Carbon Partitioning Into Structural and Nonstructural Compounds in *Leucaena leucocephala* Seedlings as Affected by Water Stress

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ABSTRACT

On October 2001, carbon partitioning into nonstructural and structural carbon compounds was studied in *Leucaena leucocephala* (Lam.) de Wit. seedlings that were subjected to water stress treatments through a pot experiment. These treatments were moderate and severe water stress in which trees were watering every ten or 15 days, respectively, comparing with watering every other day in well water treatment. Nonstructural and structural carbon compounds in leaves, stem and roots were quantified and the proportion of each of dry matter was calculated as well as the ratio of nonstructural/ structural. Water stress increased nonstructural carbon compounds in the leaves at the expense of those in stem and roots with an opposite trend was found for structural carbon compounds. The ratio of nonstructural/ structural carbon compounds in leaves was significantly greater than that in either stem or roots. It was also decreased significantly with increasing the intensity of water stress. The results of the present study suggest modifying carbon partitioning as a mechanism by which trees cope with water stress.

INTRODUCTION

Leaf photosynthesis is generally the main source of carbon for growth and storage in other parts of the plant. Thus, factors affecting photosynthesis and partitioning of carbon play important roles in forest productivity. Growth of plants is constrained primarily through photosynthetic performance either directly, as in the case of insufficient illumination, or indirectly via water stress or nutrient shortage (Krner and Menendez-Riedl 1989). Water limits growth ultimately because water loss or transpiration is inextricably tied to carbon gain through photosynthesis (Fishcer 1980). However, the production of plant biomass is not only a function of carbon metabolism but is significantly determined by concurrent fluxes of water and nutrients and the process by which these resources are partitioned (Schulze 1986). Cumulative carbon assimilation and the subsequent distribution of dry matter among plant organs, therefore, are of prime importance when considering the effects of water stress on productivity and yield of any crop. Thus, it is essential to quantify how assimilate exported from the source leaves are modified when plants are subjected to limiting environmental factors. Assimilate export is partitioned between different sinks, and even within sinks where the incoming carbon is partitioned between different chemical constituents. All of the dry matter in a tree, whether in the form of major constituents such as cellulose and lignin or as minor extractives, is derived from the carbon and energy which is made available by photosynthesis (Kremers 1963). The concept of dry matter partitioning into structural and nonstructural compounds, therefore, may be a more appropriate approach to understand carbon partitioning within plants in relation to physiological activity of the organ or whole-plant as well as its morphological characteristics. Moreover, this new approach may eliminate the problem of determining both starch and sugars in small samples, particularly when their concentrations are low in plant material. Quantifying both structural and nonstructural carbon compounds simultaneously provides more information on absolute amounts and concentrations of both as well as the ratio of one to another in the investigated organ (or in the whole plant) which may offer a greater insight into physiological responses (Ibrahim 1995). This may differ from the conventional one which considers plant body as consisting of components of carbon that are divisible into two major components structural material and storage material, the latter including soluble sugars (de Wit *et al.* 1971; Warren-Wilson 1972; Fick *et al.* 1973 and Thornley 1976, 1977). It is also differed from the model for carbon partitioning in plant which was proposed by Farrar (1980) that adopting separating components of carbon into soluble, storage and structural components. Unfortunately, determination of these components requires many procedures and would be expensive and very time consuming.

The present study aims at quantifying structural and nonstructural carbon compounds as the dry weight components in leaves, stem and roots of *Leucaena leucocephala* (Lam.) de Wit. trees and to find out the relationship between both components under water stress conditions.

MATERIALS AND METHODS

Plant material

Leucaena leucocephala (Lam.) de Wit. seedlings were planted in pots filled with sandy loam soil mixed with peat moss with ratio of 2:1 (w:w). In October 2001, dried leaves, stems and roots of five months old *Leucaena leucocephala* (Lam.) de Wit. seedlings which were irrigated either every two or 10 or 15 days for three months (El-Juhany and Aref, 1999) were used to evaluate the effects of water stress on carbon partitioning.

Quantification of structural and nonstructural carbon compounds

The estimation of structural and nonstructural carbon compounds in the leaves, stems and roots of *Leuceena leucocephala* seedlings was carried out through the extraction procedure described by Browning (1967) in order to separate the two groups quantitatively.

Preparation of samples

The dried samples of the different tree components were ground using Wiley mill and screened through a set of sieves which ranged from 20 to 60-mesh, respectively.

