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Water contents of wood of tropical deciduous forest species during the dry season

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RESUMEN. Se determinaron tres características de la madera: el contenido máximo de agua, el contenido relativo de agua y el agotamiento absoluto de agua, para 41 especies leñosas de bosque tropical caducifolio. Se encontró una correlación significativa entre el contenido máximo de agua y el peso específico de la madera. También se encontraron correlacionados el agotamiento de agua (por peso) con el peso específico de la madera. Se encontró que, con base en el volumen, los árboles caducifolios usan más agua del tallo que los árboles que almacenan agua. Los datos se discuten en relación con la frecuencia de diferentes hábitos y formas de vida de las plantas en esta vegetación.

ABSTRACT. The maximum water content, the relative water content and the water depletion of wood were studied in 41 species of a tropical deciduous forest during the dry season. There is a significant correlation between the maximum water content and the specific wood weight. Also, water depletion per wood weight is significantly correlated with the specific wood weight. On a wood volume basis, deciduous trees use more stem water than water-storing trees. These data are discussed with respect to the dominance of life forms in this forest type.

Water storage can be of considerable significance for the water relations and the water use of trees. This has been most clearly demonstrated for tall trees of *Pseudotsuga menziesii*, which have sufficient stored water available to avoid severe stress during a dry summer period in a temperate climate zone (Waring and Running, 1978). Seasonal and diurnal changes of stem circumference have been observed in many tree species and have been discussed in terms of water use during periods when transpiration exceeds

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water uptake (Hinckley *et al.*, 1978). This may lead to relative water deficits of more than 40% (Gibbs, 1958). Considering the poor elastic properties of wood, this implies embolism ocurrence (Zimmermann and Milburn, 1982).

Most observations on the use of stored water in woody species have been made in forests of temperate latitudes where severe deficits occur in late winter (Tranquillini, 1982; Kozlowski, 1982). In contrast, very little is known of water depletion from wood of tropical deciduous forest plants, where the dry season may extend for over six months. Daubenmire (1972) reported that the stem shrinkage during the dry season exceeded the net annual growth increments of several deciduous tropical species, but no reports are known to us where the depletion of water has been measured in wood of tropical dry forest species (Kozlowski, 1982; Hinckley *et al.*, 1978). Thus, we surveyed relative water contents and water use of woody species, in the middle of the dry season, in a tropical deciduous forest including a variety of habits and growth forms. Since our intention was to characterize life forms and not particular species, we approached the problem not by taking many replicates per species, but rather by sampling as many species as possible per life form.

MATERIALS AND METHODS

Research was conducted at the Estación de Biología Chamela, located 122 km northwest of Manzanillo on the west coast of mainland Mexico (19°30'N, 105°03'W). The climate is Köppen type Aw, with an average annual rainfall of 748 mm and six to seven months drought (Bullock, 1986). The vegetation, a tropical deciduous forest (*sensu* Rzedowski, 1978; Lott *et al.*, 1987), is dominated by drought deciduous trees, but evergreen species, arborescent succulents and water-storage plants co-occur. The Chamela forest is very diverse in species and life forms; the flora, of 758 angiosperm species, is about equally divided among herbs, shrubs, vines and trees, plus more than 25 epyphytes (Lott, 1985 and personal communication).

During the dry season of 1984, when most trees had no leaves, wood samples were collected during midday from plants growing on a southeast-facing slope in a dense forest. Hilltops and canyon bottoms were avoided. Samples were also collected from trees growing close to the station which were regularly irrigated. The following 41 species were studied, including various life forms and a large range of specific wood weights:

Deciduous trees with dense wood:
Apoplanesia paniculata, *Caesalpinia platyloba*, *C. pulcherrima*, *Haematoxylum brasiletto*, *Lysiloma microphylla* (Leguminosae); *Exostema caribaeum* (Rubiaceae); *Guapira* sp. (Nyctaginaceae); *Heliocarpus pallidus* (Tiliaceae); *Lippia mcvaughii* (Verbenaceae); *Ruprechtia fusca* (Polygonaceae); *Thouinia paucidentata* (Sapindaceae); *Trichilia trifolia* (Meliaceae).

