THE ROLE OF EMERGENT AQUATIC VEGETATION IN THE NUTRIENT BUDGETS OF MANAGED MARSHES

BY

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ABSTRACT

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Wetlands have been used as sites for the disposal of nutrient-enriched waters. The emergent vegetation is important in the nutrient budgets and hydrology of these systems. However, little is known about how most emergent plant species respond to variations in the absolute quantities and proportions of substrate macronutrients. More information is also needed on the establishment and harvesting of the vegetation.

Nutrient uptake experiments were conducted on *Phragmites australis*, *Zizania aquatica*, *Typha latifolia*, *Typha angustifolia*, and *Sparganium eurycarpum*. Plants were grown outdoors in a sand substrate in 30 l polyethylene tubs during the 1980-82 growing seasons. Nitrate, phosphate and potassium fertilizers were supplied using a factorial treatment arrangement. Nitrate-N levels were 0, 7.8, 23.4, 46.8 or 93.6 g m^{-2}; phosphate-P was 0, 2.1, 6.3, 12.5 or 25.0 g m^{-2}; K was 0, 7.8, 23.4 or 41.6 g m^{-2}.

Nitrate and phosphate treatments and their interaction strongly affected plant growth. Potassium treatment had little or no effect. Nitrate strongly controlled distribution of dry weight. The ratio of belowground to aboveground dry weight within a species varied by a factor of

about 3 with highest ratios associated with low nitrate. Tissue content of N or P was increased 2 to 3 times over that necessary to obtain maximum biomass production. N:P ratios less than about 4 were found with severely N limited growth; ratios were greater than about 12 with severely P limited growth. _S. eurycarpum_ was least able to tolerate extremely high nitrate levels.

Attempts to establish the above 5 species plus _Spartina pectinata_ in a clay-lined man-made marsh had mixed success. _S. eurycarpum_ rapidly established itself but was subject to decline and invasion by other species. _Typha_ spp. established stands more slowly but maintained better stand density and purity. _P. australis_ sent out mainly floating tillers from propagule clumps rather than rhizomes and vertical shoots. _S. pectinata_ and _Z. aquatica_ failed to establish.

Multiple harvests of _Typha_ spp. resulted in biomass removal of 130% of single harvest controls and N and P removal of about 150% of the controls.

Nutrient budgets developed for three man-made marsh-ponds showed a net removal of fixed N from flow-through waters but a variable situation with total P.

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INTRODUCTION

Emergent aquatic vegetation has potential for nutrient and other contaminant removal from sewage-enriched substrates (Wile et al.,1981). In addition, wetland systems can have other beneficial effects on water quality and hydrology. They may serve as retention structures that detain water during flood periods and reduce peak flows of streams. During storage, substantial improvements in water quality may occur. Certain nutrients such as phosphorus may be sorbed to or precipitated into the sediments. Other nutrients such as nitrogen, sulfur, and carbon may be lost to the atmosphere as gases due to microbial transformations which also reduce the oxygen demand of the water. A large proportion of the sediment load may be dumped into the marsh as the water velocity declines. Tchobanoglous and Culp (1980) found that natural wetlands used for treatment of wastewater removed 60% to 90% of the suspended solids. This sediment load may include adsorbed P, heavy metals, and organic toxicants. Wetlands may also act to reduce pathogens (Seidel, 1976a, 1976b; de Jong, 1976; Wellings, 1976; Wile et al, 1981) Because of these properties, both natural and artificial marshes have been used for a variety of purposes such as treatment of urban stormwater runoff (e.g. Hickock, 1978; Tolman, 1978), treatment of municipal and industrial wastewater (e.g. Grant and Patrick, 1970; Lee et al., 1976; Steward and Ornes, 1975; Ewel, 1976; de Jong, 1976; Farnham and Boelter, 1976; Richardson et al., 1976; Small, 1976; Seidel, 1976a, 1976b; Spangler et al, 1976a, 1976b; Whigham and Simpson, 1976a, 1976b; Turner et al., 1976; Cederquist, 1977; Fetter et al., 1978; Sloey et al., 1978; Wile et al, 1981), pretreatment of drinking water (Czerwenka and Seidel, 1976), and for management of dredge slurries (Lee et al., 1976).

Since emergent plants represent a harvestable and potentially valuable biomass resource (Pratt and Andrews, 1981 Farnham, 1978) as well as a potential means of removing nutrients from a system, information is needed on their growth and nutrient uptake over wide ranges of nutrient supply. The nutrient uptake characteristics are most critical for nutrients such as phosphorus and potassium which have no volatile forms and therefore cannot be removed from a system in the gaseous state. Although 80-90% of the phosphorus detained by a marsh is usually trapped in the sediments or stored in belowground plant tissues and not easily removeable by harvest (Steward, 1976; Turner et al., 1976; Sloey et al., 1976, 1978), harvest may nevertheless be desireable if uses exist for the biomass. Marshes have natural rates of primary production that are among the highest of all ecosystems (Westlake, 1963; Whittaker and Likens, 1973). Some uses for the biomass as a source of fiber or energy have already been established (Bjork, 1967; Pratt and Andrews, 1981). However, there is a need for more information concerning the optimal means of establishment, nutrient application, and best harvesting. It may be valuable to study interspecific differences in nutrient utilization since it has been shown by Garten (1978) that certain species of emergent macrophytes are quite distinct in their leaf mineral compositions. These differences may be of practical importance in designing artificial wetland systems or in planning the utilization of natural systems for the improvement of water quality.

The focus of this dissertation research was to gather the necessary data for the culture of emergent marsh vegetation with the primary goal of removing unwanted macronutrients from artificially enriched systems. Major hypotheses that were tested included the hypothesis that nutrient treatments affect both net primary production and distribution of this production. Also, the hypothesis that nutrients would be taken up in excess of needs for maximum growth was examined. To accomplish these goals, a number of common, highly productive emergent plant species that showed promise as species for cultivation in highly enriched waters were selected. The species most thoroughly studied prior to this investigation included several species of bulrush (Scirpus). Many species of Scirpus have the advantages of high productivity and nutrient uptake. They also are receptive to frequent harvesting with rapid shoot regrowth from the cut stubs so that stands can be maintained with young nutrient-rich tissues (Hanseter, 1975). S. lacustris has an extensive literature and history of culture in Europe (e.g. Seidel, 1976; de Jong, 1976). In Wisconsin, S. validus, S. acutus, and S.

fluviatilis have been examined in some detail (e.g. Spangler et al., 1976a, 1976b; Sloey et al., 1978). S. robustus has been investigated in California (Cederquist, 1977). The present study was directed towards other promising taxa, most of which have had more limited research into their nutrient removal capabilities.

Phragmites australis (Cav.) Trin. ex Steudel, appeared to be an ideal species for this purpose because of its cosmopolitan distribution, and its capacity for high rates of biomass production (Bjork, 1967). Primary production and nutrient uptake in natural P. australis (= P. communis) stands (Mason and Bryant, 1975; Dykyjova, 1978) and the effects of these stands on sediment and water chemistry (Bayly and O'Neill, 1972; Banoub, 1975) have been extensively examined. Changes in nutrient content with physiological age and differences between tissue types have also been studied (Kvet, 1973). Dykyjova et al (1971; 1972) grew P. australis in outdoor hydroponic culture using a standard culture nutrient solution with a variety of dilutions. However, they did not vary the ratios of any of the supplied nutrients. Stands apparently recover well after harvesting and may even show an increase in the size and density of new shoots (Dykyjova and Husak, 1973). However, P. australis does not respond well to multiple harvests within a single growing season.

Wild rice (Zizania aquatica L.) was selected because it was one of the few marsh grasses with established economic uses as a crop species and also because of its value as a wildlife food (Fasset, 1957; Correll and Correll, 1972). Because it is an annual, most of its production remains aboveground where harvest should be relatively easy. Peak biomass can reach over 2000 g m^{-2} and averages about 1200 g dry weight m^{-2} (Whigham and Simpson., 1977). Whigham and Simpson (1976a) conducted some experiments on the ability of this species to accept municipal wastewater irrigation. Lee and Stewart (1981, 1983) have looked for correlations between sediment and plant tissue nutrients in natural _Z. aquatica_ stands. There has also been considerable research done on _Z. aquatica_ at the University of Minnesota (e.g. Grava and Raisanen, 1978). However, their research has focused on maximizing grain production and control of disease rather than whole plant production and nutrient uptake. There exists limited data on nutrient uptake variability and growth patterns over widely variable nutrient application rates. One major difficulty with the use of wild rice is its high susceptibility to disease, especially _Helminthosporium_ blight (Kernkamp _et al_, 1976).

Species of cattail (_Typha_) have received some attention for use in wastewater treatment. Spangler _et al_ (1976b) investigated _T. latifolia_ L. growth on artificial substrates but rejected its use primarily on the basis of its regrowth characteristics. Cut shoots (mostly leaves) showed very limited regrowth because they generally lacked active intercalary meristems at the time of cutting. Most new growth came from shoots developing from underground buds which surfaced several weeks after the harvests. They were unable to sustain a high biomass yield with biweekly harvests. Hanseter (1975) also found that (in _Typha_ spp. stands) shoot density and size decreased after harvest. However, even with their limited capacity for rapid regrowth after harvest, _Typha_ spp. warrant more attention because of their large peak standing crops and ability to maintain nearly pure stands. Two temperate circumboreal species of cattail (_T. latifolia_ and _T. angustifolia_ L.) have overlapping ranges which includes the northeastern one-third of the U.S. Ecological differences between _T. latifolia_ L. and _T. angustifolia_ L. have been documented (Grace and Wetzel, 1981,1982; McNaughton, 1975). It is of interest to know if these differences extend to factors of importance in the culture of these species for wastewater renovation. That is, what are the differences between these two species in nutrient uptake, tissue production, distribution of production, ease of establishment, and regrowth after harvest. Even if _Typha_ dominated marshes are not appropriate for multiple harvest systems to maximize P removal, they may be valuable for their N stripping abilities. For example, a _Typha_ dominated Wisconsin marsh (Spangler _et al_, 1976b) reduced ammonium-N values from 8 mg N l^{-1} in the influent to below levels of detection in the effluent and reduced nitrate-N values from 0.2 to 2.1 mg l^{-1} in the influent to 0.1 to 0.2 mg l^{-1} in the effluent (Sloey _et al._,1978).

The genus _Sparganium_ is taxonomically related to the cattails and is sometimes included in the family Typhaceae rather than being placed in the monogeneric Sparganiaceae (Voss, 1972). S. eurycarpum is the largest and most robust of the North American burreeds (Fasset, 1957). It is potentially worthy of cultivation due to its often high primary productivity (van der Valk and Davis, 1978) and resultant potential for removal of nutrients from artifically enriched substrates. It resembles Typha spp. in its poor regrowth characteristics when using multiple harvests (Hanseter, 1975).

S. eurycarpum often forms large, nearly monospecific stands in waters up to 1 m deep. In Pentwater Marsh (Oceana County, Michigan), a Lake Michigan riverine coastal marsh, it is the dominant cover type in the deepest water of the emergent vegetation zone. This marsh is receiving extensive study of its vegetation and the effects of the vegetation on the nutrient budget of the marsh as part of the Michigan Sea Grant Program (Burton and Kelley, 1983). A second reason for studying this plant was therefore to provide information on the growth and nutrient uptake of this plant species under controlled conditions so that this information might be used to help predict the response of Pentwater marsh to additional influxes of nutrients.

Prairie cordgrass (Spartina pectinata Link) is a productive wetland grass species chosen for study in comparison with the other two grass species. It is a perennial C4 grass and it was desired to examine how this species would differ from the C3 species studied in properties important to its growth on sewage-enriched substrates.

MATERIALS AND METHODS

NUTRIENT UPTAKE EXPERIMENTS

The response of 5 species of emergent aquatic plants to varying rates of nitrate, phosphate, and potassium fertilization was examined using a series of experiments with each experiment in an individual tub. These experiments were conducted outdoors at the Water Quality Management Facility (WQMF) of the Institute of Water Research at Michigan State University. Plants were grown in 30 l polyethylene tubs (.125 m opening area) using 20 l of sand as a growth medium. The sand contained $<.44$ g m^{-2} of available P, <1.1 g m^{-2} of available N, and <2.3 g m^{-2} of available K as determined by the Michigan State University Soil Testing Laboratory.

During 1980, experiments were conducted on *P. australis* and *Z. aquatica*. *P. australis* propagules consisted of 5 cm long size-matched rhizome sections with 20 cm of shoot attached. Rhizomes were collected locally from a single clump growing in water 20 cm deep. It is unknown if all of the propagules were of the same clone. Average dry weight was 1.2 g (s=0.4g). Average total N, P, and K fractions of the propagules were 3.12%, 0.51%, and

2.47% respectively. Rhizomes were planted immediately after collection with 15 cm of vertical shoot extending above the sand surface.

Five Z. aquatica seeds were introduced to each tub used for this species. Once established, wild rice plants in each tub were thinned to one seedling. Seeds of the Netum variety were obtained from the University of Minnesota. All tubs were partially submerged in the water-level controlled marshes of the WQMF in order to provide a uniform and more natural temperature regime. Tubs were arranged in double rows extending through the shallow terrace in areas where all vegetation had been removed. Assignment of species and chemical treatments was completely random. The sand medium in the tubs was completely isolated from the surrounding marsh water.

Treatments consisted of single applications of nitrate ($CaNO_3$), phosphate (Na_2HPO_4) and potassium (KCl) solutions mixed into the sand prior to the rhizome or seed planting. A 4x4x4 factorial arrangement of the three nutrient treatments was used. The amount of nitrate-N added to each tub was 0, 7.8, 23.4, or 46.8 g m^{-2} of sand surface (equivalent to 0, 48.8, 147, or 293 g m^{-3} of sand); the amount of phosphate-P added was 0, 2.1, 6.3, or 12.5 g m^{-2} (equivalent to 13.1, 38.8, or 78.1 g m^{-3}); the amount of potassium, added was 0, 7.8, 23.4, or 41.5 g m^{-2} (equivalent to 0, 48.8, 147, or 260 g m^{-3}). There were five replicates of each treatment combination. Other necessary plant nutrients were added from a single solution to all tubs in the following amounts (g m^{-2}): $MgSO_4$ (38.5); $Fe(SO_4)_3$ (1.13); H_2BO_3 (2.48); $MnSO_4.H_2O$ (0.088); $CuSO_4 \cdot 5H_2O$ (0.096); $ZnSO_4$ (0.112); $CoCl_2.6H_2O$; (0.112); $(NH_4)_2MoO_4$ (0.080) (Modified from Dykyjova & Veber, 1978). Deionized water was added to bring the tub solution level 2 cm above the sand. During the growing season, water level in the tubs was maintained above the sand surface using deionized water to supplement the rainwater inputs.

Experiments on _T. angustifolia_ and _T. latifolia_ were conducted during 1981. The set-up of these experiments was similar to that used for _P. australis_ and _Z. aquatica_. _Typha_ propagules consisted of 5 cm long size-matched rhizome sections with 20 cm of shoot attached. All rhizomes were collected locally from monospecific clumps growing in water 10-30 cm deep. It is unknown if propagules were all of the same clone. Average propagule dry weight was 7.0 g (s=2.2g) for _T. latifolia_ and 1.1 g (s=0.3g) for _T. angustifolia_. Average total N, P, and K fractions of the propagules were 2.65%, 0.52%, and 2.42% respectivley for _T. latifolia_ and 2.33%, 0.51%, and 2.35% for _T. angustifolia_. Experimental treatments were the same as those used for _P. australis_ and _Z. aquatica_. However, instead of being placed in marshes, 1981 tubs were partially buried in a pit filled with water-saturated sand. Tubs were again arranged in double rows with chemical treatments and species assigned at random. This relocation was necessary to avoid fluctuating marsh water levels, damage to experimental plants by muskrats, and contamination by blackbird droppings experienced during 1980.

During 1982, initial nutrient uptake experiments were conducted on S. eurycarpum. In addition, further experiments were conducted on T. latifolia, T. angustifolia, and on P. australis at higher levels of nitrate and phosphate treatments than were previously used. S. eurycarpum propagules also consisted of 5 cm long size-matched rhizomes with 20 cm of shoot attached. Rhizomes were collected locally from a clump started two years earlier from a single rhizome collected from Pentwater Marsh and grown in one of the WQMF marsh-ponds. Thus, all propagules were genetically identical. Average propagule dry weight was 2.0 g (s=0.8 g). Average N and P fractions of the propagules were 1.81% and 0.22% respectively. Propagules were planted and tubs positioned as described for the Typha spp.

Experimental treatments for the S. eurycarpum tubs consisted of single applications of nitrate ($CaNO_3$) and phosphate (Na_2HPO_4) solutions mixed into the sand prior to the rhizome planting. A 5x5 factorial treatment arrangement was used. The amount of nitrate-N added to each tub was 0, 7.8, 23.4, 46.8 or 93.6 g m^{-2} of sand surface (equivalent to 0, 48.8, 147, 293, or 156 g m^{-3} of sand); the amount of phosphate-P added was 0, 2.1, 6.3, 12.5 or 25.0 g m^{-2} (equivalent to 0, 13.1, 38.8, 78.1 or 156 g m^{-3}). There were seven replicates of each treatment combination for a total of 175 tubs planted with S.

eurycarpum. Other necessary nutrients were added from a single solution to all tubs as with the previous experiments except that 46.8 g m^{-2} of K as KCl was also added to each tub. Other aspects of the experimental setup were identical with that used during 1981. Only the two highest treatment levels of nitrate and phosphate were used on *P. australis*, *T. angustifolia*, and *T. latifolia* during 1982.

Shoot growth rates for each species in all three years were estimated from meter stick measurements of shoot height above sand level (sand surface to tip of longest leaf) and caliper measurements of maximum shoot diameter at tub rim level. Measurements were made at intervals of about three weeks. These measurements were used in conjunction with weights of shoots from the parent stands to develop multiple regression expressions to estimate shoot dry weight accumulation. Equation 1 is for *P. australis*, equation 2 for *Z. aquatica*, equation 3 for *T. latifolia*, equation 4 for *T. angustifolia*, and equation 5 for *S. eurycarpum*. 95% confidence intervals on slopes and intercepts are shown below each equation.

$$\ln W = 1.83 \ln H + 0.70 \ln D - 8.17 \quad (r=.98; p>.99) \quad (1)$$
$$(1.72;1.94) \quad (0.57;0.83) \quad (-8.47;-7.87)$$

$$\ln W = -0.86 \ln H + 1.72 \ln D + 1.74 \quad (r=.93; p>.99) \quad (2)$$
$$(-2.06;-.34) \quad (0.92;2.52) \quad (-2.67;6.15)$$

$$\ln W = 1.55 \ln H + 0.88 \ln D - 7.80 \quad (r=.98; p>.99) \quad (3)$$
$$(1.28;1.82) \quad (0.64;1.12) \quad (-7.13;-8.46)$$

$$\ln W = 1.11 \ln H + 1.35 \ln D - 7.14 \quad (r=.98; p>.99) \quad (4)$$
$$(0.93;1.29) \quad (1.19;1.52) \quad (-6.70;-7.58)$$

$$\ln W = 1.27 \ln H + 1.36 \ln D - 9.11 \quad (r=.98; p>.99) \quad (5)$$
$$(0.86; 1.68) \quad (1.16; 1.56) \quad (-9.75; -8.46)$$

W in each equation is equal to shoot dry weight (g), H is equal to shoot height (cm) and D is equal to shoot diameter (mm). Equation 1 was developed using 98 P. australis shoots harvested during September, 1980; Equation 2 from 20 Z.aquatica shoots harvested in August, 1980; equations 3 and 4 used 70 T. latifolia and 138 T. angustifolia shoots respectively that were collected in August, 1981; equation 5 used 30 S. eurycarpum shoots cut during August, 1982. Shoots for P. australis, T. angustifolia, T. latifolia and S. eurycarpum regressions were from parent stands; Z. aquatica shoots were grown from the same seed used in the nutrient uptake experiments. Both flowering and non-flowering shoots were used. Estimates were corrected for bias introduced by the logarithmic transformations using the method of Baskerville (1973). In order that extrapolation might be possible to weights at other drying temperatures, 10 samples of each species were dried at 90 C and 105 C in addition to 60 C. It was found that the weights at the three temperatures varied by less than 1% for all species. Shoot losses over the growing season were presumed small and no attempt was made to estimate them.

During late August and early September, shoot samples of each species were obtained by clipping them at sand level while root and rhizome samples were water-sifted from the sand. All samples were dried to constant weight at 60

C. Dried samples were coarse ground in a Wiley Mill, thoroughly mixed, and subsampled for fine grinding through a .1 mm screen. A 0.2 g sample of the finely ground tissue was digested using a modified microkjeldahl digestion (Nelson and Sommers, 1973). The digestion included a reducing step so that any nitrates or nitrites present were included in the N determinations. Lithium sulfate was substituted for potassium sulfate in the digestion so that the same digestate could be used for K determinations as well as for N and P. K was determined by flame emission spectroscopy. N was determined using method 351.1 (Colorimetric, automated phenate, U.S. EPA, 1974) while P was determined using method 365.1 (colorimetric, automated ascorbic acid, U.S. EPA, 1974). As a check on the procedure, U.S. National Bureau of Standards standard plant materials (pine needles, orchard leaves and tomato leaves) of known elemental composition were carried through the same analysis procedures. The procedures used in this study resulted in average recoveries of 105% (s=5.7%), 103% (s=6.3%), and 97% (s=6.6%) of the standard N, P, and K respectively.

ESTABLISHMENT AND HARVEST EXPERIMENTS

Experiments on the establishment and harvest of *P. australis*, *Z. aquatica*, *T. latifolia*, *T. angustifolia*, *S. eurycarpum*, and *S. pectinata* were conducted on three man-made marshes (M1, M2, M3) on the WQMF. The marshes were constructed in 1973. All three were 0.4 ha in surface area with a terrace design. The outer, shallow terrace occupied 25% of the total marsh surface area and was designed to operate at a depth of 15 cm but can be filled to 45 cm. The second terrace occupied 50% of the total area with a designed operation depth of 60 cm while the middle terrace was designed to operate at a depth of 90 cm. All marshes were sealed with low organic matter clays during construction.