Procedure

Organic solvent extraction

A sample (2-5 g) of particle size 40-60-mesh was weighed in a glass thimble and placed into a medium Soxhlet extractor (100 cm^3). 125 ml of 95% ethanol was placed in a 250-ml round bottom distillation flask. Extraction was carried out for 4-8 hours. After extraction, the thimble was removed from the extractor and placed upright on an absorbent tissue for approximately three days to air dry at the room temperature. The thimble and its contents were weighed and the ethanol soluble extractives were calculated.

Hot water extraction

The contents of the thimble (extracted previously with ethanol) were transferred to a 250-ml Pyrex glass beaker and 100 ml distilled water added, then the beakers were placed in a bath of boiling water and heated for 3 hrs. After hot water extraction, the contents of the beaker were filtered through a medium fast filter paper (Whatman No. 43) and washed with small portions of hot water then the filter paper and the precipitant placed in an Aluminum can and dried at 105°C ±1 to constant weight.

Calculations

The weight of structural carbon compounds (SCC) was obtained by subtracting the can weight from the oven dry weight of the can and its contents. The weight of the nonstructural carbon compounds (NSCC) is equal to the difference between the dry weight and SCC weight. The latter can also be obtained from the dry weight minus the sum of both ethanol and water extractives which represents the NSCC weight.

Statistical design and analysis

36 samples in three replicates were investigated using randomized complete block design in factorial arrangement and included treatments at three levels (WW, WS1 and WS2) and tree parts at three levels (leaves, stem and roots). The obtained data were analyzed using SAS (SAS Institute, 1987) General Model (GLM). Means of different factors were compared by L. S. D. test. Data were arcsine transformed when necessary.

RESULTS

Analysis of variance revealed that water stress treatment significantly affected carbon partitioning in *Leucaena leucocephala* seedlings. Quantity and concentration (percentage of dry matter) of both structural and nonstructural carbon compounds were significantly varied between trees due to water stress. They also varied among different tree parts.

Dry weight production of trees decreased with increasing the intensity of water stress ($P<0.0001$) and was greater in stem and roots than in leaves ($P<0.05$) (Table 1). The quantity of nonstructural carbon compounds (NSCC) showed a trend was similar to that of dry water where decreased steadily with increasing the intensity of water stress ($P < 0.0001$) and from 1.40 to 0.85 and 0.42 g in well water to moderate and severe water stress treatments, respectively. Structural carbon compounds (SCC) had similar trend ($P=0.0006$) where its quantity decreased from 1.50 to 1.01 and 0.80 g in the same direction (Table 1). The leaves of *Leucaena* trees had a quantity of NSCC (1.16g) was significantly greater than that in either stem (0.82g) or roots (0.68g) ($P< 0.006$). Structural carbon compounds (SCC) of the same seedling had an opposite trend to that of NSCC where decreased from 1.27 g in the roots to 1.40 g in the stem to 0.64 g in the leaves ($P< 0.0002$) (Table 1).

NSCC as a percentage of dry weight decreased steadily with increasing the intensity of water stress ($P<0.05$) and from 49.1% in well water treatment to about 46.3 and 36% in moderate and sever water stress treatments, respectively. An opposite trend was obtained for SCC concentration ($P<0.05$) where it increased from 50.9% in well water to about 53.7 and 64% in moderate and sever water stress treatments, respectively (Table 1).

As a percentage of dry weight, NSCC decreased from about 58% in the leaves to 39.2 and 34.2% in stem and roots ($P= 0.0002$), respectively. On the contrary, SCC percentage increased across the same direction and from 41.9% in the leaves to about 61 and 66% in stem and roots, respectively ($P= 0.0002$) (Table 1). There were treatment × tree parts interactions for the quantity of NSCC ($P<0.01$) and SCC ($P=0.0017$) and for the percentage of both ($P=0.013$) (Table 1) indicating changing the magnitude of treatment effects on quantity and percentage of nonstructural and structural carbon compounds in different tree parts (Figure 1).

The ratio of nonstructural/structural carbon compounds (NSCC/SCC) differed significantly as a result of water stress ($P<0.05$) (Table 1). The seedlings in severe water stress treatment had a NSCC/SCC ratio (0.56) was lower compared with that of the seedlings in well water treatment (1.4). While the same ratio of the seedlings in moderate water stress treatment had a value

Table 1. Partitioning of dry weights of leaves, stem and roots of *Leucaena leucocephala* trees into nonstructural (NSCC) and structural (SCC) carbon compounds (quantities and percentages of dry weight) and the ratio between them (NSCC/SCC) under water stress treatment. Treatments were well water, moderate and severe water stress in which trees were watering every other day, ten and 15 days, respectively. Each value is a mean of nine observations.

