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Source: *The American Midland Naturalist*, Oct., 1979, Vol. 102, No. 2 (Oct., 1979), pp.
263-272

Published by: The University of Notre Dame

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Comparative Carbohydrate Storage and Utilization Patterns in the Submersed Macrophytes, *Myriophyllum spicatum* and *Vallisneria spiralis*

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ABSTRACT: A prolonged dormant period for *Vallisneria spiralis* is one of the conspicuous differences between it and *Myriophyllum spicatum*, another submersed macrophyte with which it co-occurs in the littoral zones of lakes of Madison, Wisconsin. To test the hypothesis that ample storage of total nonstructural carbohydrates (TNC) by *V. spiralis* could support a growth flush to compensate for its shorter growing season, plant tissues were collected over two annual cycles and analyzed for TNC. Both species exhibited marked seasonal patterns in % TNC in above- and below-sediment plant parts. Mean TNC values in *M. spicatum* tissues ranged from 1.6-19.0% for roots and 2.0-20.0% for shoots. The low values were associated with the spring growth flush. Analysis of variance revealed significant differences in these TNC storage and utilization patterns for roots and shoots, plants collected at different sites and plants collected at different times. *Vallisneria spiralis* tissues ranged from 4%-28% TNC during the growing season, while winter bud TNC values were ca. 45%. By virtue of low winter biomass, however, the total reserves in the *Vallisneria* community were inadequate to permit compensation for a late start in the spring, prompting us to reject our hypothesis.

INTRODUCTION

Submersed macrophyte communities are often characterized by low species diversity (Curtis, 1959), probably related to the tendencies of many submersed macrophytes to reproduce vegetatively and to the demands of seedling establishment. In Lake Wingra and University Bay (Lake Mendota) of Madison, Wisconsin, two of the dominant species have been the Eurasian water milfoil (*Myriophyllum spicatum*) and wild celery (*Vallisneria spiralis*). The introduction of *M. spicatum* into the Madison lakes has resulted in the partial replacement of *V. spiralis* (Lind and Cottam, 1969; Nichols and Mori, 1971). The interactions between these two species are complex. It now appears that *V. spiralis* is regaining its position as an important species in Lake Wingra (Titus, 1977; P. Johnsen, pers. comm.), and remains a dominant in University Bay despite a decline in its relative importance. These species are both undoubtedly active participants in carbon cycling, but very likely differ in ancillary roles such as provision of habitat for macroinvertebrates and *Aufwuchs* organisms, shelter for small fishes and food for fishes and wildfowl (Fassett, 1957). We seek to understand the environmental factors and plant adaptations which govern the relative importance of these two macrophytes and thus may contribute to the regulation of community structure.

We adopted an approach similar to that advocated by Mooney (1972) to gain insight into relations between these two species. Mooney suggested that understanding patterns of resource gain and allocation is necessary to allow predictions of the outcome of competition between species. Investigations of resource gain and allocation may also answer the question, "What are the characteristics of species which permit them to co-occur in the diversity of nature?" (Harper, 1967). Our focus has been primarily on the gain and allocation of carbon, as "carbon is the vehicle by which organisms store and transfer energy" (Mooney, 1972). The purpose of this paper is to examine aspects of the allocation of carbon among and within plant tissues.

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Several researchers have investigated allocation of resources between vegetative and reproductive plant parts (Harper and Ogden, 1970; Solbrig, 1971; Abrahamson and Gadgil, 1973; Anderson and Loucks, 1973; Gaines *et al.*, 1974; Ogden, 1974; Hickman, 1975). Application of this approach to these macrophytes is difficult because of the tremendous importance of vegetative reproduction. Vegetative reproduction, a term Harper (1977, p. 26) rejects, shares features with each pole of the vegetative growth/sexual reproduction dichotomy, and thus cannot readily be classified by that dichotomy. In addition, the production by *Myriophyllum spicatum* of abscission fragments, which may double as photosynthetic and reproductive tissues, is difficult to quantify. We have examined another aspect of allocation among plant tissues which is clearly relevant to plant fitness and is operationally more straightforward: the division between above- and below-sediment plant parts. In a general discussion of root/shoot ratios, Monk (1966) elaborated on the potential significance of roots in competitive interactions. In submersed macrophytes, below-sediment plant parts may have important functions in anchoring, nutrient uptake, carbohydrate storage, reproduction and, in some cases, uptake of photosynthetic carbon sources (Wium-Andersen and Andersen, 1972). A high proportion of shoot tissue, on the other hand, should permit more carbon fixation and shading of potential competitors.

