THE QUANTITY AND NUTRITIVE QUALITY OF *VALLISNERIA AMERICANA* BIOMASS, IN NAVIGATION POOL NO. 9 OF THE UPPER MISSISSIPPI RIVER

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ABSTRACT

Vallisneria americana Michx. (wild celery) was studied to determine biomass, productivity, and the nutritive potential of all morphological structures.

The study area was located in the southern portion of Navigation Pool No. 9 of the Upper Mississippi River. A 2.6 hectare (0.1 mi^2) stand of monotypic V. americana was selected for study. Sampling was done monthly or bi-monthly during the summer and autumn of 1980 and the spring and summer of 1981. The nutritive potential of V. americana was assessed from these samples by determining dry matter, neutral-detergent fiber, crude protein, ash, and caloric concentrations of each plant organ.

The maximum production rate of 3.2 $g \cdot m^{-2} \cdot d^{-1}$ was observed during mid to late July 1980 and was coincident with rapid rosette production and flowering. The maximum biomass of 217.3 g/m^2 was sampled on 1 September when fruit development was at a maximum. Shoot:root (S:R) ratios reached a peak of 8.7 at mid-July during rapid leaf production. By the end of July, a negative correlation existed between water depth and rosette number and a positive correlation between depth and the S:R ratio. The maximum leaf area index (LAI) of 17 paralleled the peak biomass on 1 September 1980. Leaves were the dominant plant organ composing 60-70% of the summer biomass, whereas winter buds constituted all of the winter biomass.

The nutritive potential of leaves, rootstocks, peduncles, and stolons were reduced because of high moisture (less than 8% dry matter), ash, and fiber concentrations. Staminate inflorescences and pistillate flowers were high in crude protein (averaged 21.8 and 18.2% of the dry weight, respectively) and ash-free non-cell wall fractions (digestible components), but they accounted for minimum V. americana biomass. In contrast, winter buds and fruits had high nutritive potential. Both organs contained relatively high dry matter concentrations and were low in ash (less than 10%) and fiber contents. The potentially digestible ash-free non-cell wall fraction (NCF) composed an average of 75.7 and 82.2% of the dry weight of fruits and winter buds, respectively. The maximum caloric content of V. americana was approximately 765 kcal/m^2 at peak biomass on 1 September 1980.

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INTRODUCTION

Objectives

Aquatic vascular plants (macrophytes) frequently produce large standing crops and cover extensive areas in shallow bodies of water (Boyd 1969). Macrophytes perform various ecological functions, and several genera provide food for wetland fauna (Hotchkiss 1941). Approximately 3,672 hectares of the submergent macrophyte *Vallisneria americana* Michx. (wild celery) were in Pools 7, 8 and 9 of the Upper Mississippi River during 1980-1981 (Korschgen pers. comm., Northern Prairie Wildlife Research Center, La Crosse, Wisconsin 1982). Korschgen estimated that up to 75% of the North American canvasback ducks (*Aythya valisineria*) temporarily utilize this area during their migratory flight in autumn. During that time they feed primarily on the winter bud of *V. americana*. In addition, all parts of *V. americana* have been consumed by waterfowl (Martin et al. 1951).

The present investigation was conducted to obtain data on the quantity and nutritive quality of *V. americana* biomass in Navigation Pool No. 9 of the Upper Mississippi River. The primary objectives of the present study were as follows:

(1) To determine the biomass of *V. americana* at various times throughout a one year period.

(2) To determine the biomass of the various organs that make-up *V. americana*.

(3) To determine the production rates of *V. americana*.

(4) To assess the nutritive potential of each V. americana organ.

Description of Study Area

Navigation Pool No. 9 of the Upper Mississippi River is bordered by Crawford and Vernon counties in Wisconsin, Houston County in Minnesota and Allamakee County in Iowa. The pool extends 49.9 km from Lock and Dam No. 8 at Genoa, Wisconsin (Rm 679.2; $43^{\circ}34'$N, $91^{\circ}14'$W) to Lock and Dam No. 9 downstream of Lynxville, Wisconsin (Rm 648; $43^{\circ}12'$N, $91^{\circ}6'$W). Maximum width of the pool is approximately 6.4 km (Claflin et al. 1981). In Wisconsin, the Mississippi River has an average slope of .006% (Martin 1965). Discharges range from 280 cms to greater than 2,240 cms during the navigation season. Steep-sided, limestone bluffs ascend approximately 152 m above the floodplain. These bluffs delineate the flat-bottomed Mississippi River gorge that ranges from 11 to 13 km in width.

According to Rada et al. (1980), Navigation Pool No. 9 is a hard (130 to 258 mg/L $CaCO_3$), slightly alkaline (pH range: 7.7-8.3), nitrogen and phosphorous enriched body of water (Table 1). Nitrogen and phosphorous concentrations exceed the generally accepted critical concentrations, that when combined with morphological, hydrological and climatic factors may lead to excessive primary production (Vollenweider 1968). The main channel, side channel, and backwater areas of the pool are similar with respect to water quality. The overall chemical characteristics of Navigation Pool No. 9 are homogenous to others in the Upper Mississippi River.

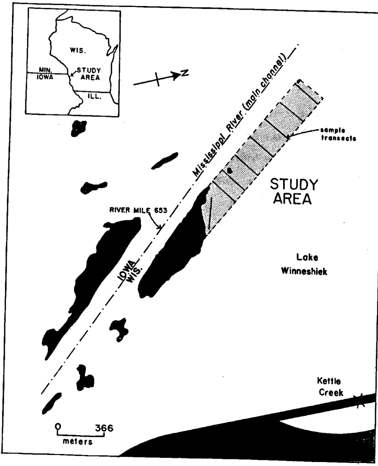
The study area was located in the southern portion of the pool between River Miles 653 and 654 (Fig. 1). The site was adjacent to the main channel in a large expanse of open water known as Lake Winneshiek.

Table 1. Mean and range of selected water quality variables in the main channel (MC), side channels (SC), backwater areas (BW) and river tributaries (RT) of Navigation Pool No. 9 during Summer 1980.[a]

Variable	Areas in Pool No. 9			
	MC	SC	BW	RT
KSP (umhos/cm)	396.1 315-440	388.2 285-430	397.5 300-440	447.1 450-525
Turbidity (NTU)	28.2 14-48	28.9 11-64	31.8 16-48	29.5 6-84
TFR (mg/L)	268.8 200.5-408.0	245.9 184.5-338.0	261.6 183.8-362.7	260.8 207-334
Ca^{++} (mg/L)	48.6 34.4-54.5	48.9 35.2-58.9	49.7 40.8-54.5	57.9 50.1-73.6
TP (mg/L)	0.236 0.180-.289	0.241 0.160-.289	0.249 0.195-.289	0.247 0.075-.470
TKN (mg/L)	1.66 0.76-3.44	1.59 0.82-3.28	1.30 0.82-2.01	2.24 0.58-7.60
NO_3-N (mg/L)	0.464 0.116-2.216	0.470 0.055-1.459	0.515 0.129-.894	1.392 0.263-3.405

[a]Taken from Rada et al. (1980).

Fig. 1. A map of the *Vallisneria americana* study area in Lake Winneshiek, Navigation Pool No. 9, Upper Mississippi River.


WIS.
MIN.
IOWA
STUDY
AREA
ILL.
N
Mississippi River (main channel)
sample
transects
STUDY
AREA
RIVER MILE 653
IOWA
WIS.
Lake
Winneshiek
Kettle
Creek
0
366
meters

The study area was bounded by two islands and contained approximately 2.6 hectares (0.1 mi^2) of a relatively monotypic, continous stand of Vallisneria americana (Fig. 1). A stump field was located east of the study site and extended into the southern portion of the study area. The study area was subjected to the effects of wind, waves, and barge traffic, except for the southern portion of the study site which was sheltered by a large island. An area composed of Nymphaea tuberosa Paine. approximately 50 ft. in diameter was located in the protected region. Trace amounts of Ceratophyllum demersum L., Elodea canadensis Michx., Potamogeton nodosus Poin., Potamogeton richardsonii (Benn.) Rydb., and Heteranthera dubia Tacq. were found at various locations within the study area. By mid-summer 1980, much of the surface of the study area was covered with Cladophora. In contrast, a thick blanket of Lemna spp. overlaid parts of the V. americana bed during August 1981. Other areas heavily populated with V. americana were evident in Lake Winneshiek.

The mean water depth of the study area ranged from 95-120 cm from 28 May 1980 to 6 June 1981 (Table 2). The minimum depth was 30 cm and the maximum depth was 170 cm. Sandy sediments (at least 75% sand) prevailed in areas less than one meter in depth. Conversely, silt and clay sediments were common in the deeper portions of the study area (Appendix I).

Table 2. The mean and range of water depth from which Vallisneria americana was sampled, Navigation Pool No. 9, Upper Mississippi River, 28 May 1980 - 6 June 1981.

Date	Depth (cm) (range)
1980	
28 May	120 (70-150)
27 June	95 (40-160)
13 July	115 (50-155)
29 July	105 (50-169)
14 August	115 (60-160)
1 September	100 (45-150)
6 October	105 (30-160)
9 November	120 (80-150)
1981	
12 April	115 (60-150)
6 June	110 (45-170)

LITERATURE REVIEW

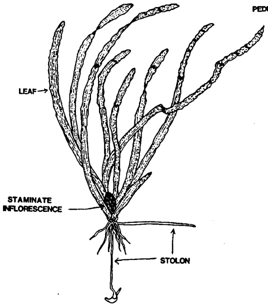
Description

Vallisneria americana Michx. (wild celery) is a dioecious, stoloniferous, perennial plant of the Hydrocharitaceae. This family is composed of approximately 14 genera and 75 species, and all are aquatic (Gleason 1968). The genus Vallisneria contains 6-10 species (Cook 1974) of which Vallisneria americana Michx. and Vallisneria spiralis L. have been most extensively studied. Vallisneria americana is found primarily in eastern North America, but it ranges west from Novia Scotia to South Dakota and south to the gulf of Mexico (Fassett 1957). Vallisneria spiralis is primarily distributed in southern Europe, but its range extends eastward into Russia and throughout India and Ceylon (Hadidi 1968)

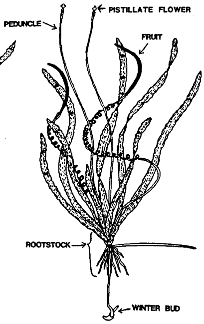
Despite the fact that Michaux in 1903 first described the North American plant as the distinct species, V. americana (Fernald 1918), numerous authors have included the new world plants in the European V. spiralis. Svendelius (1932) and Kausik (1939) cite flower morphology and variation in pollination as major differences between this species pair. Sculthorpe (1967) suggests that V. americana may be a geographical race of V. spiralis. Current treatment, however, is to recognize the new world population as a distinct and valid species under the name V. americana.

Hutchinson (1975) classified Vallisneria as a submersed plant with short stems and ribbonlike leaves that are arranged in a rosette (Fig. 2). Vallisneria americana overwinters as a winter bud at a depth

Fig. 2. A schematic diagram of staminate and pistillate rosettes of Vallisneria americana.



STAMINATE ROSETTE



PISTILLATE ROSETTE

of approximately 8-10 cm in the sediment (Titus 1977). The second internode of the bud elongates during the following spring to form a stolon which carries a compact rosette of leaves to the sediment-water interface (Fig. 2). Roots are subsequently produced at the base of the shoot (Wilder 1974). Ribbonlike leaves reach the water surface in early to mid-summer at southern Wisconsin latitudes. A rosette produces its first stolon in the axil of leaf No. 4. Three leaves intervene between each subsequent stolon. The bifurcation of stolon apical meristems gives rise to additional rosettes and stems (Wilder 1974). Vegetative reproduction of this type may result in six or more rosettes that are connected by stolons (Titus 1977). The initial leaf on a new rosette is small. The second leaf is pointed at the tip and is transitional in character. Other foliage has pointed, elongated, flattened blades and basal sheaths; they are defined as adult leaves. Numerous small roots develop acropetally at the base of a new shoot (Wilder 1974). In addition, Shannon (1953) observed root hairs on a number of aquatic macrophytes including V. americana. He concluded that they function in the absorption of water and solutes as well as in anchorage. By mid-summer, shoots form unisexual flowers on separate plants.

Pistillate epigynous flowers consist of sepals, rudimentary petals, carpels, and staminodia arranged in groups of three's (Witmer 1937). A mucilagenous ovary, measuring 20-25 mm in length, contains 200-450 ovules (Wylie 1917). Each flower is subtended by a spathe of two enveloping bracts and is born on a peduncle (scape) (Fig. 2). The peduncle increases its length by cell elongation thereby carrying the flower to the air-water interface for pollination.

Male inflorescences are submerged in the axils of leaves (Witmer 1937) (Fig. 2). Each inflorescence consists of approximately 2,000 flowers attached to a spadix and is surrounded by a spathe. Each flower is less than one millimeter in length and is composed of three sepals, one rudimentary petal, two stamens, and one staminodium (Wylie 1917). Upon maturity, the spathe curls back, the male flowers break from their pedicels, and they float to the surface before anthesis (Kaul 1970). Pollination takes place at the water surface. The peduncle contracts into a spiral following pollination, thus retracting the flower under water where fruit development occurs. During late summer or early fall, the gelatinous fruits rupture and release seeds which settle to the bottom (Kaul 1978).

Winter buds are produced at the thickened end of a stolon sector during late summer (Wilder 1974). Following winter bud formation, the remaining plant tissue degenerates, breaks off, and floats to shore (Titus and Adams 1979a).

