ALLOCATION OF ENERGY RESOURCES IN THE FRESHWATER ANGIOSPERMS *VALLISNERIA AMERICANA* MICHX. AND *POTAMOGETON PECTINATUS* L. IN FLORIDA.

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ABSTRACT: Vallisneria americana *Michx. and* Potamogeton pectinatus *L. were collected over a four-year period in the winter and summer from a spring-fed river in central Florida and analyzed for proximate constituents (dry weight, ash, protein, soluable carbohydrate, lipid, fiber and lignin) from which energy content was determined. The stolon of the freshwater species did not store carbohydrate seasonally, and kiloJoules per g dry weight were substantially lower in both winter and summer samplings in blades and stolons than reported for seagrasses of the same taxonomic families. Although leaf biomass increased significantly in the summer, a similar increase was not noted for the stolon again in contrast to their marine counterparts. Blade fiber levels in* V. americana *were higher (to 34%) than that reported for seagrasses or even some terrestrial grasses, suggesting that the broad, linear blades have adapted to high water movement by allocation of a large part of their organic content to structural carbohydrate.*

MONOCOTYLEDONS of the families Hydrocharitaceae and Potamogetonaceae occur as submerged angiosperms in both freshwater and marine systems (Cronquist 1981). Thus similarities and differences might be expected in species found in the two aquatic environments. Seagrasses show distinct allocation of energy at different times of the year to various plant organs (Dawes and Lawrence 1980; 1983). Information on energy allocation in freshwater angiosperms is more limited as shown in the reviews by Boyd and Scarsbrook (1975) and Little (1979). Boyd (1970) reported the levels of kilocalories per g dry weight for three species of *Potamogeton* but did not distinguish among plant components or seasonal variation. Donnermeyer and Smart (1985) averaged the energy levels for the different plant components for the entire year for *Vallisneria americana* Michx. from the northern U. S. and presented seasonal proximate composition and relative sizes of the plant components.

The seasonal study presented here involved the rooted aquatic angiosperms *Vallisneria americana* and *Potamogeton pectinatus* L., which are common submerged plants in northern and central Florida streams (Godfrey and Wooten 1979). We compare the seasonal composition and energy levels of the two species collected at the same site with Floridia seagrasses from the same taxonomic families, and also *V. americana* in Florida with populations from the northern U. S.

MATERIALS AND METHODS—Summer and winter collections were made from January, 1982 to August, 1985. At each collection, entire plants of *Vallisneria americana* and *Potamogeton pectinatus* were collected from about 1 m depth of water in the Juniper Run approximately 10 km downstream from the spring source of the Ocala National Forest (29° N Lat. 82° W Long.), Florida U. S. A. Eight plants from one population of each species were taken to the laboratory and cleaned of epiphytes and sand. *Vallisneria americana* was divided as described by Donnermeyer and Smart (1985) into the broad (1-2 cm) blades, a 2 cm section of stolon on each side of the shoot, and the fleshy root stock and roots if distinct. *Potamogeton pectinatus* was divided into the erect photosynthetic portion consisting of a green stem with the narrow (1-3 mm) linear leaves, a 2 cm section of stolon on each side of the stem, and the fleshy base or root stock.

The roots of all plants were pooled. The plant samples were weighed, dried under vacuum over concentrated sulphuric acid at room temperature and reweighed. After grinding the dried tissue to a powder (Wiley Micromill, #40 mesh), it was analyzed for ash, protein, soluble carbohydrate, and lipid, and energy levels calculated as described by Dawes and Lawrence (1980; 1983) and Brody (1964). Insoluble carbohydrate was estimated by difference. Fiber and lignin were determined according to Goering and van Soest (1970) using the acid detergent method to remove hemicelluloses. All constituents are expressed as percent dry weight. Standard one and two way analyses (ANOVA's) were used to ascertain statistical significance ($P < 0.05$).