Biomass quality also warrants serious consideration and is the principal subject of this paper. Of the many qualitative features of plant biomass we singled out non-structural carbohydrate content for detailed study. Total nonstructural carbohydrates (TNC) consist of sugars and nonstructural polysaccharides, such as starches and fructosans (Smith, 1969). They represent a labile pool of carbohydrates available for the accretion of structural materials as well as for the respiratory costs of plant maintenance and growth. Several mathematical production models have incorporated a pool of photosynthate as a carbon source for various growth processes (*e.g.*, de Wit *et al.*, 1970; Titus *et al.*, 1975; Fick *et al.*, 1975). The presence of a large storage TNC pool provides flexibility to the timing of structural growth and thus enhances plant plasticity and resistance to unfavorable environmental conditions. The fundamental importance of this carbohydrate pool in regulating growth (Hunt and Loomis, 1976), coupled with a general ignorance of pool sizes and dynamics in submersed aquatic macrophytes, stimulated our study on seasonal changes in TNC content for *Myriophyllum spicatum* and *Vallisneria spiralis*.

SITE AND SPECIES DESCRIPTIONS

Lake Wingra and University Bay are approximately the same size (137 ha and 106 ha, respectively) and are both relatively shallow, alkaline and eutrophic. In University Bay, part of the much larger Lake Mendota, water transparency is somewhat greater than in Wingra most of the year. Inadequate quantities of *Vallisneria spiralis* in Wingra, the site of intensive IBP studies on *Myriophyllum spicatum*, necessitated collections of the former species from University Bay. Collection sites were 1.4-1.6 m deep in Wingra and 1.2-1.5 m in University Bay, and within dense monospecific stands of their respective species.

Myriophyllum spicatum, with its long branched stems and dissected leaves, overwinters in Lake Wingra as a mass of roots with short but healthy shoots. Most plant stems are ca. 20-50 cm long in winter, though some may exceed 1 m. These plants grow toward the surface, which they usually reach in late May or early June at a rooting depth of 1.5 m in the W end of Lake Wingra. Two loosely defined flowering periods usually occur each summer (June and August-September) and are followed by partial autofragmentation of shoots. The resulting abscission fragments are particularly evident in October and November.

Vallisneria spiralis provides a morphological and phenological contrast to

Myriophyllum spicatum, in that the *V. americana* plants overwinter as winter buds buried ca. 8-10 cm in the sediment. These buds break dormancy in late May in University Bay to produce root systems and vertical stems which grow to the sediment/water interface. Ribbonlike leaves from basal rosettes reach the surface in early to midsummer at the collection site. Such rosettes sequentially produce stolons (Wilder, 1974) which bear new shoots through the summer. Mature rosettes flower and develop fruit in late July and August, then senesce in late summer and autumn at the time of winter bud formation. Thus, *V. americana* has a much shorter growing season than *M. spicatum*, which always has photosynthetic tissues in the water column.

The evergreen nature and physiological responses of *Myriophyllum spicatum* to low temperature provide it with a distinct advantage in spring and autumn. It is not clear why *M. spicatum* fragments do not colonize *Vallisneria* sites in late autumn. In this report we test the hypothesis that *V. americana* winter buds contain enough TNC to support a burst of growth in the spring that is sufficient to overcome the disadvantage of its late start and short growing season.

METHODS

To follow seasonal changes in TNC content, we collected entire plants of *Myriophyllum spicatum* with a rake at a rooting depth of 150 cm in the W end of Lake Wingra at one site in 1974 and two sites during the 1975 growing season. The two sites, A and B, were distinguished because A was closer (by ca. 100 m) to Nakoma Creek, a significant source of nutrients for Lake Wingra. During the 1975 and 1976 winters we sampled *M. spicatum* from beneath the ice in ca. 150 cm of water.

We sampled *Vallisneria* in University Bay in 1974 and 1975 at one site. At times it was necessary to dive to collect the tenacious *Vallisneria* plants intact. We used an Ekman dredge to collect winter buds. We generally sampled plants of both species between 1100 and 1600 hr. On one occasion (19 August 1974) we sampled *Myriophyllum spicatum* at different times throughout the day to evaluate the extent of diurnal changes in TNC content. In all cases, intact plants were collected at approximately monthly intervals (somewhat less frequently in the winter), returned to the laboratory, washed thoroughly, separated into above- and below-sediment components, oven-dried at 70C, weighed and ground with a Wiley mill to pass through 40-mesh screen. Surprisingly, preliminary studies showed little difference in TNC content of growing tips, older shoots, and leafless stems for *M. spicatum*. We thus combined all shoot material for analysis. Levels of TNC were higher in rhizomes and stolons than in roots of *V. americana*, but roots were lumped with them because of the limited contribution of roots to below-sediment biomass. Thus, the "shoot" category includes leaves, stems and (sexual) reproductive structures for *Myriophyllum*, but only leaves and (sexual) reproductive structures for *Vallisneria*. The "root" category for *Myriophyllum* consists primarily of roots with a few stem bases, but primarily of rhizomes and developing buds with short stems and small root systems for *Vallisneria*.