Biomass and Productivity

According to Westlake (1965b) primary production is the weight of new organic matter synthesized by photosynthesis and chemosynthesis, or the energy this represents. Conversely, primary productivity is the rate at which new organic matter is synthesized (Odum 1971). Gross primary productivity is the total rate of organic matter produced, whereas net primary productivity is the amount of organic matter remaining after respiratory needs of the plant have been satisfied. Biomass is the weight of all living matter in a unit area at a given time (Wetzel 1975). If organic matter losses other than respiration are minimal, net productivity can be determined from differences in biomass over a period of time (Westlake 1969b).

Early quantitative studies of aquatic macrophytes investigated the relationships between V. americana and ecological variables such as water depth and sediment type. Rickett (1921, 1924) determined the biomasses and depths of various aquatic plants in Lake Mendota and Green Lake, Wisconsin, respectively. Bumby (1977) examined Green Lake and found that Myriophyllum spicatum, V. americana, and Potamogeton crispus had the largest relative biomass increases as compared to Rickett's study. Wilson (1935, 1937, 1941) investigated macrophytes, including V. americana, in several northeastern Wisconsin lakes. Relationships among dry matter, depth, sediment type, incident radiation, and wave action were reported. Andrews (1946) gave an account of vegetational changes in University Bay of Lake Mendota. He concluded that V. americana was evenly distributed over the bay, but it did not become dominant until August.

The partial replacement of V. americana with the nuisance Eurasian water milfoil (Myriophyllum spicatum) has led to recent investigations of some Madison lakes, Wisconsin. Lind and Cottam (1969) gathered frequently and community compositional data in Lake Mendota and found that Myriophyllum sp. composed 98% of the plant biomass. In contrast, Rickett (1921) and Denniston (1921) observed V. americana as the dominant macrophyte 50 years earlier. Similar patterns were noted in Lake Wingra. The vegetation once dominated by V. americana and Potamogeton spp. was found to be composed of Myriophyllum spicatum (Nichols and Mori 1971). Nichols (1971) did not report V. americana in his investigations of biomass in Wingra. The interaction between these two species is complex, and it now appears that V. americana may be regaining its position as an important species in Lake Wingra (Titus 1977).

Quantitative studies of aquatic macrophytes have only recently been conducted on the Upper Mississippi River. Sohmer (1975) studied frequency of occurrence and relative biomass of vegetation across the midsection of Navigation Pool Nos. 7 and 8. Sefton (1976) studied the biomass of aquatic plants in Navigation Pool No. 8. She found that V. americana was one of the most frequently occurring species. Furthermore, it composed 14.3% of the total biomass, second only to Sagittaria latifolia. Wile (1978) and Kawatski and Schall (1980) studied the effects of mechanical harvesting on V. americana in Lake Chemung, Ontario and Pool No. 7 of the Upper Mississippi River, respectively. Neither study found that mechanical harvesting caused significant decreases in V. americana biomass at subsequent sampling dates.

Some biomass and productivity studies utilize leaf area indices (LAI) and shoot:root (S:R) ratios as structural measurements of production. Leaf area index is defined as the surface area of live leaves (one side only) per unit area (Nicholson and Best 1974). According to Odum (1971), maximum net productivity is probably reached when LAI's = 4 (i.e. when the leaf surface exposed to light is 4 times the ground surface). Maximum gross production is obtained when LAI's = 8-10. Leaf area indices vary from 4-7 for herbaceous communities, 4-6 for deciduous forests, 7-8 in temperate evergreen forests and greater than 12 in tropical forests (Mooney 1972). Nicholson and Best (1974) and van der Valk and Bliss (1971) reported LAI's of 5-7 and 3-4, respectively, for aquatic plants.

Shoot:root biomass may be significant in a variety of ecological processes. Monk (1966) suggests that succession can be partly explained through root competition caused by a decrease in the S:R ratio. According to Mooney (1972), shoot:root ratios increased as light became limiting. Bray (1963) demonstrated an increase in the S:R ratio as plant age increased. Titus and Adams (1979a) determined shoot:root biomass as part of a competition study between V. americana and Myriophyllum spicatum in Madison lakes. They reported that below-sediment parts of submersed aquatic plants may function in anchoring, nutrient uptake, carbohydrate storage, and reproduction. Nicholson and Best (1974) measured shoot:root biomass for several plants including V. americana in Chautauqua lake. They found that the S:R ratio decreased in shallow water and increased as plant size increased.

Nutritive Quality

Net productivity and biomass determinations yield useful data for descriptive energetic studies and for comparing plant productivities. These measurements, however, neglect the nutritive quality of biomass in regard to herbivores. For general ecological purposes, the determination of crude protein (percent total nitrogen x 6.25) and non-cell wall material provides valuable information on the quality of plant biomass (Boyd and Goodyear 1971).

Proteins of primary producers are important in nutritive studies because they are considered to be essential compounds in the diets of herbivores. Approximately 80-90% of the nitrogen in plants is in the form of protein (Boyd and Goodyear 1971). Thus, crude protein can be used as an approximation of true protein (sum of amino acids) even though it may overestimate the latter by 10-20% (Boyd 1970).

Dry matter can be divided into cell wall (CWF) and non-cell wall (NCF) fractions. Cell wall material (neutral-detergent fiber) is composed primarily of hemicellulose, cellulose, and lignin (Van Soest and Wine 1967). This fraction is essentially not digestible for nonruminants and only partly available to ruminants. In contrast, the NCF consists of soluble carbohydrates, proteins, starches, lipids, and other soluble materials that are highly digestible (Van Soest 1967). In addition to nutritional availability, neutral-detergent fiber has been negatively correlated with voluntary intake by herbivores. For example voluntary intake decreases when dry matter consists of approximately 60% fiber (Van Soest and Marcus 1964, Van Soest 1965). According to Crampton (1938) and Van Soest (1966), the frequently cited crude fiber (CF) and nitrogen-free extract (NFE) methods of determining digestibility are inadequate.

Dry matter can be partitioned into inorganic (ash) and organic matter (Muztar et al. 1978a). Aquatic plants photosynthetically precipitate ash (primarily $CaCO_3$) and deposit it on surface tissues (Muztar et al. 1978c). This mechanism lowers the relative organic content and nutritional quality of the plant; consequently, herbivores must consume more plant material to meet their nutritional requirements (Muztar et al. 1978a). Caloric data alone supplies little information on nutritional value because only energy in the form of digestible nutrients are available to herbivores (Boyd and Goodyear 1971). Chemical analyses of V. americana have provided insight into the quality of its biomass. Birge and Juday (1922) and Schuette and Alder (1927) analyzed V. americana from Lake Mendota. They found similar ash concentrations but the crude protein content varied considerably. Gortner (1934) and Nelson and Palmer (1939) found high crude protein and low fiber concentrations in V. americana. Lathwell (1973) observed low levels of nitrogen and high ash concentrations in V. americana in artificial plant marshes. Gerloff and Krombholz (1966) found that nitrogen and phosphorous levels above 1.3 and 0.13% of the dry weight, respectively, represented luxury uptake by V. americana. Boyd and Blackburn (1970) discussed changes in nitrogen (crude protein) during the life history of macrophytes. Polisini and Boyd (1972) analyzed various macrophytes and plant organs for neutral-detergent fiber and nitrogen content. Linn et al. (1975) compared several nutritive variables including crude protein, ash, and neutral-detergent fiber among several aquatic plants and alfalfa. Muztar et al. (1976) fed diets composed of 5-10% V. americana to chickens. They found that the weight gain from this diet was similar to a corn-soybean mixture. Muztar et al. (1978b) determined differences between true and crude protein for numerous macrophytes including V. americana.

Vallisneria americana has usually been considered as an important food source for waterfowl. McAtee (1939) studied 19 species of wild ducks and found wild celery in their stomachs. Martin and Uhler (1939) examined stomachs of 7,998 ducks of 18 species throughout the United States and Canada. They found that V. americana accounted for approximately two percent of the food ingested, ranking it as the seventh most popular plant consumed. Vallisneria americana has often been associated with the canvasback duck Aythya valisineria. Kubichek (1933), Bellrose (1976) and Palmer (1976) reported that V. americana consisted of 10.8, 9.0, and 8.8%, respectively, of the food in canvasback stomachs. Martin et al. (1951) stated that _V. americana_ composed 25-50% of the _Aythya valisineria_ diet in the northeastern United States; however, wild celery was absent from the diet of canvasbacks elsewhere in the country. Bartonek (1968) and Bartonek and Hickey (1969) examined ducks from Manitoba, Canada and found that _Potamogeton_ spp. composed 71% of the esophageal contents of the autumn-collected canvasbacks. They concluded that, because of its wide distribution, _Potamogeton_ is a more important food for canvasbacks than _V. americana_. All parts of _V. americana_ are eaten by waterfowl, but the most frequently consumed organs are winter buds, leaves, and rootstocks.

METHODS AND MATERIALS

Field sampling was initiated on 28 May 1980 and continued through 3 October 1981. Samples collected from 28 May 1980 through 6 June 1981 were analyzed to determine biomass, productivity, shoot:root (S:R) ratios, and the nutritive quality of the plant organs. Samples taken from 30 June through 3 October 1981 were analyzed to determine the biomass of Vallisneria americana, leaf area indices, and additional nutritive data.

Field Methods

Vallisneria americana was sampled at monthly intervals during 1980, but it was sampled at bimonthly intervals during July, August, and September (Table 3). Sampling was terminated on 9 November 1980 and resumed on 12 April 1981. The final sampling date on which total biomass was determined was 6 June 1981. In addition V. americana rosettes were randomly collected on a monthly basis from 30 June to 3 October 1981 (Table 3).

Twenty initial samples were taken on 28 May 1980. From 27 June to 6 October 1980, and on 6 June 1981 approximately 40 samples were collected at 5 sites along each of 8 transects (Fig. 1). Sixteen randomly selected sites were sampled along the transects on 9 November 1980 and 12 April 1981. Each sample covered 0.17 m^2 and consisted of 10 subsamples (grabs) taken with an extended post hole digger. All sampling was

Table 3. Sample dates, sample size (N), and the <u>Vallisneria americana</u> collected, Navigation Pool No. 9, Upper Mississippi River, 1980-1981.

Date	N	Plant material
1980		
28 May	20	Total biomass and plant organs
27 June	40	Total biomass and plant organs
13 July	40	Total biomass and plant organs
29 July	40	Total biomass and plant organs
14 August	37	Total biomass and plant organs
1 September	40	Total biomass and plant organs
16 September	-[a]	Plant organs
6 October	36	Total biomass and plant organs
9 November	16	Total biomass (winter buds)
1981		
12 April	16	Total biomass (winter buds)
6 June	37	Total biomass and plant organs
30 June	-	Entire rosettes and plant organs[b]
31 July	-	Entire rosettes and plant organs[b]
10 August	-	Plant organs
28 August	-	Entire rosettes and plant organs[b]
3 October	-	Entire rosettes and plant organs[b]

[a] Samples were randomly taken throughout the study area.
[b] Entire nonmutilated rosettes were collected.

separated from sediment by sieving with a 6.4 mm mesh screen. All plant material was rinsed, placed in polyethene bags, and transported to the laboratory. Additional organs of V. americana were collected at various sites and were not included in the previously described samples. Depth measurements were taken at each site and sediment samples were collected on 29 July 1980. Voucher specimens of staminate and pistillate V. americana were pressed and deposited in the herbarium at the University of Wisconsin-La Crosse.

Laboratory Methods

Biomass. Samples were refrigerated for a maximum of 96 h before analysis (Jones and Steyn 1973). Plants were then placed on a 2 mm mesh screen and sprayed with a jet of water to rid them of soil, epiphytes, and animals (Westlake 1969a). Each sample was separated into photosynthetic (leaves, peduncles, fruits, and pistillate flowers) and nonphotosynthetic (winter buds, stolons, staminate inflorescences, and rootstocks) parts. Wet weights of all organs were determined on a triple beam balance to the nearest 0.1 g. Rosettes and winter buds were enumerated. Subsequently, samples were frozen to stop respiration and the resultant loss of biomass (Sefton 1976, Strodthoff 1978). Samples were thawed and placed in a force draft oven at 60-80° C for approximately 48 h or until a constant weight was obtained. Dry weights were determined on a top loading balance to the nearest 0.1 g, and biomass was reported as g dry weight per square meter (g/m^2).

Organ samples. Plant organs were refrigerated for a maximum of 24 h before they were processed. Separate samples of V. americana organs from each sampling date were counted and processed as previously described. Dry weights were determined to the nearest .01 g. Rootstocks were defined as the basal portion of the rosette including all roots (Fig. 2). All types of organs except for fruits were ground in a Wiley mill to pass a 40-mesh screen (.4 mm) (Jackson 1958). Fruits were triturated with a porcelain mortar and pestle because they obstructed the mill. All samples were then frozen until further analyses. In addition, the number of individual organs per plant were counted and weighed during 1981. Leaves were measured (L x W) for surface area determinations (Whitwer 1955). Early rosettes (initial rosettes produced from winter buds) and late rosettes (rosettes not produced from winter buds, but produced vegetatively during the growing season) were analyzed separately on 31 July 1981. All organ samples were redried at 65° C for 24 h prior to nutritive analyses.