One of the three marshes (M2) had little emergent vegetation established in it as of the spring of 1980. This resulted from a 1974 drawdown to repair a control structure that had killed most of the originally planted vegetation. All three of the marshes were originally stocked with T. latifolia by transplanting approximately 600 rhizomes per marsh into the shallow terrace during October and November, 1973 (McNabb et al, 1975). At the start of this project, the shallow terrace of M2 contained only scattered patches of T. latifolia, T. angustifolia, P. australis, and other minor emergent components. Because of the availability of unoccupied space, M2 was chosen for the establishment experiments. Immediately prior to the start of experiments, the other two marshes (M1 and M3) had nearly continuous and dense stands of T. latifolia, T. angustifolia, and shoots of intermediate morphology which may have been the hybrid T.x glauca growing on the shallow terraces and extending out over part of the middle terraces. These two marshes were utilized for harvest experiments on established stands of *Typha*.

The shallow terrace of M2 was prepared for plant establishment by first removing all existing vegetation from areas where experiments were to be conducted. With the water drained, the sediments of the shallow terrace were fertilized with urea at the rate of 45 g N m^{-2} by raking granulated urea evenly into the sediments. Other nutrients were assumed to be already present in excess since the marsh had previously been repeatedly flushed with secondary municipal wastewater during 1973-1975. Wastewater inputs to the marshes are normally low in N because the water flows through two sewage lagoons with high N stripping properties before entering the marshes (King and Burton, 1979).

The shallow terrace of M2 was divided into plots 2.5 m long around the circumference of the marsh. The plots extended about 5 m from land to the edge of the shallow terrace. Nine plots were prepared for each of the six previously mentioned species. Plots were assigned to species in blocks of 3 contiguous plots. During the early summer of 1980, an attempt was made to establish the five perennial species selected for study (*P. australis*, *T. latifolia*, *T. angustifolia*, *S. eurycarpum*, and *S. pectinata*). *P. australis*, *T. latifolia*, and *T. angustifolia* propagules were collected locally from shallow water populations by digging up belowground sections from monospecific stands. *S. eurycarpum* was collected from Pentwater Marsh and *S. pectinata* was collected from a ditch along a local railroad right-of-way. Clumps of roots and rhizomes about 20 cm in diameter were transplanted into the prepared plots. Each plot had 10 evenly spaced clumps imbedded into the clay/organic surface layer.

During April, 1980 Z. aquatica plots were planted with about 500 g per plot of Netum variety seeds. The seed was spread evenly over the surface and then raked into the clay/organic surface sediments.

Also during 1980, harvest experiments were begun on plots of Typha spp. growing on the shallow terraces of M1 and M3. Nine 5 m long plots with dense stands of Typha spp. were selected in each marsh for two different harvesting regimes and controls with three replicates in each marsh. Plant harvesting began during early June, 1980. Three plots were harvested four times each at three week intervals while three other plots were harvested twice each at six week intervals with the remaining three plots in each marsh serving as controls. Biomass removed and N, P, and K content of this biomass was determined for all plots. Control plots were also sampled for standing crop and nutrient content.

During 1981, the plots in M1 and M3 were monitored for recovery from the harvest treatments. Samples were taken during both early and late summer to measure standing crop and nutrient content.

Similar harvest experiments were conducted on M2 plots during 1981 on the newly established vegetation. Only plots of T. latifolia, T. angustifolia, and S. eurycarpum were dense enough to conduct reasonable harvest experiments. Recovery of M2 plots was monitored during 1982 by measurement of standing crop and nutrient content.

MARSH NUTRIENT BUDGETS

Nutrient budgets for M1, M2, and M3 were constructed for 1980, 1981 and 1982 by measuring controlled inputs and outputs of nutrients and water. All three marshes were flushed periodically except during the winter months using water from Lake 2 of the four lake WQMF facility. This was done on a rotating basis with each marsh receiving inputs for one week at a time while the other two marshes received no inputs. Inputs were measured at the control structure of Lake 2 and outputs were measured at the output channels of the three marshes using water level recorders and V-notched weirs. Water samples were collected daily when water was flowing from these input and output structures. Laboratory analyses of water samples included determinations of pH, specific conductivity, nitrate-N, nitrite-N, ammonium-N, total Kjeldahl nitrogen, total P, soluble molybdate reactive P, chloride, potassium, alkalinity, and hardness. These data were used to construct input/output budgets for the marshes.

RESULTS AND DISCUSSION

NUTRIENT UPTAKE EXPERIMENTS

Phragmites australis

The original emergent shoot generally died but new shoots typically appeared from the rhizome in about two weeks. The number of shoots per tub in September varied from 1 or 2 to over 50. There was no significant growth response to K^+ fertilization (Table 1). Total K uptake by *P. australis* in pots not fertilized with K exceeded the 1.31 g m^{-2} supply of exchangeable and soluble K of the sand. Thus, more K was available to the plants than was indicated by the sand nutrient analysis, possibly due to mineral weathering or input from precipitation. Since it was found that K^+ treatment did not significantly affect growth, growth values for the nitrate and phosphate treatments were averaged over all levels of K treatment (Figure 1). There were strong and significant (Table 1) growth responses to the nitrate and phosphate treatments and to the interaction of nitrate and phosphate treatments (Table 1). *P. australis* growth responded to nitrate and phosphate fertilization in much the manner predicted by the Mitscherlich (1954) "rule" for many crop plants. That is, growth increase per unit increase in nitrate and phosphate fertilization declines at higher treatment levels.

Root and rhizome production of *P. australis* increased

Table 1. Analysis of Variance on the effects of treatments and their interactions on estimates of *P. australis* cumulative shoot dry mass after 108 days growth (n=246).

Source of Variation	DF	F	Sig. of F
N Treatment	3	166.561	.99
P Treatment	3	79.073	.99
K Treatment	3	1.128	.66
N-P Treatment Interaction	9	21.740	.99
N-K Treatment Interaction	9	0.894	n.s.
P-K Treatment Interaction	9	0.374	n.s.
N-P-K Treatment Interaction	27	1.891	.99

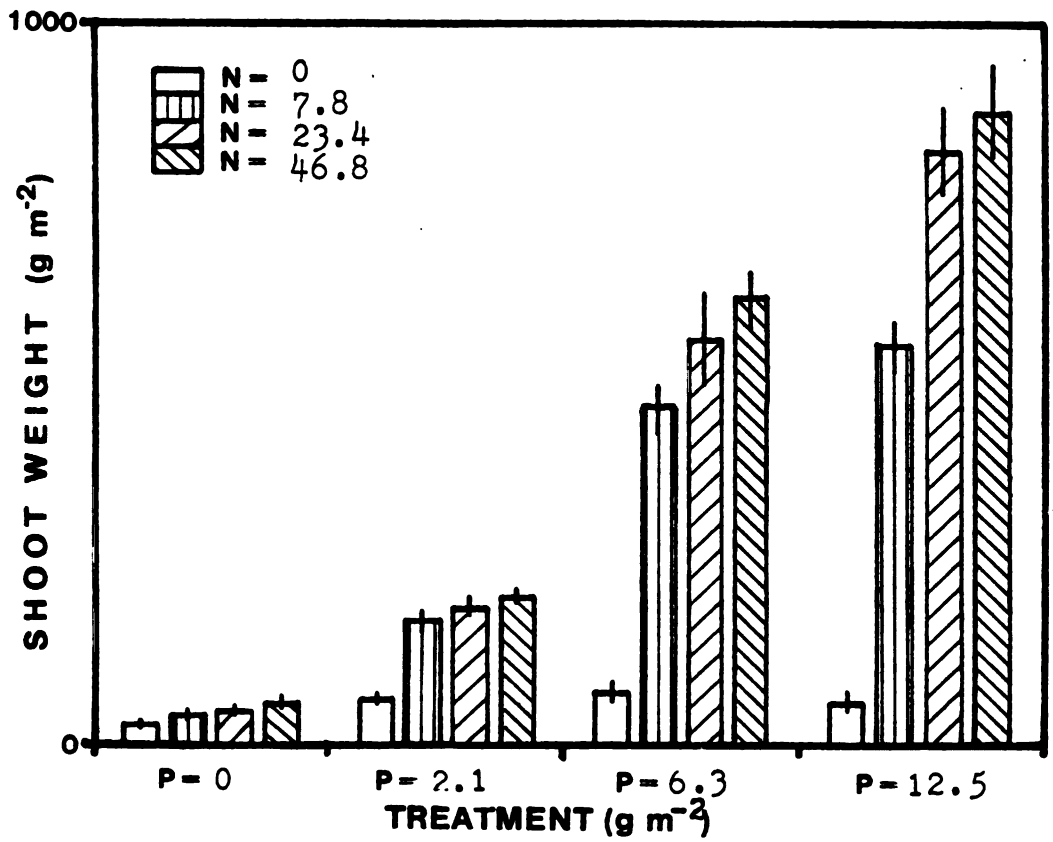

Figure 1. Average areal dry weight (60 C) of P. australis shoots after 106 days growth during 1980 with variable combinations of nitrate and phosphate fertilization. Vertical lines are standard errors of the means.

with nitrate-N content of the substrate but only through the intermediate level of 14.6 g m^{-2} (Figure 2). Root and rhizome production as a fraction of total production declined with increasing nitrate treatment (Figure 3). Root and rhizome production increased with phosphate supply only up to the 1.31 g m^{-2} treatment level (Figure 2). The fraction of the total production in the roots and rhizomes showed no significant (Table 2) relationship to phosphate treatment (Figure 3). Fiala (1976) found the lowest root and rhizome to shoot biomass ratios associated with the most productive habitats in natural P. australis stands in Czechoslovakia. N content of the top 20 cm of sediment was found to be the best predictor of root and rhizome biomass of all parameters examined by Fiala. No simple pattern could be discerned by Fiala with respect to the effects of a number of habitat variables on the growth of underground organs of P. australis. Thus, the importance of substrate nitrogen in determining the distribution of production in P. australis was suggested both by the present study and by Fiala's (1976) results.

Shoot N and P concentrations were not significantly affected by the level of K treatment (Table 3). Therefore, shoot levels of N and P were averaged over all levels of K treatment (Figures 4 and 5). Lowest tissue N concentrations occurred with the lowest level nitrate treatment only when no phosphate was added. Otherwise, tissue N concentrations were lowest at intermediate rates of nitrate addition. This patterm of lowest N at

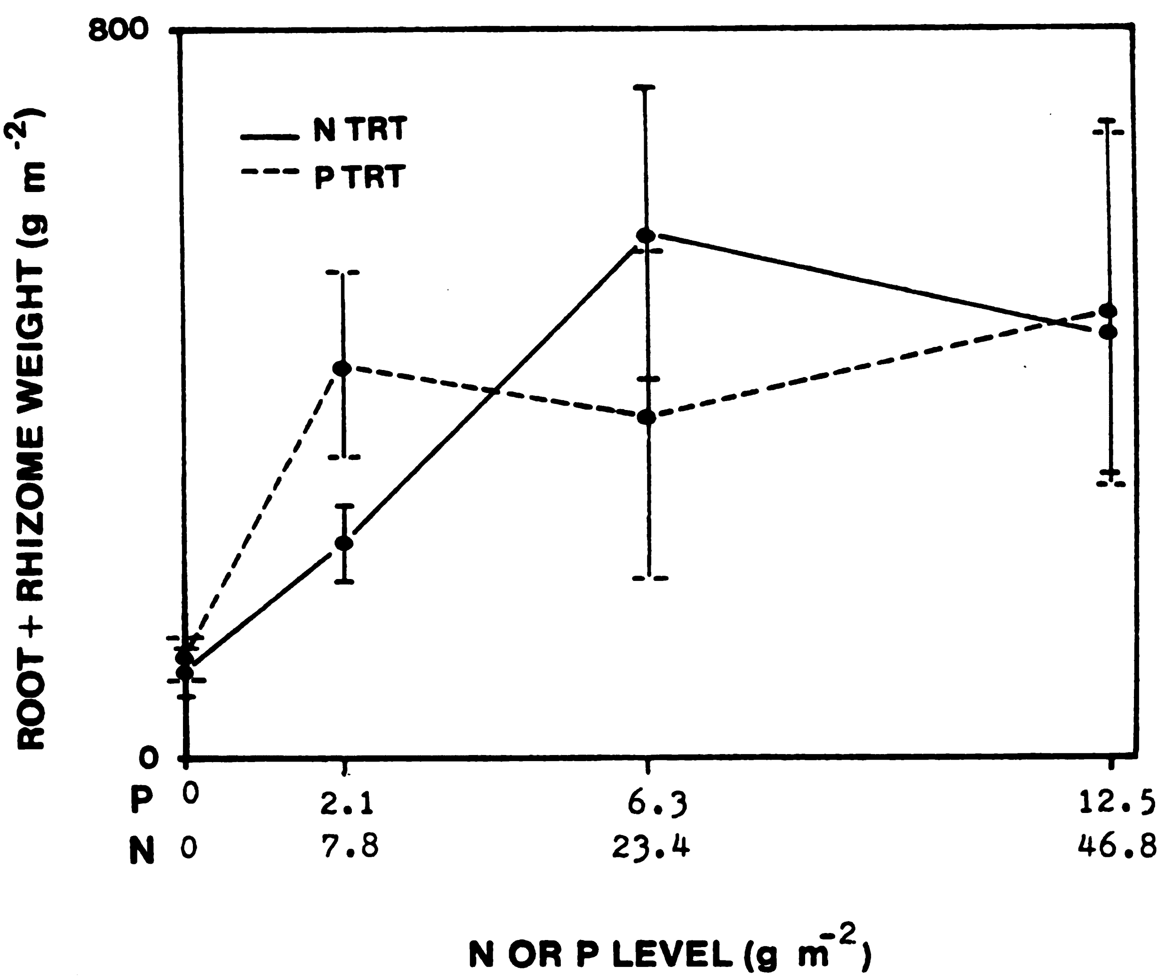

Figure 2. Total areal seasonal belowground production of P. australis as a function of nitrate or phosphate treatment level during 1980. Vertical lines are standard errors of the means.

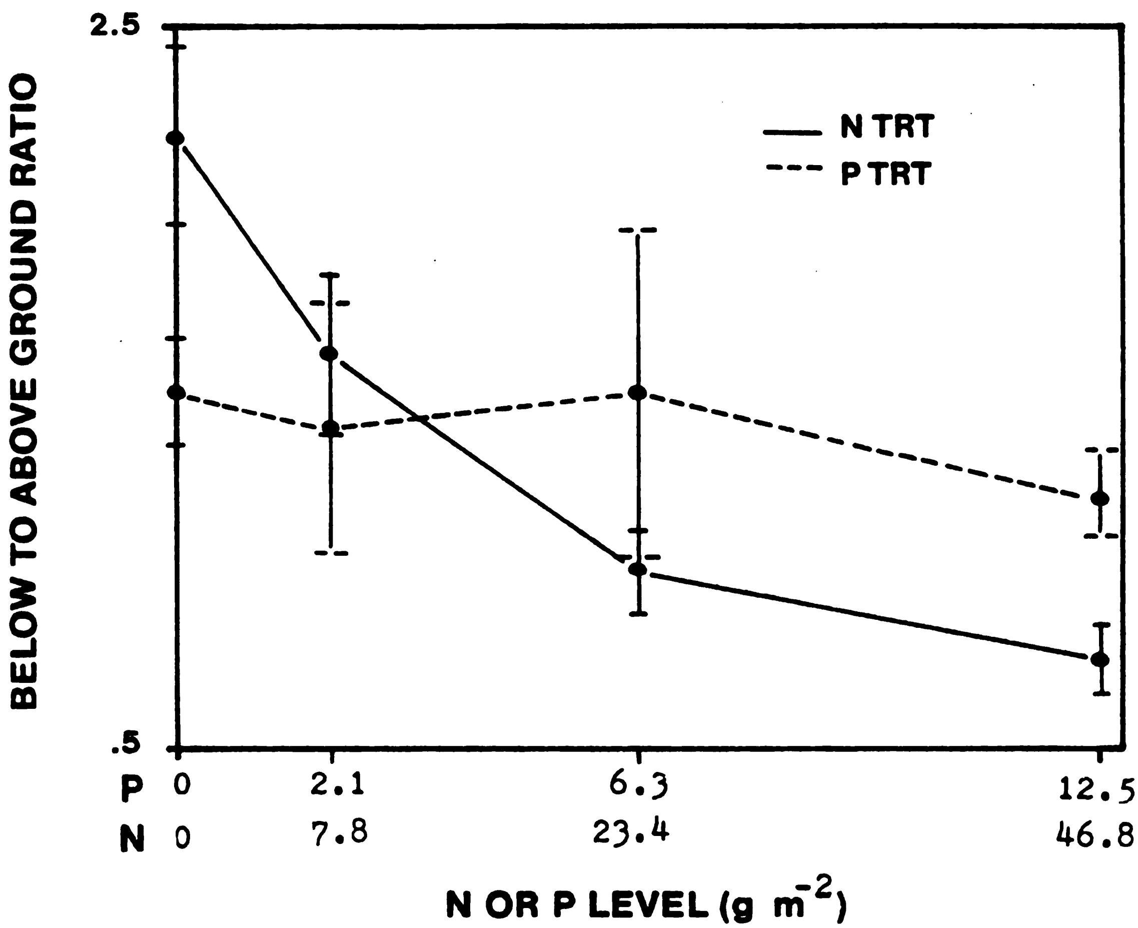

Figure 3. Relationship at end of 1980 growing season between nitrate or phosphate treatment level and distribution of production aboveground and belowground by P. australis. Vertical lines are standard errors of the means.

Table 2. Results of analysis of variance on the effects of treatments on the ratio of *P. australis* root + rhizome dry weight to shoot dry weight. Based on weights of materials harvested at end of experiments and arcsin transformed prior to statistical analysis.

Source of Variation	Effect	n	df	F	Sig. of F
N Treatment	R.+R./Shoot Ratio	34	3	8.21	.99
P Treatment	R.+R./Shoot Ratio	34	3	0.93	n.s.
K Treatment	R.+R./Shoot Ratio	34	3	1.07	n.s.

Table 3. Results of analyses of variance on the effects of treatments on %N, %P, and %K of P. australis shoots and roots plus rhizomes. Based on weights of materials harvested at end of experiments.

Source of Variation	Effect	n	df	F	Sig. of F
N Treatment	Shoot %N	41	3	7.41	.99
N Treatment	R.+R. %N	34	3	8.96	.99
P Treatment	Shoot %N	41	3	2.18	.89
P Treatment	R.+R. %N	34	3	1.59	.89
K Treatment	Shoot %N	41	3	0.41	n.s.
K Treatment	R.+R. %N	34	3	0.15	n.s.
N Treatment	Shoot %P	41	3	0.62	n.s.
N Treatment	R.+R. %P	34	3	4.40	.99
P Treatment	Shoot %P	41	3	1.75	.83
P Treatment	R.+R. %P	34	3	6.67	.99
K Treatment	Shoot %P	41	3	0.76	n.s.
K Treatment	R.+R. %P	34	3	0.19	n.s.
N Treatment	Shoot %K	41	3	4.13	.99
N Treatment	R.+R. %K	34	3	0.96	n.s.
P Treatment	Shoot %K	41	3	1.72	.82
P Treatment	R.+R. %K	34	3	0.57	n.s.
K Treatment	Shoot %K	41	3	5.43	.99
K Treatment	R.+R. %K	34	3	5.31	.99

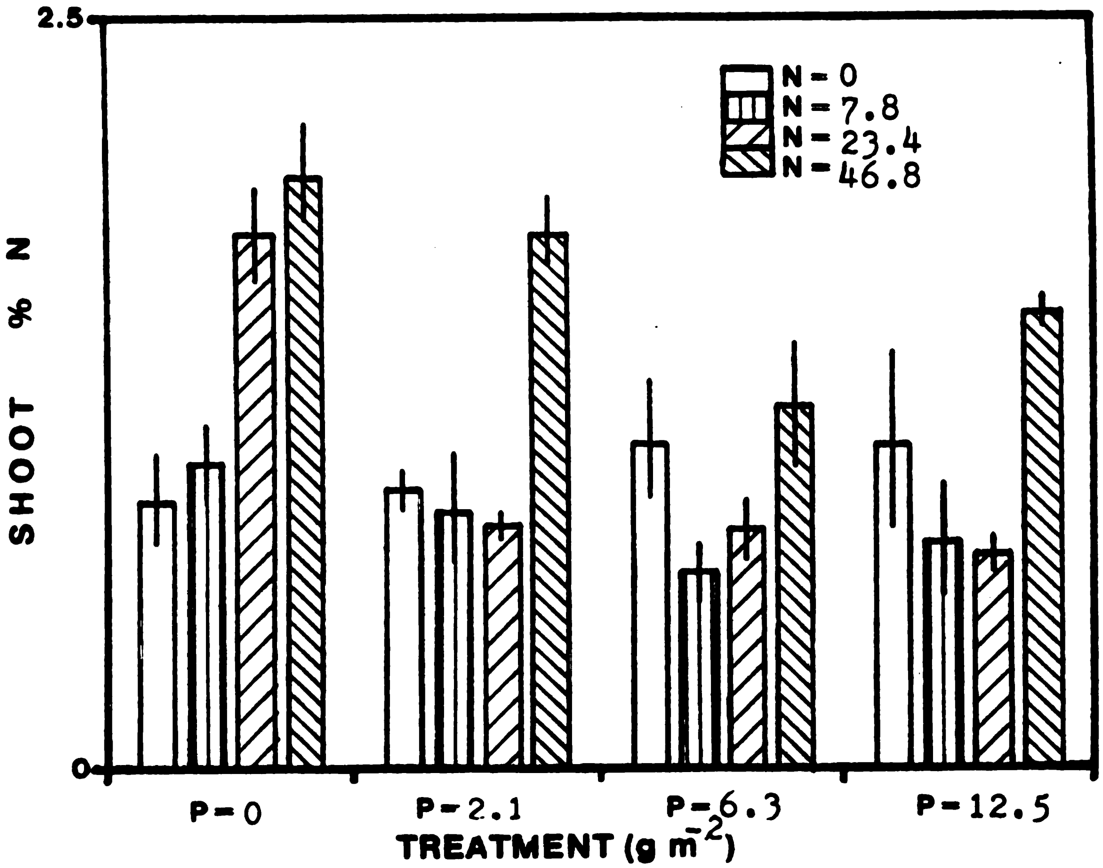

Figure 4. P. australis shoot concentration of N as per cent of dry weight (60 C) at end of 1980 growing season for different combinations of nitrate and phosphate fertilization. Vertical lines are standard errors of the means.