Our sampling program afforded an opportunity to quantify shoot/root ratios, defined operationally as above-sediment/below-sediment biomass ratios. We generally collected three separate *Myriophyllum* plants at each site on each sampling date, while *Vallisneria* samples were composite samples, each consisting of several plants. Dried samples were stored in sealed vials until analyzed according to Smith (1969) for TNC. At least two 200-mg subsamples were analyzed for each field sample. Dextrose was used as a standard.

RESULTS AND DISCUSSION

Total nonstructural carbohydrates.—Carbohydrate storage and utilization patterns

have been investigated for arctic and alpine plants (*e.g.*, Mooney and Billings, 1960, 1961; Shaver and Billings, 1976), desert and chaparral plants (*e.g.*, Dina and Klikoff, 1974; Mooney and Hays, 1973; Mooney and Chu, 1974), and emergent macrophytes (Linde *et al.*, 1976; McIntire and Dunstan, 1976; Gustafson, 1976). We are aware of no previous studies involving submersed macrophytes. Seasonal cycles may be pronounced, with high storage levels accumulated prior to an unfavorable season, or poorly developed, generally associated with relatively low carbohydrate levels. This latter pattern has been observed both for the evergreen California live oak (*Quercus agrifolia*) (Mooney and Hays, 1973) and for cordgrass (*Spartina alterniflora*) (McIntire and Dunstan, 1976), active the year round where studied. The importance of TNC storage in supporting subsequent growth is great for cattails (Linde *et al.*, 1976; Gustafson, 1976) and alpine plants (Mooney and Billings, 1960) but minimal for *Q. agrifolia* and *S. alterniflora*.

Myriophyllum spicatum TNC content as a percent of dry weight showed distinct seasonal patterns for 1974 (Fig. 1). Values of TNC ranged from near 20% under winter ice cover and again in early October to about 5% in early summer and late autumn. We did not expect TNC values as high as 20% for *M. spicatum*, which has no conspicuous storage organs and is evergreen. Shoots apparently may be used for winter storage of TNC. The rapid depletion after the spring thaw corresponds to the May growth flush, and subsequent storage in the summer is presumably a reflection of the exploitation of favorable conditions after plants have reached the surface. This pattern is consistent with the notion of a resource accumulation prior to a season of stress, in this case presumably due to unfavorable light and temperature regimes of winter, cycling with a rapid depletion following the onset of more favorable conditions. The TNC depletion in the autumn before winter ice cover is surprising, however, and precludes the return of 1975 winter TNC to 1974 values. A full interpretation of this decline would require more information on biomass, transparency and water temperature. It is possible that much of this loss could be due to potentially reproductive abscission fragments, which are dispersed abundantly in the autumn. Shoot and root TNC values were not substantially different except on the July, August and September collection dates. Shoots initiated a steady accumulation of TNC in July, whereas roots accumulated TNC much more slowly until early autumn, when shoots apparently translocated carbohydrates to the roots rapidly before these shoots were sloughed from the plants.

TNC storage and use patterns for *Myriophyllum spicatum* were different in 1975 (Fig. 2). Plant tissues had low winter TNC levels which were further depleted to about 2% in May. *Myriophyllum* was then able to accumulate TNC rapidly to levels of 20% in shoots by late summer. A steady rise in root TNC followed that in the shoots. Shoot and root curves crossed in October, but maintained higher levels in the winter of 1976 than in the previous winter. Thus, *M. spicatum* recovered from the surprising decline in TNC content which was observed in the autumn of 1974. Evidently TNC accumulation and utilization patterns are not the same from year to year.

Analysis of variance for TNC content of *Myriophyllum spicatum* samples collected on 19 August 1974 (data not shown) showed no significant diurnal variation, in contrast to diurnal TNC changes in *Spartina alterniflora* (McIntire and Dunstan, 1976). Analysis of variance for the 1975 TNC data for *M. spicatum* (Table 1) revealed significant differences between sites A and B, between roots and shoots, and among sampling dates. The significance of the plant part/sampling date interaction is related to the crossovers of root and shoot TNC content (Fig. 2). The significant differences between nearby sites at the same rooting depth serve to caution against generalization from data based on restricted sampling areas. The TNC data for site A (not shown) were consistently lower for both roots and shoots than at site B,

although these same plants had higher levels of tissue phosphorus than those at site B (Titus, 1977). These differences may be due to increase siltation and periphyton growth observed on plant surfaces at site A (the site nearer to the Nakoma Creek inlet to Lake Wingra), but this is not certain.

