

Biomass, Nitrogen, and Phosphorus Allocation in Parrotfeather (*Myriophyllum aquaticum*)

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ABSTRACT

Seasonal patterns in allocation of biomass, nitrogen, and phosphorus in parrotfeather, *Myriophyllum aquaticum* (Vell.) Verd., were determined in a north-central California lake. Submersed rhizomes comprised 72 to 98% of the total biomass. Emergent biomass never comprised more than 24% of the total biomass. Allocation to emergent biomass was greater in shallow (<0.5 m) than in deep (0.5-1.5 m) sites on the dates sampled. The submersed growth form was an important component of the biomass only during winter when it accounted for a maximum of 3% of the biomass. There was no accumulation of biomass between June and September 1989, which suggests that biomass loss rates equalled production rates during the growing season. Rhizome N concentration, but not P or C concentrations, increased during the growing season. Allocation of N and P in parrotfeather varied with season and depth. Rhizomes contained 42 to 89% of the total N pool. The proportion of N in emergent tissues from deep plots decreased from 30% in June to <10% in September. Rhizomes contained only 3% of the total P pool, 80% of the parrotfeather P was in emergent tissues. Parrotfeather appeared to rely upon current uptake of P for growth rather than on stored P, which suggests that reduction in P supply may effectively reduce growth, and may partially explain the limited distribution of parrotfeather and its lack of aggressive invasion of aquatic macrophyte communities in some areas. The allocation of P and the lack of P storage may make parrotfeather susceptible to a harvesting strategy that removes only the emergent growth, especially in P-limited stands.

Key words: resource storage, perennation, nutrient cycling, emerged and submersed growth.

INTRODUCTION

Allocation of biomass and resources are fundamental aspects of competitiveness and the nuisance characteristics of aquatic plants. Problem macrophyte species often allocate a large portion of their biomass to canopy formation and rely upon stored resources to support the rapid spring growth that allows them to suppress competing species (Nichols and Keeney 1976, Granéli et al. 1983, Nichols and Shaw 1986, Perkins and Sytsma 1987, Garver et al 1988, Smith et al. 1988, Madsen 1991). Allocation of

photosynthate and biomass may be more important in growth, competitive success, and manifestation of nuisance characteristics than high photosynthetic rate and productivity (Smith and Barko 1990, Grace 1991). Changes in patterns of resource allocation have been proposed to explain natural declines in macrophyte abundance (Johnstone 1982), and are one of the major mechanisms by which plants adjust to resource imbalance (Chapin et al. 1980). Understanding resource and biomass allocation may be important in development of successful management plans. The efficacy of control measures may be enhanced if they are applied at points in the lifecycle that disrupt resource allocation patterns that are necessary to sustain competitiveness (Nichols 1991).

Parrotfeather (*Myriophyllum aquaticum* (Vellozo) Verdcourt; syn: *M. brasiliense* Cambess. and *M. proserpinacoides* Gilles ex Hook. & Arn.) (Aiken 1981) is not an aggressive invader over much of its range in North America (Nelson and Couch 1985), but in California (Anderson 1990) and elsewhere in its current range (Fernandez et al. 1990) it is an increasingly troublesome species. In addition to the adverse impacts commonly associated with excessive macrophyte growth, parrotfeather also provides mosquito larvae a refuge from predation (Orr and Resh 1989), which creates a human health hazard (Gangstad and Carderelli 1990). The association of parrotfeather and mosquitoes has provided much of the impetus for control measures in California.

Most research on parrotfeather biology and ecology has been conducted in the laboratory or greenhouse (Sutton 1985, Maberly and Spence 1989, Saito et al. 1989, Yen and Myerscough 1989, Fernandez et al. 1990, Kane et al. 1991), or in wastewater treatment systems (Nuttal 1985). Reports of biomass development in naturalized populations are few (Shibayama 1988, Monteiro and Moreira 1990). We are aware of no reports of seasonal patterns in parrotfeather biomass and resource allocation. The objectives of this study were to examine allocation of biomass, nitrogen and phosphorus in a naturalized population of parrotfeather.