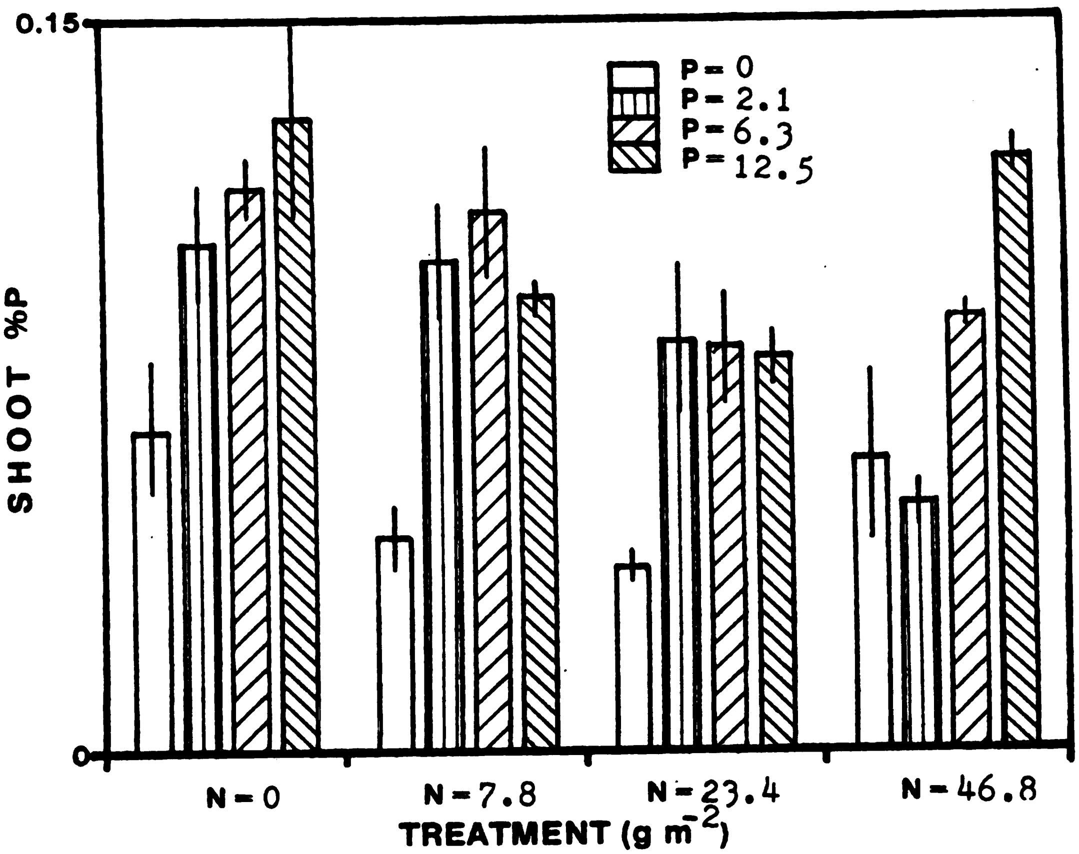

Figure 5. P. australis shoot concentration of P as per cent of dry weight (60 C) at end of 1980 growing season for different combinations of nitrate and phosphate fertilization. Vertical lines are standard errors of the means.

intermediate rates of N fertilization often occurs under conditions of severe soil nutrient deficiencies with crop plants when whole plants are sampled for nutrients (Smith, 1962). N is normally transported from mature tissues to active growth areas resulting in a "dilution" of N during growth (Smith, 1962). Since plants with poor N supply grow very slowly, the transport of N from mature tissue to actively growing areas of <u>P. australis</u> was depressed, resulting in higher per cent N at the lowest treatment level compared to intermediate treatment levels. In contrast, total N uptake was directly correlated with level of nitrate added (Figure 6) because of the overriding effect of the quantity of tissue produced (Figure 1).

Except with a nitrate-N level of 46.8 g m^{-2}, minimum shoot P concentrations were found to be associated with the lowest level of phosphate at a given level of nitrate treatment (Figure 5). Association of the lowest shoot P concentrations with the lowest phosphate treatment level may reflect the relative N as compared to P shortage existing in the untreated sand. Otherwise, tissue P levels might be expected to exhibit a pattern similiar to that of the tissue N levels since both nutrients are mobilized from older tissues. The total quantity of N uptake was strongly dependent on the phosphate treatment (Figure 6). This was especially true at the higher nitrate treatment levels. The same type of relationship exists for P uptake (Figure 7). That is, the amount of P taken up is dependent strongly on both the nitrate and the phosphate treatment

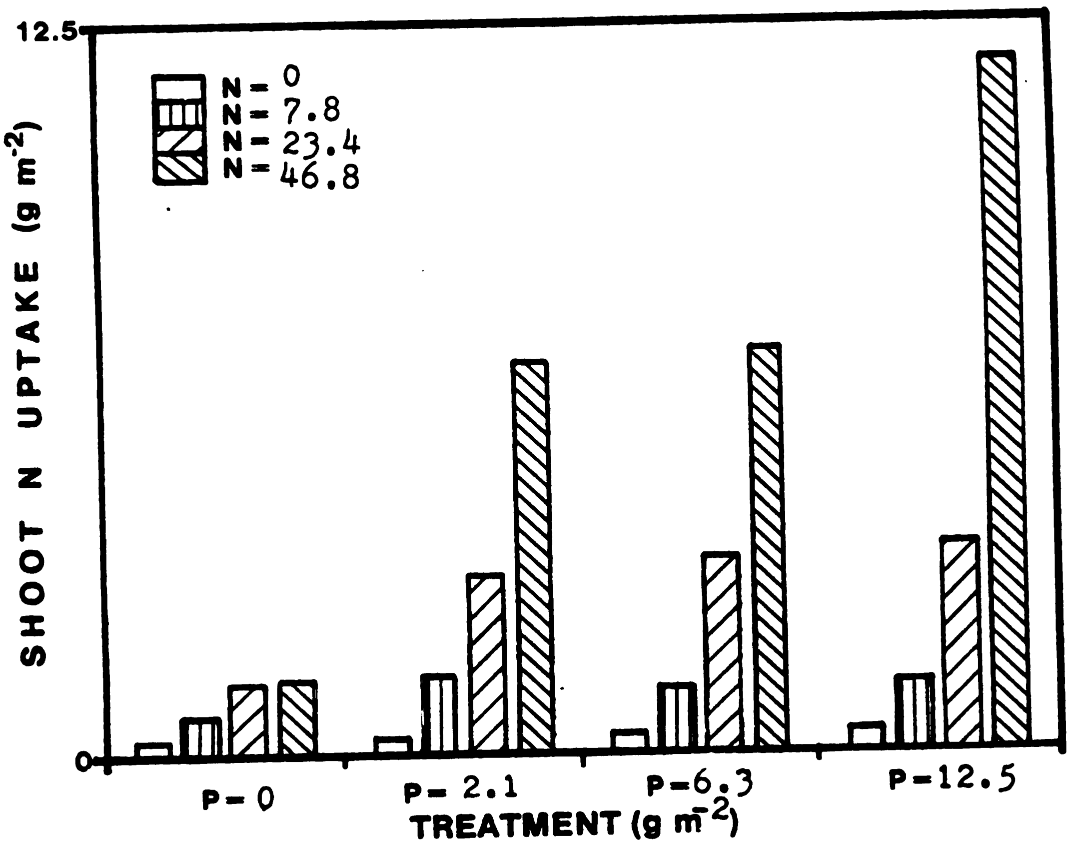

Figure 6. Seasonal areal uptake of N by P. australis shoots under variable combinations of nitrate and phosphate fertilization during 1980.

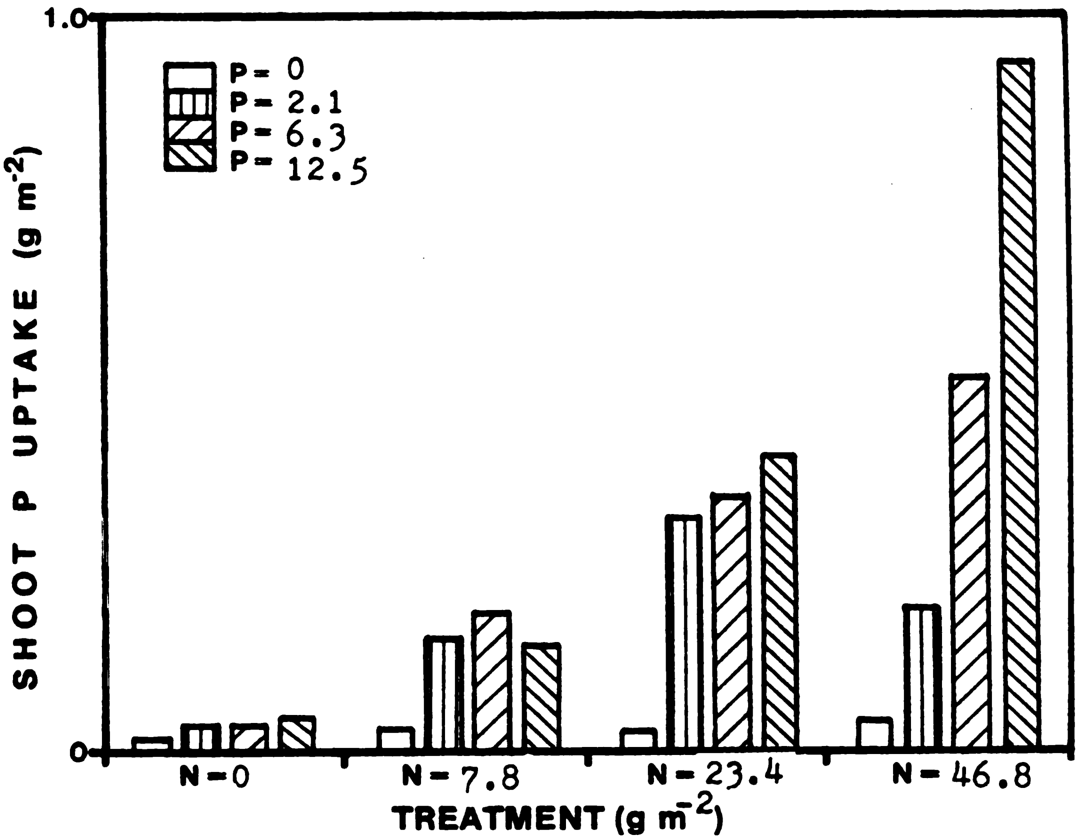

Figure 7. Seasonal areal uptake of P by P. australis shoots under variable combinations of nitrate and phosphate fertilization during 1980.

level.

Shoot N concentrations were found to be significantly higher than root plus rhizome N concentrations (Figure 8). P and K concentrations showed no significant between tissue differences.

Zizania aquatica

Z. aquatica differed from all the other species studied in that it is an annual established from seed. Its biomass production response to individual treatment combinations was also markedly lower, probably due to the much smaller propagule size. Since Z. aquatica did not approach its maximum areal biomass production, production values are given on a per plant basis (Table 4).

Extremely low production values and high mortality with certain treatments of Z. aquatica did not allow for reliable nutrient analysis on samples from every treatment. However, nutrient content patterns were similar to those found with the species started from rhizomes. That is, tissue P was highest with high phosphate-low nitrate treatment while tissue N was greatest with low P-high N treatment. However, P showed a much greater range than did N (Table 5).

Typha spp.

For both T. angustifolia and T. latifolia, N, P and K

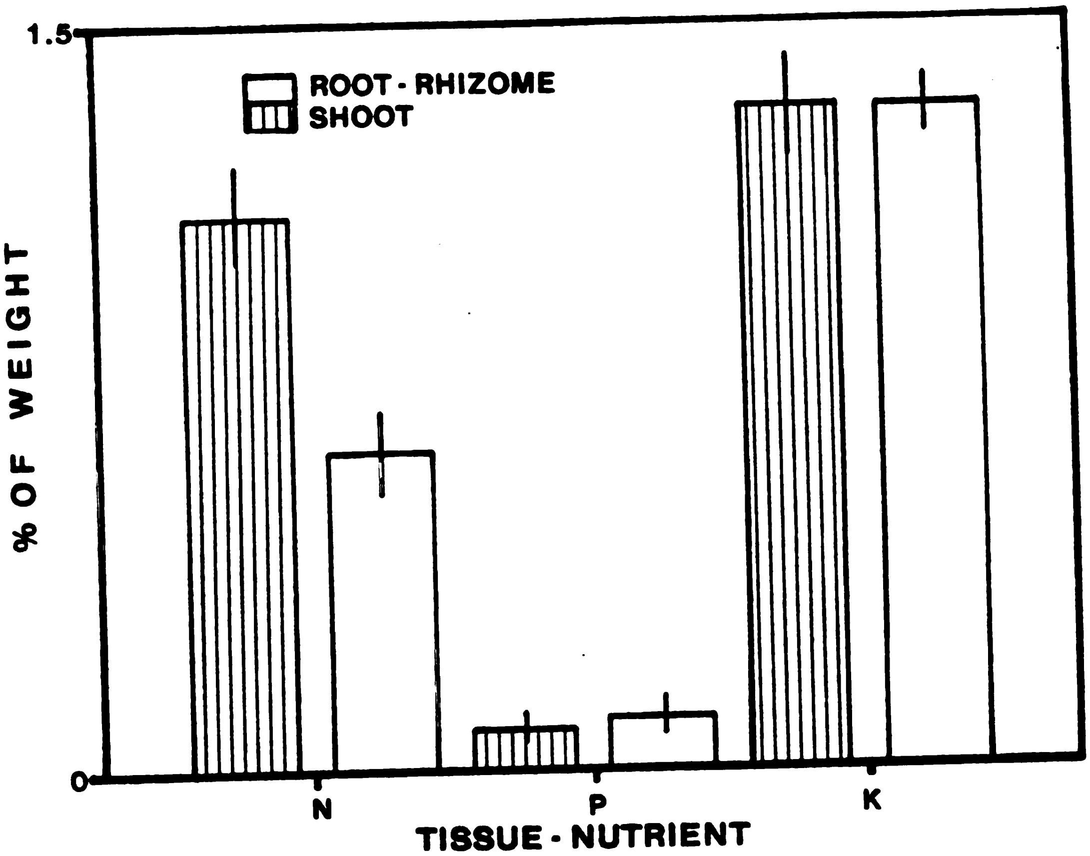

Figure 8. Comparison of the average 1980 N, P, and K content of *P. australis* shoots with that of roots plus rhizomes. Vertical lines are standard errors of the means.

Table 4. Results of analyses of variance on the effects of treatments on harvest weight, %N, %P, and %K of *Z. aquatica* shoots (n=66,30,29,30, respectively).

Source of Variation	Effect	DF	F	Sig. of F
Treatment	Shoot Weight	58	2.414	.99
Treatment	Shoot %N	27	1.66	.91
Treatment	Shoot %P	26	0.50	n.s.
Treatment	Shoot %K	26	2.64	.99

Table 5. Effects of variable nitrate, phosphate, and potassium treatments on Z. aquatica shoot dry weight, root dry weight and tissue content of N, P and K. Weight values are in g per plant; percentges are as per cent of 60 C dry weight.

Treatment (g m-2)		Shoot				Root			
		Dry Wt.	%N	%P	%K	Dry Wt.	%N	%P	%K
0	0	0.08	-	-	-	0.21	-	-	-
0	2.1	0.14	-	-	-	0.12	-	-	-
0	6.2	0.15	1.6	0.33	1.7	1.0	0.92	0.18	0.72
0	12.3	0.14	2.4	0.42	2.9	0.24	1.7	0.22	2.7
7.8	0	0.06	-	-	-	0.08	-	-	-
7.8	2.1	0.70	1.6	0.11	2.9	0.60	1.3	0.12	1.7
7.8	6.2	2.8	1.5	0.21	2.5	0.95	1.0	0.13	3.0
7.8	12.3	2.4	1.4	0.35	2.5	0.90	0.89	0.19	1.8
23.4	0	0.05	-	-	-	0.04	-	-	-
23.4	2.1	0.20	1.8	0.08	2.6	0.18	-	-	-
23.4	6.2	4.7	1.3	0.36	2.0	1.2	0.77	0.16	1.0
23.4	12.3	5.9	1.5	0.31	2.5	1.7	1.4	0.20	1.2
46.8	0	0.17	-	-	-	0.06	-	-	-
46.8	2.1	0.27	2.7	0.27	1.9	0.35	-	-	-
46.8	6.2	2.8	2.2	0.24	2.3	0.44	1.0	0.18	2.0
46.8	12.3	3.2	2.0	0.25	2.6	2.0	1.1	0.22	1.2

treatment factors showed significant effects on end of experiment shoot weight and on root plus rhizome weight (Tables 6 and 7). All first and second order interactions were also significant (Tables 6 and 7). This shows that growth response to N, P or K fertilizers was dependent upon levels of the other two fertilizers. The magnitude of the production response to nitrate treatment was far greater than the response to phosphate treatment which was in turn far greater than the response to K treatment. Because of the small increase in plant growth as a function of added K, production responses to nitrate and phosphate treatments were averaged over all levels of K treatment (Figure 9). Both species showed similar patterns of response. However, significant differences did occur. For example, T. angustifolia distributed a significantly greater (Table 8) proportion of its net primary production to belowground tissues (Figure 9). The T. angustifolia belowground to aboveground dry weight ratio averaged 2.58 compared to 1.97 for T. latifolia (Figure 10). The difference in the two ratios largely resulted from the higher aboveground production of T. latifolia. Over all treatments, the average aboveground dry weight of T. latifolia of 440 g m^{-2} ($s_{\bar{x}}$=28) was significantly greater (Table 8) than the 360 g m^{-2} ($s_{\bar{x}}$=25) mean aboveground dry weight of T. angustifolia. There was no significant difference in the belowground ground production of T. angustifolia and T. latifolia (Table 8).

Averaged over all levels of other factors, belowground

Table 6a. Analysis of variance on the effects of treatments and their interactions on *T. angustifolia* cumulative above ground dry mass at the end of the growing season (n=174).

Source of Variation	DF	F	Sig. of F
N Treatment	3	1186.4	.99
P Treatment	3	42.4	.99
K Treatment	3	6.9	.99
N-P Treatment Interaction	9	14.2	.99
N-K Treatment Interaction	9	4.8	.99
P-K Treatment Interaction	9	2.6	.95
N-P-K Treatment Interaction	27	2.8	.95

Table 6b. Analysis of variance on the effects of treatments and their interactions on *T. angustifolia* cumulative below ground dry mass at the end of the growing season (n=174).

Source of Variation	DF	F	Sig. of F
N Treatment	3	1110.3	.99
P Treatment	3	28.6	.99
K Treatment	3	6.8	.99
N-P Treatment Interaction	9	7.0	.99
N-K Treatment Interaction	9	3.0	.99
P-K Treatment Interaction	9	1.9	.95
N-P-K Treatment Interaction	27	1.8	.98

Table 7a. Analysis of variance on the effects of treatments and their interactions on *T. latifolia* cumulative above ground dry mass at the end of the growing season (n=173).

Source of Variation	DF	F	Sig. of F
N Treatment	3	1142.7	.99
P Treatment	3	31.9	.99
K Treatment	3	5.4	.99
N-P Treatment Interaction	9	15.7	.99
N-K Treatment Interaction	9	3.7	.99
P-K Treatment Interaction	9	3.1	.98
N-P-K Treatment Interaction	27	4.3	.99

Table 7b. Analysis of variance on the effects of treatments and their interactions on *T. latifolia* cumulative below ground dry mass at the end of the growing season (n=173).

Source of Variation	DF	F	Sig. of F
N Treatment	3	189.2	.99
P Treatment	3	20.8	.99
K Treatment	3	4.0	.99
N-P Treatment Interaction	9	9.6	.99
N-K Treatment Interaction	9	4.9	.99
P-K Treatment Interaction	9	1.9	.95
N-P-K Treatment Interaction	27	3.3	.99

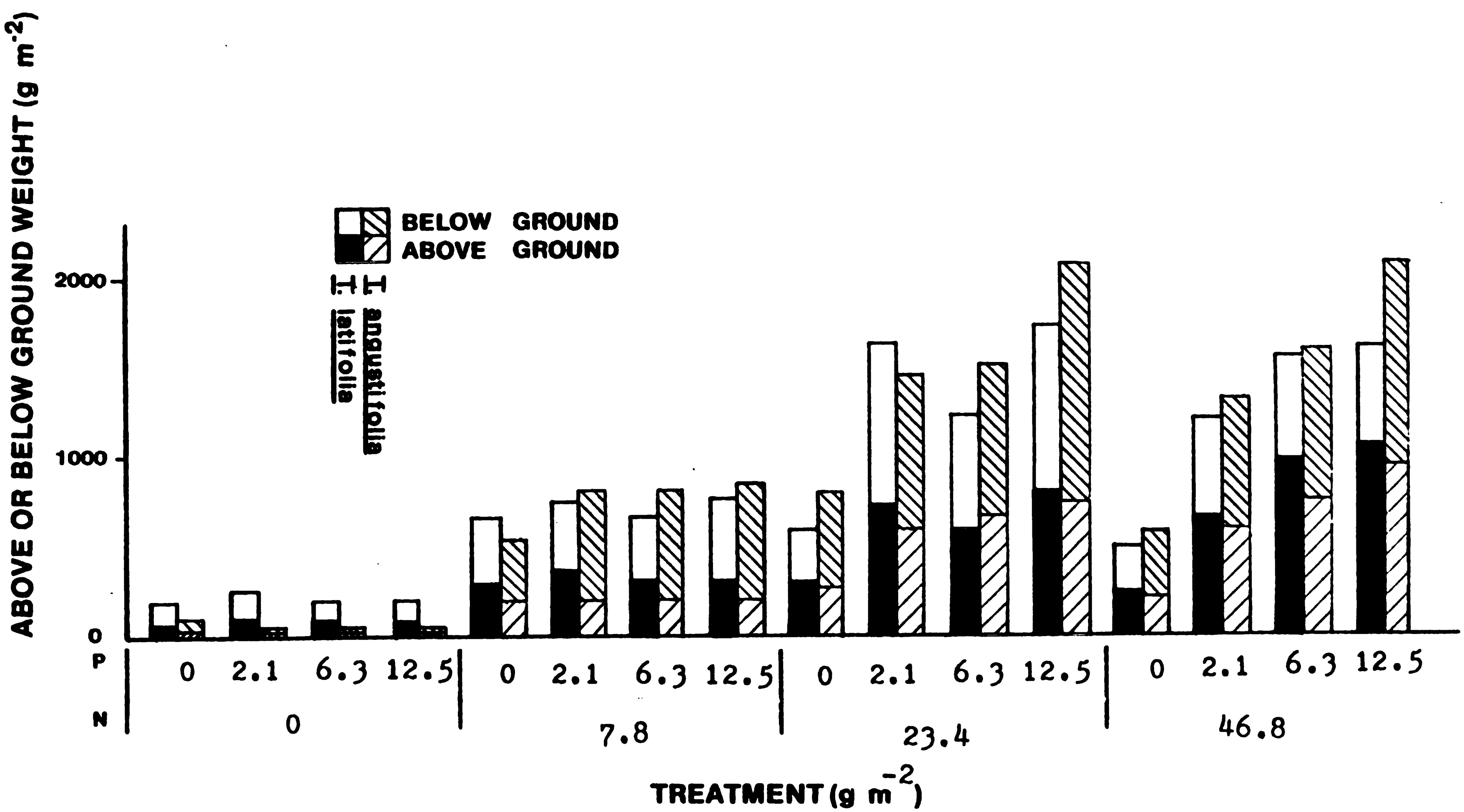

Figure 9. Average areal dry weight (60 C) of *T. latifolia* and *T. angustifolia* aboveground and belowground tissues in early September, 1981 with variable combinations of nitrate and phosphate fertilization.