Because the formation of winter buds on new rhizomes in the autumn by *Vallisneria* plants is followed by degeneration of original plant tissues, *V. americana* can be

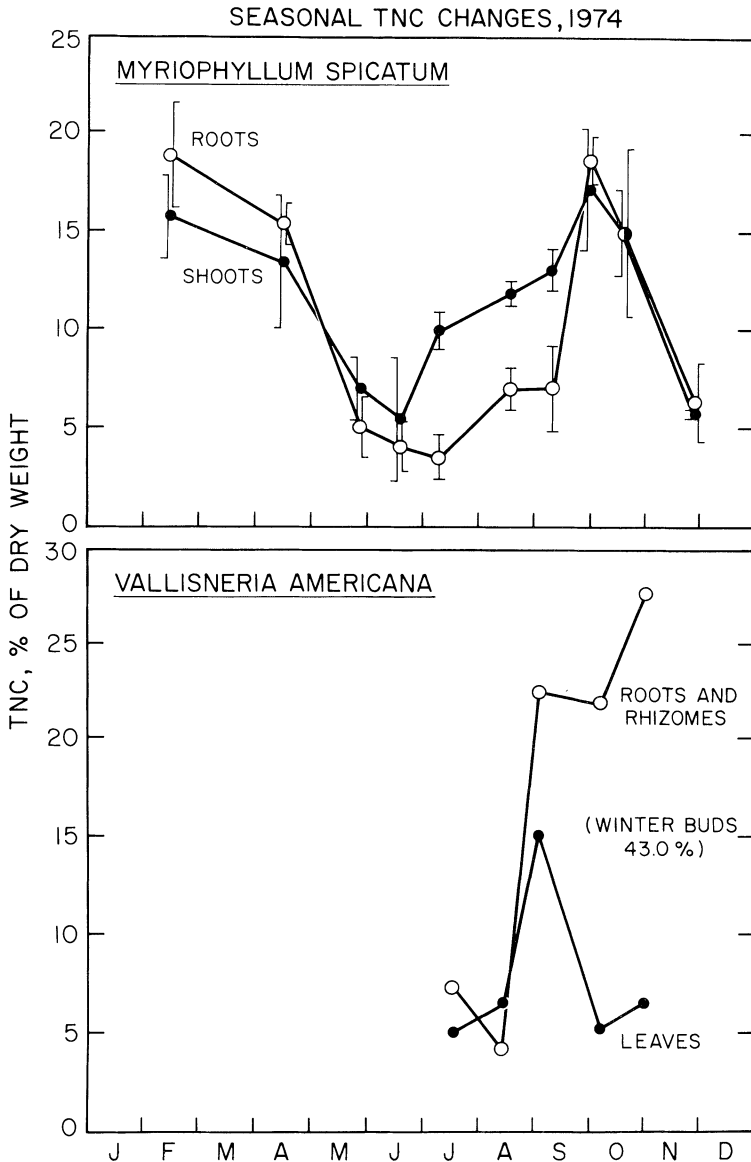


Fig. 1.—Seasonal changes in tissue total nonstructural carbohydrate (TNC) content for shoots and “roots” of *Myriophyllum* and *Vallisneria* in 1974. For *Myriophyllum*, means are shown with their standard errors. For *Vallisneria*, means represent several plants in composite samples

considered a "vegetative annual" (Hutchinson, 1975). In such plants, TNC storage for subsequent spring growth must be concentrated in rhizomes and winter buds. Observed TNC levels for 1974 (Fig. 1) confirm this expectation. Levels of TNC in below-sediment parts exceeded 25% during the 1974 growing season. The 1975 data (Fig. 2) showed a rapid depletion of TNC from the below-sediment component, presumably in support of the establishment of rosettes in late spring. This depletion was followed by TNC accumulation, first observed for leaves. This prior accumulation of TNC in leaves is expected, as the leaves must act as the TNC source for roots