METHODS

The study was conducted in Park's Lake, located on Beale Air Force Base, near Marysville, California. The physical and chemical characteristics of Park's Lake were described by Sytsma (1992). Briefly, the lake is divided into two basins, approximately 2 ha each, with emergent parrotfeather growth over about 80% of the surface of both basins. During summer, there is no surface inflow to the lake and water level is maintained by groundwater inflow (maximum summer depth = 1.8 m). Growth of parrotfeather in Park's Lake is P-limited, presumably as a re-

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sult of the N:P ratio of the groundwater inflow and sediment characteristics (Sytsma 1992).

The primary biomass sampling site, in the southern basin of the lake, was 50 m long and extended 10 to 15 m from the shore. Maximum depth was 1.5 m. The sampling area was originally divided into six plots of approximately equal size. In June 1989 we noticed that emergent stem length and density were greater in near-shore areas of the plots; therefore, plot boundaries were adjusted to provide 10 plots, five each in shallow (0.5 m) and deep (0.5-1.5 m) areas. All samples collected prior to June 1989 were from deep areas. One sample was randomly collected from each plot on each sampling date. Total parrotfeather biomass was sampled in the southern basin in September 1988; February, June and September 1989; and September 1990. Five random samples were collected in a visually uniform stand of emergent parrotfeather along the north-western shore of the northern basin in June and September 1989 (depth <0.5 m).

All sampling was done from a boat to minimize disturbance of the plots. Samples were collected with a 33.6 cm diameter (0.09 m²) PVC pipe, fitted with a circumferential saw blade on one end. The pipe was lowered to the sediment with a twisting motion that permitted the saw blade to cut through the mat of parrotfeather in the water column. All plant material was collected from within the pipe with a rake and seive. Sediment roots were collected by disturbing the sediment within the sampler with a pitchfork.

Samples were returned to the laboratory where they were separated into emergent stems, rhizomes, submersed stems with submersed leaves (the submersed growth form), and roots. Rhizomes were old emergent stems that had been pushed under water by elongation of the aerial stems. Rhizomes in the water column could easily be differentiated from submersed stems; rhizomes were more dense and rigid than submersed stems. Rhizomes bore adventitious roots and submersed branch stems with submersed leaves but no submersed leaves directly. Adventitious roots, (formed on rhizomes in the water column) and sediment roots (formed on rhizomes on or in the sediment) were not differentiated. Adventitious, water-column roots were never observed on the submersed growth form. Tissues were dried for a minimum of 48 hours at 80 C and weighed.

Dynamics of N, P, and C concentrations in rhizomes during the 1989 growing season were followed by monthly hand-collection of three rhizome samples in the shallow and deep sites from March through September 1989. Each sample consisted of ten, 1-m rhizome sections. Adventitious roots were removed, samples were rinsed thoroughly in lake water to remove periphyton and debris, and transported on ice to the laboratory where they were frozen at -70 C prior to drying at 80 C. After drying, tissues were ground to a powder and analyzed for P, N, and C. Phosphorus was determined by the ascorbic acid method (Murphy and Riley 1962) after combustion at 550 C for 3 hours and dissolution of the ash in HNO₃ (Chapman and Pratt 1961). Total N and C were determined on a Perkin-Elmer Model 2400 Elemental Analyser calibrated with acetanilide.

In June and September, 1989, emergent leaves and stems, and adventitious water roots, were also collected for nutrient analysis. Three samples of each were collected. Each leaf and stem sample consisted of leaves and stems from a minimum of 25 emergent stems. Root samples consisted of the adventitious roots removed from the rhizome samples. Field rinsing, transport, drying, and analysis procedures for emergent and root tissues were the same as described for the rhizome samples. Nitrogen and phosphorus pool sizes were estimated by multiplying mean dry weight biomass estimates for plant tissues by the mean tissue nutrient concentration.

Differences in total September biomass in the plots between years, and between June and September in 1989, were assessed by analysis-of-variance of log-transformed data (p=0.05).

RESULTS AND DISCUSSION

Total parrotfeather biomass in the primary sampling site ranged from 234±74 g m⁻² (±1 standard error) in February 1989 in the deep plots to 1001±84 g m⁻² in September 1990 in the shallow site (Figure 1). Year-to-year differences in total September biomass in the deep and shallow plots were not significant. Shibayama (1988) reported total parrotfeather fresh weight of 13.3 kg m⁻² in drainage ditches in Japan, and Monteiro and Moreira (1990) found total fresh weights of 22 to 26 kg m⁻² in Portugal. Assuming a dry weight: fresh weight ratio of 0.21 (Sytsma unpublished data), maximum total parrotfeather biomass in Park's Lake was about one-fifth of that reported in Japan and Portugal.