TABLE 1. Proximate constituents as percent of dry weight and energy levels (kiloJoules g dry wt^{-1}) from winter and summer collections over a 4-yr period of *Vallisneria americana* growing in Juniper River, Florida. $N = 8 \pm 1S.D.$

	Blade		Stolon		Roots		Root Stocks	
	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer
Dry Wt (%)	11 ±3.1	12 ±3.4	9 ±3.6	11 ±5.2	9 ±3.2	11 ±4.7	12 ±1.0	20 ±9.2
Ash (%)	24 ±9.4	25 ±10.4	24 ±9.7	23 ±9.5	28 ±10.1	28 ±9.2	25 ±15.2	18 ±11.3
Sol Carbo. (%)	26 ±11.6	24 ±5.4	30 ±17.1	32 ±9.7	28 ±13.0	18 ±1.1	28 ±10.8	—
Insol Carbo. (%)	41	40	37	35	31	40	34	—
Protein (%)	8 ±3.8	9 ±2.4	8 ±3.7	10 ±3.5	7 ±2.7	2 ±4.5	10 ±8.8	12.5
Lipid (%)	1.6 ±0.4	2.3 ±0.6	1.2 ±0.7	1.0 ±0.6	5.8 ±6.9	2.0 ±0.7	1.7	2.9
Energy (kJ)	13.4	13.6	13.3	13.7	13.8	10.7	13.3	15.8

RESULTS—The average water temperature at the Juniper Run site was 10.0 C° (winter) and 23.5 C° (summer). The percent dry weight of blades, stolons, and root stocks and roots of the two species were lower in the winter, but the differences were not significant (Tables 1, 2).

Ash levels in the blades ranged from 21 to 29% (*Potamogeton pectinatus*, winter and summer, Table 2). Stolon ash levels ranged from 16% (*P. pectinatus*, summer, Table 2) to 24% (*Vallisneria americana*, winter, Table 1). Ash levels in the root stock ranged from 18% (*V. americana*, summer, Table 1) to 27% (*P. pectinatus*, winter, Table 2).

Protein levels were not significantly different between winter and summer collections or between blades and stolons for any species. Protein levels ranged from 8% (*Vallisneria americana*, winter, Table 1) to 10% (*V. americana*, summer; *Potamogeton pectinatus*, winter, Table 1 and 2 for blades and

TABLE 2. Proximate constituents as percent of dry weight and energy levels (kiloJoules g dry wt^{-1}) from winter and summer collections over a 4-yr period of *Potamogeton pectinatus* growing in Juniper Run, Florida. N = 8 ± 1S.D.

	Blade		Stolon		Root Stock	
	Winter	Summer	Winter	Summer	Winter	Summer
Dry Wt (%)	11 ±2.6	12 ±3.3	13 ±3.3	16 ±6.4	10 ±2.1	12 ±2.0
Ash (%)	21 ±6.6	29 ±9.7	22 ±11.8	16 ±11.0	27 ±10.5	22 ±11.9
Sol Carbo. (%)	21 ±8.1	23 ±7.2	29 ±14.1	40 ±9.7	23 ±8.4	23 ±1.4
Insol Carbo. (%)	48	35	40	33	35	57
Protein (%)	7 ±4.6	10 ±1.9	7 ±4.8	9 ±3.0	7 ±2.1	13 ±5.0
Lipid (%)	1.5 ±0.8	2.6 ±0.6	1.8 ±1.1	2.3 ±0.6	8.8 ±1.6	2.3 ±1.2
Energy (kJ)	13.9	12.9	13.9	15.2	14.6	17.1

stolons. Root stock protein levels ranged from 7 to 13% (*P. pectinatus*, winter and summer, Table 2). The roots and root stocks of *V. americana* had intermediate protein values.

Soluble carbohydrate levels were highest in the stolon (30 to 40%) and root stocks (23 to 28%) for both species. The stolon had significantly higher levels of soluble carbohydrate when compared with the blades and root system of *Potamogeton pectinatus.* Summer collections of stolons of the two species had significantly higher levels than their blade counterparts. However, there were no significant seasonal differences in the levels of soluble carbohydrate between the winter and summer stolon samples for each species.