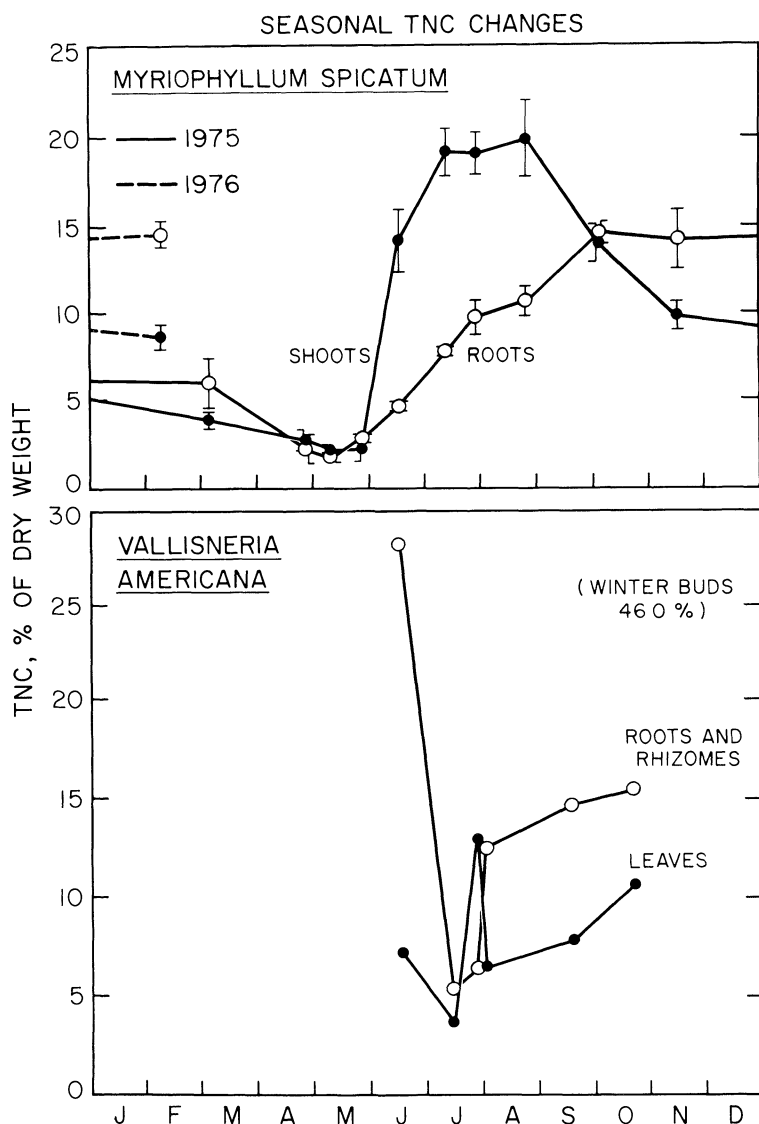


Fig. 2.—Seasonal changes in TNC content for shoots and "roots" of *Myriophyllum* (site B) in 1975-1976 and *Vallisneria* in 1975. Means and standard errors are represented as in Figure 1

and rhizomes. Unlike *Myriophyllum spicatum* shoots, however, *V. americana* leaves do not maintain TNC values comparable to their respective below-sediment parts. The disparity between 1974 and 1975 root and rhizome TNC values is difficult to understand, especially in view of similar winter bud TNC values for the 1975 and 1976 winters. Water level in Lake Mendota was unusually high in 1975, which could have resulted in a less favorable carbon balance for *V. americana* in that year. The comparable TNC values of winter buds for the 2 years appear to contradict this explanation. It is possible, however, that *V. americana* responds to adverse conditions by producing fewer winter buds, rather than by producing winter buds with lower TNC content. Winter TNC levels of 43% and 46% are quite high, and approach maximum values recorded for *Aesculus californica* (48%, Mooney and Hays, 1973) and *Typha glauca* (52%, Linde *et al.*, 1976).

Both differences and similarities emerge from the comparison of annual TNC cycles of *Myriophyllum spicatum* and *Vallisneria americana*. *Myriophyllum* has generally higher %TNC in shoots, but has no storage to compare with winter buds of *V. americana* with their very high TNC content. Aside from winter buds, however, the annual TNC ranges are very similar for the two species. Thus in some respects, *M. spicatum* behaves comparably to the "vegetative annual" *Vallisneria americana*, and in other respects to terrestrial plants which are active year-round.

Shoot:root ratios and biomass estimates.—Seasonal changes in shoot:root (S:R) ratio for *M. spicatum* in 1975 (Fig. 3) correspond approximately to seasonal changes in biomass observed for 1972 (Titus *et al.*, 1975), suggesting that root biomass changed little through the growing season. If root biomass is indeed a conservative quantity, changes in the S:R ratio indicate shoot biomass changes. On this assumption, shoots apparently began growing rapidly in May, more than a month after the spring thaw, and continued growing until late July when the S:R ratio peaked at 9.05. This high ratio is in line with values reported by Wetzel (1975, p. 379) for rooted submersed macrophytes, and is in good agreement with the ratio of 9.1 for *Myriophyllum* sp. in Chautauqua Lake (Nicholson and Best, 1974). In general such ratios are very high in comparison to those of terrestrial herbaceous plants, and suggest the lesser importance of roots for submersed macrophytes.