Table 8a. Results of analysis of variance on the effects of treatments on the ratio of *T. angustifolia* root + rhizome dry weight to shoot dry weight. Based on weights of materials harvested at end of 1981 experiments and arcsin transformed prior to statistical analysis.

Source of Variation	Effect	n	df	F	Sig. of F
N Treatment	R.+R./Shoot Ratio	110	3	28.9	.99
P Treatment	R.+R./Shoot Ratio	110	3	5.8	.99
K Treatment	R.+R./Shoot Ratio	110	3	3.9	.99

Table 8b. Results of analysis of variance on the effects of treatments on the ratio of *T. latifolia* root + rhizome dry weight to shoot dry weight. Based on weights of materials harvested at end of 1981 experiments and arcsin transformed prior to statistical analysis.

Source of Variation	Effect	n	df	F	Sig. of F
N Treatment	R.+R./Shoot Ratio	111	3	6.07	.99
P Treatment	R.+R./Shoot Ratio	111	3	0.62	.99
K Treatment	R.+R./Shoot Ratio	111	3	0.64	.99

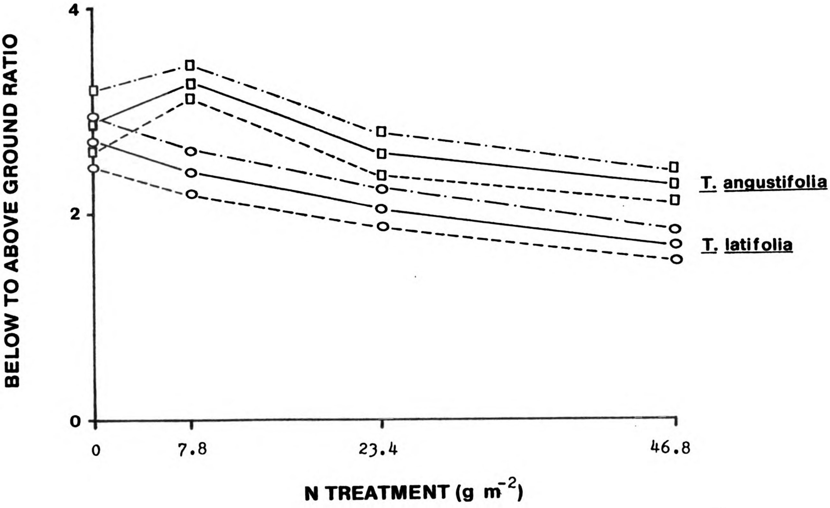

Figure 10. Average aboveground to belowground tissue dry weight ratios in early September, 1981 for T. latifolia and T. angustifoia at various levels of nitrate treatment.

production in both species increased only up to the 23.4 g m^{-2} treatment level of nitrate (Figure 11). Shoot production continued to increase up to the highest treatment level of nitrate. Nitrate was the only factor that significantly (Table 8) affected the proportion of biomass distributed aboveground as compared to belowground. This effect of nitrate appears to be at least partially independent of the increased production brought about by the nitrate fertilization.

Aboveground shoot weight from the May planting to the September harvest resembled a logistic type of increase following an initial lag period (Figure 12). The shape of this response curve was very similiar for both species. Total shoot dry weight produced was slightly greater for *T. latifolia* with *T. angustifolia* producing more numerous but lighter shoots.

Although shoot dry weight production averaged over all levels of phosphate and K leveled off at 23.4 g m^{-2} N, total N content of the tissues continued to increase up to the 46.8 g m^{-2} treatment level in both *T. latifolia* and *T. angustifolia* (Figures 13 and 14). Reaction to phosphate treatment was similar. Dry weight increases leveled off after the 2.1 g m^{-2} treatment level while total P content increased up to the highest treatment level of 12.5 g m^{-2} of phosphate (Figures 13 and 14).

There was no significant difference (Table 8) between *T. latifolia* and *T. angustifolia* in aboveground or belowground %N (Figure 15) or %P (Figure 16) when these

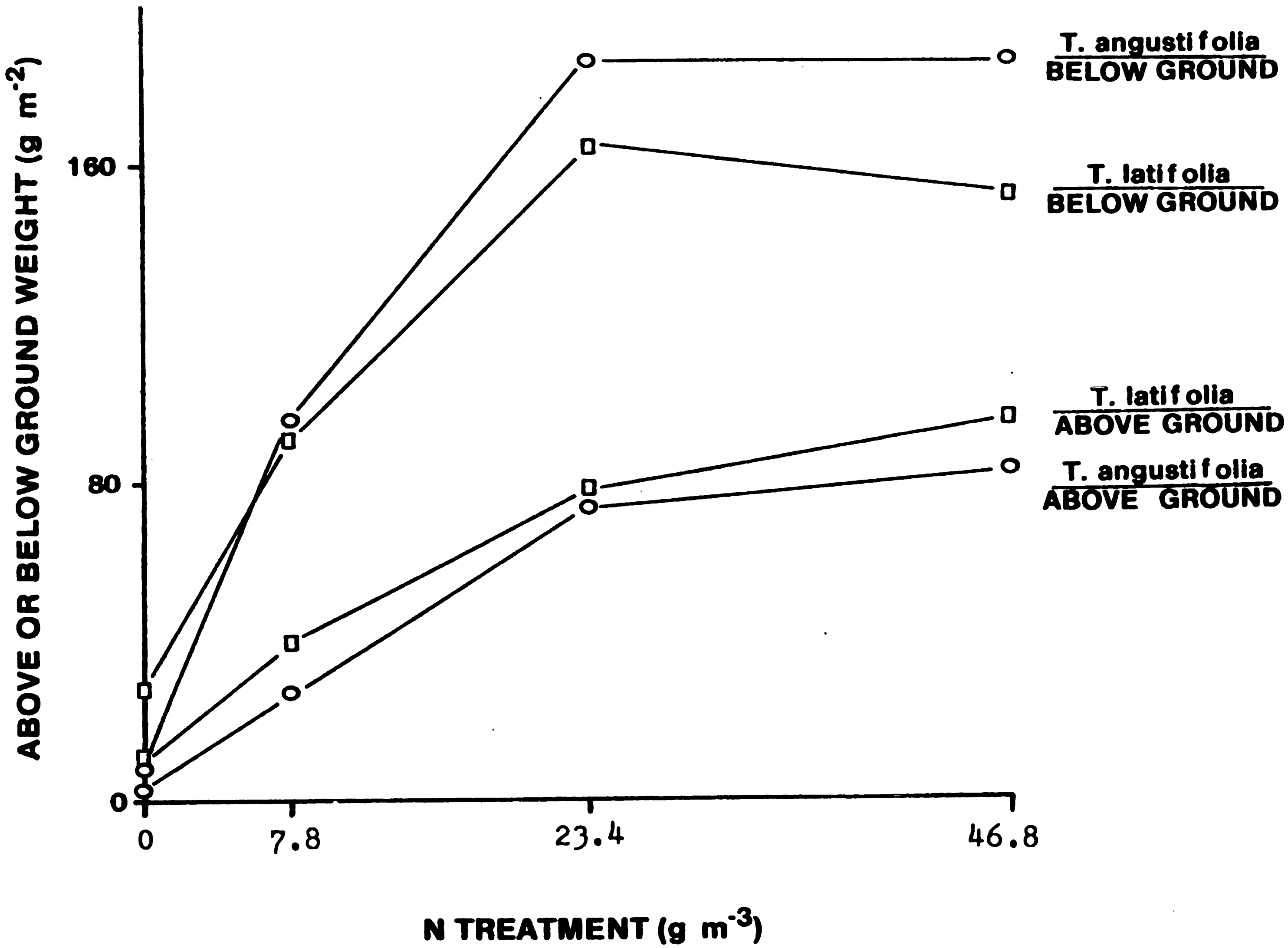

Figure 11. Average aboveground and belowground tissue dry weights in early September, 1981 for T. latifolia and T. angustifolia at various levels of nitrate treatment.

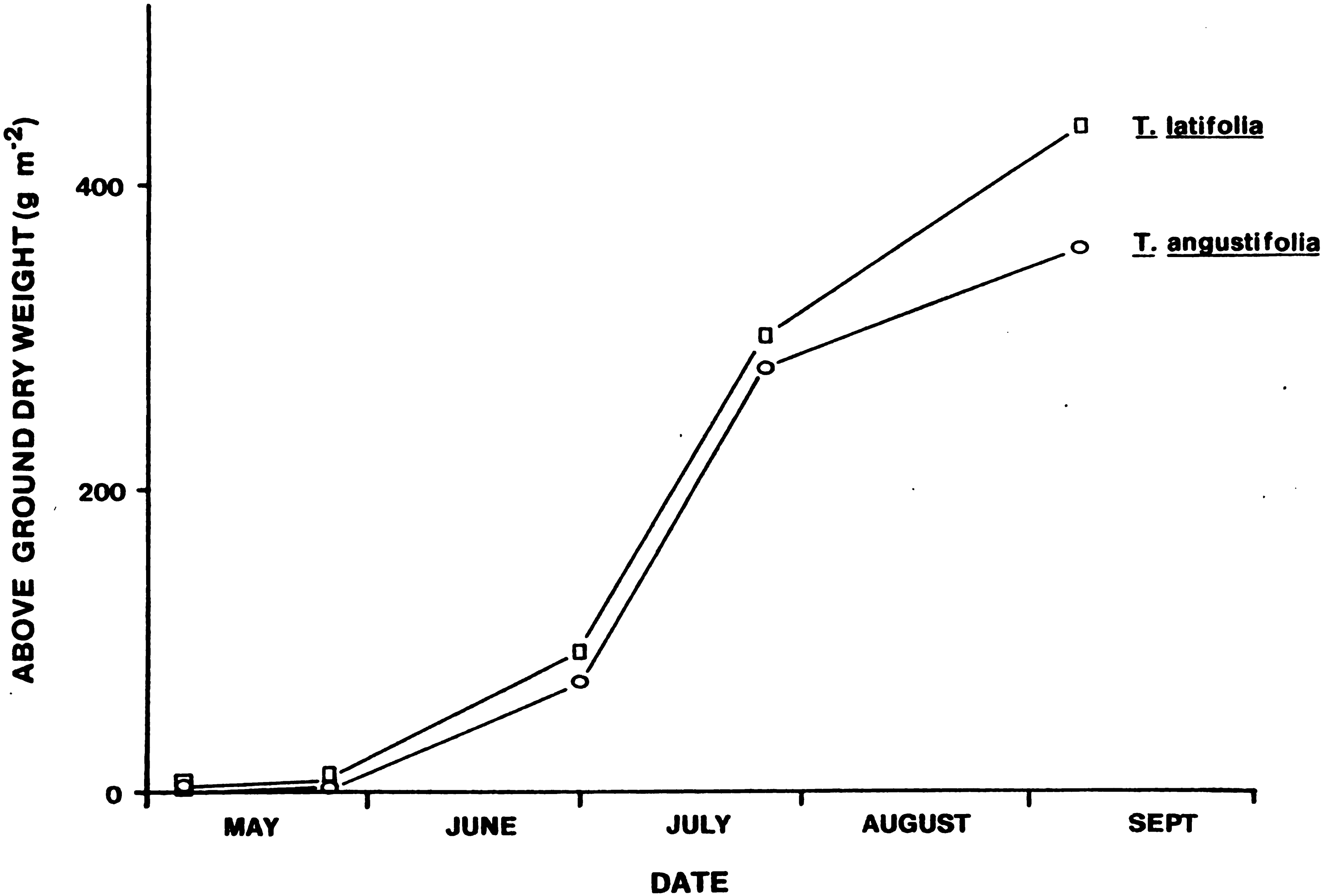

Figure 12. Seasonal accumulation of aboveground dry weight by _T. latifolia_ and _T. angustifolia_ during 1981 tub experiments.

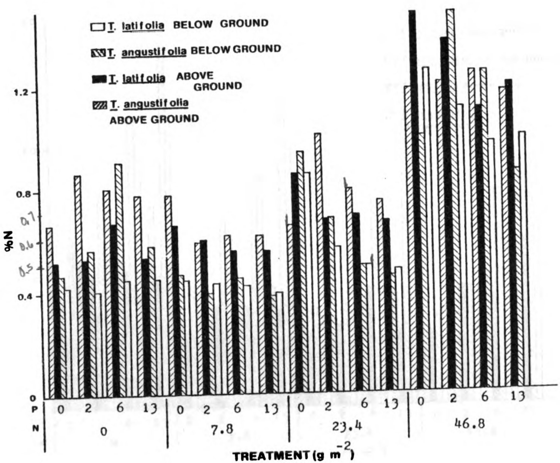

Figure 13. Aboveground and belowground N content as a function of dry weight for *T. latifolia* and *T. angustifolia* tissues harvested during early September, 1981 from tub experiments.

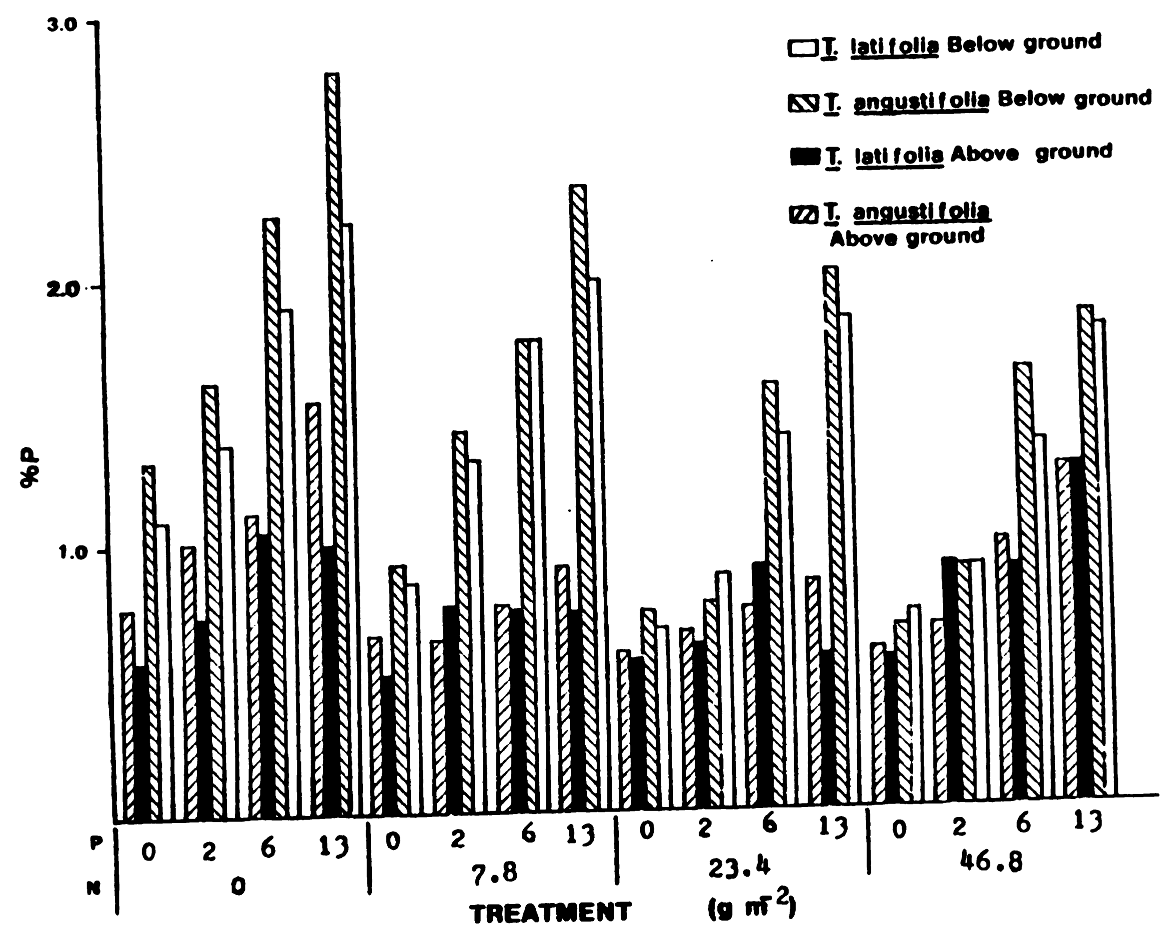

Figure 14. Aboveground and belowground P content as a percentage of dry weight for *T. latifolia* and *T. angustifolia* tissues harvested during early September, 1981 from tub experiments.

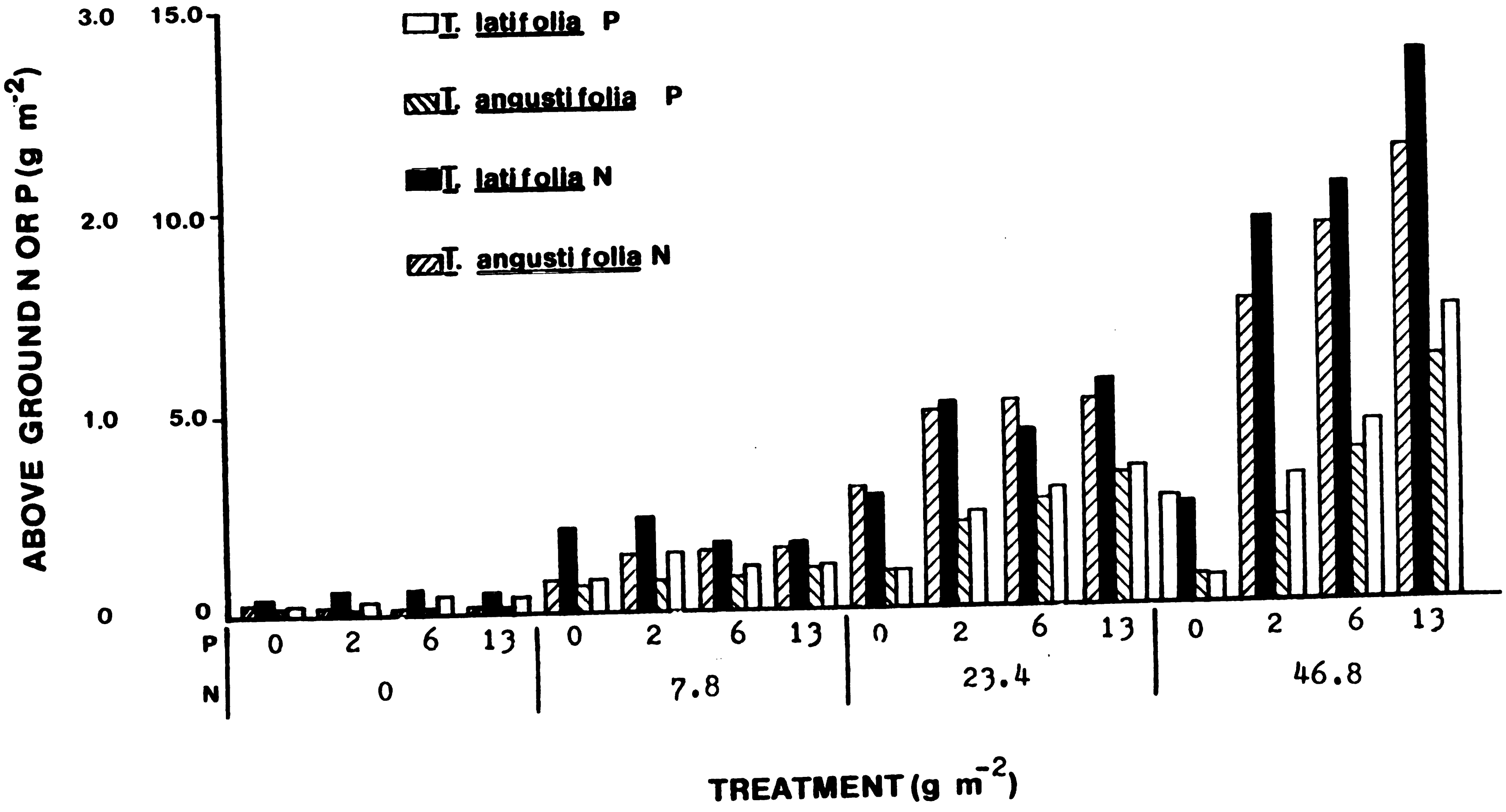

Figure 15. Areal content of N and P of *T. latifolia* and *T. angustifolia* aboveground tissues during early September, 1981 with variable nitrate and phosphate treatments.