Source of variation	Dry weight (g)	NSCC (g)	SCC (g)	NSCC (%)	SCC (%)	NSCC/SCC ratio
Treatments:						
Well water	*2.91^{a}	1.40^{a}	1.50^{a}	49.10^{a}	50.90^{b}	1.4^{a}
Moderate water stress	1.85^{b}	0.85^{b}	1.01^{b}	46.34^{a}	53.66^{b}	1.01^{ab}
Severe water stress	1.22^{c}	0.42^{c}	0.80^{b}	36.06^{b}	63.95^{a}	0.56^{b}
Probability level	$P< 0.0001$	$P< 0.0001$	$P= 0.0006$	$P< 0.05$	$P< 0.05$	$P< 0.05$
Tree parts:						
Leaves	1.80^{b}	1.16^{a}	0.64^{b}	58.08^{a}	41.92^{b}	2.21^{a}
Stem	2.22^{a}	0.82^{b}	1.40^{a}	39.18^{b}	60.82^{a}	0.67^{b}
Roots	1.96^{ab}	0.68^{b}	1.27^{a}	34.24^{b}	65.77^{a}	0.65^{b}
Probability level	$P< 0.05$	$P< 0.006$	$P= 0.0002$	$P= 0.0002$	$P= 0.0002$	$P< 0.0001$
Probability level of treatment × tree parts interaction	$P= 0.007$	$P< 0.0099$	$P= 0.0017$	$P< 0.05$	$P< 0.05$	n. s.

*Means followed by the same superscript small letter within each box are not significantly different at $P<0.05$.

(1.02) did not differ from those of the trees in the other two treatments (Table 1). NSCC/SCC ratio also varied significantly between tree parts ($P<0.0001$). The ratio was 2.21 in the leaves compared with 0.67 and 0.65 in stem and roots, respectively (Table 1).

DISCUSSION

Under water stress, Leucaena trees in the present study allocated more nonstructural carbon compounds to their leaves and less structural carbon compounds to their stems and roots. Increasing carbon allocation to the roots of the roots of water-stressed trees was due to their relatively large investment of biomass in structures necessary to absorb nutrients and water or to protect themselves against adverse conditions Konings (1989).

Water-stressed seedlings had less structural and nonstructural carbon compounds in the different organs compared with the well-watered trees. This was expected, as both structural and nonstructural carbon are components of total dry matter of the tree and highlights the large contribution of structural carbon compounds to dry matter accumulation below-ground under limited water supply.

Increasing the concentration of structural carbon compounds in dry matter of any organ indicates the accumulation of structural compounds at the expenses of nonstructural carbon compounds. Water-stressed trees had lower levels of structural carbon compounds, as a proportion of dry weight in leaves and higher levels in roots. This result concurs with the results of Ibrahim *et al.* (1997) who found that the proportion of nonstructural carbon compounds increased from 59 in leaves of well-watered poplar trees to 63% in leaves of drought-stressed trees. Increasing the concentration of nonstructural carbon compounds in the leaves of water-stressed trees at the expense of structural carbon compounds may be explained as osmotic adjustment to maintain turgour. Accumulation of nonstructural carbon compounds in the leaves of water-stressed trees can be also resulted from a slow-down in translocation. A number of workers have reported that water stress decrease translocation (*e.g.* Weibe and Wihrheim 1962, and Plaut and Reinhold 1965). Moreover, Roberts (1964) observed that water stress inhibited movement of ^{14}C-photosynthate from leaves of potted yellow poplar seedlings; distance and velocity as well as amount of transport were lowered. Decreasing the concentration of nonstructural carbon compounds in the roots of water-stressed trees may support this interpretation. Increasing the concentration of nonstructural carbon compounds in the leaves of water-stressed trees through loss of water could be another possible interpretation (*e.g.* Turner and Jones 1980). Increasing the concentration of structural carbon compounds in the roots of water-stressed trees, on the other hand, follows the increased allocation of carbon to the roots as a strategy for acclimation to water stress. According to Kramer (1980) the plant develops the ability to maintain higher water status by lessening the loss and increasing the uptake of water.

Thus, increasing partitioning of structural carbon compounds to roots will increase root growth and in turn increase water uptake.