Based on the maximum biomass of 407 g•m⁻² for 1972 at 150 cm (Titus *et al.*, 1975) and the maximum S:R value of 9.05, we estimate root biomass at 39 g•m⁻². If root biomass does not change seasonally, overwintering shoot biomass based on a S:R ratio of 1.39 (6 March 1975) should be approximately 54 g•m⁻².

Above sediment: below sediment weight ratios (also referred to as S:R) for *Vallisneria americana* in 1975 and 1976 (Fig. 3) present a similar pattern, at least for the summer. In both years, the S:R ratio rises rapidly in June and July, peaks in late July and declines by late August. The high ratio of ca. 5.5 is considerably lower than 9.05 for *Myriophyllum*. The high ratio for 18 September 1975 is puzzling. The 26 August 1976 ratio of 3.5 is higher than the 1.1 obtained by Nicholson and Best (1974)

TABLE 1.—ANOVA results for *Myriophyllum* total nonstructural carbohydrate content, 1975-1976

Source of variation	df	Mean square	F
Sites (A)	1	239.8	68.2**
Plant parts (B)	1	139.9	39.8**
Dates (C)	8	179.2	51.0**
AxB	1	.8	.2n.s.
AxC	8	18.9	5.4**
BxC	8	159.2	45.3**
AxBxC	8	8.5	2.4*
Within groups	72	3.5

n.s.: not significant; *: $P < .05$; **: $P < .01$

for *V. americana* in late August in Chautauqua Lake. The *Vallisneria* S:R ratio drops to zero in winter, unlike that of *M. spicatum*.

By counting the number of *Vallisneria* rosettes m^{-2} in early June, we estimated the number of winter buds m^{-2} at 101 ± 10 (SD). In conjunction with the average fresh weight of winter buds (0.89 g for 30 buds) and an assumed dry weight: fresh weight ratio of 0.20, this yielded an estimate of overwintering biomass of $18.0 \text{ g} \cdot \text{m}^{-2}$. For maximum biomass, samples on 30 July 1976 yielded an average of 344 ± 78 (SD) $\text{gdw} \cdot \text{m}^{-2}$. Based on a S:R value of 5.4, ca. 54 g should have been below the sediment/water interface. Thus root and rhizome biomass is by no means conservative for *Vallisneria*.

On the basis of overwintering biomass estimates, winter bud TNC levels, and the assumption that this stored carbohydrate was converted with 100% efficiency to leaf biomass capable of shading shoots of *Myriophyllum spicatum*, $8.3 \text{ gdw} \cdot \text{m}^{-2}$ of *Vallisneria americana* leaves could have been produced by stored TNC in the spring of 1976. Use of a more realistic efficiency of conversion to leaf biomass would result in an even lower leaf biomass. This does not compare favorably with the estimated $54 \text{ gdw} \cdot \text{m}^{-2}$ of overwintering *M. spicatum* shoots. Thus we must reject our hypothesis that higher TNC levels in *Vallisneria* winter buds compensate for its later start relative to *M. spicatum*. This interpretation is, of course, not appropriate for interactions between an established stand of *Vallisneria* and isolated propagules of *M. spicatum*, but should be applicable to areas transitional between those dominated by the two species. The role of TNC storage in *V. americana* appears related to establishing a small rosette of leaves near the sediment. The success of this rosette would