Biomass turnover was high in Park's Lake. There were no significant changes in biomass between June and September 1989 in any of the sampling areas. Emergent stems exhibited no obvious herbivory or senescence, and there was no change in area of the parrotfeather stand during the growing season. Although not measured, biomass loss

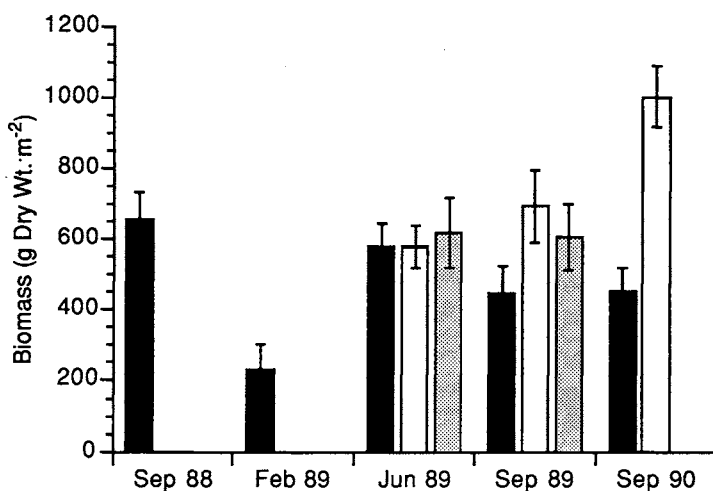


Figure 1. Total dry weight biomass of parrotfeather collected in deep (black) and shallow (open) plots in the southern basin and shallow plots in the northern basin (stipled) of Park's Lake (Mean±1 SE, n=6 in September 1988 and February 1989, n=5 on all other sampling dates).

rates, primarily of submersed tissues, must have approximated productivity rates reported by Sytsma (1992). Similarly, Monteiro and Moreira (1990) found no biomass accumulation during the growing season in the parrotfeather they studied, which suggests that high biomass turnover is a general feature of parrotfeather.

Most of the biomass in Park's Lake was in rhizome tissues. Emergent tissues never comprised more than 24% of the total parrotfeather biomass (Table 1). Emergent tissues generally comprised a greater portion of the total biomass in the shallow site than in the deep site. Rhizome tissues made up 72 to 95% of the total parrotfeather biomass in summer. Roots never comprised >12% of the total biomass. Submersed stems bearing leaves (submersed growth form) accounted for 3 and 1% of the total biomass in February and September 1989, respectively. The submersed growth form was absent or represented less than 1% of the biomass on the other sampling dates.

There was substantial variation in allocation to emergent biomass between years (Table 1). Allocation to emergent biomass was lowest in September 1989 and highest in September 1990. Flooding occurred in March 1989 that severely perturbed the parrotfeather stand and may have altered sediment composition in Park's Lake. Changes in sediment composition may have altered nutrient availability and plant allocation patterns. If perturbation was indeed the cause of the reduced allocation to emergent biomass in 1989, the parrotfeather stand was quite resilient, biomass allocation patterns in 1990 were similar to those in 1988.

Rhizome concentrations of N increased during the growing season, while concentrations of P and C were relatively stable (Figure 2). Concentrations of P were generally greater in rhizomes from the shallow plots, possibly reflecting the ability of the 25 to 30-cm long adventitious roots,