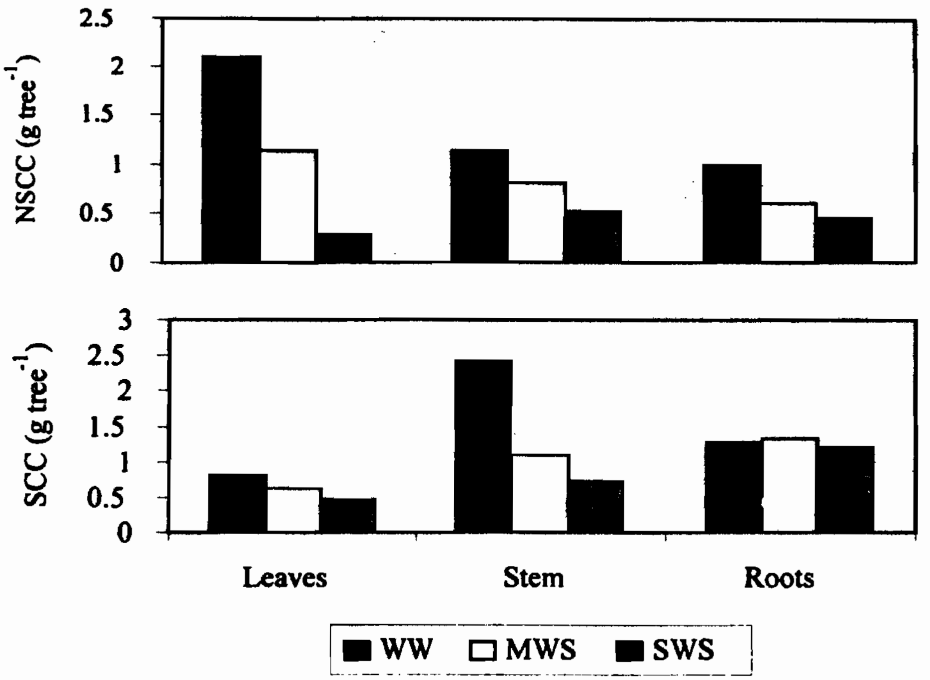

Figure 1. Quantity of nonstructural (NSCC) (above) and structural carbon compounds (SCC) (below) in leaves, stem and roots of *Leucaena leucocephala* seedlings as affected by water stress. The seedlings were watering every other day in well water treatment (WW) and every ten and 15 days in moderate (MWS) and severe (SWS) water stress treatments, respectively. Values are means of three determinations.

Nonstructural /structural carbon compounds ratio

Decreasing the ratio of nonstructural/structural carbon compounds with increasing the intensity of water stress is a result of decreases of about 39 and 65% in the quantity of nonstructural carbon compounds in moderate and severe water stress treatments, respectively. While the decreases the quantity of structural carbon compounds in the same treatments were only 34 and 36%.

On the other hand, increasing this ratio in leaves by more than three times as much as that in roots was a consequence of decreasing concentrations of structural carbon compounds in leaves and increased it in roots at the expense of nonstructural carbon compounds due to water stress. Similar results were obtained for poplar trees under water stress (Ibrahim 1995).

CONCLUSION

The results of the present study show changing carbon chemistry in different tree parts due to water stress. Increasing nonstructural carbon in leaves at the expense of that in stem and roots and conversely increasing structural carbon manly in root (and to a less extent to stem) at the expense of that in leaves may add more understanding of the performance of plants under water stress. It can also employed to explain the morphological modifications in plants under different environmental stresses.

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الملخّص العربي

توزيع الكربون في أشجار اللوسينا إلى مركبات بنائيّة و غير بنائيّة تحت تأثير الإجهاد المائي

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في أكتوبر ٢٠٠١ درس توزيع الكربون في شتلات اللوسينا إلى مركبات كربونيّة بنائيّة و غير بنائيّة التي تعرّضت لمعاملات إجهاد مائي خلال تجربة أصص. هذه المعاملات كانت إجهاد مائي متوسط و شديد حيث رويت فيهما الشتلات كل عشرة أيام و كل ١٥ يوماً، على التوالي بالمقارنة مع الري كل يومين كري كاف. و قد قدرت كمية و نسبة المركبات الكربونيّة البنائيّة و غير البنائيّة في المادة الجافّة لأوراق و ساق و جذور الشتلات، كما حسبت النسبة بين المركبات الكربونيّة غير البنائيّة و البنائيّة. و قد أظهرت النتائج أنّ الإجهاد المائي سبّب زيادة في كميّة المركبات الكربونيّة غير البنائيّة على حساب كميها في الساق و الجذور مع اتجاه عكسي للمركبات الكربونيّة البنائيّة. و كانت نسبة المركبات الكربونيّة غير البنائيّة / المركبات الكربونيّة البنائيّة في الأوراق معنوياً أعلى من تلك التي في الساق أو الجذور. كما انخفضت هذه النسبة معنوياً مع زيادة شدة الإجهاد المائي. و تدل نتائج هذه الدراسة على أنّ تحوّر توزيع الكربون كآليّة بها تتعامل الأشجار مع الإجهاد المائي.