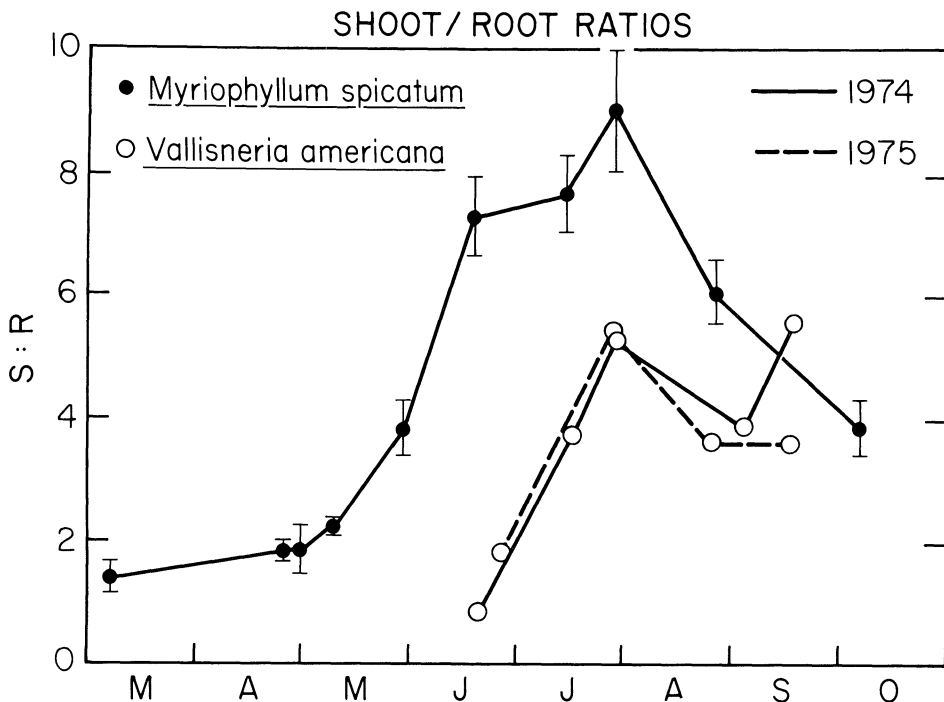


Fig. 3.—Seasonal changes in shoot:root weight ratio for *Myriophyllum spicatum* in the W end of Lake Wingra and *Vallisneria* in University Bay. Means and standard errors are represented as in Figure 1

depend entirely on subsequent assimilation. These contrasts exacerbate the distinction made elsewhere (Titus, 1977) between *M. spicatum* and *V. americana*: the latter is more dependent on water transparency than the former, and probably more susceptible to a decline should water transparency decrease.

Thus, no apparent physiological basis is derived from our study to explain the failure of *Myriophyllum spicatum* to expand into the *Vallisneria* community in late autumn or early spring. Alternative explanations include the possibility that allelopathic agents produced by *Vallisneria* inhibit the growth of *Myriophyllum*, or even that herbivores may play a role. It seems more likely that *Vallisneria* has an inherently higher productivity than *Myriophyllum* during the summer months (Titus, 1977), or that the greater allocation of biomass to below-sediment parts in *V. americana* allows it to maintain itself in shallow waters with relatively great wave action while the less robust anchoring systems of *M. spicatum* do not permit this.

Acknowledgments.—This research was supported by National Science Foundation grant DEB-19-777 to the University of Wisconsin - Madison, and by the Eastern Deciduous Forest Biome, US-IBP, funded by the National Science Foundation under Interagency Agreement AG 199, 40-193-69 with the Energy Research and Development Administration - Oak Ridge National Laboratory. We thank Cathy Carnes, Richard Hueschen and Billie Lofland for technical assistance.

LITERATURE CITED

- ABRAHAMSON, W. G. AND M. D. GADGIL. 1973. Growth form and reproductive effort in golden-rod (*Solidago*, Compositae). *Am. Nat.*, **107**:651-661.
- ANDERSON, R. C. AND O. L. LOUCKS. 1973. Aspects of the biology of *Trientalis borealis* Raf. *Ecology*, **54**:798-808.
- CURTIS, J. T. 1959. The vegetation of Wisconsin. Univ. of Wisconsin Press, Madison. 657 p.
- DINA, S. J. AND L. G. KLIKOFF. 1974. Carbohydrate cycle of *Plantago insularis* var. *fastigiata*, a winter annual from the Sonoran Desert. *Bot. Gaz.*, **135**:13-18.
- FASSETT, N. C. 1957. A manual of aquatic plants. Univ. of Wisconsin Press, Madison, 405 p.
- FICK, G., R. S. LOOMIS AND W. A. WILLIAMS. 1975. Sugar beet, p. 259-295. In: L. T. Evans (ed.). Crop physiology—Some case studies. Cambridge Univ. Press, New York.
- GAINES, M. S., K. J. VOGT, J. L. HAMRICK AND J. CALDWELL. 1974. Reproductive strategies and growth patterns in sunflowers (*Helianthus*). *Am. Nat.*, **108**:889-894.
- GUSTAFSON, T. D. 1976. Production, photosynthesis and the storage and utilization of reserves in a natural stand of *Typha latifolia* L. Ph.D. Thesis, Univ. of Wisconsin, Madison. 102 p.
- HARPER, J. L. 1967. A Darwinian approach to plant ecology. *J. Ecol.*, **55**:247-270.
- . 1977. The population biology of plants. Academic Press, London. 892 p.
- AND J. OGDEN. 1970. The reproductive strategy of higher plants. I. The concept of strategy with special reference to *Senecio vulgaris* L. *J. Ecol.*, **58**:681-698.
- HICKMAN, J. C. 1975. Environmental unpredictability and plastic energy allocation strategies in the annual *Polygonum cascadenae* (Polygonaceae). *Ibid.*, **63**:689-701.
- HUNT, W. F. AND R. S. LOOMIS. 1976. Carbohydrate-limited growth kinetics of tobacco (*Nicotiana rustica* L.) callus. *Plant Physiol.*, **57**:802-805.
- HUTCHINSON, G. E. 1975. A treatise on limnology, Vol. 3. Limnological Botany. John Wiley and Sons, New York. 660 p.
- LIND, C. T. AND G. COTTAM. 1969. The submerged aquatics of University Bay: A study in eutrophication. *Am. Midl. Nat.*, **81**:353-369.
- LINDE, A. F., T. JANISCH AND D. SMITH. 1976. Cattail—The significance of its growth, phenology and carbohydrate storage to its control and management. Tech. Bull. 94, Department Nat. Res., Madison, Wisconsin.
- McINTIRE, G. L. AND W. M. DUNSTAN. 1976. Non-structural carbohydrates in *Spartina alterniflora* Loisel. *Bot. Mar.*, **19**:93-96.
- MONK, C. D. 1966. Ecological importance of root/shoot ratios. *Bull. Torrey Bot. Club*, **93**:402-406.

