BIOLOGIA PLANTARUM 37 (2): 291-295, 1995

BRIEF COMMUNICATION

Seasonal differences in nitrogen storage in deciduous and evergreen species of a tropical dry forest

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Abstract

Reserves of twig nitrogen of drought-deciduous species changed seasonally and provided some of the nitrogen required for canopy reconstruction after drought relief. By contrast, in evergreen species, nitrogen mobilization from old leaves and use in expanding leaves occurred simultaneously at the time of leaf exchange and twig nitrogen remained constant.

Key words: Beureria cumanensis, Capparis aristiguetae, Coursetia arborea, Lonchocarpus dipteroneurus, Morisonia americana, Pithecellobium dulce

Tropical dry forests are dominated by woody drought-deciduous species (DC) in coexistence with few evergreen species (EG). In DC, with a seasonal development, storage of resources should support flowering and fruit set after leaf fall as well as construction of new leaves when rains start. Thus, they should set aside stores before leaf fall as insurance to meet demand when resources acquisition is cut down by drought (Bloom *et al.* 1985). Conversely, conservancy of resources in a long-lived EG leaf is *per se* an adaptative feature to nutrient-poor environments (Monk 1966, Mooney and Hay 1983, Mooney and Rundel 1979). Nitrogen is costly and plants maximize benefits by optimizing its investment (Field 1983). This also may be achieved by efficient mobilization mechanisms to prolong its use. Nitrogen storage and translocation is common in woody plants (Taylor 1967, Chapin and Kedrowski 1983). By contrast, lipids are also expensive compounds and despite of this, mobilization from leaves to storage does not seem to occur (Bloom *et al.* 1985). This

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Received 14 June 1994, *accepted* 17 September 1994.
Acknowledgements: Financial support was provided by Decanato de Investigaciones-USB (DI-CB-73-94). Technical help by Mr. T. Perez and Mr. M. Edreida in the laboratory and in the field and to Dr. D. Henriquez for correcting the English grammar is sincerely thanked.

study examines the seasonal levels of twig reserves of nitrogen in a dry mass and compare them to lipids reserves in DC and EG species in a tropical forest of Venezuela. Crude fiber to protein ratios and glucose equivalents (GE) were used to characterize leaves and twigs, respectively.

The study site was a seasonal forest located in Charallave, Venezuela (10 °N, 67 °W, 400 m elevation) with a mean rainfall of 900 mm falling from May to October. The species were four DC (*Coursetia arborea* Leguminosae, *Lonchocarpus dipteroneurus* Leguminosae, *Pithecellobium dulce* Leguminosae and *Beureria cumanensis* Boraginaceae) with leaf longevities from 6 to 9 months and remaining leafless during the dry season. The two EG species (*Capparis aristiguetae* and *Morisonia americana* both Capparidaceae) exchange leaves each 12 months. More details about ecophysiology of these species could be found elsewhere (*e.g.* Sobrado 1986, 1991,1992, 1993, 1994).

Samples were taken from the upper part of the plant and from three individuals per species. Leaves were sampled at full maturity stage and just before abscission. Water contents of leaves and twigs were calculated as the difference between fresh and dry mass per unit dry mass from samples collected during wet and dry seasons. Twig parts were sampled on four dates (wet, wet-dry transition, dry and following wet seasons) from the distal section by considering that they should reflect more accurately short term nitrogen and lipids storage-remobilization dynamics (Mooney *et al.* 1992). The chemical analyses were performed after plant material was oven dried at 80 °C, ground and homogenized. Proteins were measured by micro-Kjeldahl analysis and nitrogen (N) contents assessed by dividing that value by 6.25 (Williams 1984). Crude lipids estimates were obtained gravimetrically on soluble diethyl ether extracts (Williams 1984). The energy contents were evaluated as heats of combustion with a *Parr Adiabatic Calorimeter Model 1241* (*Parr Instruments Co.*, Moline, USA). Leaf crude fiber was determined after digesting in both, acid and basic media (Williams 1984). Twig glucose equivalents were calculated from nitrogen and ash-free combustion heat (Williams *et al.* 1987).

Leaf and stem water contents underwent larger depletion during drought in DC than in EG (Table 1). This relates to water sources used by EG during drought which are not available to DC (Sobrado and Cuenca 1979). Twig glucose equivalents were slightly different between DC and EG species indicating comparable chemical composition and carbon cost of wood from both plant groups (Table 1).