Analytical Procedures

Crude protein. Percent crude protein was calculated as percent total nitrogen x 6.25 (Boyd and Goodyear 1971). Nitrogen from samples collected in 1980 was digested by the total Keldahl process and was analyzed with an NH_3 probe (EPA 1979). A 0.100 g sample was analyzed. Nitrogen in samples harvested in 1981 was digested and analyzed according to the total persulfate nitrogen (TPN) procedure (Smart et al. 1982). Samples sizes ranged from 20-60 mg.

Fiber. The cell wall fraction (CWF) was determined using the Neutral-detergent fiber procedure (Van Soest and Wine 1967). This procedure was modified for winter buds, stolons, staminate inflorescences, and pistillate flowers in the following manner. After the reflux step, the organs were cooled to 32° C, and a 0.2% diatase of malt solution

(Merck USP) was added for 30 min. The enzyme digested the starch that otherwise persisted and contaminated the extracted fiber. Sample size was approximately 0.5 g.

Ash. An organ sample was weighed, placed in a muffle furnace, and combusted at 500-550° C for six hours (Wood 1975). The amount of ash was reported as the weight of the material remaining after combustion. Sample size ranged from 0.5-2.0 g. The fiber ash content was determined by combustion at 500-550° C for three hours (Van Soest and Wine 1967).

Caloric content. Caloric values were determined with an adiabatic bomb calorimeter (Parr Instrument Co. 1968). Sample size ranged from 0.8-1.2 g. Unground organs were compressed in a pellet for analysis.

Grain size. Sediment was analyzed using a modified sieve-pipette procedure (Guy 1969). Results were expressed as the percentage of silt, sand, and clay in each sample. Sample size ranged from 5-20 g.

Analytical precision. A minimum of 35% of the samples for each nutritive variable were analyzed in triplicate (Table 4). Relative standard deviations (RSD's) among triplicate analyses ranged from .6% for caloric determinations to 8.4% for the Keldahl procedure.

Frozen and nonfrozen samples. During 1981, subsamples of *V. americana* organs were dried immediately (not frozen) to determine the effects of freezing on nutritive characteristics. Frozen samples yielded significantly greater fiber concentrations than nonfrozen organs (Table 5). In contrast, the crude protein and caloric content of both frozen and nonfrozen organs were not significantly different ($p<0.05$). Twenty-five percent of the ash samples were also significantly unequal.

Table 4. Analytical precision of four independent nutritive variables of Vallisneria americana, Navigation Pool No. 9, Upper Mississippi River, 1980-1981.

Variable	N[a]	$\bar{X}$ RSD[b]	percent of total samples done in triplicate
Neutral-detergent fiber	32	3.2	50
Crude protein			
TKN	39	8.4	100
TPN	25	4.8	92
Ash	41	2.8	65
Caloric content	15	.6	35

[a]Number of samples analyzed in triplicate.
[b]Mean relative standard deviations among triplicate subsamples.

Table 5. A direct pairwise comparison between frozen and nonfrozen samples of <u>Vallisneria americana</u> organs, 1981.

Variable	Frozen $\bar{x}^a$ (% dry weight)	Frozen CI	Frozen RSD (%)	Nonfrozen $\bar{x}^a$ (% dry weight)	Nonfrozen CI	Nonfrozen RSD (%)
<u>Neutral-detergent fiber N=8</u>						
Leaves						
6-6[b]	33.5	.98	1.2	29.6	2.0	2.7
7-31[b]	38.8	1.2	1.3	34.5	2.1	2.8
Stolons						
6-6[b]	32.6	1.7	2.1	28.8	1.9	2.6
7-31[b]	40.0	2.9	2.9	35.1	2.9	3.3
Winter buds						
6-6	14.9	1.3	3.6	15.7	1.2	3.2
Fruits						
7-31	15.0	.4	1.1	14.5	1.7	4.6
Peduncles						
7-31[b]	37.7	1.1	1.2	30.7	1.2	1.6
Rootstocks						
7-31[b]	42.3	2.6	2.5	37.6	1.6	1.7
<u>Crude protein N=8</u>						
Leaves						
6-6	21.8	1.6	3.0	24.6	3.2	5.3
7-31	17.9	2.4	5.4	17.7	.86	2.0
Stolons						
6-6	19.6	1.7	3.5	19.2	.86	1.8
7-31	14.1	2.4	6.9	12.5	1.5	4.8
Winter buds						
6-6	10.8	1.7	6.4	13.1	1.6	5.0
Fruits						
7-31	14.4	1.5	4.2	14.6	2.3	6.3
Peduncles						
7-31	13.4[c]	12.1	-[d]	12.8[c]	20.3	-
Rootstocks						
7-31	13.6	2.4	7.2	12.9	2.0	5.8
<u>Ash N=7</u>						
Leaves						
6-6	23.5	1.4	2.4	22.7	3.1	5.5
7-31	24.3	1.0	1.7	25.0	.3	.5
Stolons						
6-6[b]	16.5	.2	.6	14.8	1.1	3.1
Winter buds						
6-6	7.9[c]	.3	-	7.4[c]	7.3	-
Fruits						
7-31	9.9	1.2	5.1	9.2	.2	.8
Peduncles						
7-31[b]	18.3	.4	.8	22.2	.1	.2
Rootstocks						
7-31	27.6	5.8	8.4	31.9	5.1	6.4
<u>Caloric content N=3</u>	<u>calories/g</u>					
Leaves						
6-6	3,628.4	100.6	1.1	3,577.7	55.6	.6
Stolons						
6-6	3,688.6[c]	112.6	-	3,701.7[c]	60.2	-
Winter buds						
6-6	3,965.9	60.0	.6	3,957.1	68.4	.7

[a]Values are the means of triplicate analyses.

[b]The means of frozen samples are significantly different than nonfrozen samples ($p < .05$).

[c]Values are the means of duplicate analyses.

[d]-No RSD because N=1.

Data Analysis

The percent dry weight of the total biomass and individual plant organs were determined from the following expression:

$$\text{Dry weight (\%)} = \frac{\text{dry weight}}{\text{wet weight}} \times 100$$

Productivity was determined as the change in biomass over a period of time (Westlake 1963).

$$\text{Net productivity} = \frac{B}{T}$$

where B: change in biomass (B_2-B_1)

T: number of days between T_1 and T_2

Shoot:root ratios were determined according to Titus and Adams (1979a), except for male inflorescences which were considered part of the root biomass in this study. The following expression was used:

$$\text{Shoot:root (S:R) ratio} = \frac{\text{photosynthetic biomass}}{\text{nonphotosynthetic biomass}}$$

The leaf surface area was determined by the following relationships:

$$LSA_m = LSA_l \times L_r \times R_m$$

where LSA_m: mean leaf surface area per square meter

LSA_l: mean leaf surface area per leaf

L_r: mean No. of leaves per rosette

R_m: mean No. of rosettes per square meter

The mean leaf surface area/m^2 was used to estimate the leaf area index (LAI).

$$LAI = \frac{\text{surface area of leaves (one side only)}}{\text{unit area}}$$

The biomass of a plant organ (g/m^2), on a specific sampling date during 1981, was estimated by the following expression:

$B_o = B_p \times B_t$

where B_o: estimated organ biomass (g/m^2) on a specific sampling date (1980)

B_p: percentage an organ composed of the total biomass on that sampling date (1980)

B_t: total biomass (g/m^2) on that sampling date (1980)

Some of the organ percentages (B_p) were determined from similar sampling dates a year later (1981). Therefore:

$B_o = B_p1 \times B_t$

where B_o: estimated organ biomass (g/m^2) on a specific sampling date (1980)

B_p^1: percentage an organ composed of the total biomass, on a similar sampling date, a year later (1981)

B_t: total biomass (g/m^2) on the specific sampling date (1980)

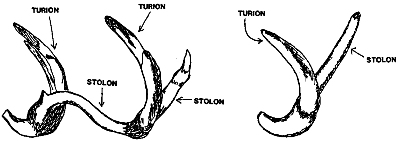
Winter buds. Winter bud estimations (turion, stolon, and a portion of the stolon that produced the turion) were made by counting the number of both rosettes and winter buds in late May 1980 and early June 1981 (Fig. 3). It was estimated that 79.3% of the winter buds, at each sampling site were being harvested. The total number of winter buds were estimated by the following expression:

$$\text{Total No. of winter buds} = \frac{\text{No. of winter buds recovered} \times 100}{79.3}$$

The mean winter bud biomass (g/m^2) was determined by the following:

$B_{wb} = DW_{wb} \times N_{wb}$

Fig. 3. A schematic diagram of _Vallisneria americana_ winter buds.



TWO WINTER BUDS BORNE ON THE SAME STOLON

ONE WINTER BUD

WINTER BUDS

where B_{wb}: mean winter bud biomass (g/m^2)

DW_{wb}: mean dry weight per winter bud

N_{wb}: mean number of winter buds per square meter

The non-cell wall fraction (NCF) was determined from fiber concentrations.

Non-cell wall fraction (%) = 100 - fiber content (%)

Organic matter was calculated from the ash content.

Organic matter (%) = 100 - ash (%)

Nutritive parameters (g/m^2) for the total V. americana biomass were estimated from organ analyses from samples taken on a monthly basis.

Ash-free (organic) fiber and NCF were determined by subtracting the ash content from both variables. Therefore:

Ash-free (organic) fiber (%) + ash-free (organic) NCF (%) + ash (%) = 100.

Ash-free crude protein and ash-free caloric content were determined by the following:

$$\text{Ash-free crude protein (\%)} = \frac{\text{crude protein (\%)}}{\text{organic matter (\%)}} \times 100$$

$$\text{Ash-free caloric content (cal/g)} = \frac{\text{calories/g}}{\text{organic matter (g)}} \times 100$$

Relative standard deviations (RSD), confidence intervals, t-tests, and correlations were determined according to standard procedures.

RESULTS

Biomass and Productivity

Vallisneria americana was characterized by a high moisture content. During 1980, photosynthetic (shoot) biomass contained an average of 7.7% dry matter (92.3% water) (Appendix II). In contrast, dry matter concentrations were greater in the nonphotosynthetic (root) biomass and ranged from a minimum of 8.3% of the wet weight in August to a maximum of 26.6% in November.

Vallisneria americana production was low early in the growing season. By mid-summer net primary productivity had increased, and it reached the maximum of 3.2 $g \cdot m^{-2} \cdot d^{-1}$ during the latter half of July (Fig. 4). Growth continued and the maximum seasonal biomass of 217.3 g/m^2 was observed on 1 September (Table 6 and Fig. 5). Both photosynthetic and nonphotosynthetic biomass peaked with the maximum biomass on 1 September. Total productivity from 28 May to 1 September averaged 2.2 $g \cdot m^{-2} \cdot d^{-1}$. The greatest rate of shoot production was 2.9 $g \cdot m^{-2} \cdot d^{-1}$, and it occurred from late June to mid-July. The maximum nonphotosynthetic production rate of 0.9 $g \cdot m^{-2} \cdot d^{-1}$ was observed from mid-August to early September (Fig. 4). Senescence and death were evident from 1 September through 9 November. The photosynthetic biomass was lost at a rate of 2.6 $g \cdot m^{-2} \cdot d^{-1}$. Root biomass losses were less, and approximately 20 g/m^2 overwintered in the sediment.

Variation among biomass samples (g/m^2) for any given sampling period was high (Table 6). Relative standard deviations (RSD) usually

Fig. 4. Total productivity, photosynthetic productivity, and nonphotosynthetic productivity of Vallisneria americana, Navigation Pool No. 9, Upper Mississippi River, 1980-1981.

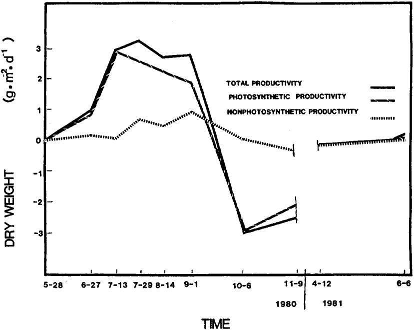
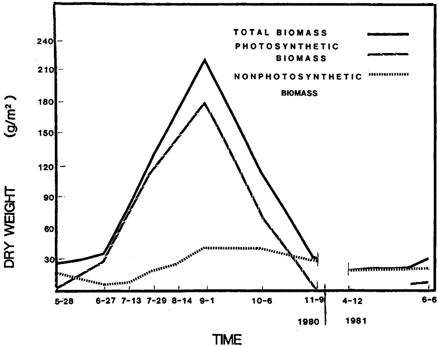

DRY WEIGHT (g·m⁻²·d⁻¹)
3
2
1
0
-1
-2
-3
TOTAL PRODUCTIVITY
PHOTOSYNTHETIC PRODUCTIVITY
NONPHOTOSYNTHETIC PRODUCTIVITY
5-28
6-27
7-13
7-29
8-14
9-1
10-6
11-9
4-12
6-6
1980
1981
TIME

Table 6. The biomass (g/m^2) of Vallisneria americana, Navigation Pool No. 9, Upper Mississippi River, 1980-1981.

	1980								1981	
Date	5-28	6-27	7-13	7-29	8-14	9-1	10-6	11-9	4-12	6-6
N	20	40	40	40	37	40	36	16	16	37
Total biomass	20.9	42.4	86.3	131.9	173.6	217.3	113.4	30.3	20.0	27.3
Total biomass without winter buds from previous growing season	7.2	35.9	80.3	129.1	169.9	217.3	113.4	30.3	20.0	10.9
Photosynthetic biomass	4.1	28.6	72.0	111.0	144.5	176.6	73.1	1.9	-[a]	6.7
RSD (%)	53.7	61.9	58.9	46.6	53.9	38.5	62.5	277.5	-	85.7
Nonphotosynthetic biomass	16.8	13.7	14.2	20.9	29.1	40.7	40.3	28.4	20.0	20.6
RSD (%)	72.2	87.0	55.6	48.2	48.9	35.2	37.1	63.8	48.1	79.6
Nonphotosynthetic biomass without winter buds from previous growing season	3.1	7.2	8.3	18.1	25.4	40.7	40.3	28.4	20.0	4.1

[a]-No photosynthetic biomass was present.