- MOONEY, H. A. 1972. The carbon balance of plants. *Annu. Rev. Ecol. Syst.*, **3**:315-346.
- AND W. D. BILLINGS. 1960. The annual carbohydrate cycle of alpine plants as related to growth. *Am. J. Bot.*, **47**:594-598.
- AND ———. 1961. Comparative physiological ecology of arctic and alpine populations of *Oxyria digyna*. *Ecol. Monogr.*, **31**:1-29.
- AND C. CHU. 1974. Seasonal carbohydrate allocation in *Heteromeles arbutifolia*, a California evergreen shrub. *Oecologia (Berl.)*, **14**:295-306.
- AND R. I. HAYS. 1973. Carbohydrate cycles in two California Mediterranean-climate trees. *Flora*, **162**:295-304.
- NICHOLS, S. A. AND S. MORI. 1971. The littoral macrophyte vegetation of Lake Wingra. An example of a *Myriophyllum spicatum* invasion in a southern Wisconsin lake. *Trans. Wis. Acad. Sci. Arts Lett.*, **59**:107-119.
- NICHOLSON, S. A. AND D. G. BEST. 1974. Root:shoot and leaf area relationships of macrophyte communities in Chautauqua Lake, New York. *Bull. Torrey Bot. Club*, **101**:96-100.
- OGDEN, J. 1974. The reproductive strategy of higher plants. II. The reproductive strategy of *Tussilago farfara* L. *J. Ecol.*, **62**:291-324.
- SHAVER, G. R. AND W. D. BILLINGS. 1976. Carbohydrate accumulation in tundra graminoid plants as a function of season and tissue age. *Flora*, **165**:247-267.
- SMITH, D. 1969. Removing and analyzing total nonstructural carbohydrates from plant tissues. *Wis. Agric. Exp. Stn. Res. Rep.*, **41**:1-11.
- SOLBRIG, O. T. 1971. The population biology of dandelions. *Am. Sci.*, **59**:686-694.
- TITUS, J. E. 1977. The comparative physiological ecology of three submersed macrophytes. Ph.D. Thesis, Univ. of Wisconsin, Madison. 195 p.
- , R. A. GOLDSTEIN, M. S. ADAMS, J. B. MANKIN, R. V. O'NEILL, P. R. WEILER, JR., H. H. SHUGART AND R. S. BOOTH. 1975. A production model for *Myriophyllum spicatum*. *Ecology*, **56**:1129-1138.
- WETZEL, R. G. 1975. Limnology. W. B. Saunders Co., Philadelphia. 743 p.
- WILDER, G. J. 1974. Symmetry and development of pistillate *Vallisneria americana* (Hydrocharitaceae). *Am. J. Bot.*, **61**:846-866.
- WIT, C. T. DE., R. BROUWER AND F. W. T. PENNING DE VRIES. 1970. The simulation of photosynthetic systems, p. 47-70. In: The prediction and measurement of photosynthetic productivity. Proceedings of the IBP/PP Technical Meeting. Trebon, 1969. Wageningen Centre for Agricultural Publishing and Documentation.
- WIUM-ANDERSEN, S. AND J. M. ANDERSEN. 1972. The influence of vegetation on the redox profile of the sediment of Grane Langso, a Danish *Lobelia* lake. *Limnol. Oceanogr.*, **17**:948-952.

SUBMITTED 17 JULY 1978

ACCEPTED 9 FEBRUARY 1979