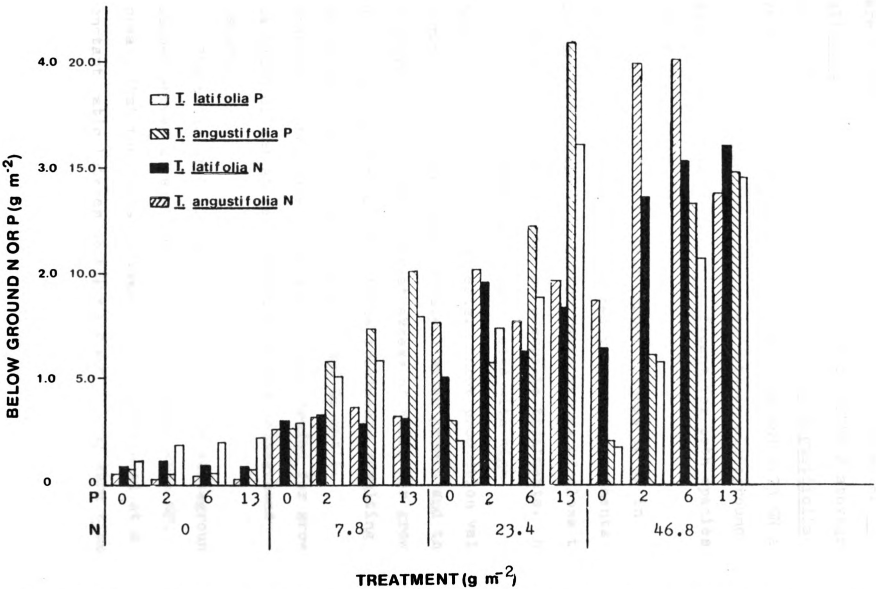

Figure 16. Areal content of N and P of T. latifolia and T. angustifolia during early September, 1981 with variable nitrate and phosphate treatments.

were averaged over all treatments. Early September T. latifolia tissues averaged 0.75% N and 0.078% P aboveground and 0.63% N and 0.136% P belowground. T. angustifolia averaged 0.86 %N and 0.086 %P aboveground and 0.73 %N and 0.157 %P belowground. Differences between aboveground and belowground %N and %P were significant for both species (Table 8).

The ratio of %P in belowground tissues to %P in aboveground tissues varied markedly between treatments for both species (Table 8). Lowest ratio values of close to 1 occurred with high nitrate-low phosphate treatments. High ratio values of over 3 were associated with high phosphate-low nitrate treatments. Shoot production values (Figure 9) indicated that nitrate limited growth and that phosphate was present in great excess of needs for growth in the high phosphate-low nitrate treatments resulting in the highest belowground to aboveground %P ratio. Apparently, phosphate in excess of that needed for growth was taken up and stored primarily in the belowground tissues.

The ratio of %N in belowground to %N in aboveground tissues showed a relative constancy compared with %P. It appears that the excess N taken up is distributed at a near constant ratio between aboveground and belowground tissues in both T. latifolia and T. angustifolia.

Maximum values of %N and %P within a species and tissue type with various combinations of nitrate and phosphate treatments were 2 to 4 times the minimum values

(Figure 15). Highest %N values occurred with low phosphate treatment and high nitrate treatment. Similarly, highest %P values occured with low nitrate and high phosphate treatment (Figure 16).

Tissue content of N and P expressed on an areal basis (Figures 13 and 14) showed much greater variability between treatments than did N or P expressed as a percentage of tissue dry weight (Figures 15 and 16). This areal variability was due to the large variability in tissue production between treatments. Typha spp. aboveground areal N or P content can be more than doubled by increasing the respective fertilizer application beyond that needed for maximum growth (compare Figure 9 with Figure 13). For example, T. angustifolia aboveground dry weight production was approximately equal with treatments of either 12.3 g m^{-2} of phosphate and 23.4 or 46.8 g m^{-2} of nitrate. However, the N content with the lower nitrate treatment was only 5.6 g m^{-2} compared with 13.6 g m^{-2} for the higher nitrate treatment. Belowground N or P tissue content can also be increased substantially without increasing dry weight by addition of fertilizer beyond that needed for maximum growth (compare Figure 9 with Figure 16). This trend for belowground P is especially significant due to the differential concentration of excess P in belowground tissues.

Sparganium eurycarpum

Early September mean shoot dry weight for <u>S. eurycarpum</u> ranged from 20 to 1035 g m^{-2} while belowground dry weight ranged from 55 to 1280 g m^{-2} (Figure 17). Both nitrate and phosphate treatments and their interactions significantly affected production levels (Table 9). The addition of nitrate resulted in a production response range from near zero growth with zero added nitrate to maximum belowground production at 23.4 g m^{-2} and maximum aboveground production at 46.8 g m^{-2} to a high mortality rate or stunted growth at the 93.6 g m^{-2} treatment level. Phosphate at the highest level did not result in any increased mortality. Only relatively small increases in aboveground or belowground dry weight occurred with phosphate treatment levels greater than 6.3 g m^{-2}.

The ratio of early September dry weight belowground to dry weight aboveground was strongly and significantly (Table 9) affected by nitrate treatment but not by phosphate treatment (Figure 17). This response was especially evident when comparing dry weight production responses as the nitrate treatment level increased from 23.4 to 46.8 g m^{-2} (Figure 17). Above the 2.1 g m^{-2} treatment level of phosphate there was both an increase in the aboveground dry weight and a decrease in the belowground dry weight.

Tissue concentrations of N as per cent of dry weight reached their maximum with the higher treatment levels of nitrate combined with the lowest treatment levels of phosphate (Figure 18). Similarly, tissue concentrations of

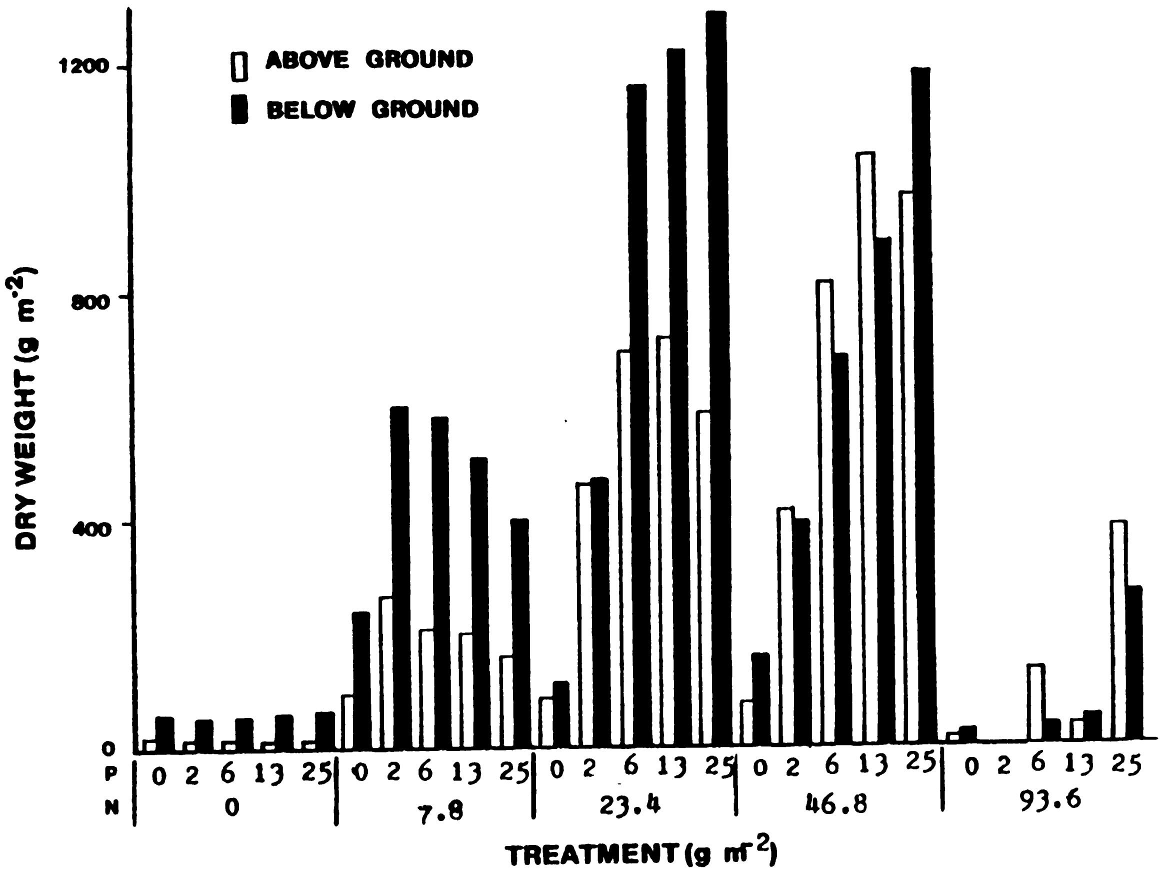

Figure 17. Average areal dry weight (60 C) of S. eurycarpum aboveground and belowground tissues in early September, 1982 with variable nitrate and phosphate treatments.

Table 9a. Analysis of variance on the effects of treatments and their interactions on S. eurycarpum cumulative above ground dry mass at the end of the growing season (n=144).

Source of Variation	DF	F	Sig. of F
N Treatment	4	132.4	.99
P Treatment	4	95.5	.99
N-P Treatment Interaction	16	179.0	.99

Table 9b. Analysis of variance on the effects of treatments and their interactions on S. eurycarpum cumulative below ground dry mass at the end of the growing season (n=64).

Source of Variation	DF	F	Sig. of F
N Treatment	4	135.9	.99
P Treatment	4	29.1	.99
N-P Treatment Interaction	16	49.0	.99

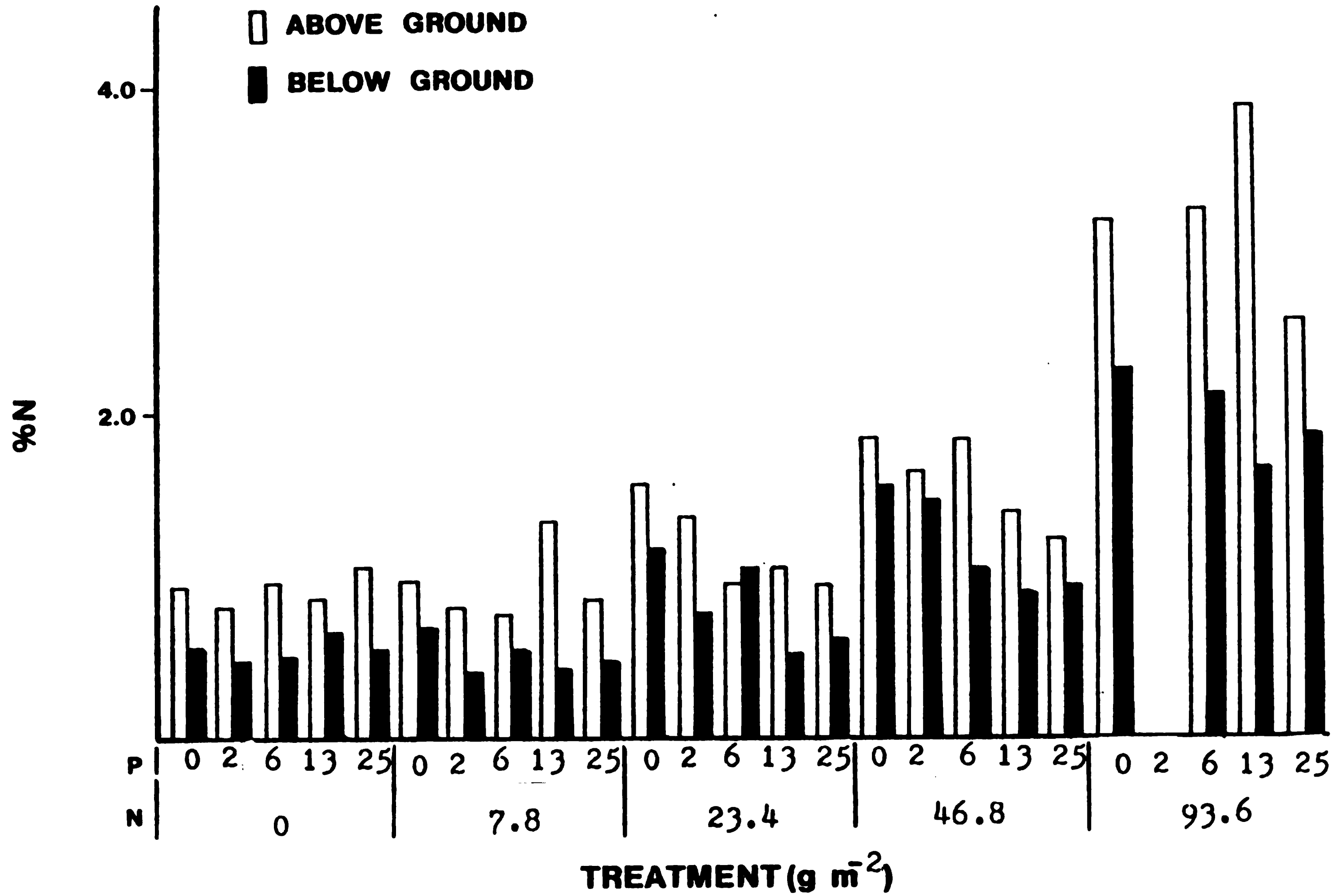

Figure 18. Aboveground and belowground N content as a percentage of dry weight for *S. eurycarpum* tissues harvested during early September, 1982.

P peaked with high phosphate treatment levels combined with low nitrate treatment levels (Figure 19). These maxima corresponded with very low dry weight values (Figure 17). This association explains the contrasting situation found when areal uptake of N (Figure 20) or of P (Figure 21) was compared with %N (Figure 18) or %P (Figure 19). Figures 20 and 21 are very similar and indicate the close interdependence of nitrate and phosphate on the uptake of one another. High uptake of one of the nutrients is dependent upon high uptake of the other. %N was consistently higher aboveground than belowground. %P was not consistently higher either aboveground or belowground. There was no tendency for excess phosphorus to be differentially concentrated in belowground tissues as was found with Typha spp.

General Discussion

Since N or P is believed to be the nutrient limiting growth in most wetlands (Sculthorpe, 1967), the ratio of %N to %P should resemble the ratio found under controlled conditions of similiar nutrient supply in emergent aquatics such as S. eurycarpum (Figure 22). This ratio may be a better indicator of nutrient limitation than are the "critical concentrations" of N or P used by others to determine nutrient deficiencies in submerged species (Gerloff and Krombholz, 1966). N:P ratios show less variability between tissue types of different physiological

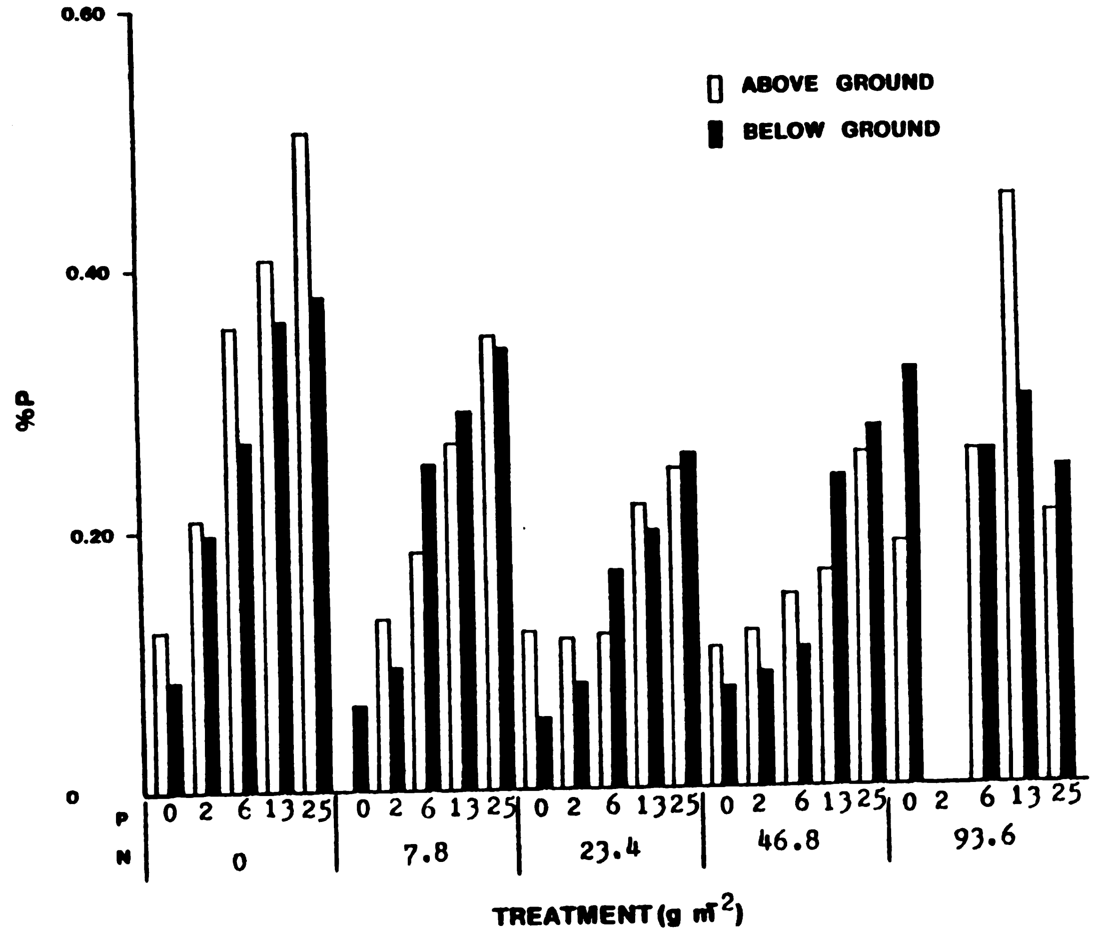

Figure 19. Aboveground and belowground P content as a percentage of dry weight for *S. eurycarpum* tissues harvested during early September, 1982.

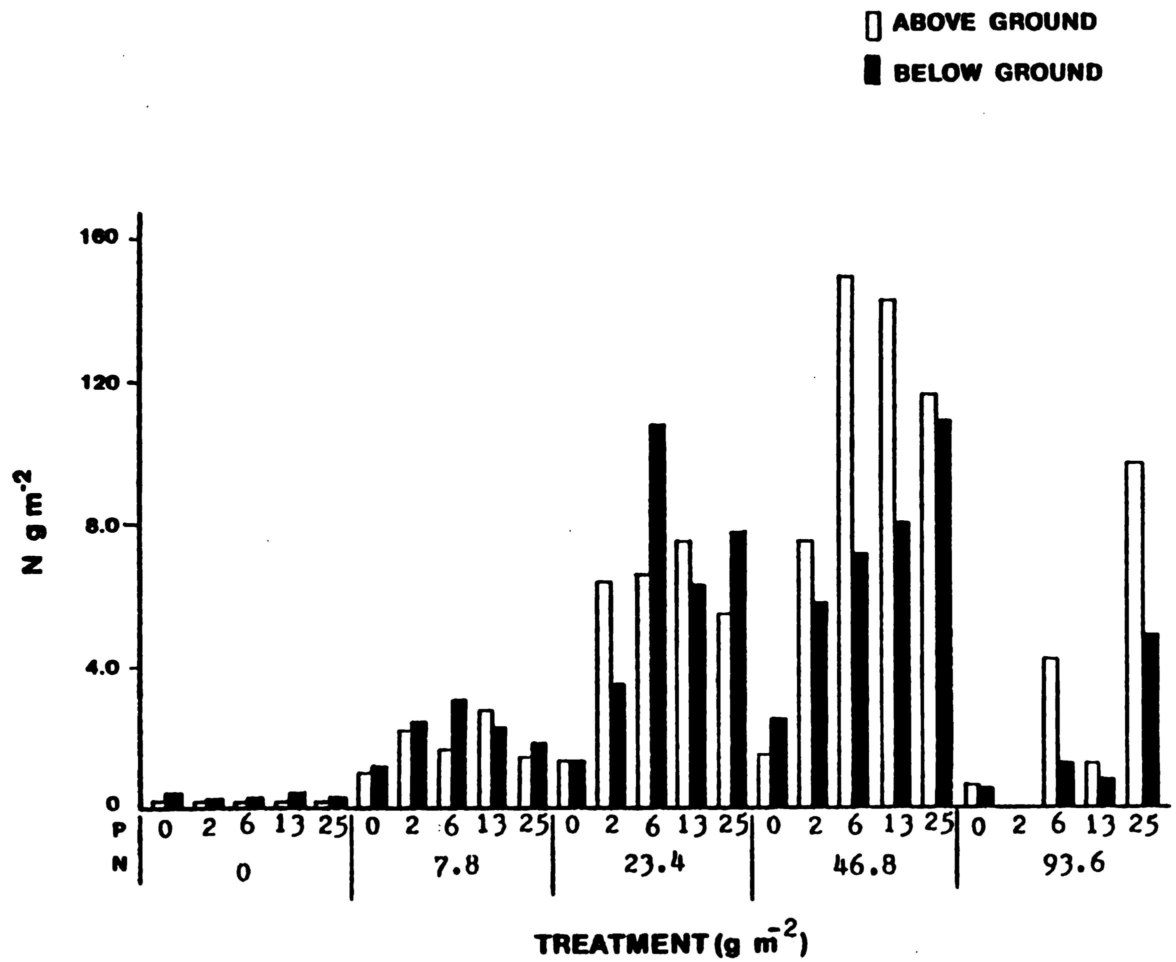

Figure 20. Early September, 1982 areal content of N in S. eurycarpum aboveground and belowground tissues with variable nitrate and phosphate treatments.