Decidous trees with low-density wood:
Amphipterygium adstringens (Julianiaceae); *Bursera instabilis* (Burseraceae); *Cnidoscolus spinosus*, *Jatropha standleyi* (Euphorbiaceae); *Cochlospermum vitifolium* (Cochlospermaceae); *Ficus cotinifolia* (Moraceae); *Ipomoea wolcottiana* (Convolvulaceae); *Tabebuia chrysantha* (Bignoniaceae).

Evergreen and heliophile trees:
Coccoloba liebmannii (Polygonaceae); *Forchhammeria pallida* (Capparidaceae); *Jacquinia pungens* (Theophrastaceae).

Vines:
Entadopsis polystachya, *Mimosa micheliana* (Leguminosae); *Marsdenia astephanoides*, *Gonolobus* sp. (Asclepiadaceae); *Euphorbia colletioides* (Euphorbiaceae); *Gouania rosei* (Rhamnaceae); *Ipomoea bracteata* (Convolvulaceae); *Serjania brachycarpa* (Sapindaceae); *Lasianthea* sp. (Compositae); *Aristolochia taliscana* (Aristolochiaceae); *Hiraea reclinata* (Malpighiaceae).

Water-storage plants:
Jacaratia mexicana (Caricaceae); *Philodendron warscewiczii* (Araceae); *Spondias purpurea* (Anacardiaceae).

Arborescent succulents:
Cephalocereus purpusii, *Opuntia excelsa*, *Pachycereus pecten-aborigenum*, *Stenocereus* sp. (Cactaceae) (representing all such species present in this forest).

The samples were two centimeters in lenght. For trees, cores were taken with an increment borer out of the sapwood at 1.3 m above ground. The cambium and bark were removed from the core and the core was stored in a small glass vial within seconds after removal from the tree. For vines, longitudinal sections of stem were cut, taking care to cut the upper and lower ends simultaneously; the bark was peeled off before storing the sample. After measuring the fresh weight and the volume, the samples were allowed to saturate for 24 hrs with water entering the samples from one end only, such that air bubbles were not trapped in the wood. The adequate filling of the xylem vessels was checked for a number of samples by microscopic observation. The samples were weighted again to obtain the saturated weight, and subsequently were dried for 24 hrs at 80°C for assessment of the dry weight.

We are aware that the method of taking wood samples with an increment borer may create errors due to compression of the sample during coring or expansion of the sample following extraction from the trunk; such errors would be largest in succulents and water-storage plants. They may cause an underestimate of the fresh weight and an overestimate of the saturated weight. Therefore, water deficits may be overestimated in low density wood. In dense wood the core may become heated during removal; this could affect the fresh weight of the sample although the time for evaporating water from the fresh sample was very short. Again, this error would tend to overestimate water deficits in dense woods. We did not distinguish differences in the amount of parenchyma between species.

The relative water content (RWC) of wood was calculated from the fresh weight (FW), dry weight (DW), and saturated weight (SW) of the samples: RWC = (FW-DW) / (SW-DW). The maximum water content (MWC) was calculated from the saturated weight and dry weight: MWC = (SW-DW) / DW. The specific wood weight (SWW) was calculated from the dry weight and the sample volume (V): SWW = DW / V. The use of stored water was calculated as the absolute water depletion per dry weight or volume: AWD = (SW-FW) / DW or (SW-FW) / V. Differences between life form/habit groups were tested by analysis of variance using the SPSS / PC statistical package.

Results and discussion

The maximum water content (table 1) is significantly correlated with the inverse of the specific wood weight:

$$\text{MWC} = -0.93 + 1.02 / \text{SWW};\ r^2 = 0.98;\ P < 0.01$$

The very close correlation suggests that water storage capacity could be estimated very accurately from specific wood weight for a broad range of wood types without going trough resaturation experiments. Species are different by a factor of 50 with respect to water storage, *Philodendron warscewiczii* having a maximum water content of almost 17 g H_2O g^{-1} wood dry weight versus 0.34 g H_2O g^{-1} in the dense wood of *Caesalpinia platyloba*.