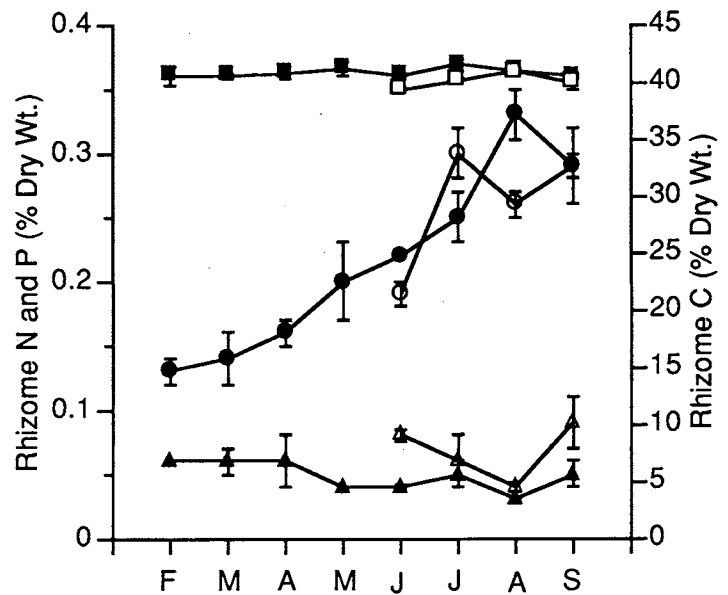


Figure 2. Variation in N (○), P (△) and C (□) concentrations in rhizomes of parrotfeather collected in deep (filled symbols) and shallow (open symbols) plots in the southern basin of Park's Lake (Mean ± 1 SE, n=3).

formed in the water column, to gain access to sediment P in shallow water (Sytsma 1992). Nitrogen concentrations in rhizomes nearly tripled over the period of study in shallow and deep plots. There were no consistent differences in rhizome N concentrations between depths.

The parrotfeather N pool was dominated by rhizome N (Figure 3). Allocation of N differed with both season and depth. In June, rhizomes contained 52% of the total N pool in the deep plots and 42% in the shallow. By September, rhizome N had increased to 89 and 53% of the total N pool in deep and shallow sites, respectively. The proportion of the total N pool in emergent growth in the

TABLE 1. ALLOCATION OF PARROTFEATHER BIOMASS (%) BETWEEN EMERGENT AND SUBMERSED BIOMASS AND ALLOCATION OF SUBMERSED BIOMASS BETWEEN RHIZOMES, SUBMERSED STEMS WITH SUBMERSED LEAVES¹, AND ROOTS IN PARK'S LAKE. BASED ON MEAN BIOMASS IN DEEP AND SHALLOW PLOTS IN THE SOUTHERN BASIN.

Date Depth	% of Total biomass			
	Emergent	Submersed	Rhizomes	Roots
Sep 88 Deep	13	87	83	4
Feb 89 Deep	3	97	82	12
Jun 89 Deep	10	90	82	8
Shallow	20	80	74	6
Sep 89 Deep	2	98	95	2
Shallow	11	89	85	4
Sep 90 Deep	20	80	74	6
Shallow	24	76	72	4

¹Submersed stems with leaves (submersed growth form) comprised 3 and 1% of the total biomass in the deep plot in February and September 1989, respectively. Submersed stems with leaves were not present in samples on the other sampling dates.

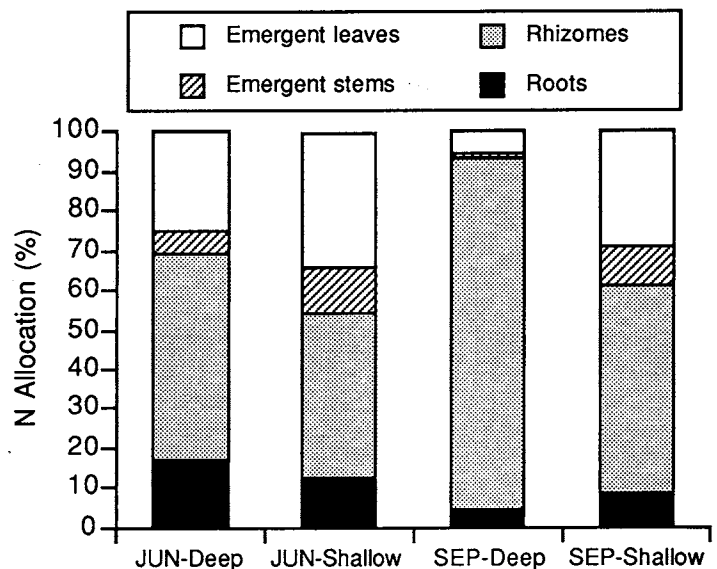


Figure 3. Allocation of the total N pool in parrotfeather collected in shallow and deep plots in the southern basin of Park's Lake in June and September 1989.

deep plots decreased from 30% in June to < 10% in September. The proportion of the total N pool in emergent tissues in the shallow site was relatively constant in June and September. The total N pool in the deep plots was 2 g N m⁻² in June and 1.5 g N m⁻² in September. In the shallow plots, the total N pool was 2.5 g N m⁻² and 3 g N m⁻² in June and September, respectively.