Fig. 5. Total biomass, photosynthetic biomass, and nonphotosynthetic biomass (including old winter buds from the previous growing season) of *Vallisneria americana*, Navigation Pool No. 9, Upper Mississippi River, 1980-1981.



TOTAL BIOMASS
PHOTOSYNTHETIC BIOMASS
NONPHOTOSYNTHETIC BIOMASS
DRY WEIGHT (g/m²)
240
210
180
150
120
90
60
30
5-28
6-27
7-13
7-29
8-14
9-1
10-6
11-9
4-12
6-6
1980
1981
TIME

ranged from 35-87%. Variation among the 10 subsamples (grabs) that constituted a sample were also considerable (Table 7). The mean RSD's ranged from 59.7-79.8% for photosynthetic and nonphotosynthetic biomass, respectively.

Maximum shoot production rates were coincident with minimum root productivities, and both occurred during June and July. The result was an increase in S:R ratios from 1.3 in late May to 8.7 in mid-July (Fig. 6). A subsequent decrease of the ratio to 4.3 by 1 September was largely due to vegetative reproduction and winter bud formation. No ratio was calculated for 12 April 1981, because all of the overwintering biomass was nonphotosynthetic. Shoot:root ratios were considerably lower from May through mid-July when overwintering buds from the previous season were included in the S:R calculations (Fig. 6). At the end of July, greater mean concentrations of nonphotosynthetic (root) biomass were found in shallow portions (depth $\leq$ 1 m, sandy sediments) of the study area when compared to deeper regions (water > 1 m, clay and silt sediments) (Table 8). In contrast, concentrations of photosynthetic biomass were similar in both deep and shallow areas during that time. Conversely, by 1 September, greater concentrations of photosynthetic biomass were found in deep portions of the study area, whereas nonphotosynthetic biomass were similar in both deep and shallow regions. Consequently, a positive correlation between the shoot:root ratio and depth was observed from 29 July to 1 September (Table 8).

Approximately 80 rosettes/m^2 were found on 28 May 1980 (Table 8). Following vegetative reproduction during the summer, rosettes reached a maximum concentration of 214/m^2 on 1 September. A negative correlation was observed between the number of late rosettes produced in July

Table 7. Percent relative standard deviation (%RSD) of photosynthetic and nonphotosynthetic biomass among 10 grabs comprising a sample.

Date	Sample Site	Photosynthetic biomass (%RSD)	Nonphotosynthetic biomass (%RSD)
June 27	23	38.3	107.5
	9	83.0	95.6
July 13	1	89.4	81.2
	10	71.0	134.9
July 29	11	45.1	64.4
	25	47.1	66.5
August 14	10	43.2	92.8
	27	40.3	35.2
September 1	26	56.5	57.6
	8	64.2	86.7
October 6	26	89.8	78.1
	34	48.7	56.9
Mean		59.7	79.8

Fig. 6. Shoot:root (S:R) ratios of _Vallisneria americana_ with and without old winter buds (produced in the previous growing season) included in the root biomass, Navigation Pool No. 9, Upper Mississippi River, 1980-1981.

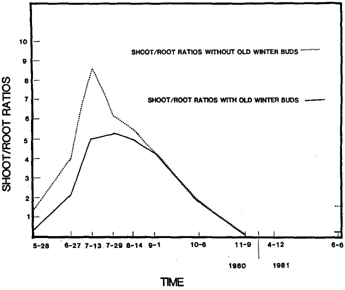

SHOOT/ROOT RATIOS WITHOUT OLD WINTER BUDS
SHOOT/ROOT RATIOS WITH OLD WINTER BUDS
SHOOT/ROOT RATIOS
10
9
8
7
6
5
4
3
2
1
5-28
6-27
7-13
7-29
8-14
9-1
10-6
11-9
4-12
6-6
1980
1981
TIME

Table 8. Rosette number and biomass in deep (water > 1 m, clay and silt sediments) and shallow (water ≤ 1 m, sand sediments) regions of the study area, leaf area indices (LAI), and correlation coefficients (r) between shoot:root ratios and water depth and between number of rosettes and water depth for *Vallisneria americana*, Navigation Pool No. 9, Upper Mississippi River, 1980-1981.

	1980								1981	
Date	5-28	6-27	7-13	7-29	8-14	9-1	10-6	11-9	4-12	6-6
N	20	40	40	40	37	40	36	16	16	37
No. of rosettes/m^2	80	82	138	212	197	214	122	trace	0	96
No. of rosettes/m^2 (depth ≤ 1 m)	–[a]	91	187	300	243	266	–[b]	–[b]	0	126
No. of rosettes/m^2 (depth > 1 m)	–[a]	64	113	129	183	157	–[b]	–[b]	0	78
No. of late rosettes/m^2 (depth ≤ 1 m)	0	0	92	–[c]	–[c]	–[c]	–[b]	–[b]	0	0
No. of late rosettes/m^2 (depth > 1 m)	0	0	33	–[c]	–[c]	–[c]	–[b]	–[b]	0	0
r between rosette No. and depth	–[a]	-0.38[d]	-0.51[d] -0.62[e]	-0.68[d]	-0.56[d]	-0.74[d]	–[b]	–[b]	–[f]	–[c]
Photosynthetic biomass/m^2 (depth ≤ 1 m)	–[a]	–[c]	–[c]	118.5	102.8	149.3	–[b]	–[b]	0	–[c]
Photosynthetic biomass/m^2 (depth > 1 m)	–[a]	–[c]	–[c]	109.8	174.3	206.8	–[b]	–[b]	0	–[c]
Nonphotosynthetic biomass g/m^2 (depth ≤ 1 m)[h]	–[a]	–[c]	–[c]	25.6	30.2	38.3	–[b]	–[b]	–[g]	–[c]
Nonphotosynthetic biomass g/m^2 (depth > 1 m)[h]	–[a]	–[c]	–[c]	14.5	23.2	37.2	–[b]	–[b]	–[g]	–[c]
r of shoot:root ratio and depth	–[a]	–[c]	–[c]	+0.80	+0.78	+0.59	–[b]	–[b]	–[g]	–[c]
Leaf area indices	–[c]	4	–[c]	8	–[c]	17	–[b]	–[b]	–[c]	< 1

[a]-The depth was primarily > 1 m.

[b]-Values were not determined because of biomass loss.

[c]-Values were not determined.

[d]r between total rosettes and depth, ($p < .05$).

[e]r between late rosettes and depth, ($p < .05$).

[f]-No rosettes were present in the biomass.

[g]-Only winter buds were present in the biomass.

[h]Values are not adjusted for winter buds missed during sampling.

and water depth ($r = -0.62$, $p < 0.05$). The maximum correlation between total rosette density and depth was observed on 1 September 1980 ($r = -0.74$, $p < 0.05$). The number of leaves per rosette also increased during the growing season. An average of 6 leaves/plant were produced in spring which increased to 13 in late August, 1981. Increases in numbers of leaves and rosettes paralleled increases in leaf area indices. Leaf area indices ranged from 1 in early June 1981 to 17 on 1 September 1980 (Table 8).

Organ Biomass

Leaves, rootstocks, stolons, peduncles, pistillate flowers, and staminate inflorescences averaged less than 8% dry matter during 1980 (Appendix III). In contrast, the average dry matter of winter buds and fruits were 24.8 and 12%, respectively.

Leaves constituted 60-70% of the biomass (dry weight) from late June to early October (Table 9). The maximum leaf standing crop of 146.7 g/m^2 was sampled on 1 September (Fig. 7). The greatest leaf productivity (2.9 $g \cdot m^{-2} \cdot d^{-1}$) was observed from late June to mid-July when foliage accounted for 100% of the photosynthetic biomass (Fig. 4). By 9 November, leaves could only be collected from sheltered areas adjacent to islands. At that time only 1.9 g/m^2 was observed.

Maximum winter bud biomass (30.1 g/m^2) occurred on 6 October 1980 (Fig. 7). A maximum of 158 buds/m^2 were observed at that time. Winter bud density declined to approximately 105 per square meter by 12 April 1981 (Fig. 8). The largest decrease occurred after 9 November 1980. Buds composed 100% of the winter biomass (Table 9). After breaking

Table 9. The percentage contribution of each organ to the total Vallisneria americana biomass, Navigation Pool No. 9, Upper Mississippi River, 1980-1981.

	1980						1981	
Date	5-28	6-27	7-29	9-1	10-6	11-9	4-12	6-6
Organs								
Leaves	19.5	67.6	70.8[a]	67.5[a]	61.6[a]	6.3	-[b]	26.2
Winter buds	65.5	15.5	2.2	5.9	26.5	91.4	100	55.5
Rootstocks	-	14.4[a]	11.4[a]	7.3[a]	3.8[a]	2.32[c]	-	-
Stolons	15.0[d]	2.6[a]	2.7[a]	4.1[a]	5.2[a]		-	18.3[d]
Fruits	-	-	5.3[a]	10.9[a]	2.5[a]	-	-	-
Peduncles	-	-	4.9[a]	4.2[a]	.4[a]	-	-	-
Staminate inflorescences	-	-	2.1[a]	0.1[a]	-	-	-	-
Pistillate flowers	-	-	0.6[a]	-	-	-	-	-

[a]Percentages from 1980 that were estimated from 1981 samples (See materials and methods).
[b]-Specific organ not present in biomass.
[c]Percentage represents the summation of rootstocks and stolons.
[d]Represents stolons growing directly from winter buds.

Fig. 7. Estimated biomass of winter buds, leaves, and other organs of *Vallisneria americana* on 8 select sampling dates, Navigation Pool No. 9, Upper Mississippi River, 1980-1981.

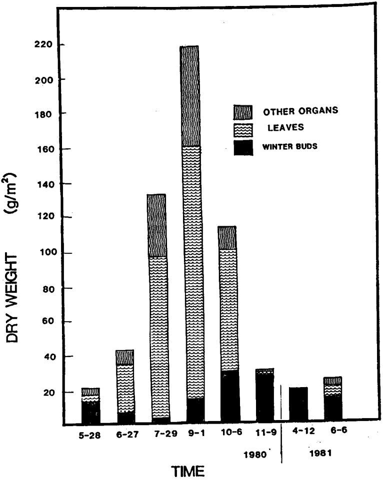
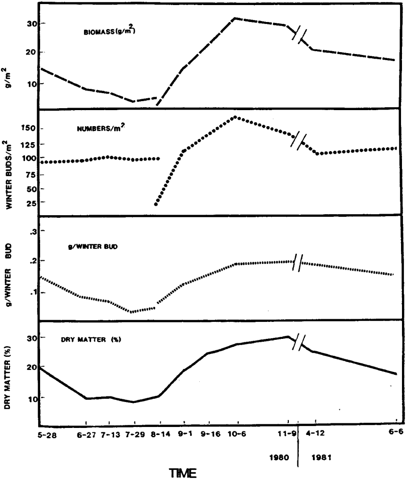

220
200
180
160
140
120
100
80
60
40
20
DRY WEIGHT (g/m²)
OTHER ORGANS
LEAVES
WINTER BUDS
5-28
6-27
7-29
9-1
10-6
11-9
4-12
6-6
1980
1981
TIME

Fig. 8. Biomass, density, and percent dry matter fluctuations for winter buds of *Vallisneria americana*, Navigation Pool No. 9, Upper Mississippi River, 1980-1981.


BIOMASS (g/m²)
g/m²
30
20
10
NUMBERS/m²
WINTER BUDS/m²
150
125
100
75
50
25
g/WINTER BUD
g/WINTER BUD
.3
.2
.1
DRY MATTER (%)
DRY MATTER (%)
30
20
10
5-28
6-27
7-13
7-29
8-14
9-1
9-16
10-6
11-9
4-12
6-6
1980
1981
TIME

accounted for only 2.2% (2.8 g/m^2) of the total biomass observed at the end of July. The dry matter of winter buds increased with maturity. The minimum dry matter concentration (18.7%) was observed on 1 September 1980, and the maximum (29.5%) occurred on 9 November (Fig. 8 and Table 13). The mean biomass of individual winter buds increased from 0.06 g in mid-August to 0.20 g in November.

Rootstocks were not sampled until 27 June 1980. The maximum rootstock biomass was coincident with peak biomass on 1 September and only a trace remained by 9 November. Rootstocks composed a maximum of 14.4% of the plant material on 27 June. A steady decline in the relative contribution of rootstocks to the total biomass was observed during the remainder of the growing season (Table 9).

The stolons of V. americana that were formed from winter buds composed 15% of the biomass in late May. In contrast, stolons that were produced during vegetative reproduction later in the summer rarely constituted over 5% of the total crop. Furthermore, they never exceeded a biomass of 9 g/m^2. On the average, each rosette had 2.5 stolons at the end of August.

Maximum fruit biomass was observed on 1 September and made-up 10.9% of the total plant biomass at that time. During fruit development, the dry matter of fruits increased from 9.5 to 14.3%. The biomass of each fruit increased from 0.04 to 0.30 g during the same period (Appendix III). Other organs associated with flowering (peduncles, staminate inflorescences, and pistillate flowers) did not exceed a biomass of 10 g/m^2 when analyzed individually. Collectively, these organs rarely accounted for over 7% of the total V. americana biomass. Pistillate plants contained an average of 4.3 peduncles with attached flowers.