Lipid levels were low in the blades, ranging from 1.5 to 2.6% (*Potamogeton pectinatus*, winter, Table 2) and 1.0% (*Vallisneria americana*, summer, Table 1) to 2.3% (*P. pectinatus*, summer) in the stolon. Lipid levels were highest in the root stock of *P. pectinatus* in the winter (9%, Table 2).

Fiber in *Vallisneria americana* accounted for 29 and 30% in the blades and 30 and 40% in the stolon (winter and summer respectively). In *Potamogeton pectinatus,* fiber levels were 31 and 23% in the blades and 39 and 22% in the stolon (winter and summer respectively). Lignin levels were highest in the winter collections of the blades of both species (*V. americana:* 6 and 2%; *P. pectinatus:* 4 and 3%, winter and summer) with lower levels in the stolons (*V. americana:* 0.2 and 2%; *P. pectinatus*: 3 and 2%, winter and summer).

The blades of summer plants had significantly higher dry weights in *Vallisneria americana* (27 and 7 g) and *Potamogeton pectinatus* (0.7 and 0.4 g) when compared to the winter levels, or the stolons of the same plants (*V.*

americana: 0.1 and 0.04 g; *P. pectinatus:* 0.1 and 0.02 g, summer and winter). Total energy levels in the stolon were low (*V. americana:* 0.6 and 0.2 kilojoules; *P. pectinatus:* 0.1 kilojoules, summer and winter) when compared with the blades of both species (*V. americana:* 206 and 39 kilojoules; *P. pectinatus:* 6 and 2 kilojoules, summer and winter).

Energy values expressed per g dry weight did not differ much seasonally for the blades of both species (Tables 1, 2), but did show a summer high for stolons of *Potamogeton pectinatus* and for the root stocks of both species. The roots of *Vallisneria americana* had lower kilojoules in the summer.

Discussion—Differences in allocation of energy are evident when comparisons are made between *Vallisneria americana* and the seagrass *Thalassia testudinum* Banks ex Konig, both in the family Hydrocharitacae, and between *Potamogeton pectinatus* and the seagrass *Halodule wrightii* (Ascherson) Ascherson, both in the family Potamogetonaceae (Cronquist 1981). Unlike the marine macrophytes found at the same latitude, there is no seasonal shift in constituents in the freshwater macrophytes. Due to the influence of the Ocala Springs, the Juniper Run has a very limited temperature range, and the seasonal changes in irradiances are assumed to be similar when compared with the marine environment on the west coast of Florida although water transparency can vary in seagrass beds.

Blade biomass did increase in the summer in both species in a manner similar to that reported for seagrasses (Dawes and Lawrence 1980), and for *Vallisneria americana* from the Mississippi River (Donnermeyer and Smart 1985). However, there was never complete die back to a "winter bud" in the Florida *V. americana* as in the Mississippi plants. In fact, the plants showed new leaf growth in winter collections, unlike their marine counterparts. Stolon biomass did not show any major increase in dry weight and the level of soluble carbohydrate did not increase significantly in the summer. The stolon of these freshwater macrophytes apparently does not function as a storage organ for growth as shown in the marine macrophytes (Dawes and Lawrence 1980) although soluble carbohydrate is higher than in the blades. The blades, in fact, contain the majority of the plant's organic constituents in both summer and winter, unlike the seagrasses.

Protein levels of blades and stolons in the freshwater macrophytes were similar or less than (Dawes and Lawrence 1980; Dawes 1986) levels found in the two seagrasses. The root stocks, when a fleshy stem base was separable, had the highest protein levels. The generally lower levels of protein and ash in the freshwater macrophytes over their marine counterparts suggest a lower energy allocation in growth. Blade protein levels reported here are less than half when compared with the data presented by Donnermeyer and Smart (1985). Perhaps it is because these authors calculated protein based on total nitrogen (Kjeldahl method) while we report soluble protein based on the Folin Ciocalteau reaction.

