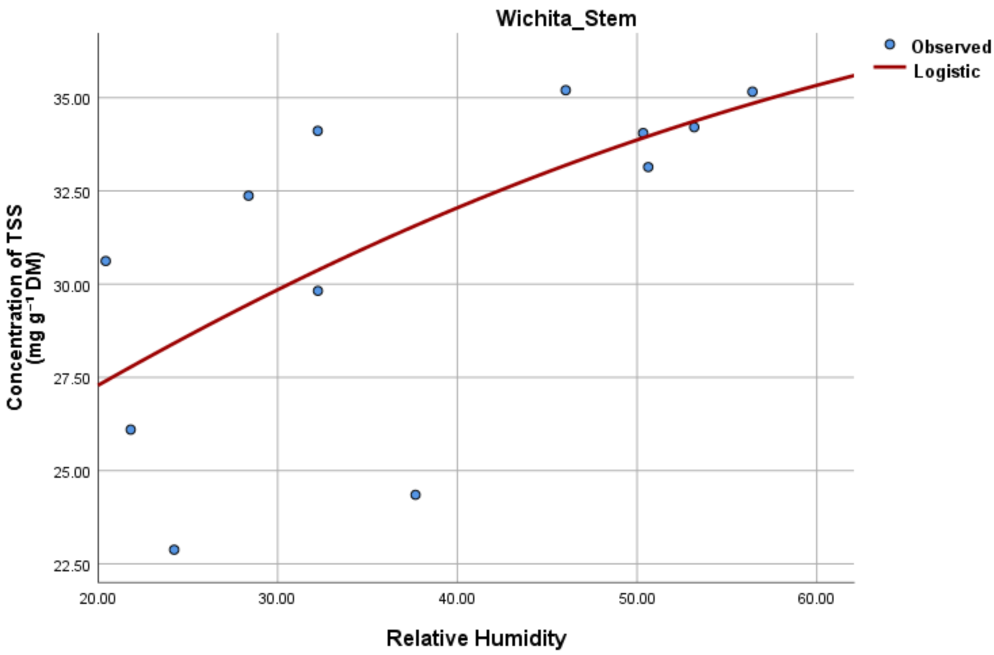

Figure 8. Correlation between relative humidity and TSS concentration in walnut stem of the Wichita variety.

The results are consistent with those mentioned by Furze et al. [6], who indicate that, in addition to the seasonal dynamics being different in each organ, each organ carries out different physiological and metabolic processes during the months of the year, given the climatic characteristics, as well as the foliar habit and the anatomy of the wood; on the other hand, they mentioned that stress factors such as drought could have an influence on it, as observed in this study, that there was a significant difference only for the Western variety, perhaps due to the different capacity to adapt to the changes in humidity present in the place between this and the Wichita variety that did not show a statistical difference.

Morales et al. [17] mentioned that there is a strong relationship between temperature and the behavior of stomata in carbohydrate-producing organs. When temperatures are very high, they tend to close to prevent water loss. Gahir et al. [33] commented that when there is an increase in atmospheric demand, that is, low relative humidity, plant species can close their stomata to prevent water loss. However, there are anisohydric species that maintain open stomata despite this atmospheric demand, which causes water stress and consequently affects their leaf water potential and physiological processes. Furthermore, within the same species, there may be varieties with different responses to these atmospheric changes.

Regarding the correlation between relative humidity and the concentrations of total soluble sugars (TSS) in the stems and roots of *C. illinoinensis* in the Western variety, as well as in the root of the Wichita variety, no statistically significant correlation was detected.

4. Conclusions

Environmental factors significantly influence TSS reservoirs in pecan trees, with varying effects on roots and stems, among varieties, and over time during a production cycle. Environmental factors, particularly temperature, and irradiation, profoundly influence TSS reservoirs in pecan trees. These carbohydrates are critical for tree survival, growth, and nut production, as they are used to support metabolic processes when photosynthetic supply is insufficient.

Temperature is the environmental factor with the greatest influence on TSS concentrations in pecan trees. Low temperatures in the spring damage developing tissues. Trees may respond to freeze stress by mobilizing sugars from roots and stems to the twigs to enhance cold tolerance.

Pecan varieties exhibit varying capacities for storage and tolerance to environmental stress. The Western variety showed a greater influence of environmental factors on its TSS storage capacity, while relative humidity had a greater impact on the Wichita variety.

Author Contributions

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

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Informed Consent Statement

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Data Availability Statement

Data is unavailable due to privacy or ethical restrictions.

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Conflicts of Interest

The authors declare no conflict of interest.

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