Approximately one-half of the pistillate flowers had developed into fruits by 31 July 1981. By the end of August, receptive pistillate flowers were no longer observed; only peduncles with mature fruits were evident. Staminate plants collected on 31 July contained an average of 5.7 inflorescences. All inflorescences had opened and released their flowers by the end of August.

Nutritive Quality

Ash. Annual mean ash concentrations of winter buds and leaves ranged from 4.7% to 29.1%, respectively (Table 10 and 13). Leaves contained the greatest ash concentrations (38.7%) in mid-July. Staminate inflorescences, stolons, peduncles, and rootstocks contained mean annual ash concentrations that ranged from 17 to 25.4% of the dry matter. Ash composed less than 12% of the biomass in the remaining organs. Ash levels of most organs fluctuated during the growing season.

Fiber and non-cell wall fractions. Leaves, rootstocks, stolons, and peduncles had the greatest fiber concentrations (Table 11). Means ranged from 33-40% of the dry weight. Fiber comprised 14-22% of the dry weight of the other organs. Most of the fiber contained less than 10% ash (Appendix IV). Therefore, the potentially digestible non-cell wall fraction (NCF) contained the majority of the nondigestible ash (Table 11). The non-cell wall fractions are reported below on an ash-free dry weight basis. Winter buds and reproductive structures contained the most non-cell wall material (Tables 10, 12, and 13). Overwintering buds contained a relatively constant NCF and averaged 82.2% of the dry weight. A decrease in the NCF was paralleled by an increase in ash and fiber concentrations. This was due to decomposition that occurred the

Table 10. Some nutritive variables of Vallisneria americana organs, Navigation Pool No. 9, Upper Mississippi River, 1980[a]

Date	5-28	6-27	7-13	7-29	8-14	9-1	9-16	10-6	$\bar{X}$	RSD (%)
Leaves										
Ash (%)	23.7	36.3	38.7	30.6	27.5	22.9	24.5	28.2	29.1	20.1
Ash-free NCF (%)	54.5	37.0	31.6	34.4	37.7	39.8	41.4	39.8	39.5	17.3
Ash-free fiber (%)	21.8	26.7	29.7	35.0	34.8	37.2	34.1	32.0	31.4	16.3
Rootstocks										
Ash (%)	-[b]	26.6	31.6	30.0	20.2	19.1	23.7	26.7	25.4	18.5
Ash-free NCF (%)	-	42.4	31.6	33.4	39.0	40.0	41.6	34.0	37.4	11.7
Ash-free fiber (%)	-	31.0	36.8	36.7	40.8	40.9	34.7	39.3	37.2	9.6
Stolons										
Ash (%)	12.7	17.1	21.5	20.1	17.2	15.9	22.0	25.1	19.0	21.0
Ash-free NCF (%)	64.5	55.7	41.5	41.3	51.7	54.7	45.0	41.4	49.5	17.3
Ash-free fiber (%)	22.8	27.1	37.0	38.6	31.1	29.4	33.0	33.4	31.6	16.3
Fruits										
Ash (%)	-	-	-	9.3[c]		8.2	8.6	8.4	8.6	5.9
Ash-free NCF (%)	-	-	-	77.3		72.1	75.9	77.4	75.7	3.3
Ash-free fiber (%)	-	-	-	13.4		19.7	15.6	14.2	15.7	18.0
Peduncles										
Ash (%)	-	-	-	20.1		20.8[d]		23.9	21.6	9.3
Ash-free NCF (%)	-	-	-	45.8		45.2		40.2	43.8	7.1
Ash-free fiber (%)	-	-	-	34.1		34.0		36.0	34.7	3.2

[a] All data was derived from either triplicate, duplicate or single analyses.

[b] -Specific organs were not present in biomass.

[c] Fruits from 7-29 and 8-14 were combined for analyses.

[d] Peduncles from 9-1 and 9-16 were combined for analyses.

Table 11. The neutral-detergent fiber and non-cell wall fraction (NCF) contents on a dry weight basis, of Vallisneria americana organs, Navigation Pool No. 9, Upper Mississippi River, 1980-1981.

	Fiber		NCF	
Organ	Mean	Range	Mean	Range
Leaves N=8	34.0	23.5-39.5	66.0	60.5-76.5
Rootstocks N=7	40.3	32.8-43.4	60.7	56.6-67.2
Stolons N=8	33.0	24.0-40.1	67.0	59.9-76.0
Winter buds N=5	13.8	11.5-17.2	86.2	82.8-88.5
Peduncles N=3	36.0	35.2-37.3	64.0	62.7-64.8
Fruits N=4	16.4	14.4-20.2	83.6	79.8-85.6
Pistillate flowers N=2	21.0	17.2-24.9	79.0	75.1-82.8
Staminate inflorescences N=2	22.2	20.2-24.3	77.8	75.7-79.8

[a]Samples were taken during 1980.

[b]Sampled from 1 September 1980 through 12 April 1981.

[c]Samples were taken during 1980 and 1981.

Table 12. Some nutritive variables of <u>Vallisneria americana</u> flowers and inflorescences, Navigation Pool No. 9, Upper Mississippi River, 1980-1981.

	1980	1981	$\bar{X}$
<u>Pistillate flowers</u>[a]			
Ash (%)	12.2	11.3	11.8
Ash-free NCF (%)	72.8	65.3	69.0
Ash-free fiber (%)	15.0	23.4	19.2
Crude protein (%)	14.9	17.3	16.1
Crude protein (% ash-free dry weight)	17.0	19.5	18.2
<u>Staminate inflorescences</u>[a]			
Ash (%)	-[b]	17.1	
Ash-free NCF (%)	63.9[c]	60.1	62.0
Ash-free fiber (%)	19.0[c]	22.8	20.9
Crude protein (%)	19.2	24.5	21.8
Crude protein (% ash-free dry weight)	-	29.5	

[a]N=1 composite sample taken at different times during flowering.
[b]-No sample was analyzed.
[c]Estimated using ash concentrations from 1981.

Table 13. Nutritive data of winter buds for Vallisneria americana, Navigation Pool No. 9, Upper Mississippi River, 1980-1981.[a]

	1980								1981								
Date	5-28	6-27	7-13	7-29	9-1	9-16	10-6	11-9	4-12	6-6	6-30	7-31[b]	8-10	8-28	10-3	$\bar{x}$[c]	RSD[c] (%)
Dry matter (%)[d]	19.2	9.5	9.6	7.9	18.7	24.0	27.2	29.5	24.5	16.9	9.0	7.2	13.2	19.6	27.0	24.8	16.4
Ash (%)	7.3	21.3	25.9[e]		6.2	4.7	4.0	4.2	4.6	7.9	-[f]	24.6	7.3	4.8	-	4.7	18.2
Ash-free NCF (%)	82.4	51.2	47.4		77.6	80.2	83.9	84.7	84.7	78.3	-	42.2	73.7	78.3	-	82.2	3.9
Ash-free fiber (%)	10.3	27.5	26.7		16.2	15.0	12.1	11.1	10.7	13.8	-	33.2	19.0	16.9	-	13.0	18.9
Fiber (% of dry weight)	11.2	30.3	29.0		17.2	16.0	12.7	11.9	11.5	14.9	-	36.6	20.0	17.6	-	13.8	18.5
Crude protein (%)	11.8	11.8	10.6		10.2	8.3	9.4	9.1	12.6	10.9	-	10.9	12.4	11.0	-	9.9	16.8
Crude protein (% ash-free dry weight)	12.7	15.0	14.2		10.9	8.7	9.8	9.5	13.2	11.9	-	14.4	13.4	11.6	-	10.4	16.9
Calories (cal/g dry weight)	-	-	-		3,929	3,977	3,970	4,026	3,985	3,965	3,436	2,250	3,907	3,989	-	3,978	.9
Calories (cal/g ash-free dry weight)	-	-	-		4,188	4,172	4,133	4,204	4,178	4,305	-	2,984	4,214	4,190	-	4,175	.6

[a]All data was derived from either triplicate, duplicate or single sample analyses.

[b]Values are for winter buds decomposing from 30 June through 10 August 1981.

[c]Values were calculated for samples taken 1 September 1980 through 4 April 1981.

[d]A minimum of 20 winter buds were analyzed.

[e]Winter buds from 13 July to 29 July were combined for analyses.

[f]-Values were not determined.

following summer (Fig. 9). Fruits also had large NCF's, averaging 75.7% of the dry weight. The NCF concentrations in stolons reached a maximum of 64.5% in late May and a minimum of 41.3% in July, 1980 (Table 10). Minimum NCF's were in organs with great ash and fiber concentrations. Leaves, rootstocks, and peduncles had annual mean NCF's of 39.5, 37.4, and 34.7%, respectively. Young leaves, however, reached a maximum NCF of 54.5% in late May.

Crude protein. Vallisneria americana harvested during the summer of 1980 and 1981 ranged from 6.3% crude protein (CP) in stolons to 24.5% in male inflorescences (Tables 12 and 14). Annual averages for samples taken in 1980 ranged from 9.3% crude protein in peduncles to 16% in leaves. Crude protein concentrations of leaves and stolons decreased from May through September 1980. Protein content in rootstocks, however, fluctuated throughout the growing season. Winter buds, peduncles, and fruits remained relatively constant. The annual mean concentration of ash-free crude protein in leaves was 22.7%. New winter buds harvested from 1 September 1980 through 12 April 1981 contained the minimum of 10.4% ash-free CP.

Caloric content. Caloric content of the plant organs ranged from a mean of 3,276 cal/g in peduncles to 4,318 cal/g in staminate inflorescences (Table 15). Reproductive structures and winter buds had greater caloric value than other organs. Leaves and stolons contained more calories in early summer 1981 than later in the growing season of 1980 (Appendix V). Winter buds sampled from September 1980 through April 1981 averaged 3,979 cal/g (Tables 13 and 15). During decomposition the

Fig. 9. Ash-free non-cell wall fraction (NCF), ash-free neutral-detergent fiber, and ash content fluctuations for winter buds of *Vallisneria americana*, Navigation Pool No. 9, Upper Mississippi River, 1980-1981.

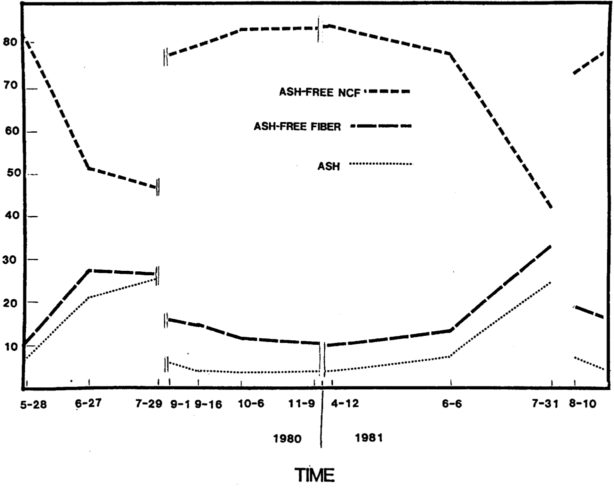

ASH-FREE NCF
ASH-FREE FIBER
ASH
80
70
60
50
40
30
20
10
5-28
6-27
7-29
9-1
9-16
10-6
11-9
4-12
6-6
7-31
8-10
1980
1981
TIME

Table 14. Crude protein content of _Vallisneria americana_ organs, Navigation Pool No. 9, Upper Mississippi River, 1980[a]

Date	5-28	6-27	7-13	7-29	8-14	9-1	9-16	10-6	$\bar{X}$	RSD (%)
Leaves										
Crude protein (%)	21.4	16.4	16.0	14.4	16.5	15.8	14.0	13.5	16.0	15.5
Crude protein (% ash-free dry weight)	28.1	25.8	26.1	20.7	22.8	20.4	18.5	18.8	22.7	16.0
Rootstocks										
Crude protein (%)	-[b]	12.8	10.4	12.8	14.1	11.3	8.0	14.0	11.9	18.2
Crude protein (% ash-free dry weight)	-	17.4	15.3	18.2	17.6	14.0	10.5	19.1	16.0	18.8
Stolons										
Crude protein (%)	17.1	16.0	13.2	9.4	10.6	6.9	6.3	9.4	11.1	35.8
Crude protein (% ash-free dry weight)	19.5	19.3	16.9	11.7	12.8	8.2	8.1	12.5	13.6	33.1
Fruits										
Crude protein (%)	-	-	-		12.2[c]	11.8	12.1	10.9	11.7	4.8
Crude protein (% ash-free dry weight)	-	-	-		13.4	12.8	13.2	11.9	12.8	5.1
Peduncles										
Crude protein (%)	-	-	-		11.5[c]		7.4[d]	9.2	9.4	21.7
Crude protein (% ash-free dry weight)	-	-	-		14.4		9.4	12.1	12.0	20.9

[a]All values are means of triplicate analyses.

[b]-Specific organs were not present in biomass.

[c]Samples from 7-29 and 8-14 were combined for analyses.

[d]Samples from 9-1 and 9-16 were combined for analyses.

Table 15. The mean caloric content of Vallisneria americana organs, Navigation Pool No. 9, Upper Mississippi River, 1980-1981.