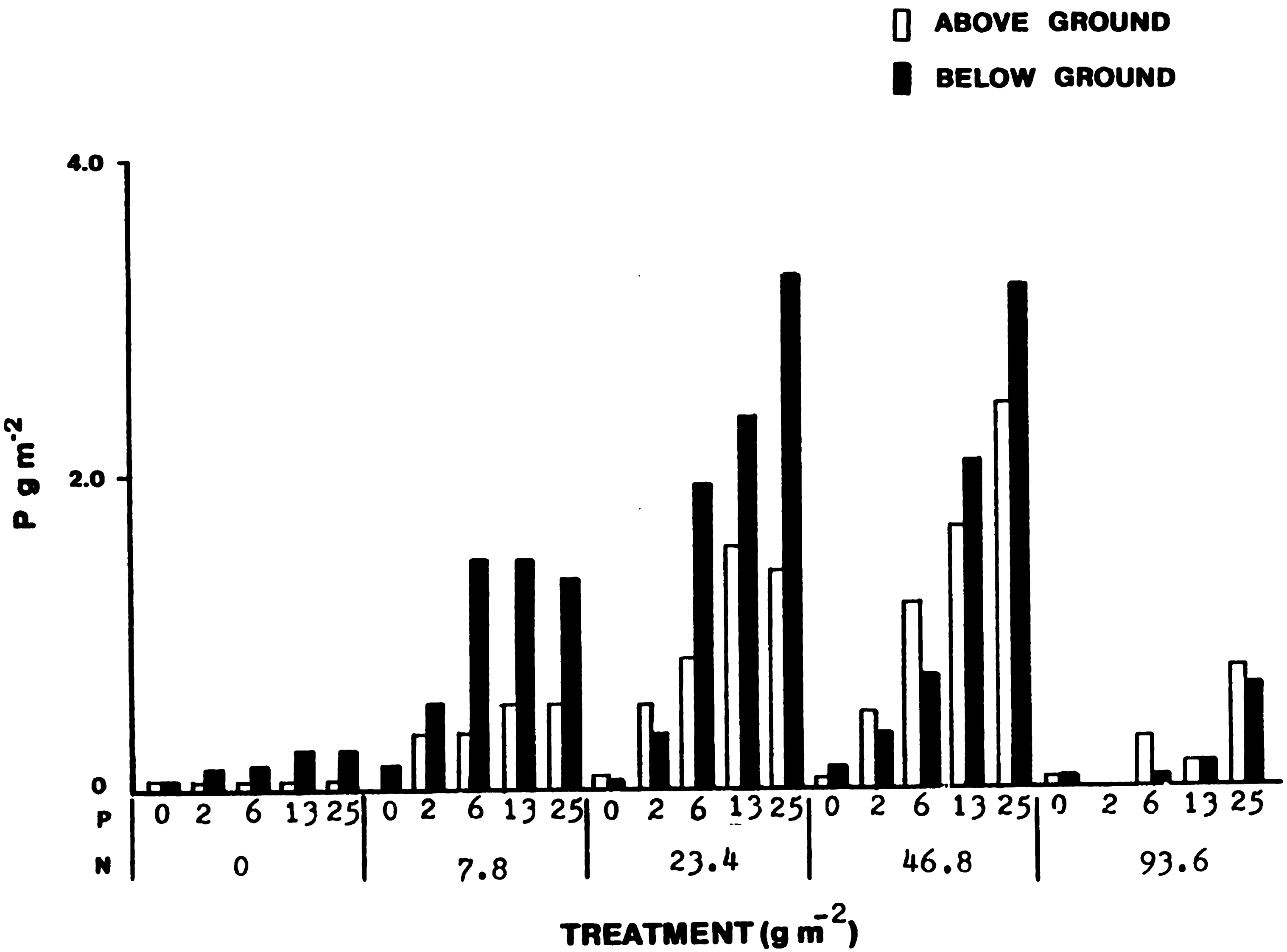

Figure 21. Early September, 1982 areal content of P in S. eurycarpum aboveground and belowground tissues with variable nitrate and phosphate treatments.

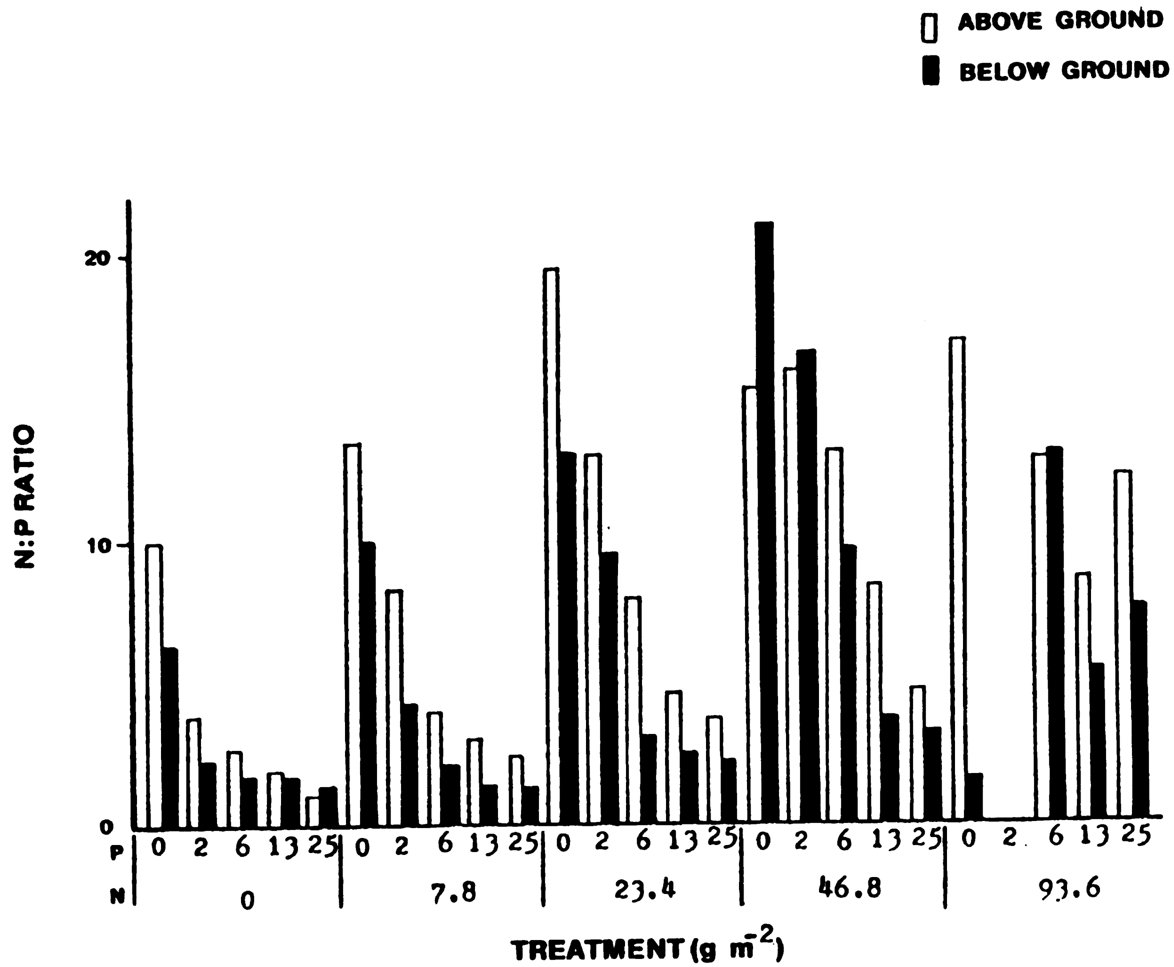

Figure 22. Variation in the ratio of %N to %P in <u>S. eurycarpum</u> aboveground and belowground tissues during early September, 1982 as a function of nitrate and phosphate treatment.

age than do absolute concentrations of N and P. "Critical concentrations" of N and P also increase with increasing concentrations of other nutrients (Bates, 1970). There is also more temporal variability in amount of structural tissues in emergent than in submergent species which results in more variability in nutrient concentrations. The shoot N:P ratio for S. eurycarpum plants with severe growth limitation due to low P ranged from 13 to 19.5. Belowground, the range for the same treatments was 9.5 to 21.1. For severely N limited treatments the same ratio ranged from 1.0 to 4.2 for shoots and 1.3 to 2.6 for combined roots and rhizomes. Intermediate values of the tissue N:P ratios were found with treatments where tissue dry weight production was less strongly inhibited by low N or P supply.

If these N:P ratios are to be used in comparisons with natural stands to determine N or P deficiencies, tissues analyzed from natural stands should ideally be of the same developmental stage as the plants in this study unless it can be demonstrated that the ratio is constant over the growing season. For most emergent aquatic plants, shoot %N during the early part of the growing season has been as much as 3 times that found at the end of the growing season (Dykyjova, 1978). This seasonality for N has been found in some instances to be coupled with a relatively constant %P which has led to a declining ratio with tissue maturity. However, once the tissue has reached maturity and before senescence, the ratio has usully remained relatively constant. Dykyjova's (1978) data for several emergent plant species showed little change in the N:P ratio from early September through October. Since S. eurycarpum tissues in this study were harvested at maturity in September for nutrient analyses, comparisons of N:P ratios of natural stands with data from this study should be based on tissues collected during the latter part of the growing season.

Shoot %N and shoot %P declined at approximately the same rate over the course of the growing season for S. eurycarpum stands in Pentwater Marsh, Michigan (Burton and Kelley, 1983). This constant ratio allowed comparison throughout the growing season with the tub-grown S. eurycarpum. From May to September, 1981 the N:P ratio in shoots ranged from 5.3 to 6.6. The N:P ratios for Pentwater Marsh of 5.3 to 6.6 for the 1981 growing season indicated that N was more limiting than was P. However, the ratio was above that found with severe N limitation with the tub grown S. eurycarpum. Therefore, it is likely that the Pentwater S. eurycarpum was only moderately deficient in N. Belowground Pentwater S. eurycarpum N:P ratios were less appropriately compared with the tub-grown data since the belowground tissues in the natural stand were the result of more than one years growth. Belowground samples from the natural stands would therefore include much senescent material which may have lost P at a rate greater than it lost N. Pentwater Marsh belowground N:P ratio showed much greater variability both temporally and between samples from the same date than did the aboveground ratio. The range during 1981 was from 5 to 11 with an average value of 8. Using these values in comparison with the tub-grown S. eurycarpum belowground tissues would point more towards a phosphorus deficiency which, on the basis of shoot nutrient comparisons, would be an incorrect diagnosis.

N:P ratios similar to those found with S. eurycarpum shoots were also found with the other species studied. The above discussion on S. eurycarpum also, therefore, applies to these other species.

Bernatowicz (1969) examined nutrient content of water plants of Lake Warniak using the "critical concentration" criteria of Gerloff and Krombholz (1966). Twelve of the sixteen species examined were below the "critical concentration" of .13% P while only the emergent species T. latifolia and P. australis were below the critical concentration of 1.3% N. The average N:P ratio was 10.5 for the Lake Warniak species. This analysis pointed out the inappropriateness of using the same "critical concentration" values for emergent and submergent plant species. It also showed that the N:P ratio is less dependent on the amount of structural tissues present than are nutrient concentrations.

Differences existed in the abilities of the four species of perennial plants studied to thrive at very high levels of nitrate fertilization. This was determined during the 1982 growing season when all four species were grown under identical conditions using higher levels of nitrate and phosphate fertilizers than had been used in either of the two preceding years. Dry weight production results are shown in Figure 17 for S. eurycarpum and in Table 10-12 for the other three species. None of the species exhibited a significantly greater production of aboveground or belowground tissues as treatment nitrate-N increased from 46.8 to 93.6 g m^{-2} or phosphate-P increased from 12.5 to 25.0 g m^{-2}. S. eurycarpum showed the most severe response to the highest nitrate level with very high mortality and stunted growth among the survivors. None of the other species produced as much total dry weight at the highest treatment level of nitrate as the same species did at the second highest level. P. australis experienced a slight decline at the highest nitrate level while the Typha spp. showed a more pronounced decrease. However, the deleterious effects were not nearly as strong as those found with S. eurycarpum.

ESTABLISHMENT EXPERIMENTS

Attempts to establish vegetation in Marsh M2 met with mixed success. Some species grew rapidly and established dense stands while others showed little growth and high mortality of propagules. Successful species included T. latifolia, T. angustifolia, and S. eurycarpum. S. eurycarpum showed the most rapid and complete establishment. Its plots were uniformly covered with

Table 10. 1982 P. *australis* aboveground and belowground dry weights, %N and %P with various combinations of nitrate-N and phosphate-P treatments. Standard errors are in parentheses.

Treatment (g m-2)		Dry Weight		%N		%P	
N	P	Aboveground	Belowground	Aboveground	Belowground	Aboveground	Belowground
0	25.0	28.3 (5.2)	35.2 (4.6)	0.57 (0.04)	0.49 (0.05)	.116 (.008)	.153 (.015)
7.8	25.0	185 (38)	124 (26)	0.64 (0.05)	0.39 (0.03)	.126 (.006)	.135 (.016)
23.4	25.0	687 (131)	200 (69)	0.84 (0.16)	0.43 (0.11)	.125 (.016)	.115 (.011)
46.8	25.0	1310 (137)	249 (72)	0.91 (0.23)	0.61 (.048)	.130 (.008)	.106 (.006)
93.6	25.0	1580 (221)	447 (25)	1.93 (0.13)	1.03 (0.13)	.155 (.009)	.108 (.015)
93.6	0	356 (50)	127 (28)	1.60 (0.17)	0.98 (0.17)	.064 (.012)	.052 (.011)
93.6	2.1	618 (161)	224 (80)	1.42 (0.36)	1.08 (0.10)	.089 (.011)	.068 (.008)
93.6	6.3	1420 (228)	291 (79)	1.60 (0.03)	0.99 (0.05)	.092 (.015)	.080 (.014)
93.6	12.5	1260 (226)	282 (65)	1.91 (.106)	1.13 (.09)	.127 (.012)	.094 (.011)
46.8	12.5	1510 (163)	353 (100)	0.89 (0.31)	0.68 (0.03)	.128 (.007)	.095 (.009)

Table 11. 1982 *T. latifolia* aboveground and belowground dry weights, %N and %P with various combinations of nitrate-N and phosphate-P treatments. Standard errors are in parentheses.

Treatment (g m-2)		Dry Weight		%N		%P	
N	P	Aboveground	Belowground	Aboveground	Belowground	Aboveground	Belowground
0	25.0	31.4 (8.0)	85.8 (45)	0.81 (0.09)	0.29 (0.03)	.143 (.015)	.144 (.070)
7.8	25.0	298 (66)	446 (157)	0.67 (0.10)	0.49 (0.09)	.143 (.022)	.242 (.014)
23.4	25.0	698 (162)	1040 (244)	0.84 (0.16)	0.48 (0.15)	.125 (.016)	.126 (.003)
46.8	25.0	1320 (137)	1140 (72)	1.05 (0.09)	0.56 (.045)	.180 (.017)	.256 (.015)
93.6	25.0	674 (330)	251 (160)	2.43 (0.34)	1.48 (0.46)	.285 (.044)	.337 (.043)
93.6	0	146 (34)	153 (21)	1.38 (0.08)	1.25 (0.17)	.089 (.008)	.076 (.017)
93.6	2.1	772 (348)	614 (317)	1.27 (0.03)	1.23 (0.09)	.084 (.005)	.115 (.013)
93.6	6.3	196 (42)	201 (72)	2.33 (0.37)	1.57 (0.19)	.190 (.026)	.164 (.018)
93.6	12.5	414 (193)	152 (53)	2.33 (.278)	1.70 (.06)	.244 (.039)	.246 (.038)
46.8	12.5	1050 (212)	1220 (145)	1.45 (0.15)	0.91 (0.14)	.175 (.018)	.179 (.026)

Table 12. 1982 <u>T. angustifolia</u> aboveground and belowground dry weights, %N and %P with various combinations of nitrate-N and phosphate-P treatments. Standard errors are in parentheses.

Treatment (g m-2) N	P	Dry Weight Aboveground	Dry Weight Belowground	%N Aboveground	%N Belowground	%P Aboveground	%P Belowground
0	25.0	33.8 (3.8)	89.4 (12)	0.82 (0.07)	0.48 (0.02)	.244 (.016)	.349 (.014)
7.8	25.0	219 (23)	629 (78)	0.60 (0.04)	0.66 (0.05)	.138 (.018)	.233 (.042)
23.4	25.0	730 (65)	1220 (111)	0.80 (0.06)	0.39 (0.07)	.156 (.016)	.243 (.008)
46.8	25.0	1060 (72)	1380 (216)	1.21 (0.15)	0.85 (0.11)	.228 (.020)	.322 (.009)
93.6	25.0	774 (13)	778 (159)	2.01 (0.04)	2.12 (0.40)	.235 (.018)	.243 (.068)
93.6	0	255 (62)	244 (100)	1.69 (0.24)	1.32 (0.06)	.124 (.024)	.108 (.014)
93.6	2.1	393 (126)	343 (145)	1.83 (0.28)	1.44 (0.11)	.141 (.041)	.147 (.042)
93.6	6.3	270 (139)	363 (220)	1.75 (0.60)	1.88 (0.09)	.184 (.071)	.268 (.051)
93.6	12.5	372 (47)	370 (133)	2.09 (.026)	1.64 (.03)	.260 (.021)	.305 (.003)
46.8	12.5	839 (19)	1020 (199)	1.70 (0.20)	1.29 (0.28)	.193 (.018)	.213 (.036)

nearly pure stands of S. eurycarpum before the end of the second month after planting. By this time, there was little evidence of the original planting pattern since all areas in each plot were homogeneously covered with vegetation.

With T. latifolia and T. angustifolia there was also considerable growth and spread from the originally planted clumps. However, these species did not completely fill in their plots by the end of the first growing season. There was still visible evidence of the original planting pattern with gaps in certain areas by the beginning of the second growing season. This was especially true in areas away from the shoreline where the water depth was greater.

Z. aquatica seeds showed low germination and high seedling mortality so that plots sown with this seed became only sparsely covered with a few Z. aquatica plants. Part of the problem with the establishment of this species may have been the presence of large amounts of submerged macrophytes which were piled onto the plots from the deeper terraces during times of strong winds resulting in shading and uprooting of Z. aquatica seedlings.

P. australis also did very poorly in M2. Many of the initial clumps died while most of the survivors did very little spreading within their plots. Some of the surviving clumps sent out numerous floating tillers over the water surface. Some of these exceeded 10 m in length. However, these same clumps showed very little local spreading within their plots. This poor establishment may have been a reflection of less than ideal substrate composition for the spread of the plants. Most of the plots had only a very thin (2 cm) soft organic layer over the heavy clay seal. This substrate may not have been conducive for the spread of *P. australis* rhizome systems.

S. pectinata was the least successful of all of the perennial species. Almost all of the initial clumps died during the first summer. The few that survived showed virtually no spread from the original clumps. Again, the nature of the substrate was suspect.

HARVEST EXPERIMENTS

A summary of the harvest experiments on *Typha* spp. plots in M1 and M3 (Table 13) showed the limited capability of cattails to sustain a high yield with multiple harvests over the course of a single growing season. After the original late June, 1981 harvest, subsequent harvests yielded an average of only 10% of the original harvest biomass with each of 4 subsequent harvests at 3 week intervals and an average of 19% with each of 2 subsequent harvests at 6 week intervals. If the harvested stands had been left standing and subjected to a single harvest in late July, an examination of the control data indicates that about 11% more biomass could have been harvested than was harvested in late June. Therefore, the total amount of biomass removal by the multiple harvests using either the 3 or 6 week harvest intervals was less than 130% of the

Table 13. Effects of harvest treatments on shoot weight and nutrient content of *Typha* spp. All units g m-2. * = material removed from plot; other values are shoot standing crops.

	Control				3 Week Harvest Interval				6 Week Harvest Interval			
	Shoot Wt.	N	P	K	Shoot Wt.	N	P	K	Shoot Wt.	N	P	K
6/25/80	670	16.3	1.89	19.9	579*	14.7*	1.71*	18.0*	591*	13.4*	1.50*	17.2*
7/11/80	-	-	-	-	62.9*	2.04*	0.24*	1.85*	-	-	-	-
7/28/80	746	16.0	1.68	14.4	65.5*	2.20*	0.27*	1.62*	144*	3.91*	0.47*	3.27*
8/20/80	-	-	-	-	84.1*	2.44*	0.33*	2.32*	-	-	-	-
9/8/80	565	10.8	1.08	9.11	21.9*	0.85*	0.09*	0.56*	83.3*	2.81*	0.28*	1.87*
SUM 1980	-	-	-	-	813*	22.2*	2.64*	24.4*	818*	20.1*	2.25*	22.3*
6/9/81	625	12.9	1.71	17.8	200	5.22	0.65	5.58	398	8.9	1.20	12.0
8/13/81	627	10.6	1.47	15.0	612	8.91	2.79	11.2	769	9.9	1.51	15.2

amount removable with a single harvest.

Increases in nutrient removal using multiple harvests were somewhat greater than increases in biomass removal. The maximum aboveground harvestable standing crop of N, P, and K occurred in the control plots on June 25. Removal of N amounted to 151% of this control mean using 3 week harvest intervals and 150% of this control mean using 6 week harvests. P removal amounted to 154% of the control mean with 3 week harvests and 150% of the control mean with 6 week intervals. K removal showed the smallest increase with multiple harvests. K removal averaged 135% of the control mean with 3 week harvest intervals and 130% of the control mean with 6 week harvest intervals.

Harvesting had a marked effect on the vegetation during the subsequent 1981 growing season (Table 13). Effects were especially pronounced at the start of the 1981 growing season with harvested plots showing much lower standing crops of nutrients and biomass. Plots that had been harvested every three weeks had, on June 9, 1981, only about 50% of the standing crop of nutrients and biomass of the plots that had been harvested every six weeks and only about 30% of that found in the unharvested plots. However, differences rapidly diminished over the course of the 1981 growing season. By mid-August there was very little difference between plots receiving the various treatments.

Results of harvest experiments on newly established stands of T. latifolia, T. angustifolia, and S. eurycarpum in M2 (Table 14) show some differences between species in

Table 14. Results of harvest experiments on vegetation established in M2. Dry weights are in kg ha-1. * = material removed from plot; other values are standing crops.

Plot Treatment		1981 Shoot Dry Wt.	1981 Nutrient Content N	P	K	8/15/82 Dry Wt.
T. latifolia	7/5/81 harvest	478*	8.61*	1.09*	13.3*	741
T. latifolia	8/12/81 harvest	618*	8.96*	1.21*	15.1*	554
T. latifolia	unharvested	-	-	-	-	670
T. angustifolia	7/5/81 harvest	483*	8.22*	1.03*	11.5*	468
T. angustifolia	8/12/81 harvest	651*	10.7*	1.35*	13.7*	531
T. angustifolia	unharvested	-	-	-	-	711
S. eurycarpum	6/28/81 harvest	215*	3.05*	0.54*	6.03*	232
S. eurycarpum	8/12/81 harvest	178*	2.15*	0.25*	4.09*	215
S. eurycarpum	unharvested	-	-	-	-	293

their response to harvesting at two different harvesting dates. T. latifolia and T. angustifolia showed greater standing crops of biomass and of N, P, and K at the mid-August harvest date compared with the early July harvest date. The opposite pattern was true for the S. eurycarpum plots. These patterns appear to be related to the establishment course of the three species in M2. T. latifolia and T. angustifolia were still expanding from their original plantings at the beginning of the 1981 growing season. S. eurycarpum, on the other hand, was experiencing a visually evident decline from the 1980 growing season. There was a noticeable deterioration in the health of the S. eurycarpum stands with some shoots appearing discolored and lacking the vigor of the previous years growth. Invasion of the S. eurycarpum stands by Scirpus spp. and Sagittaria sp. was also noticeable. It was believed that propagules for these other species were brought along with the S. eurycarpum from Pentwater Marsh but they did not initially constitute an important component of the newly established stands.

MARSH NUTRIENT BUDGETS

Input/output data for the three marshes M1, M2 and M3 (Tables 15-17) indicated that the marshes were all net importers of water carried N. N may be either stored in accumulating sediments, and/or lost as gases (NH_3, N_2, N_2O) to the atmosphere. The three marshes reacted somewhat

Table 15. Input/output balance of water and water-borne chemical constituents of M1 during 1980-82. Water is reported as 10^6 l; all other units are kg.