During the dry season the relative water content of deciduous trees and vines decreased to 70-75%. It was significantly higher in evergreen trees (*i. e.* 94%) and it did not decrease at all in the arborescent succulents. The relative water content is significantly correlated with the logarithm of the maximum water content, but the correlation is not as close:

$$\text{RWC} = 75.2 + 6.10 * \ln(\text{MWC}),\ r^2 = 0.41,\ P < 0.05$$

TABLE 1. Specific wood weight (SWW; g cm^{-3}), maximum water content (MWC; g H_2O g^{-1}), relative water content (RWC; %), and absolute water depletion (AWD; g H_2O g^{-1} and g H_2O cm^{-3}) of different plant life forms and habits. In each column, values differing significantly ($P < 0.01$) are followed by different letters

	Number of species	*Specific wood weight*	*Water content maximum*	*Water content %*	*Absolute water depletion per weight*	*Absolute water depletion per volume*
Deciduous trees						
high-density wood	12	0.67 a	0.67 a	69.5 a	0.20 a	0.13 a
low-density wood	8	0.34 b	2.15 b	71.0 a	0.62 c	0.21 b
Vines	11	0.49 c	1.26 a	75.4 a	0.31 b	0.15 c
Evergreen trees	3	0.65 a	0.84 a	94.0 b	0.05 a	0.03 d
Water-storage plants	3	0.11 d	11.03 c	87.0 b	1.24 d	0.13 a
Arborescent succulents	4	0.26 d	3.24 d	99.0 c	0.00 a	0.00 d

The scatter of this correlation is due to deciduous trees of low density wood having lower relative water contents and evergreen trees having higher water contents than the regression line. The high relative water content of evergreen and heliophile trees indicates that they may be reaching some water which is not accessible to deciduous trees (see also Fanjul and Barradas, 1985).

There is a correlation between the logarithm of the maximum water content and the absolute water depletion, excluding the arborescent succulents:

$$\text{AWD} = 0.31 + 0.39 * \ln(\text{MWC}),\ r^2 = 0.88,\ P < 0.01$$

All the cacti were fully hydrated. The water depletion is also small in evergreen trees, which again indicates access to water. Water-storage plants use two to four times as much water per wood weight as deciduous trees or vines. It is quite interesting to note that the water use per wood volume is identical for deciduous trees with dense wood and water-storage plants (0.13 g H_2O cm^{-3}), and it is much higher in deciduous trees with low-density wood (0.21 g H_2O cm^{-3}).

The effective water use from stem water may be smaller than that indicated in table 1, since irrigated trees do not show maximum water contents (as defined in this study) in their wood, and since cavitation may occur in trees even if watered. Only 11 irrigated species were sampled. When compared to the watered counterpart, deciduous tree species with dense wood (six species) depleted only 0.08 g H_2O g^{-1} (0.05 g H_2O cm^{-3}), less than half the value in table 1. Deciduous trees with low-density wood (three species) depleted 0.43 g H_2O g^{-1} which is about as much as found in water-storing trees of *Spondias purpurea* (0.57 g H_2O g^{-1}) when compared to watered trees. On a volume basis, deciduous trees deplete their stems almost three times as much as water-storage plants (0.15 g H_2O cm^{-3} in deciduous trees *versus* 0.06 g H_2O cm^{-3} in water-storage plants).

Cavitation and use of stored water from the stem seems to be a characteristic feature in the deciduous dry forest. Apparently, species which are very conservative in their water use, such as arborescent succulents, are less dominant in this vegetation with respect to species number and cover (Lott *et al.*, 1987) than species which use water rather extensively. It is likely that their stems contain a large proportion of living parenchyma wich cannot lose water without serious damage. The dominant vegetation of deciduous trees and vines uses more water per volume than water-storage plants, which again indicates that those species which are very conservative in their water use are less dominant in this vegetation and climate than those species which utilize water rather extensively.

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