Organ	$\bar{X}$ cal/g dry weight	RSD (%)	$\bar{X}$ cal/g ash-free dry weight	RSD (%)
Leaves N=7	3,389.2	5.9	4,488.0	4.2
Rootstocks N=4	3,416.4	4.9	4,488.9	3.3
Stolons N=6	3,394.4	8.5	4,154.7	5.2
Winter buds[a] N=5	3,977.6	.9	4,175.2	.6
Peduncles N=3	3,276.4	5.9	4,143.8	2.8
Fruits N=3	4,228.1	3.6	4,642.6	2.8
Pistillate flowers N=1	3,977.7	-[b]	4,484.9	-
Staminate inflorescences N=1	4,317.6	-	5,206.3	-

[a]Sampled from 1 September 1980 through 12 April 1981.
[b]-No RSD because N=1.

maximum caloric value of 5,206 cal/g. Most organs ranged from 4,000-4,500 cal/g ash-free dry weight.

Early and late rosettes. Both types of rosettes contained leaves, rootstocks, and stolons (Table 16). In addition, early plants contained reproductive structures and remains of overwintering buds. Leaves composed 67.7 and 72.2% of the biomass for early and late plants, respectively. Stolons constituted 11.4% of the biomass in late plants and only 2.2% in older individuals. Organs from late plants contained higher crude protein concentrations as compared to similar organs of early rosettes. Higher ash concentrations were found in younger leaves. Other nutritive variables were similar in both types of plants (Table 16).

Biomass Nutritive Quality

The digestible ash-free non-cell wall fraction (NCF) composed 85% of the biomass during late autumn and winter (Fig. 10). The maximum ash-free NCF biomass (101 g/m^2) occurred during peak biomass 1 September. Greatest fiber and ash concentrations were found during summer and early autumn. The maximum concentration of crude protein (30.3 g/m^2) was coincident with the maximum biomass on 1 September 1980. Crude protein concentrations ranged from 9.1% of the biomass on 9 November 1980 to 15.4% in early June (Table 17). On an ash-free basis, crude protein (CP) concentrations averaged 43% higher than CP on a dry weight basis during June and July. The maximum caloric con-

Table 16. Comparisons between early and late rosettes of *Vallisneria americana*, Navigation Pool No. 9, Upper Mississippi River, 31 July 1981.

Variable	Early rosettes			Late rosettes[a]		
	Leaves	Rootstocks	Stolons	Leaves	Rootstocks	Stolons
Biomass (%)[b]	67.7	12.3	2.2	72.2	16.3	11.4
Dry matter (%)	6.1	5.4	5.3	5.8	7.7	5.2
Fiber (% of dry weight)	38.8	42.3	38.2	36.5	40.7[c]	
Ash (%)	24.5	27.6	16.3	28.8	25.2	
Ash-free fiber (%)	36.1	39.7	37.0	34.4	39.0	
Ash-free NCF (%)	39.4	32.7	46.7	36.7	35.8	
Crude protein (%)	17.9	13.8	12.8	20.0	15.4	
Crude protein (% ash-free dry weight)	23.8	19.0	15.3	28.1	20.6	
Calories (cal/g dry weight)	3,333.7	3,373.6	3,578.3	3,323.7	3,491.4	
Calories (cal/g ash-free dry weight)	4,416.1	4,657.1	4,276.9	4,670.7	4,669.5	
No. of organs per rosette	12.6	1.0	2.0	7.8	1.0	1.5

[a]All of the late rosettes analyzed were less than 40cm in height.

[b]Additional organs that composed part of the biomass of early plants: peduncles-5.6%, fruits-6.0%, winter buds-2.9%, staminate inflorescences-2.5%, pistillate flowers-.6%.

[c]Rootstocks and stolons were combined for analyses.

Fig. 10. Estimated biomass of the ash-free non-cell wall fraction (NCF), ash-free neutral-detergent fiber, and ash content for the total biomass of Vallisneria americana on 8 select sampling dates, Navigation Pool No. 9, Upper Mississippi River, 1980-1981.

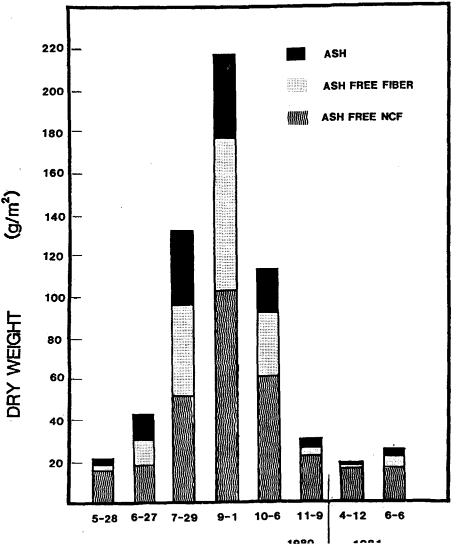

ASH
ASH FREE FIBER
ASH FREE NCF
DRY WEIGHT (g/m^2)
220
200
180
160
140
120
100
80
60
40
20
5-28
6-27
7-29
9-1
10-6
11-9
4-12
6-6

Table 17. Estimated crude protein and caloric content of the total <u>Vallisneria americana</u> biomass for 8 select sampling dates, Navigation Pool No. 9, Upper Mississippi River, 1980-1981.

	1980						1981	
Date	5-28	6-27	7-29	9-1	10-6	11-9	4-12	6-6
<u>Crude protein</u>								
g/m^2	3.0	6.4	18.2	30.3	13.8	2.5	2.5	4.0
Dry weight (%)	14.5	15.2	13.8	13.9	12.2	9.1	12.6	15.4
Ash-free dry weight (%)	16.4	22.4	19.2	17.3	15.3	9.5	13.2	17.8
<u>Caloric Content</u>								
kcal/g dry weight	80.6	152.2	446.9	765.4	337.0	111.4	79.6	98.3
kcal/g ash-free dry weight	90.9	223.9	622.6	952.3	422.5	116.3	83.4	113.7

DISCUSSION

Biomass and Productivity

The maximum biomass observed in this study (217.3 g/m^2) is among the highest cited for Vallisneria americana (Table 18). Similar results were observed in Navigation Pool No. 7 and in adjacent pools of the Upper Mississippi River (Korschgen, pers. comm., Northern Prairie Wildlife Research Center, La Crosse, Wisconsin 1982). Titus and Adams (1979a) reported the maximum V. americana biomass of 344 g/m^2 in Lake Mendota. Lower values, however, have been reported in northern Wisconsin lakes (Table 18). Moyle (1945) stated that V. americana grows optimally in hard water environments (90-150 mg/L $CaCO_3$), but it can also grow in soft waters (40 mg/L $CaCO_3$). This probably explains the great differences between the biomass of V. americana in the Mississippi River as compared to lakes of northeastern Wisconsin (Table 18).

Vallisneria americana biomass increased sharply during July and August, and its maximum crop was sampled at what appeared to be peak fruit development on 1 September. Maximum productivity of 3.2 $g \cdot m^{-2} \cdot d^{-1}$ was during late July at the time of flowering and rapid vegetative reproduction. In contrast, a relatively constant V. americana biomass was observed during August in Pool No. 8 of the Upper Mississippi River (Sefton 1976). She also reported that peak biomass (93.6 g/m^2) occurred during maximum fruit development early in that month. Maximum pro-

Table 18. Vallisneria americana biomass from various locations.

Site	Average biomass dry weight (g/m^2)		Source
Trout L., N.E. Wis.	0.001		Wilson (1941)
Silver L., N.E. Wis.	0.02		Wilson (1935)
Sweeny L., N.E. Wis.	0.04		Wilson (1934)
Green L., S.E. Wis.	0.5		Rickett (1924)
Green L., S.E. Wis.	3.9		Bumby (1977)
Lake Mendota, S.E. Wis.	67.0		Rickett (1921)
Navigation Pool No. 8 Upper Mississippi River	93.6		Sefton (1976)
Navigation Pool No. 7 Upper Mississippi River	170.3[a] 149.5[a]	1980 1981	Korschgen (pers. comm.)
Navigation Pool No. 8 Upper Mississippi River	171.1[a] 176.0[a]	1980 1981	Korschgen (pers. comm.)
Navigation Pool No. 9 Upper Mississippi River	154.6[a] 109.7[a]	1980 1981	Korschgen (pers. comm.)
Navigation Pool No. 9 Upper Mississippi River	176.6[b] 144.5[c]		Present study
Navigation Pool No. 9 Upper Mississippi River	217.3[d] 173.6[e]		Present study
Lake Mendota, S.E. Wis.	344		Titus and Adams (1979a)

[a] Shoot biomass only (August 1980).
[b] Shoot biomass only (1 Sept. 1980).
[c] Shoot biomass only (14 August 1980).
[d] Total biomass (1 September 1980).
[e] Total biomass (14 August 1980).

Titus and Adams (1979b) found that maximum photosynthetic rates for wild celery were found at the summer temperature of 32.6° C. They also demonstrated that wild celery could efficiently photosynthesize at low light intensities. Similarily, Meyer et al. (1943) found V. americana to be well adapted to shading. In the present study, V. americana was shaded by Cladophora sp. and Lemna spp. during mid to late summer.

Large increases in leaf biomass resulted in rapid increases in the shoot:root ratio (S:R) during June and July 1980 (Fig. 6). Ratios began to decrease by mid-summer when nonphotosynthetic stolons were produced. Ratios continued to decline with the production of winter buds in late summer and the loss of shoot biomass during autumn. Titus and Adams (1979a) reported similar trends, but lower ratios during early summer for V. americana in Lake Mendota. Conversely, Nicholson and Best (1974) noted a low S:R ratio of 1.1 during August in Chautauqua Lake, New York.

The S:R ratio was positively correlated with water depth by the end of July 1980 (Table 8). On 13 July 1980 shallow reaches of the study area (depth $\leq$ 1 m, sandy sediments) contained approximately three times the density of late rosettes than were found in deep areas (depth $>$ 1 m, clay and silt sediments). Nonphotosynthetic organs composed 28% of the late rosette biomass (Table 16). In contrast, these organs constituted 17% of the biomass in older (early) plants. This resulted in a decline in the S:R ratio in late rosettes. Nicholson and Best (1974) reported similar trends for Potamogeton richardsonii. Nonphotosynthetic fractions were low in older plants (5-15%), but they constituted up to 30% of the total biomass in recently formed shoots.

In deeper portions of the study area, V. americana rosettes were taller and contained greater mean values of photosynthetic biomass/m^2 by mid-August (Table 8). Similarily Nicholson and Best (1974) reported increased S:R ratios for V. americana with increased size of the plant. Monk (1966) observed the same phenomenon in herbaceous terrestrial plants. Therefore the decline in the S:R ratio from deep to shallow water was probably due to the presence of rosettes in deep water that were taller and contained a greater proportion of photosynthetic biomass than those in shallow areas. Furthermore, late rosettes which had a higher proportion of nonphotosynthetic biomass, were found in greater densities in shallow depths. Nicholson and Best (1974) also noted a decrease in the S:R ratio from deep to shallow water.

Denniston (1921) found that V. americana grew in various sediment types to depths in excess of 5 m in Lake Mendota. Richett (1921) determined that V. americana was the dominant macrophyte in Lake Mendota, and it composed 46% of the plant biomass. Fifty years later, Lind and Cottam (1969) reported that Myriophyllum sp. had replaced V. americana as the dominant macrophyte in Lake Mendota. They observed that V. americana was limited to water depths less than 2.5 m and usually occurred in sandy sediments. Schuette and Alder (1929) stated that Myriophyllum flourished in muddy sediments, whereas V. americana thrived equally well in sandy and mud substrates. The replacement of V. americana by Myriophyllum spicatum appears to have occurred primarily in deep water where non-sandy sediments occur. The allocation of biomass to nonphotosynthetic organs allows V. americana to maintain itself in shallow water subjected to wave action. This mechanism also permits V. americana to overwinter and establish a small rosette of leaves at the sediment surface in May (Titus and Adams 1979a).

Increases in leaf biomass also resulted in the increase of leaf area indices (LAI). Leaf area indices increased from 4 to 8 during periods of maximum productivity during July. The maximum LAI (17) was coincident with the maximum biomass on 1 September. In comparison, Hannan and Dorris (1970) calculated a LAI of 29 at the time of maximum productivity in a Texas river. These studies are in agreement with Nicholson and Best (1974) who stated that highly productive aquatic environments may promote high LAI's and a high biomass accretion rate in submersed macrophyte communities. They reported LAI's of 5-7 in the less productive Chautauqua Lake. In contrast, Odum (1971) reported that a LAI of 4 was optimal for net production and LAI's of 8-10 were optimal for maximum gross production in terrestrial plants. In the present study, the maximum LAI of 17 represented 170,000 cm^2 of leaf surface area/m^2. Therefore, when both sides of a leaf were considered, 340,000 cm^2 of leaf surface area/m^2 were available for epiphytic colonization.

Nutritive Quality

In the present study, V. americana was characterized by high moisture concentrations that ranged from 92.6% to 75.5%. The latter number was noted when winter buds composed all of the plant material. The biomass averaged 9% dry matter during the growing season. All organs averaged over 92% water except for fruits and winter buds which had relatively high dry matter concentrations (Table 21 and Appendix III). Aquatic macrophytes typically range from 5-15% dry matter. These low concentrations decrease nutritive quality (National Academy of Sciences 1976).