Fiber to protein ratio was higher in EG (2.3 to 2.5) than in DC (0.5 to 1.4) as shown in Table 1. This is a typical characteristic of sclerophyll evergreen leaves with low specific leaf area (Loveless 1961, 1962). Despite the larger protein contents in mature DC leaves, the proteins were diminished before leaf fall by 68 % in *C. arborea*, 48 % in *L. dipteroneurus*, 60 % in *P. dulce* and 31 % in *B. cumanensis*. In EG having longer leaf life-spans, protein content decreased by 20 % before abscission. Thus, both DC and EG resorbed part of their nitrogen from leaves before they were shedded. The constancy between seasons of twig N in EG was remarkable, while reserves in DC were significantly increased with leaf fall (Fig. 1a). The increments were higher in *C. arborea* (61 %) and *P. dulce* (56 %) compared to *L. dipteroneurus* (28 %) and *B. cumanensis* (21 %). This trend is observed in tropical

Table 1. Leaf crude-fiber and protein content, and twig glucose equivalents (GE) measured in samples taken during the rainy season on three trees per species. Water contents [g(H_2O) g^{-1}(d.m.)] were measured during rainy (wet) and drought (dry) seasons on ten replicates per species. Least statistically significant differences (LSD) at $P < 0.05$ are indicated for each parameter.

Species	Leaves				Twigs		
	Fiber [g m^{-2}]	Protein [g m^{-2}]	Water [g(H_2O) g^{-1}(d.m.)]		GE [g(glu) g^{-1}(d.m.)]	Water [g(H_2O) g^{-1}(d.m.)]	
			Wet	Dry		Wet	Dry
Deciduous							
C. arborea	9.2	8.5	1.78	1.04	1.20	1.20	0.59
L. dipteroneurus	9.8	8.5	2.36	1.14	1.19	1.19	0.50
P. dulce	17.3	11.9	1.71	0.99	1.23	0.92	0.45
B. cumanensis	7.9	16.9	1.98	0.91	1.23	1.41	0.76
Evergreen							
C. aristiguetae	42.5	19.2	0.88	0.80	1.19	0.90	0.87
M. americana	48.7	18.4	1.12	1.09	1.18	0.89	0.90
LSD	7.2	8.4	0.76	0.41	0.03	0.38	0.30

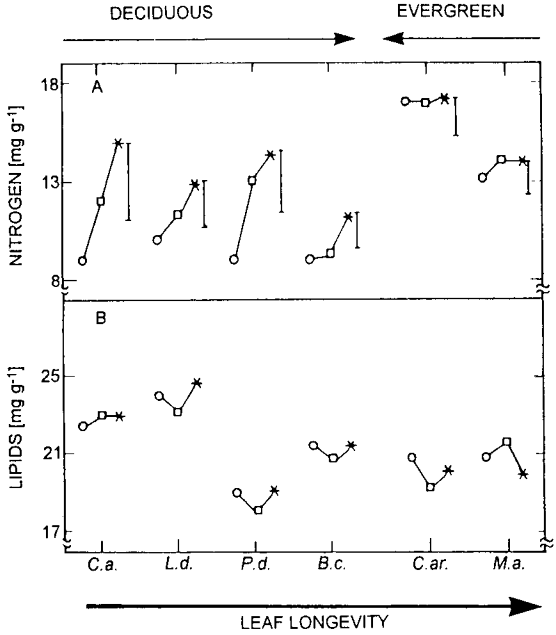

Fig. 1. Twig nitrogen (*A*) and lipid (*B*) content as a function of leaf longevity in four deciduous (*C.a.* - *C. arborea*, *L.d.* - *L. dipteroneurus*, *P.d.* - *P. dulce* and *B.c.* - *B. cumanensis*) and two evergreen (*C.ar.* - *C. aristiguetae* and *M.a.* - *M. americana*) species. Values are the mean of samples from three trees per species taken during wet (*circles*), wet-dry transition (*squares*) and dry (*asterisks*) seasons. Bars indicate the least significant difference at $P < 0.05$ for each species.

deciduous vines as well (Mooney *et al.* 1992). At the time of emergence of new leaves in DC, twig N was curtailed to comparable values [8 - 9 mg g^{-1}(dry mass)] of that from the previous wet season. Such reduction may reflect N mobilization to growing leaves. Twig non-structural carbohydrates reserves of DC are replenished by surplus during the wet season as well as by retranslocation on drought onset, but seasonal changes of EG are slight (Mooney and Hay 1983, Olivares 1987). Consistent with this carbon isotopic composition reveals that during early stages of leaf development, carbohydrates are imported from stored reserves (Sobrado and Ehleringer unpublished). Conversely, twig lipids remained constant over seasons in both DC and EG (Fig. 1b).