Time & Flow	H2O	NO3-N	NO2-N	NH3-N	TKN-N	PO4-P	Total P	K+	Cl-
7/80 Inputs	2.76	1.57	0.44	2.84	8.30	1.24	2.48	25.1	331
7/80 Outputs	1.75	0.04	1.14	0.22	4.47	1.02	1.25	18.4	212
8/80 Inputs	3.40	7.07	0.20	0.51	9.08	3.67	4.90	32.6	377
8/80 Outputs	3.20	0.12	0.58	0.16	7.00	2.00	3.46	36.5	369
9/80 Inputs	0.38	0.30	0.09	0.20	1.29	0.31	0.47	3.7	39
9/80 Outputs	0.30	0.02	0.08	3.18	0.37	0.17	0.19	3.2	33
1980 Inputs	6.54	8.94	0.73	3.55	18.7	5.22	7.85	61.4	747
1980 Outputs	5.25	0.18	1.80	3.56	11.8	3.19	4.90	58.1	614

Table 15 (cont'd.).

Time & Flow	H2O	NO3-N	NO2-N	NH3-N	TKN-N	PO4-P	Total P	K+	Cl-
4/81 Inputs	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0	0
4/81 Outputs	0.27	0.26	0.00	0.06	0.30	0.16	0.18	4.7	16
5/81 Inputs	1.95	2.61	0.54	3.11	6.43	0.74	1.88	17.4	225
5/81 Outputs	1.75	1.15	0.11	0.50	2.02	0.87	1.93	18.2	122
6/81 Inputs	2.47	1.27	0.31	1.14	8.23	0.39	0.68	21.2	289
6/81 Outputs	1.95	0.27	0.09	0.25	4.10	1.37	2.53	21.1	201
7/81 Inputs	3.17	1.81	0.56	3.26	9.54	1.44	2.84	29.2	381
7/81 Outputs	2.44	0.24	0.24	0.26	7.20	2.39	3.44	26.8	278
8/81 Inputs	2.41	5.71	0.13	0.36	6.80	3.03	3.97	23.4	269
8/81 Outputs	1.85	0.08	0.02	0.31	3.70	1.30	2.16	21.6	165
9/81 Inputs	5.11	5.02	0.88	0.57	13.09	5.04	6.34	51.6	519
9/81 Outputs	4.84	4.31	0.05	0.07	7.21	3.53	4.47	50.3	397
10/81 Inputs	4.08	4.57	0.04	0.06	6.18	3.77	4.69	36.3	347
10/81 Outputs	3.96	3.53	0.04	0.06	5.90	2.89	3.65	34.1	325
11/81 Inputs	1.11	1.29	0.01	0.01	1.73	0.98	1.58	9.9	99
11/81 Outputs	1.41	1.43	0.01	0.02	1.96	1.03	1.86	12.7	124
1981 Inputs	20.30	22.28	2.47	8.51	52.00	15.39	21.98	189	2129
1981 Outputs	18.47	11.27	0.56	1.53	32.39	13.54	20.22	190	1628

Table 15 (cont'd.).

Time & Flow	H2O	NO3-N	NO2-N	NH3-N	TKN-N	PO4-P	Total P	Cl-
6/82 Inputs	3.90	0.44	0.04	0.47	6.34	1.63	2.78	318
6/82 Outputs	2.96	0.46	0.12	0.46	3.78	1.54	3.15	214
7/82 Inputs	2.99	0.29	0.04	0.25	3.59	1.20	1.71	255
7/82 Outputs	3.10	0.06	0.06	0.33	4.84	2.94	4.05	257
8/82 Inputs	0.87	0.09	0.07	0.06	0.84	0.34	0.40	80
8/82 Outputs	0.35	0.12	0.03	0.02	0.61	0.23	0.26	31
1982 Inputs	7.76	0.82	0.15	0.78	10.77	3.17	4.89	653
1982 Outputs	6.41	0.64	0.21	0.81	9.23	4.71	7.46	502

20.27
17.30

Table 16. Input/output balance of water and water-borne chemical constituents of M2 during 1980-82. Water is reported as 10^6 l; all other units are kg.

Time & Flow	H20	NO3-N	NO2-N	NH3-N	TKN-N	PO4-P	Total P	K+	Cl-
7/80 Inputs	2.92	1.66	0.47	3.01	8.79	1.31	2.63	30.5	350
7/80 Outputs	2.50	0.06	0.57	2.23	6.67	1.33	2.99	37.2	304
8/80 Inputs	7.96	16.6	0.48	1.20	21.3	8.60	11.5	75.7	884
8/80 Outputs	7.17	4.57	4.58	0.11	11.8	7.69	9.71	81.1	805
9/80 Inputs	0.16	0.13	0.04	0.09	0.55	0.13	0.20	1.6	17
9/80 Outputs	0.43	1.35	0.01	0.54	0.20	1.43	1.34	4.6	45
1980 Inputs	11.0	18.4	0.99	4.30	30.6	10.0	14.3	108	1251
1980 Outputs	10.1	5.98	5.16	2.88	18.7	10.5	14.0	123	1154

84.3

70% N P 5%

Table 16 (cont'd.).

Time & Flow	H2O	NO3-N	NO2-N	NH3-N	TKN-N	PO4-P	Total P	K+	Cl-
4/81 Inputs	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0	0
4/81 Outputs	0.17	0.26	0.00	0.05	0.30	0.25	0.30	2.5	10
5/81 Inputs	1.94	2.60	0.54	3.09	6.39	0.73	1.87	14.0	225
5/81 Outputs	1.36	0.38	0.08	0.32	1.86	1.48	2.11	14.7	134
6/81 Inputs	4.14	2.29	0.79	3.33	18.1	0.92	1.93	35.6	485
6/81 Outputs	3.79	0.08	0.11	0.80	4.55	1.33	2.27	40.6	447
7/81 Inputs	3.85	2.31	0.67	5.98	13.7	2.38	4.08	35.4	463
7/81 Outputs	2.95	0.03	0.03	0.71	4.28	1.75	2.89	31.0	348
8/81 Inputs	4.89	6.53	0.05	6.17	8.62	4.95	6.42	47.4	492
8/81 Outputs	4.21	0.04	0.04	0.38	7.79	1.93	2.43	41.7	427
9/81 Inputs	1.18	1.25	0.29	0.21	4.90	1.51	1.89	11.9	117
9/81 Outputs	1.07	0.02	0.01	0.06	1.41	0.84	1.11	10.2	102
10/81 Inputs	0.21	0.17	0.00	0.00	0.31	0.19	0.23	1.9	17
10/81 Outputs	0.28	0.02	0.00	0.01	0.38	0.28	0.32	2.3	22
1981 Inputs	16.21	15.15	2.34	18.78	52.02	10.68	16.42	146	1799
1981 Outputs	13.83	0.83	0.27	2.33	20.57	7.86	11.43	143	1490

88.3
N = 73%

P 31%

Table 16(cont'd.).

Time & Flow	H2O	NO3-N	NO2-N	NH3-N	TKN-N	PO4-P	Total P	Cl-
6/82 Inputs	3.04	1.19	0.09	0.55	4.51	1.69	2.38	255
6/82 Outputs	2.82	0.06	0.08	0.48	3.08	1.23	1.63	219
7/82 Inputs	1.42	0.19	0.02	0.14	1.65	0.54	0.92	121
7/82 Outputs	1.10	0.01	0.01	0.13	1.66	0.25	0.37	92
8/82 Inputs	2.40	0.46	0.11	0.10	2.17	0.78	1.06	212
8/82 Outputs	1.80	0.17	0.04	0.09	1.94	0.44	0.59	157
9/82 Inputs	1.08	0.11	0.04	0.08	1.16	0.36	0.50	95
9/82 Outputs	1.03	0.01	0.01	0.16	1.57	0.97	1.09	99
1982 Inputs	7.94	1.95	0.26	0.87	9.49	3.37	4.86	683
1982 Outputs	6.75	0.25	0.14	0.86	8.25	2.89	3.68	567

Table 17. Input/output balance of water and water-borne chemical constituents of M3 during 1980-82. Water is reported as 10 6 l; all other units are kg.

Time & Flow	H2O	NO3-N	NO2-N	NH3-N	TKN-N	PO4-P	Total P	K+	Cl-
7/80 Inputs	4.65	2.65	0.74	4.79	14.0	2.09	4.18	41.8	558
7/80 Outputs	4.04	8.01	0.21	0.04	7.74	3.37	4.10	35.1	498
8/80 Inputs	5.86	12.2	0.35	0.88	15.6	6.33	8.43	56.2	650
8/80 Outputs	5.25	0.23	1.47	6.30	10.0	8.03	9.88	49.2	617
9/80 Inputs	0.47	0.37	0.11	0.25	1.61	0.38	0.58	4.7	49
9/80 Outputs	0.43	0.66	0.59	0.20	1.32	0.88	1.00	4.3	46
1980 Inputs	11.0	15.2	1.20	5.92	31.2	8.80	13.2	102.7	1257
1980 Outputs	9.72	8.90	2.27	6.54	19.1	12.3	15.0	88.6	1161

Table 17 (cont'd.).

Time & Flow	H2O	NO3-N	NO2-N	NH3-N	TKN-N	PO4-P	Total P	K+	Cl-
6/81 Inputs	3.87	1.87	0.63	2.34	16.9	0.86	2.00	33.3	453
6/81 Outputs	2.93	0.03	0.03	0.64	3.55	0.82	1.03	24.3	322
7/81 Inputs	4.63	1.33	0.68	4.34	13.1	1.62	3.24	42.6	557
7/81 Outputs	4.25	0.04	0.04	1.00	4.78	1.85	2.75	37.4	480
8/81 Inputs	6.82	9.09	0.07	8.59	12.0	6.88	8.43	66.2	684
8/81 Outputs	6.07	0.13	0.06	1.30	10.2	4.03	5.70	57.1	621
9/81 Inputs	2.58	0.69	0.04	0.37	7.27	2.99	3.44	26.1	249
9/81 Outputs	2.51	0.71	0.25	0.24	4.57	3.20	4.28	25.4	234
10/81 Inputs	0.85	0.83	0.01	0.01	1.28	0.76	0.95	7.6	71
10/81 Outputs	0.95	0.60	0.01	0.02	1.36	0.91	1.17	7.6	73
1981 Inputs	18.75	13.81	1.43	15.65	50.55	13.11	18.06	176	2014
1981 Outputs	16.71	1.51	0.39	3.20	24.46	10.81	14.93	152	1730

Table 17 (cont'd.).

Time & Flow	H2O	NO3-N	NO2-N	NH3-N	TKN-N	PO4-P	Total P	Cl-
6/82 Inputs	1.57	0.11	0.02	0.23	2.70	0.72	1.08	131
6/82 Outputs	0.91	0.01	0.01	0.11	0.99	0.19	0.27	63
7/82 Inputs	1.44	0.15	0.02	0.16	1.93	0.55	0.81	124
7/82 Outputs	1.23	0.01	0.01	0.17	1.39	0.35	0.46	100
8/82 Inputs	0.53	0.08	0.01	0.03	0.47	0.15	0.29	46
8/82 Outputs	0.09	0.02	0.01	0.00	0.08	0.04	0.05	8
1982 Inputs	3.54	0.34	0.05	0.42	5.10	1.42	2.18	301
1982 Outputs	2.23	0.04	0.03	0.28	2.46	0.58	0.78	171

differently for phosphorus. The import/export balance of total P varied between net input and net output between marshes and between years. Unbalanced chloride budgets for some years probably indicate some unmonitored losses of water and water carried nutrients since chloride is not generally detained to any great extent by any physical, chemical, or biological processes occurring in marshes. These losses could represent seepage through muskrat tunnels, around weirs, etc.

CONCLUSIONS

This research has revealed both similarities and differences between the species in their abilities to establish themselves from rhizome sections, incorporate nutrients into their tissues, and recover from the stress of multiple harvests. Some of these differences should receive consideration when the role or potential role of these species in natural and artificial systems is discussed. For example, when establishing stands for the purpose of maximizing biomass or nutrient uptake, it is necessary to consider the substrate texture, operational water depth of the system, and nutrient supply. All of the perennial species studied may be easily propagated using rhizome cuttings. However, they differ in other properties.

In this study, all species spread about equally rapidly through the sand substrate used in the tub experiments. However, there were great differences between the species in their abilities to colonize a heavy clay substrate. S. eurycarpum spread very rapidly in such a situation and may be the best species of those studied for use in a situation where a clay substrate cannot be avoided and rapid establishment is necessary. Both species of cattail are also suitable for such a substrate if rapid establishment is not essential. Plantings of T. latifolia and T. angustifolia at the WQMF eventually resulted in very dense, nearly monospecific stands. P. australis appears to be a very poor colonizer of clay substrates. When placed in such a substrate the plants sent out floating horizontal tillers rather than roots, rhizomes and vertical shoots. At the WQMF P. australis is much more successful in the looser soils immediately adjacent to the marshes than in the heavy clay sediments of the marshes.

Differences in success on different substrates for the species used in this study have been reported in the literature. Around Danish lakes it was found that T. angustifolia did better in softer sediments that did P. australis (Boye-Peterson, 1917). In Finland, the capacity of P. australis to invade coarser sediments has been used as an explanation of its greater development along open shores than is found with Schoenoplectis lacustris (Maristo, 1941). Somewhat contradictory is the finding of Brand (1896) that Scirpus lacustris has harder rhizomes that Phragmites australis and can therefore grow in gravelly areas where _P. australis_ cannot. The natural substrates of most common occurrence for _Z. aquatica_ are sand and organic (Fasset, 1957). It has been reported that _T. angustifolia_ grows on more organic substrates than _T. latifolia_. Most of the literature reports on substrate preference are descriptive rather than experimental and often do not account for such covariates as degree of disturbance and substrate chemistry. Substrate texture should therefore be examined more carefully and under more controlled conditions before recommendations are made for artificial plantings in a prepared substrate.

While all of the species overlapped in their water depth utilization, _S. eurycarpum_ appeared to be the most successful in the deepest waters of the WQMF marshes while _P. australis_ was most successful at the land-water interface. There was no clear depth separation of the cattails at the WQMF but it has been reported from other studies that _T. angustifolia_ has a greater depth tolerance that _T. latifolia_ (Grace and Wetzel, 1982) At the WQMF the two _Typha_ species did not grow in as deep of water as was found with _S. euraycarpum_ or extend onto dry land as did _P. australis_. Penetration into the sod of the area surrounding the WQMF marshes was accomplished only by _P. australis_. It has been reported in other situations that _P. australis_ is capable of invading stands of other species (Buttery and Lambert, 1965). Thus, either a tolerance for low water level or the penetrating abilities of the _P. australis_ rhizomes may be responsible for its appearance in the sod. In many areas of Europe P. australis has been reported to be the dominant species in deeper water areas (Bjork, 1967). This contrasting situation is probably due to the greater resistance of P. australis to wind and wave stress due to its more linear form when compared to Typha spp. (Hutchinson, 1975).

The ranges of chemical environments of occurrence for some of the species of this study have been roughly mapped out (Hutchinson, 1975; Moyle, 1945). In the north central U.S., P. australis is typical of low alkalinity to moderately hard waters. The two species of Typha occupy the above type of waters plus harder waters and waters very high in sulfate. There is no sharp distinction between T. latifolia and T. angustifolia in chemical environment of occurrence (Hutchinson, 1975) although they have been reported to have somewhat different pH (Hotchkiss and Dozier, 1949) and salinity tolerances (McMillan, 1959). S. eurycarpum and Z. aquatica are typical species in areas of low sulfate and low alkalinity and hardness. The natural range of S. eurycarpum in low nutrient water relates to the present findings of the tub experiments where S. eurycarpum did the most poorly of the species studied at high nutrient concentrations.

Most wetlands have anaerobic substrates with large amounts of organic matter present. Under these conditions, nitrate is rapidly denitrified and ammonia is the dominant form of available nitrogen (Patrick and Mahapatra, 1968). Our tubs differed from this situation in that there was initially almost no organic matter present in the substrate and most of the added nitrate was therefore not denitrified. It is therefore of interest what the response of the plants would have been had ammonia been used as the nitrogen source. Some differences would have occurred because of differences in toxicity and uptake paths of the two nitrogen forms. Ammonia is normally the more toxic of the two forms (Mengel and Kirkby, 1979) and might be tolerated only at lower maximum levels. However, since most emergent aquatics are normally found associated with high ammonia levels, they might be more tolerant than typical land plants of high ammonia levels. Ammonium ions are positively charged while nitrate ions are negatively charged. This difference leads to different antagonist/protagonist relationships (to plant uptake) with other ions in solution. Because of the ionic charges, nitrate would be expected to stimulate potassium uptake and depress phosphate uptake while the opposite would be true for ammonium. This could result in different N:P ratios in plants in tubs with the same N:P fertilizer ratios but using ammonia instead of nitrate as the nitrogen source.

The spacing of fertilizer applications over the course of the growing season could also make a difference in the total nutrient uptake. Some of the tub experiment plants took up over 80% of the applied nitrogen which indicates that little was available for the plants by the end of the growing season. Emergent aquatics in natural stands normally take up most of their nutrients in the spring.

However, the tub grown plants represented expanding colonies which sent up new shoots later in the season than most natural stands. The tub grown plants would also, therefore, have been expected to take up more nutrients later in the season.

As has been found in other studies, these new data indicate that very large stands of vegetation would be needed to remove the amount of phosphorus loading resulting from the domestic sewage of a large population. Spangler et al (1976c) estimate that the phosphorus removable by *Scirpus validus* shoot harvests would accommodate only 25 persons ha^{-1} if all of the input P was to be removed in the shoots. This assumes shoot removal of 3.5 g m^{-2} and a per capita P input of 1.3 kg per annum. Others have achieved removal of up to 5 g P m^{-2} yr^{-1} with emergent marsh species (Sloey *et al*, 1978). Several harvests per season were needed to achieve even this removal. Maximum shoot P uptake in the tub experiments were in the range of 1 to 2 g m^{-2} for each of the species studied. This study therefore reinforces the concept that marshes and other wetlands are not suitable for the long term treatment of large quantities of high P wastewaters.

It is likely that different plants of the same species studied but collected from different sites could vary markedly in their growth responses to various levels of fertilization. *P. australis* is known to be exceptionally diverse genetically (Bjork, 1967). Polyploidy is widespread with the basic number of chromosomes considered to be either 6 (Love and Love, 1961) or 12 (Bjork, 1967). The tetraploid (48 chromosomes) is apparently the most common worldwide but other variations including triploidy, hexaploidy, heptaploidy, and octaploidy (based on n=12) have been reported. Substantial genetically determined morphologic differences between shoots have also been found within a ploidy level as well as between levels (Bjork, 1967). Ecotypic differences have also been found to exist for *Typha* spp. (McNaughton, 1966) and *Z. aquatica* (Elliot, 1977) and probably also exist for *S. eurycarpum*. Care must therefore be exercised in extending these results to other populations.

P. australis, *T. angustifolia*, *T. latifolia*, and *S. eurycarpum* remain as species with good promise for cultivation in artificial marshes. Their utilization in such systems should consider the interspecific differences found in this study. In addition, attempts should be made to develop new varities or find naturally occurring ecotypes with greater nutrient uptake capabilities and/or aboveground production potential.

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Table A1. 1980 *P. australis* aboveground dry weight (g m-2) estimates from regressions. Number of replicates and standard errors are in parentheses.

Treatment (g m-2)			Days After Planting			
N	P	K	14	35	49	63
0	0	0	6.4(5;2.4)	13.6(5;4.0)	18.0(5;3.2)	19.2(5;4.0)
0	0	7.8	4.8(5;1.6)	5.6(5;0.8)	10.2(5;2.9)	18.4(4;5.6)
0	0	23.4	9.6(4;3.2)	13.6(4;5.6)	18.2(5;6.3)	23.2(4;7.8)
0	0	41.6	12.8(4;3.2)	8.8(4;2.4)	14.2(4;3.6)	15.2(3;0.8)
0	2.1	0	12.0(5;0.8)	9.6(5;0.8)	14.4(5;2.2)	16.0(3;1.6)
0	2.1	7.8	11.2(4;4.0)	15.2(4;4.0)	20.0(4;4.8)	23.2(4;5.6)
0	2.1	23.4	8.0(4;0.8)	16.0(4;7.2)	12.0(4;1.9)	18.4(4;0.8)
0	2.1	41.6	7.2(4;2.4)	7.2(4;1.6)	11.8(4;1.2)	16.0(4;1.6)
0	6.2	0	6.4(5;2.4)	8.8(3;4.0)	17.2(5;3.8)	20.0(4;6.4)
0	6.2	7.8	6.4(5;1.6)	8.8(5;3.2)	13.2(5;4.4)	16.8(5;5.6)
0	6.2	23.4	6.4(5;1.6)	8.0(5;1.6)	10.2(5;1.9)	10.4(4;1.6)
0	6.2	41.6	7.2(4;0.8)	32.8(4;3.2)	14.1(4;2.8)	18.4(4;2.4)
0	12.5	0	4.0(5;0.8)	24.8(5;4.8)	11.5(5;2.7)	16.0(4;3.2)
0	12.5	7.8	11.2(5;1.6)	14.4(5;3.2)	19.9(5;4.5)	22.4(5;5.6)
0	12.5	23.4	6.4(6;0.8)	9.6(6;2.4)	11.7(6;2.7)	14.4(5;3.2)
0	12.5	41.6	8.8(5;1.6)	11.2(5;1.6)	15.0(5;2.0)	19.2(5;2.4)
7.8	0	0	5.6(5;0.8)	10.4(5;1.6)	18.0(5;2.0)	31.2(4;4.0)
7.8	0	7.8	9.6(5;1.6)	17.6(5;4.0)	29.3(5;4.3)	42.4(4;8.0)
7.8	0	23.4	6.4(5;2.4)	18.4(5;5.6)	27.4(5;7.2)	39.2(5;9.6)
7.8	0	41.6	6.4(5;2.4)	12.0(5;0.8)	14.7(5;3.5)	28.0(5;2.4)
7.8	2.1	0	8.0(5;1.6)	21.6(5;3.2)	56.5(5;9.5)	110(5;20.0)
7.8	2.1	7.8	12.0(5;0.8)	36.8(5;6.4)	87.8(5;10.7)	134(5;27.2)
7.8	2.1	23.4	5.6(5;0.8)	15.2(5;4.8)	42.6(5;10.6)	57.6(5;9.6)
7.8	2.1	41.6	8.8(6;2.4)	24.0(6;9.6)	63.3(6;19.5)	87.2(6;17.6)
7.8	6.2	0	7.2(5;2.4)	14.4(5;4.0)	39.2(5;12.4)	84.8(5;16.0)
7.8	6.2	7.8	6.4(5;1.6)	28.0(5;8.0)	90.3(5;20.8)	111(5;17.6)
7.8	6.2	23.4	16.0(4;3.2)	24.0(4;3.2)	74.1(4;10.9)	129(4;33.6)
7.8	6.2	41.6	11.2(4;2.4)	25.6(4;4.0)	69.3(5;9.8)	129(4;28.0)
7.8	12.5	0	5.6(5;0.8)	30.4(4;8.8)	71.9(5;19.4)	126(4;26.4)
7.8	12.5	7.8	8.8(5;1.6)	27.2(5;6.4)	87.1(5;19.6)	131(4;25.6)
7.8	12.5	23.4	8.0(5;1.6)	32.8(3;4.8)	78.9(3;27.2)	97.6(4;11.2)
7.8	12.5	41.6	7.2(5;0.8)	21.6(5;1.6)	84.7(5;6.3)	107(5;11.2)

Table A1 (cont'd.).