In addition to high moisture, aquatic plants often contain high concentrations of ash that lower nutritive quality (Muztar et al. 1978c). Muztar et al. (1977) fed unwashed V. americana (38% ash) to chickens and ducks and concluded that the amounts of metabolizable energy were low. The high ash content lowered the concentration of organic matter and may have interfered with digestion and absorption of energy contributing nutrients. Crowder et al. (1977) and Forest (1977) found ash concentrations that ranged from 10-50% of the macrophyte biomass. According to Westlake (1965a), ash usually composes 15-25% of the dry matter. The ash content is dependent upon the age, species of macrophyte, and environmental factors such as water hardness and trophic status. In hard water lakes, vigorous uptake among plants for available CO_2 results in an increased rate of $CaCO_3$ deposition on the plant tissue (Muztar et al. 1978a).

Westlake (1965b) recommends using organic matter (ash-free dry weight) as the most accurate measurement of production because it eliminates errors caused by ash when reporting dry weight. In the present study, the ash content of V. americana averaged approximately 22.3% of the total biomass during the growing season (Table 19). The maximum ash concentration was observed during mid-July when approximately 35% of the biomass was inorganic residue. Ash concentrations steadily declined as new rosettes were produced during the summer. During the winter months, the ash content composed less than 5% of the dry weight. These values are similar to other ash concentrations reported of V. americana (Table 19). Biomass and productivity were higher when expressed as dry weight (g/m^2) when compared to ash-free dry weight

Table 19. Nutritive variables of _Vallisneria americana_ from various sources.

Site	Part of plant	Dry matter (%)	Dry weight (%)				Source
			Crude protein	Ash	CWF (fiber)	Calories Kcal/g	
L. Mendota, S.E. Wis.	-[a]	-	17.5	20.7	-	-	Birge and Juday (1922)
L. Mendota, S.E. Wis.	-	-	11.8	25.2	-	-	Schuette and Alder (1927)
Minnesota Lakes	-	-	15.0	28.6	-	-	Gortner (1934)
Lake Owasso St. Paul Minnesota	Photosynthetic biomass	5.2	15.2	15.6	-	-	Nelson and Palmer (1939)
L. Mendota, S.E. Wis.	Entire plant	-	12.4-24.1 (17.2)	-	-	-	Gerloff and Krombholz (1966)
Fort Lauderdale Florida	Shoot biomass	8.0-12.0	17.6-27.0 (21.1)	-	-	-	Boyd and Blackburn (1970)
New York	Above ground parts	-	8.0-12.4 (10.0)	21.8-40.3 (31.0)	-	-	Lathwell et al. (1973)
Minnesota Lakes	Aerial parts	-	15.2	3.1	41.0	-	Linn et al. (1975)
Lake Chemung Ontario	-	4.1-9.8 (7.0)	18.1-19.8 (19.1)	23.3-43.1 (33.2)	34.4	3.1-3.8 (3.4)	Muztar et al. (1978a)
Navigation Pool No. 9 Upper Mississippi River	Entire plant	7.4-12.9 (9.0)	12.2-15.2 (13.9)	11.4-32.0 (22.3)	15.5-36.2 (29.3)	3.5[b]	Present study
	Leaves	3.2-9.5 (6.2)	13.5-21.4 (16.0)	22.9-38.7 (29.1)	23.9-39.5 (34.0)	3.4[c]	Present study

[a]-Data not available.

[b]Mean caloric content on 1 September 1980.

[c]Mean caloric content from 1980-1981 (N=7).

(Table 20).

Approximately 92% of the ash content of V. americana was in the soluble non-cell wall fraction (NCF) of the dry matter. Muztar et al. (1978a) reported that an average of 85% of the ash was NCF when they analyzed several macrophytes. In the present study, ash content was substracted from the non-cell wall fraction (NCF) after fiber and ash concentrations were determined. This method provided a more refined estimate of the digestible portion of each organ (Tables 10, 12, and 13). The non-cell wall fraction contains proteins, lipids, sugars and starches which are readily digested by herbivores. The cell wall fraction (neutral-detergent fiber) includes the structural components of the plant (cellulose, hemicellulose and lignin). Neutral-detergent fiber is not digestible by nonruminant animals, whereas ruminants can partially digest the cellulose and hemicellulose components (Van Soest 1966).

The ash-free NCF in both leaves and rootstocks averaged less than 40% of the dry weight. The greatest concentration of the ash-free NCF in leaves and stolons occurred early in the growing season. The fiber and ash content of leaves increased during June and July and resulted in a decrease of the ash-free NCF to a minimum of 31.6% by mid-July. The maximum fiber content of leaves was observed on 1 September 1980 and paralleled the period of maximum biomass. The concentration of ash, fiber, and ash-free NCF's remained relatively constant in reproductive structures (Table 12). The ash-free NCF decreased in winter buds during the period of decomposition (Fig. 9). The average ash-free NCF's of fruits and winter buds composed 75.7 and 82.7% of their biomass, respectively (Table 21).

Table 20. A comparison between dry weight and ash-free dry weight (organic) of biomass (g/m^2) and productivity ($g \cdot m^{-2} \cdot d^{-1}$) for *Vallisneria americana*, Navigation Pool No. 9, Upper Mississippi River, 1980.

Date	5-28		6-27		7-29		9-1		10-6
Biomass (dry weight)	7.2		35.9		129.1		217.3		113.4
Biomass (ash-free dry weight)	5.8		23.7		92.6		174.6		90.4
Productivity (dry weight)		1.0		3.0		2.7		-3.1	
Productivity (ash-free dry weight)		.6		2.2		2.5		-2.5	

Ingestion of the vegetation by herbivores is decreased when neutral-detergent fiber concentrations constituted 55-60% of the dry weight of a plant (Van Soest 1965). Fiber concentrations were below the 55-60% level in all V. americana organs observed during this study (Table 11). Muztar et al. (1978a) and Linn et al. (1975) reported similar neutral-detergent fiber concentrations for V. americana (Table 19). In comparison, Muztar et al. (1978a), Polisini and Boyd (1972) and Linn et al. (1975) found greater neutral-detergent fiber concentrations for several aquatic macrophytes.

The digestible NCF contains approximately 90% of the crude protein in plants (Van Soest 1966). In contrast, the cell wall fraction is composed of small amounts of fiber-bound protein and lignified nitrogenous compounds (Van Soest 1965). This implies that most of the plant protein should be available to herbivores. Nelson and Palmer (1939) found different results when they fed photosynthetic parts of V. americana, Myriophyllum spicatum and Elodea canadensis to rats. They concluded that proteins in M. spicatum and V. americana were low in digestibility in contrast to E. canadensis that contained protein of "better nutritive" quality.

Submergent macrophytes are lower in fiber and similar to forage crops in crude protein (Boyd 1968). In the present study, V. americana ranged from 12.2-15.2% crude protein (CP) and 15.5-36.2% fiber during the growing season (Table 19). Linn et al. (1975) reported similar crude protein levels and higher fiber values for alfalfa hay. Other studies reported CP concentrations for V. americana that ranged from 8-27% of the dry weight (Table 19). Leaves were included in all analyses, but the time of harvest and the type of plant parts varied with each investigation. Muztar et al. (1978b) found that the crude protein content of V. americana from Chemung Lake, Ontario overestimated the true protein content by 37%. They determined that macrophytes usually contained lower concentrations of cystine, methionine, and lysine as compared to terrestrial plants.

In the present study, V. americana leaves were high in nitrogen and constituted approximately 70% of the summer biomass. Thus, leaves contained approximately 72% of the summer crude protein content. Staminate inflorescences and pistillate flowers contained the greatest mean concentrations of CP (21.8 and 18.2%, respectively). These organs, however, constituted a maximum of 2.7% of the total biomass at mid-summer (Table 9). Thus, flowers contained a minimum amount of the total V. americana crude protein content. Young leaves sampled during the spring of 1980 and 1981 contained high crude protein concentrations of 21.4 and 21.9% of the dry weight, respectively (Tables 5 and 14). In contrast, the crude protein values for leaves sampled during the autumn of 1980 were lower (13.5%). The decline in CP with leaf age was also evident in 1981. Young leaves contained 20% CP as compared to 17.9% for old foliage (Table 16). Gerloff and Krombholz (1966) reported similar trends in V. americana from Lake Mendota. Boyd (1968) and de la Cruz (1975) also found high crude protein concentrations in young emergent plants when compared to older vegetation. Boyd and Blackburn (1970) noted that crude protein decreased with age of emergent plants. Crude protein of submergent plants, however, can decrease, increase, or remain constant with age.

The caloric content of V. americana was approximately 3.5 kcal/g (4.4 kcal/g ash-free dry weight) when maximum biomass was observed

(Table 19). Muztar et al. (1978a) found a similar caloric value of 3.4 kcal/g for V. americana in Chemung Lake, Ontario. Boyd (1968) found that the caloric content ranged from 2.5-3.9 kcal/g with a mean of 3.5 for 11 submersed macrophytes. The mean ash-free value was approximately 4.3 kcal/g.

In this study, the caloric value of V. americana organs expressed on an ash-free dry weight basis were contained within a narrow range (4,144-5,206 cal/g) (Table 15). These results agree with Westlake (1963) who reported that plant tissues usually contain 4.1-5.2 kcal/g on an ash-free dry weight basis. Golley (1961), de la Cruz and Gabriel (1974), and Muztar et al. (1978a) found higher caloric values in young plants when compared to old plants. Higher crude protein concentrations in younger plants apparently resulted in higher caloric values. In the present study, young leaves, stolons, and peduncles contained greater protein and caloric values as compared to older organs.

Only energy in the form of digestible nutrients are available to herbivores (Boyd and Goodyear 1971). Approximately 765 kcal/m^2 were present when maximum biomass was sampled on 1 September (Table 17). It was estimated that ash-free fiber and the potentially digestible ash-free NCF composed approximately 34 and 47% of the biomass, respectively, at that time (Fig. 10). Therefore, a large amount of the energy was not available to the nonruminant herbivore.

Nutritive Summary

Submersed aquatic macrophytes are nutritionally characterized by high moisture and ash concentrations. Herbivores generally feed on selected plant parts; therefore, specific organs must be analyzed in order to determine nutritive quality (Boyd and Goodyear 1971).

Unlike leaves, rootstocks, and stolons, winter buds and fruits have high nutritional potential (Table 21). Winter buds and fruits are high in dry matter and are low in ash and fiber content. The digestible ash-free non-cell wall fraction (NCF) constituted an average of 75.7 and 82.2% of the biomass of fruits and winter buds respectively. On a dry weight basis, fruits and winter buds also had higher caloric values than most other organs. The protein content of winter buds and fruits may be available to herbivores because of the low ash content.

Both winter buds and fruits contributed significant biomass to the total V. americana crop. Winter buds constituted all of the overwintering biomass. The maximum winter bud biomass of 30.1 g/m^2 (158 $buds/m^2$) was observed in October. By the following April, both the number and biomass of winter $buds/m^2$ had decreased by approximately 30% (Fig. 8). Similar amounts and trends of winter buds were observed in Navigation Pool No. 7 (Korschgen pers. comm., Northern Prairie Wildlife Research Center, La Crosse, Wisconsin 1982). They attributed the decrease in winter bud biomass and density from autumn to spring to waterfowl cropping.

Table 21. The mean nutritive values of fruits, winter buds, and other organs of _Vallisneria americana_, Navigation Pool No. 9, Upper Mississippi River, 1980-1981.

Organs	Dry matter (%)	Dry matter (%)				
		Crude protein	Ash-free fiber	Ash-free NCF	Ash	Calories
Leaves, rootstocks and stolons 28 May 1980 - 6 October 1980	6.5	13.0	33.4	42.1	24.5	3516.8
Fruits 29 July 1980 - 6 October 1980	12.0	11.7	15.7	75.7	8.6	4314.8[a]
Winter buds 1 September 1980 - 9 April 1981	24.8	9.9	13.0	82.2	4.7	3978.0

[a]The mean caloric content from 16 September - 6 October 1980.

CONCLUSIONS

1. The maximum biomass of 217.3 g/m^2 was observed on 1 September 1980 and is among the highest reported for Vallisneria americana.
2. Both the photosynthetic (shoot) and nonphotosynthetic (root) biomasses reached maximums of 176.6 and 40.7 g/m^2, respectively, on 1 September.
3. Vallisneria americana had a mean productivity rate of 2.2 $g \cdot m^{-2} \cdot d^{-1}$ during the growing season. Maximum productivity of 3.2 $g \cdot m^{-2} \cdot d^{-1}$ was coincident with maximum rosette and flower production.
4. The maximum photosynthetic (shoot) productivity of 2.9 $g \cdot m^{-2} \cdot d^{-1}$ occurred in early July when all of the shoot biomass was composed of leaves.
5. The maximum nonphotosynthetic (root) production rate of 0.9 $g \cdot m^{-2} \cdot d^{-1}$ was sampled from mid-August to 1 September during maximum winter bud production.
6. Shoot:root ratios reached a maximum of 8.7 at mid-July. No ratio was reported on 12 April 1981 as all of the biomass was nonphotosynthetic. By the end of July, a positive correlation existed between S:R ratios and water depth ($r = 0.80$, $p < 0.05$).
7. Rosette density increased sharply during July, and the maximum of 214 rosettes/m^2 was sampled on 1 September 1980. By the middle of July, three times the number of late rosettes were found in shallow water (depth $\leq$ 1 m, sandy sediments) than in deeper (depth $>$ 1 m, clay and silt sediments) reaches of the study area.

The maximum correlation between total rosette density and depth was observed on 1 September 1980 ($r = ^{-}0.74$, $p < 0.05$).