In conclusion, reserves of twig N in DC provided some amount of nitrogen necessary for reconstruction of the canopy after drought relief. At the time of EG leaf exchange, N mobilization from old leaves and use in expanding leaves occurred simultaneously and seasonal differences in twig N were not found. Despite their contrasting phenologies, both deciduous and evergreen species were essentially preservative of their nitrogen resources.

References

Bloom, A.J., Chapin III, F.S., Mooney, H.A.: Resource limitation in plants. An economic analogy. - Annu. Rev. Ecol. Syst. **16**: 363-392, 1985.

Chapin III, F.S., Kedrosky, R.A.: Seasonal changes in nitrogen and phosphorus fractions in autumn retranslocation in evergreen and deciduous taiga trees. - Ecology **64**: 367-391, 1983.

Field, C.: Allocating leaf nitrogen for the maximization of carbon gain: leaf age a control of the allocation program. - Oecologia **56**: 341-347, 1983.

Loveless, A.R.: A nutritional interpretation of sclerophylly based on differences in the chemical composition of sclerophyllous and mesophytic leaves. - Ann. Bot. **25**: 168-184, 1961.

Loveless, A.R.: Further evidence to support a nutritional interpretation of sclerophyly. - Ann. Bot. **26**: 551-561, 1962.

Monk, C.D.: An ecological significance of evergreeness. - Ecology **47**: 504-505, 1966.

Mooney, H.A., Chu, C., Bullock, S.H., Robichaux, R.: Carbohydrate, water and nitrogen storage in vines of a tropical deciduous forest. - Biotropica **24**: 134-139, 1992.

Mooney, H.A., Hay, R.: Carbohydrate storage cycles in two Californian mediterranean-climate trees. - Flora **162**: 295-304, 1973.

Mooney, H.A., Rundel, P.W.: Nutrient relations of the evergreen shrub, *Adenostoma fasciculatum*, in the California chaparral. - Bot. Gaz. **149**: 109-113, 1979.

Olivares, E.: [Water and nutritional relationships in woody species, with contrasting phenological patterns, from a tropical deciduous forest]. - Ph. D. Thesis. IVIC, Caracas 1987. [In Spanish].

Sobrado, M.A.: Aspects of tissue water relations and seasonal changes in leaf water potential components in evergreen and deciduous species coexisting in a tropical dry forest. - Oecologia **68**: 413-415, 1986.

Sobrado, M.A.: Cost-benefit relationships in deciduous and evergreen leaves of a tropical dry forest. - Funct. Ecol. **5**: 608-616, 1991.

Sobrado, M.A.: The relationship between nitrogen and photosynthesis in relation to leaf age in a tropical xerophytic tree. - Photosynthetica **26**: 445-448, 1992.

Sobrado, M.A.: Trade-off between water transport efficiency and leaf-span in a tropical dry forest. - Oecologia **96**: 19-23, 1993.

Sobrado, M.A.: Leaf age effects on photosynthetic rate, transpiration rate and nitrogen content in a tropical dry forest. - Physiol. Plant. **90**: 210-215, 1994.

Sobrado, M.A., Cuenca, G.: Water use in deciduous and evergreen species from a tropical dry forest in Venezuela. - Acta Cient. Ven. **30**: 302-308, 1979.

Taylor, B.K.: Storage mobilization of nitrogen in fruit trees: A review. - J. aust. Inst. agr. Sci. **33**: 25-29, 1967.

Williams, K., Percival, F., Merino, J., Mooney, H.A.: Estimation of tissue construction coasts from heat of combustion and nitrogen content. - Plant Cell Environ. **10**: 725-734, 1987.

Williams, S.: Official Methods of Analysis. - AOAC, Arlington 1984.