Except for the winter blades of *Vallisneria americana*, the energy values of blades were 90 to 92% of their marine counterparts (Dawes and Lawrence 1980). The stolons of the freshwater plants also had lower energy levels than their marine counterparts; 78% for winter stolons of *Potamogeton pectinatus* when compared with *Halodule wrightii* and 95% for summer stolons of *Vallisneria americana* when compared to *Thalassia testudinum*. Furthermore, if fiber is considered as a non-nutritive component, then the blades and stolons of the freshwater macrophytes have almost a third less of the nutritively available energy constituents than their seagrass counterparts (Dawes 1986). The levels of insoluble carbohydrate determined by difference ranged from 24 to 47% for blades and 33 to 40% for stolons while fiber levels ranged from 23 to 34% and 14 to 39% respectively. Thus, fiber does account for up to 90% of the calculated insoluble carbohydrate.

Lignin and fiber levels of winter blades of *Vallisneria americana* and *Potamogeton pectinatus* were higher than those reported for the marine counterparts while the summer levels were similar. Fiber levels in both freshwater macrophytes were also higher than true terrestrial grasses in Florida (in Dawes 1986) such as *Festuca arundinacea* (tall fescue) and *Cynodon dactylon* (Bermuda grass) but lower than the range reported for a population of *V. americana* in Mississippi by Donnermeyer and Smart (1985). However, these authors used a neutral detergent analysis which will include hemicelluloses while this study employed the acid detergent which removes the hemicelluloses. The higher fiber levels of the broad, linear blades of *V. americana*, when compared to the morphologically similar blades of *Thalassia testudinum* as well as terrestrial grasses may be indicative of adaptation to current drag in a stream. The narrow blades of *P. pectinatus* would not experience the same amount of drag.

CONCLUSIONS—The stolons of *Vallisneria americana* and *Potamogeton pectinatus* do not function as storage organs in contrast to the seagrasses. This difference may be due in part to the stable year-around production of new blade material. The higher levels of fiber found in *V. americana* blades is probably due to the current of the stream habitat.

LITERATURE CITED

BOYD, C. E. 1970. Amino acid, protein, and caloric content of vascular aquatic macrophytes. Ecology. 51:902-906.

———, AND E. SCARSBROOK. 1975. Chemical composition of aquatic weeds. Pp. 144-150. *In:* BRESONIC, P. L., AND J. L. FOX, (eds.). Proc. Symp. on Water Quality Management through Biological Control. Environmental Protection Agency, Corvallis Oregon. ENV-07-75-1.

BRODY, S. 1964. Bioenergetics and Growth. Hafner, New York. 1023 pp.

CRONQUIST, A. 1981. An integrated System of Classification of Flowering Plants. Columbia University Press. New York. 1262 pp.

DAWES, C. J. 1986. Seasonal proximate constituents and caloric values in seagrasses and algae on the west coast of Florida. J. Coastal Res. 2:25-32.

———, AND J. M. LAWRENCE. 1980. Seasonal changes in the proximate constituents of the seagrass *Thalassia testudinum*, *Halodule wrightii*, and *Syringodium filforme*. Aq. Bot. 8:371-380.

———, AND J. M. LAWRENCE. 1983. Proximate constituents and caloric content of seagrasses. Mar. Technol. Soc. J. 17:53-58.

DONNERMEYER, G. N., AND M. M. SMART. 1985. The biomas and nutritive potential of *Vallisneria americana* Michx in Navigation Pool 9 of the upper Mississippi River. Aq. Bot. 22:33-44.

GODFREY, R. K., AND J. W. WOOTEN. 1979. Aquatic and Wetland Plants of the Southeastern United States. Univ. Georgia Press, Athens. 933 pp.

GOERING, H. K., AND P. J. VAN SOEST. 1970. Forage Fiber Analyses. U. S. Department of Agriculture. Handbook No. 319. 20 pp.

LITTLE, E. C. S. 1979. Handbook of Utilization of Aquatic Plants. A Review of World Literature. Food and Agriculture Organization of the United Nations, Rome. FAO Fish. Tech. Pap. No. 187. 176 pp.

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