8. The leaf area index (LAI) reached the maximum of 17 on 1 September 1980. Therefore, when both sides of a leaf were considered, 340,000 cm^2 of leaf surface area/m^2 was available for epiphytic colonization.
9. Leaves were the dominant organ during the summer. They constituted 60-70% of the biomass from late June to early October.
10. Winter buds composed all of the biomass during the winter months. Maximum winter bud production was sampled from mid-August to 1 September, and the maximum biomass of 30.1 g/m^2 (158 buds/m^2) was observed on 6 October 1980. By 12 April 1981, the density and biomass of winter buds had declined by 30%. This may have resulted from waterfowl foraging.
11. The combined biomasses of stolons, peduncles, staminate inflorescences, and pistillate flowers rarely exceeded 10% of the total biomass on any sampling date. Fruits composed a maximum of 10.9% of the biomass on 1 September 1980.
12. Most V. americana organs contained less than 10% dry matter (90% water). Winter buds and fruits, however, reached maximums of 29.5 and 14.3% dry matter, respectively.
13. All organs contained neutral-detergent fiber concentrations below levels that may decrease intake by herbivores.
14. Fruits and winter buds possessed the greatest nutritional potential of all organs. They composed substantial percentages of the total biomass and were high in dry matter, caloric content, and ash-free non-cell wall fractions (75.7 and 82.2%,

respectively). They were also low in fiber and ash contents.

15. Staminate inflorescences and pistillate flowers contained the greatest mean crude protein concentrations (21.8 and 18.2%, respectively). Both were high in ash-free non-cell wall fractions (NCF) and caloric values. They were, however, high in moisture and composed minimal amounts of the total biomass.
16. Leaves produced the greatest quantities of biomass and contained a high crude protein concentration. Ash and fiber concentrations, however, markedly decrease nutritional quality. Leaves harvested in May had greater nutritive potential than older leaves.
17. Rootstocks, stolons, and peduncles usually composed a small percentage of the total biomass and had minimal nutritive potential.
18. The maximum caloric content of V. americana biomass was apprriximately 765 kcal/m^2 on 1 September 1980.
19. Average fiber concentrations were 14.6% higher in samples of leaves, stolons, peduncles, and rootstocks that were frozen when compared to nonfrozen samples. Therefore, fiber values for these organs in this study may be higher than in other papers.

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Appendix I. The percent silt, sand, and clay of the sediments in the *Vallisneria americana* study area, Navigation Pool No. 9, Upper Mississippi River, 29 July 1980.

Sample site	Silt (%)	Sand (%)	Clay (%)	Depth (cm)
1	0	100	0	70
2	15.3	76.7	8.0	90
3	39.1	36.1	24.9	120
4	50.4	24.0	25.6	150
5	62.7	12.8	24.4	135
6	0	100	0	80
7	46.0	28.9	25.1	150
8	22.6	63.2	14.2	125
9	30.8	40.8	28.5	130
10	39.7	21.3	39.0	135
11	50.9	17.0	32.2	125
12	51.8	15.4	32.8	160
13	50.2	11.1	38.7	145
14	47.8	11.9	40.4	145
15	40.8	19.7	39.5	135
16	62.7	12.8	24.4	160
17	46.0	23.8	30.3	140
18	59.5	18.1	22.5	145
19	50.0	17.8	32.1	145
20	64.3	8.3	27.3	145
21	0	100	0	110
22	0	100	0	80
23	0	100	0	80
24	0	100	0	100
25	45.2	22.8	32.0	95
26	35.9	41.5	22.7	90
27	49.7	23.7	26.6	90
28	-[a]	-	-	110
29	52.5	9.5	38.0	125
30	49.8	6.7	43.4	110
31	0	100	0	45
32	0	100	0	55
33	7.2	87.0	5.8	50
34	24.2	65.0	10.7	85
35	18.6	73.8	7.6	85
36	0	100	0	50
37	10.6	82.3	7.2	55
38	28.4	54.1	17.5	65
39	0	100	0	55
40	0	100	0	60

[a]-No value was determined.

Appendix II. Wet weights (g/m^2) and dry matter (%) of Vallisneria americana biomass, Navigation Pool No. 9, Upper Mississippi River.

	1980								1981	
Date	5-28	6-27	7-13	7-29	8-14	9-1	10-6	11-9	4-12	6-6
N	20	40	40	40	37	40	36	16	16	37
Total wet weight	162.0	432.2	1,102.7	1,771.1	2,153.3	2,567.6	1,306.9	133.1	81.6	279.5
Dry matter (%)	12.9	9.8	7.8	7.4	8.1	8.5	8.7	23.0	24.5	9.8
Total wet weight without winter buds from previous growing season	89.0	366.8	1,043.2	1,733.2	2,115.5	2,567.6	1,306.9	133.1	81.6	180.9
Dry matter (%)	8.1	9.8	7.7	7.4	8.0	8.5	8.7	23.0	24.5	6.0
Photosynthetic wet weight	63.2	323.0	933.7	1,522.9	1,800.7	2,155.2	1,029.5	24.9	0	127.6
Dry matter (%)	6.4	8.9	7.7	7.3	8.0	8.2	7.1	7.6	-[a]	5.3
Nonphotosynthetic wet weight	98.9	109.2	169.0	248.2	352.6	412.4	277.4	108.2	81.6	151.9
Dry matter (%)	17.0	12.6	8.4	8.4	8.3	9.9	14.5	26.6	24.5	13.5
Nonphotosynthetic wet weight without winter buds from previous growing season	25.8	43.8	109.5	210.3	314.8	412.4	277.4	108.2	81.6	53.2
Dry matter (%)	12.0	16.4	13.2	8.6	8.1	9.9	14.5	26.6	24.5	13.5

[a]-No photosynthetic biomass was present.

Appendix III. Estimated biomass (g/m^2), mean dry weight (g/organ), and dry matter (%) of each organ of *Vallisneria americana*. Navigation Pool No. 9, Upper Mississippi River, 1980-1981.[a]

Date	1980 5-28	6-27	7-13	7-29	8-14	9-1	9-16	10-6	11-9	1981 4-12	6-6	6-30	7-31	8-10	8-28	10-3	$\bar{X}$[b]	RSD[b] (%)
Leaves																		
Dry matter	3.2	9.5	6.0	6.0	7.7	6.1	5.2	5.6	-[c]	-	6.0	5.5	6.0	-	6.0	6.1	6.2	29.8
Biomass	4.1	28.6	-	93.4	-	146.7	-	69.8	-	-	6.7	-	-	-	-	-	-	-
Dry weight	.01	.10	.10	.08	.08	.11	.05	.06	-	-	-	.10	.11	-	.16	-	-	-
Rootstocks																		
Dry matter	-	7.3	11.0	7.6	6.2	6.6	6.1	6.3	-	-	-	6.1	7.1	-	7.2	7.0	7.3	23.7
Biomass	-	6.1	-	15.0	-	15.8	-	4.4	-	-	-	-	-	-	-	-	-	-
Dry weight	-	.08	.08	.08	.05	.06	.06	.04	-	-	-	.06	.09	-	-	.04	-	-
Stolons																		
Dry matter	8.4	5.5	5.9	5.1	6.8	5.9	5.4	4.3	-	-	6.6	5.4	5.6	-	5.4	5.3	5.9	20.9
Biomass	3.1	1.1	-	3.6	-	8.9	-	5.9	-	-	4.7	-	-	-	-	-	-	-
Dry matter	.04	.02	.02	.02	.05	.04	.03	.03	-	-	-	.02	.03	-	.06	.02	-	-
Winter buds																		
Dry matter	19.2	9.5	9.6	7.9	9.1[d]	18.7	24.0	27.2	29.5	24.6	16.9	9.0	7.2	13.2	19.6	27.0	24.8[e]	16.3[e]
Biomass	13.7	6.6	-	2.8	-	14.2	-	30.1	27.7	20.0	16.4	-	-	-	-	-	-	-
Dry weight	.15	.07	.06	.03	.06	.13	.15	.19	.20	.19	.15	.05	.03	.06	.13	.16	-	-
Fruits																		
Dry matter	-	-	-	-	9.5	11.4	12.7	14.3	-	-	-	-	8.7	-	11.4	14.0	12.0	17.3
Biomass	-	-	-	6.9	-	23.7	-	2.8	-	-	-	-	-	-	-	-	-	-
Dry weight	-	-	-	.04	.07	.15	.22	.30	-	-	-	-	.08	-	.17	.22	-	-
Pistillate flowers																		
Dry matter	-	-	-	8.8[f]		-	-	-	-	-	-	-	7.2	7.4	-	-	-	-
Biomass	-	-	-	.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dry weight	-	-	-	.01	.01	-	-	-	-	-	-	-	.01	.01	-	-	-	-
Peduncles																		
Dry matter	-	-	-	7.7[f]		5.8[g]		6.2	-	-	-	5.2	-	5.5	5.6	-	6.6	15.3
Biomass	-	-	-	6.4	-	9.2	-	.5	-	-	-	-	-	-	-	-		
Dry weight	-	-	-	-	-	-	-	-	-	-	-	-	.04	-	-	-		
Staminate inflorescences																		
Dry matter	-	-	-	6.9	6.4	-	-	-	-	-	-	6.3	6.0	6.4	-	-	6.7	5.3
Biomass	-	-	-	2.8	-	-	-	-	-	-	-	-	-	-	-	-		
Dry weight	-	-	-	.01	.01	-	-	-	-	-	-	.01	.01	.01	-	-		

[a] At least 20 organs of each type were weighed to determine the average dry matter (%) and dry weight (g/organ).
[b] Means and RSD for 1980 samples only, except for winter buds.
[c] -No values were determined because specific organs were not present in the biomass or the variable was not sampled.
[d] Includes decomposing and newly produced winter buds.
[e] Mean and RSD includes winter buds sampled from 9-1, 1980 to 4-12, 1981.
[f] Samples from 7-29 and 8-14 were combined for analyses.
[g] Samples from 9-1 and 9-16 were combined for analyses.

Appendix IV. The ash content (%) of neutral-detergent fiber of <u>Vallisneria americana</u> organs, Navigation Pool No. 9, Upper Mississippi River, 1980-1981.

	1980									1981				
Date	5-28	6-27	7-13	7-29	8-14	9-1	9-16	10-6	11-9	4-12	6-6	7-31	8-10	8-28
Leaves	7.2	8.8	7.3	7.9	7.4	5.9	7.4	8.9	-[a]	-[b]	-[a]	7.1	-[a]	-[a]
Rootstocks	-[b]	5.7	7.9	8.1	5.1	5.9	14.2	7.6	-[a]	-[b]	-[b]	6.0	-[a]	-[a]
Stolons	5.0	3.9	4.4	3.8	3.7	4.2	5.0	5.0	-[b]	-[b]	5.2	4.9	-[a]	-[a]
Winter buds	8.0	9.4	8.1	-[a]	-[a]	5.7	5.5	5.0	6.8	6.7	7.0	9.3	4.9	3.8
Fruits	-[b]	-[b]	-[b]	7.2[c]		2.4	3.6	3.7	-[b]	-[b]	-[b]	10.7	-[a]	-[a]
Peduncles	-[b]	-[b]	-[b]	4.0[c]		3.3[d]		3.6	-[b]	-[b]	-[b]	5.1	-[a]	-[a]
Pistillate flowers	-[b]	-[b]	-[b]	12.9[e]		-[b]	-[b]	-[b]	-[b]	-[b]	-[b]	6.0[e]		-[a]
Staminate inflorescences	-[b]	-[b]	-[b]	6.1[e]		-[b]	-[b]	-[b]	-[b]	-[b]	-[b]	-[a]	-[a]	-[b]

[a]-Values were not determined.

[b]-Specific organs were not present in the biomass.

[c]Samples from 7-9 and 8-14 were combined for analyses.

[d]Samples from 9-1 and 9-16 were combined for analyses.

[e]Composite samples that were taken at different times during flowering.

Appendix V. The caloric content (cal/g) of some Vallisneria americana organs, Navigation Pool No. 9, Upper Mississippi River, 1980-1981.

	1980				1981		
Date	8-14	9-1	9-16	10-6	6-6	6-30	7-31
Leaves							
cal/g dry weight	3,316.7	3,391.9	3,375.2	3,050.1	3,628.0	3,628.6	3,333.7
cal/g ash-free dry weight	4,572.9	4,401.1	4,468.1	4,250.4	4,747.4	-[a]	4,416.1
Rootstocks							
cal/g dry weight	-[a]	3,489.2[b]		3,203.6	-[c]	3,599.0	3,373.6
cal/g ash-free dry weight	-[a]	4,439.2		4,370.5	-[c]	-[a]	4,657.1
Stolons							
cal/g dry weight	-[a]	3,393.6	3,264.3	2,889.3	3,688.0	3,551.8	3,579.3
cal/g ash-free dry weight	-[a]	4,034.2	4,186.6	3,860.1	4,415.7	-[a]	4,276.9
Fruits							
cal/g dry weight	-[a]	-[a]	4,279.6	4,349.9	-[c]	-[c]	4,054.9
cal/g ash-free dry weight	-[a]	-[a]	4,682.3	4,746.2	-[c]	-[c]	4,499.4
Peduncles							
cal/g dry weight	-[a]	3,217.1[b]		3,118.9	-[c]	-[c]	3,493.3
cal/g ash-free dry weight	-[a]	4,060.5		4,095.7	-[c]	-[c]	4,275.2

[a]-Caloric content was not determined.
[b]Samples from 9-1 and 9-16 were combined for analyses.
[c]-Specific organs were not present in the biomass.