Allocation of P was quite different than N. Rhizomes contained only about 3% of the P pool. Greater than 80% of the P in Park's Lake parrotfeather was in the emergent tissues (Figure 4). The total P pool decreased by 70% (0.1 to 0.03 mg P m⁻²) in the deep plots by 40% (0.5 to 0.3 mg P m⁻²) in the shallow plots between June and September. Emergent leaves lost P and emergent stems gained P between June and September. In the deep plots, emergent leaf P dropped from 40 to 4 μg m⁻² emergent stem P increased from 70 to 200 μg m⁻². In the shallow plots, emergent leaf P decreased from 100 to 60 μg m⁻², while stem P increased from 20 to 200 μg m⁻².

Rhizomes were important in allocation of biomass and N in parrotfeather, however, the role of rhizomes, or old stems, in the overall survival strategy of parrotfeather is unclear. Parrotfeather lacks structures produced specifically for storage, dispersal, and perrenation (e.g., tubers, turions, and winterbuds); rhizomes serve all these functions. The storage function was limited to N, there was no evidence of seasonal P or C accumulation. Rhizomes function as a support structure for adventitious roots and provide buoyancy for emergent growth during the summer, but their role in perrenation and dispersal is probably paramount. Rhizomes stored under moist conditions in a refrigerator survived for one year (Sytsma personal observation). Parrotfeather survives overwinter drawdown in

California irrigation canals as rhizomes buried in the sediment, a strategy common to many aquatic plants in systems with seasonally fluctuating water levels (Hutchinson 1975).

Limitation of parrotfeather growth by P in Park's Lake (Sytsma 1992) and allocation of >80% of the P pool to emergent biomass suggests that a harvesting strategy, that removes only the emergent growth, could remove a major portion of the Park's Lake P pool (summer water column P concentrations were typically <20 μg l⁻¹ and water transparency was high, indicating low phytoplankton density) and reduce parrotfeather growth. Harvesting in conjunction with reduction in P loading to the system could severely impact growth. Reduction of P loading to Park's Lake is impractical because nutrient loading is primarily by groundwater; however, if the allocation patterns observed in Park's Lake are a general feature of parrotfeather biology, the technique may be effective in other systems.

Allocation of resources to storage is a common strategy in environments with periodic, stressful or inhospitable periods (Mooney 1972), and is important aspect of competitiveness in aquatic macrophytes. Parrotfeather appears to rely on current uptake of P and C for growth rather than on P and C stores. This characteristic may partially explain the failure of parrotfeather to invade areas with severe winters, and the apparent lack of characteristics that facilitate rapid and aggressive invasion of aquatic systems in areas with mild winters (Nelson and Couch 1985).

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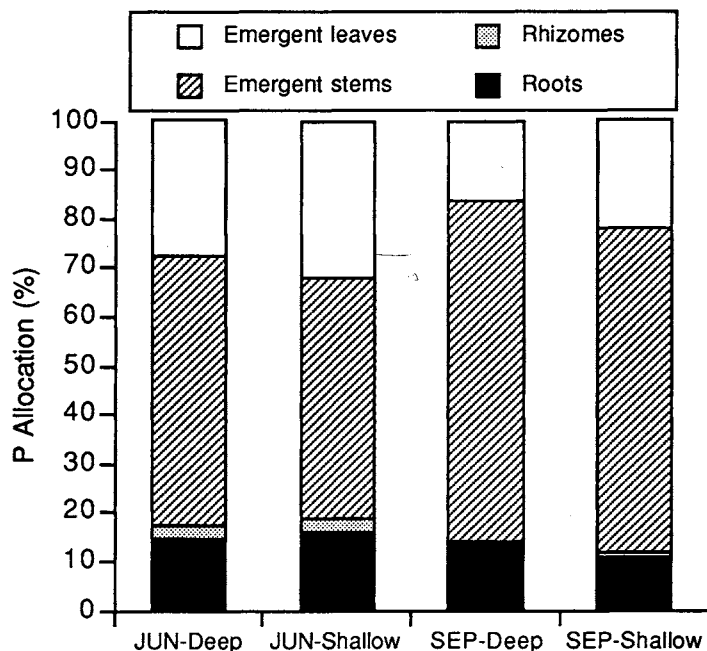


Figure 4. Allocation of the total P pool in parrotfeather collected in shallow and deep plots in the southern basin of in Park's Lake in June and September 1989.

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