Treatment (g m-2)			Days After Planting			
N	P	K	14	35	49	63
23.4	0	0	8.8(5;2.4)	16.8(4;2.4)	34.8(4;0.4)	33.6(4;11.2)
23.4	0	7.8	5.6(5;2.4)	12.0(5;4.8)	27.4(5;9.2)	33.6(5;11.2)
23.4	0	23.4	8.0(4;0.8)	17.6(4;4.0)	35.2(5;7.7)	44.8(3;11.2)
23.4	0	41.6	5.6(5;0.8)	12.0(5;4.0)	26.1(5;6.3)	60.0(4;16.0)
23.4	2.1	0	6.4(5;0.8)	17.6(5;3.2)	61.3(5;6.9)	110(5;16.8)
23.4	2.1	7.8	9.6(4;2.4)	25.6(5;8.0)	83.7(5;24.3)	185(5;48.0)
23.4	2.1	23.4	4.0(4;2.4)	5.6(5;0.8)	18.1(5;5.0)	48.0(5;13.6)
23.4	2.1	41.6	8.8(5;1.6)	16.0(5;7.2)	58.1(5;19.9)	119(5;36.8)
23.4	6.2	0	5.6(5;1.6)	15.2(4;1.6)	79.0(5;18.5)	181(4;24.8)
23.4	6.2	7.8	7.2(5;2.4)	16.0(5;4.0)	60.4(4;11.7)	130(4;54.4)
23.4	6.2	23.4	5.6(4;4.8)	16.8(2;16.0)	80.5(2;77.1)	185(2;162)
23.4	6.2	41.6	8.0(5;1.6)	16.0(5;4.8)	74.0(5;19.2)	174(6;35.2)
23.4	12.5	0	9.6(6;3.2)	23.2(6;8.8)	86.6(6;24.5)	142(6;37.6)
23.4	12.5	7.8	5.6(5;2.4)	22.4(5;5.6)	80.3(5;11.5)	228(5;41.6)
23.4	12.5	23.4	11.2(5;3.2)	36.8(5;10.4)	145(5;39.9)	262(4;50.4)
23.4	12.5	41.6	6.4(7;1.6)	20.8(7;4.8)	105(6;16.3)	244(6;35.2)
46.8	0	0	6.4(5;1.6)	8.0(5;2.4)	21.5(5;6.8)	20.0(4;8.0)
46.8	0	7.8	5.6(5;2.4)	10.4(5;2.4)	23.9(5;5.0)	34.4(4;7.2)
46.8	0	23.4	5.6(5;0.8)	7.2(5;1.6)	13.7(4;2.8)	16.0(4;1.6)
46.8	0	41.6	10.4(4;0.8)	11.2(4;3.2)	26.4(4;1.8)	40.0(3;1.6)
46.8	2.1	0	6.4(4;1.6)	15.2(5;6.4)	61.0(5;22.4)	120(5;28.0)
46.8	2.1	7.8	5.6(4;0.8)	16.0(5;8.0)	62.0(5;27.1)	142(5;71.2)
46.8	2.1	23.4	9.6(5;0.8)	23.2(6;10.4)	71.6(5;16.1)	138(5;36.0)
46.8	2.1	41.6	9.6(4;2.4)	21.6(4;9.6)	70.8(4;27.5)	437(4;92.8)
46.8	6.2	0	8.0(5;0.8)	17.6(4;8.0)	57.1(4;15.0)	166(4;36.0)
46.8	6.2	7.8	6.4(5;1.6)	24.8(5;4.8)	110(5;13.1)	331(5;85.6)
46.8	6.2	23.4	9.6(2;4.0)	8.8(2;4.0)	47.0(3;37.5)	134(2;68.8)
46.8	6.2	41.6	6.4(6;0.8)	13.6(6;4.0)	56.5(6;10.8)	182(4;22.4)
46.8	12.5	0	8.0(4;1.6)	16.8(4;8.8)	68.7(4;25.9)	170(4;67.2)
46.8	12.5	7.8	9.6(5;4.0)	23.2(5;7.2)	109(5;37.2)	160(4;8.0)
46.8	12.5	23.4	8.8(3;2.4)	33.6(3;20.0)	152(3;84.8)	238(2;142)
46.8	12.5	41.6	5.6(5;1.6)	24.8(5;11.2)	117(5;48.0)	192(5;60.0)

Table A1 (cont'd.).

Treatment (g m-2)			Days After Planting			
N	P	K	80	91	106	117
0	0	0	27.2(5;4.0)	31.2(5;4.0)	38.4(3;1.6)	43.2(4;3.2)
0	0	7.8	16.0(4;4.8)	20.8(4;5.6)	24.8(3;5.6)	30.4(3;7.2)
0	0	23.4	27.2(4;7.2)	35.2(4;8.8)	61.4(3;20.8)	45.6(2;6.4)
0	0	41.6	32.8(2;12.8)	20.0(2;0.0)	32.8(2;4.0)	4.3(1;-)
0	2.1	0	22.4(3;5.6)	17.6(2;4.0)	18.4(2;4.8)	36.8(1;-)
0	2.1	7.8	37.6(4;12.0)	50.4(4;13.6)	91.2(1;-)	126(2;50.4)
0	2.1	23.4	25.6(3;0.8)	33.6(3;2.4)	42.4(3;5.6)	46.4(3;3.2)
0	2.1	41.6	24.8(4;3.2)	28.8(3;4.8)	38.4(3;5.6)	52.8(2;2.4)
0	6.2	0	28.8(4;6.4)	30.4(4;8.0)	62.4(3;14.4)	56.0(1;0.0)
0	6.2	7.8	22.4(5;5.6)	32.0(5;8.8)	43.2(4;10.4)	48.0(3;12.8)
0	6.2	23.4	20.0(3;2.4)	32.8(1;0.0)	28.0(2;0.8)	32.8(2;0.8)
0	6.2	41.6	23.2(4;2.4)	32.0(4;3.2)	48.8(4;15.2)	60.8(3;16.8)
0	12.5	0	28.0(4;5.6)	36.8(4;9.6)	47.2(4;10.4)	43.2(2;2.4)
0	12.5	7.8	32.0(5;6.4)	36.0(4;9.6)	103(2;20.8)	92.8(3;40.8)
0	12.5	23.4	22.4(5;3.2)	30.4(5;5.6)	55.2(3;21.6)	64.0(2;36.8)
0	12.5	41.6	28.0(5;2.4)	36.8(5;4.8)	53.6(3;13.6)	68.0(3;17.6)
7.8	0	0	47.2(4;6.4)	58.4(4;4.8)	73.6(2;2.4)	88.8(3;11.2)
7.8	0	7.8	53.6(3;18.4)	82.4(4;15.2)	93.6(4;9.6)	99.2(2;23.2)
7.8	0	23.4	58.4(5;12.8)	76.0(5;13.6)	70.4(4;16.0)	60.0(2;23.2)
7.8	0	41.6	40.0(5;5.6)	48.0(5;4.8)	65.6(2;7.2)	64.0(3;12.8)
7.8	2.1	0	160(5;31.2)	177(4;26.4)	207(4;32.8)	213(4;38.4)
7.8	2.1	7.8	165(5;24.8)	188(5;19.2)	173(4;8.8)	79.2(2;31.2)
7.8	2.1	23.4	92.0(5;17.6)	107(5;20.0)	129(4;29.6)	138(4;19.2)
7.8	2.1	41.6	122(6;23.2)	154(5;28.0)	172(3;42.4)	184(1;-)
7.8	6.2	0	129(5;26.4)	159(4;37.6)	132(4;38.4)	153(2;3.2)
7.8	6.2	7.8	98.4(4;8.0)	137(2;16.0)	154(2;27.2)	154(1;38.4)
7.8	6.2	23.4	170(4;41.6)	192(4;51.2)	166(2;32.0)	154(2;40.8)
7.8	6.2	41.6	163(3;28.0)	186(3;23.2)	219(3;43.2)	194(2;69.6)
7.8	12.5	0	154(4;33.6)	179(4;30.4)	250(2;45.6)	-(-)
7.8	12.5	7.8	137(5;20.8)	112(4;15.2)	120(1;10.4)	122(1;6.4)
7.8	12.5	23.4	122(3;12.8)	137(3;16.0)	214(1;-)	197(2;36.8)
7.8	12.5	41.6	138(5;14.4)	177(5;16.0)	197(3;40.0)	-(-)

Table A1 (cont'd.).

Treatment (g m-2) N	P	K	Days After Planting 80	91	106	117
23.4	0	0	47.2(4;13.6)	56.8(4;17.6)	118(3;55.2)	135(3;32.0)
23.4	0	7.8	47.2(5;13.6)	56.8(5;17.6)	118(3;55.2)	135(2;32.0)
23.4	2.1	23.4	64.0(3;17.6)	81.6(3;22.4)	86.4(3;11.2)	97.6(2;24.8)
23.4	0	41.6	50.4(4;8.0)	68.8(5;12.0)	68.8(3;18.4)	129(1;-)
23.4	2.1	0	238(5;20.8)	356(4;45.6)	523(2;136)	707(2;49.6)
23.4	2.1	7.8	310(4;51.2)	519(3;44.8)	669(3;30.4)	667(4;74.4)
23.4	2.1	23.4	119(5;31.2)	252(5;56.8)	401(4;89.6)	371(2;127)
23.4	2.1	41.6	262(4;90.4)	421(5;93.6)	554(4;130.4)	442(2;350)
23.4	6.2	0	325(4;40.0)	469(2;45.6)	518(1;58.4)	646(1;-)
23.4	6.2	7.8	275(4;92.8)	223(2;107)	432(2;286)	-(-)
23.4	6.2	23.4	350(2;270)	497(2;344)	1040(1;-)	1016(1;-)
23.4	6.2	41.6	362(6;60.0)	445(6;70.4)	477(3;22.4)	426(2;48.8)
23.4	12.5	0	289(6;50.4)	317(3;42.4)	446(2;90.4)	406(1;-)
23.4	12.5	7.8	357(5;40.8)	487(5;52.0)	604(5;53.6)	667(4;55.2)
23.4	12.5	23.4	468(5;74.4)	590(5;96.0)	635(2;229)	903(3;438)
23.4	12.5	41.6	450(5;72.0)	514(5;34.4)	779(3;218)	793(3;208)
46.8	0	0	37.6(3;15.2)	44.8(3;17.6)	60.0(3;24.0)	71.2(3;27.2)
46.8	0	7.8	57.6(4;15.2)	92.8(4;36.8)	93.6(2;5.6)	109(3;9.6)
46.8	0	23.4	19.2(4;5.6)	36.0(4;1.6)	53.6(3;0.8)	60.0(1;-)
46.8	0	41.6	59.2(1;4.8)	80.0(2;4.0)	114(1;-)	117(2;24.8)
46.8	2.1	0	272(5;72.0)	344(5;54.4)	514(3;131)	502(2;150)
46.8	2.1	7.8	199(5;35.2)	327(5;44.8)	489(3;58.4)	515(3;71.2)
46.8	2.1	23.4	275(4;80.8)	462(4;87.2)	666(4;134)	805(4;126)
46.8	2.1	41.6	207(5;40.8)	392(4;84.0)	519(3;61.6)	697(4;130)
46.8	6.2	0	308(3;67.2)	440(3;60.8)	602(2;78.4)	534(1;-)
46.8	6.2	7.8	570(4;96.0)	690(4;178)	1011(3;165)	1404(2;66.4)
46.8	6.2	23.4	190(3;100)	462(2;108)	419(2;174)	798(2;62.4)
46.8	6.2	41.6	361(4;17.6)	598(4;76.8)	998(4;65.6)	1202(3;129)
46.8	12.5	0	381(4;122)	687(3;133)	794(3;249)	862(3;242)
46.8	12.5	7.8	513(4;58.4)	902(4;91.2)	1124(2;40.8)	1274(3;73.6)
46.8	12.5	23.4	193(1;-)	472(1;-)	-(-)	350(1;-)
46.8	12.5	41.6	419(4;97.6)	685(4;136)	1464(1;-)	-(-)

Table A2. 1980 *Z. aquatica* aboveground dry weight (g per plant) estimates from regressions. Number of replicates and standard errors are in parentheses.

Treatment (g m-2) N	P	K	Days After Planting 35	63	81	92	108
0	0	0	.34(5;.02)	.34(5;.02)	.35(4;.03)	.40(3;.08)	.40(2;.09)
0	0	7.8	.32(5;.02)	.33(5;.02)	.31(5;.02)	.33(3;.02)	.32(4;.02)
0	0	23.4	.34(5;.02)	.38(5;.01)	.45(3;.08)	.67(3;.28)	.28(1;-)
0	0	41.6	.35(5;.02)	.34(5;.02)	.34(3;.03)	.32(3;.03)	-(-)
0	2.1	0	.32(5;.01)	.30(5;.01)	.35(5;.02)	.38(5;.03)	.50(2;.20)
0	2.1	7.8	.32(5;.02)	.32(1;.02)	.36(4;.02)	.34(3;.03)	.31(2;-)
0	2.1	23.4	.35(5;.03)	.36(3;.01)	.39(4;.06)	.43(5;.08)	.48(3;.10)
0	2.1	41.6	.33(5;.03)	.38(2;.03)	.36(4;.04)	.31(3;.03)	.50(2;.19)
0	6.2	0	.31(2;.03)	.34(2;.01)	.41(2;.10)	.44(2;.09)	.43(2;.07)
0	6.2	7.8	.32(4;.02)	.34(4;.02)	.36(3;.02)	.30(4;.01)	.30(3;.03)
0	6.2	23.4	.33(6;.01)	.38(5;.01)	.40(4;.03)	.48(4;.08)	.51(3;.09)
0	6.2	41.6	.31(5;.01)	.32(5;.01)	.33(3;.02)	.42(3;.13)	.49(2;.21)
0	12.5	0	.33(4;.04)	.34(5;.04)	.32(4;.02)	.64(5;.28)	.46(2;.05)
0	12.5	7.8	.33(5;.01)	.31(5;.01)	.32(5;.01)	.33(5;.02)	.33(3;.01)
0	12.5	23.4	.32(4;.02)	.32(4;.02)	.35(4;.04)	.31(4;.01)	-(-)
0	12.5	41.6	.32(5;.02)	.36(4;.01)	.39(3;.02)	.36(3;.02)	.30(1;-)
7.8	0	0	.37(5;.01)	.34(5;.02)	.31(4;.01)	.31(3;.01)	.32(1;-)
7.8	0	7.8	.35(5;.01)	.36(5;.01)	.34(4;.02)	.33(4;.01)	.34(2;.01)
7.8	0	23.4	.37(4;.01)	.36(5;.02)	.31(5;.01)	.33(3;.01)	.36(1;-)
7.8	0	41.6	.36(5;.01)	.38(5;.03)	.36(3;.01)	.31(2;.01)	.33(2;.06)
7.8	2.1	0	.45(5;.05)	.64(5;.12)	.95(4;.26)	1.47(3;.26)	.95(3;.31)
7.8	2.1	7.8	.42(5;.02)	.63(5;.10)	.77(4;.05)	1.11(4;.09)	1.16(2;.12)
7.8	2.1	23.4	.46(5;.05)	.64(4;.10)	1.58(3;.46)	1.37(3;.37)	.88(1;-)
7.8	2.1	41.6	.39(5;.02)	.46(5;.03)	.57(5;.08)	.68(5;.14)	-(-)
7.8	6.2	0	.55(4;.06)	1.54(4;.36)	3.25(4;1.67)	3.97(4;.41)	2.70(2;.08)
7.8	6.2	7.8	.46(4;.10)	1.13(5;.61)	3.02(4;1.28)	2.93(4;1.29)	3.10(4;1.37)
7.8	6.2	23.4	.64(4;.03)	1.80(4;.56)	2.85(4;1.06)	3.92(3;1.54)	3.98(3;1.17)
7.8	6.2	41.6	.50(5;.04)	1.53(5;.28)	2.74(3;.35)	2.46(4;.20)	2.06(2;.37)
7.8	12.5	0	.37(4;.04)	.59(4;.16)	1.80(4;.84)	1.80(4;.77)	2.73(3;1.28)
7.8	12.5	7.8	.48(5;.03)	1.75(5;.22)	3.07(4;.23)	3.85(4;.18)	1.86(2;.70)
7.8	12.5	23.4	.52(4;.12)	1.16(6;.42)	2.40(5;.96)	2.52(6;.72)	2.68(3;.10)
7.8	12.5	41.6	.62(3;.20)	1.77(3;.76)	3.47(2;.79)	3.82(2;1.29)	1.21(1;-)

Table A2 (cont'd.).

Treatment (g m-2) N	P	K	Days After Planting 35	63	81	92	108
23.4	0	0	.34(4;.02)	.36(3;.04)	-(-)	-(-)	-(-)
23.4	0	7.8	.38(5;.04)	.34(5;.02)	.31(3;.02)	.30(1;-)	-(-)
23.4	0	23.4	.38(5;.03)	.33(4;.02)	.31(3;.02)	.27(3;.00)	-(-)
23.4	0	41.6	.36(4;.03)	.38(4;.07)	-(-)	.30(1;-)	1.18(1;-)
23.4	2.1	0	.36(4;.02)	.54(5;.11)	.85(5;.36)	.85(5;.19)	1.03(4;.12)
23.4	2.1	7.8	.34(4;.01)	.42(3;.07)	.60(2;.01)	.42(2;.04)	-(-)
23.4	2.1	23.4	.42(6;.06)	.52(6;.11)	.57(6;.13)	.60(5;.16)	.69(4;.18)
23.4	2.1	41.6	.38(5;.02)	.40(4;.04)	.45(5;.07)	.31(4;.03)	.58(1;-)
23.4	6.2	0	.48(6;.04)	2.04(6;.45)	3.15(5;.76)	3.78(5;.42)	3.75(3;.57)
23.4	6.2	7.8	.53(5;.03)	1.80(5;.43)	4.39(5;.75)	5.95(5;1.12)	6.61(4;.22)
23.4	6.2	23.4	.60(5;.09)	1.90(5;.81)	4.60(5;1.82)	6.11(5;2.30)	6.36(4;2.43)
23.4	6.2	41.6	.49(5;.06)	1.40(5;.43)	3.00(2;.85)	3.83(3;.34)	3.15(2;1.18)
23.4	12.5	0	1.23(5;.56)	3.06(5;.49)	6.39(5;1.29)	6.85(5;1.44)	9.10(4;2.57)
23.4	12.5	7.8	.54(4;.11)	2.24(4;.36)	5.14(4;.91)	7.14(4;1.60)	5.83(4;2.21)
23.4	12.5	23.4	.45(4;.03)	1.68(2;.20)	3.48(4;.66)	4.28(4;2.00)	6.21(5;3.30)
23.4	12.5	41.6	.58(5;.05)	3.05(3;.44)	6.04(4;1.10)	7.39(4;1.43)	6.18(5;1.55)
46.8	0	0	.36(5;.01)	.47(1;-)	.66(2;.34)	.33(1;-)	-(-)
46.8	0	7.8	.36(5;.03)	.33(5;.03)	.28(1;-)	.32(1;-)	-(-)
46.8	0	23.4	.31(4;.02)	.39(5;.07)	-(-)	-(-)	-(-)
46.8	0	41.6	.34(5;.02)	.33(5;.01)	.31(2;.01)	-(-)	-(-)
46.8	2.1	0	.39(5;.03)	.48(4;.04)	.47(3;.15)	.43(2;.13)	.30(1;-)
46.8	2.1	7.8	.45(5;.07)	.37(3;.03)	.35(1;-)	-(-)	-(-)
46.8	2.1	23.4	.34(5;.02)	.34(5;.02)	.40(2;.12)	-(-)	-(-)
46.8	2.1	41.6	.34(4;.03)	.37(4;.05)	.52(2;.19)	.46(3;.15)	.58(2;.19)
46.8	6.2	0	.54(5;.04)	.87(3;.09)	2.20(3;.70)	1.84(3;.17)	1.85(2;.17)
46.8	6.2	7.8	.58(4;.13)	1.65(5;1.04)	3.62(3;3.00)	8,88(2;7.15)	8.14(2;6.73)
46.8	6.2	23.4	.44(5;.04)	.90(3;.35)	.96(3;.36)	1.71(2;.07)	1.76(1;-)
46.8	6.2	41.6	.36(3;.04)	.40(2;.11)	.72(1;-)	-(-)	1.31(1;-)
46.8	12.5	0	.44(6;.06)	1.92(4;.26)	3.62(3;.29)	3.13(4;.51)	2.45(3;.97)
46.8	12.5	7.8	.75(4;.17)	2.24(4;.31)	3.83(4;.56)	4.31(4;.74)	3.72(2;1.86)
46.8	12.5	23.4	.59(4;.13)	1.54(5;.76)	1.34(5;.67)	2.67(4;.99)	2.00(3;.63)
46.8	12.5	41.6	.52(5;.06)	1.92(5;.48)	2.95(4;1.28)	3.71(3;1.32)	5.59(2;.02)

Table A3. 1981 T. angustifolia aboveground dry weight (g m-2) estimates from regressions. Numbers in parentheses represent number of replicates; standard error of the mean; average number of shoots per m2; and standard error of the mean for the number of shoots, respectively.

Treatment (g m-2)			Days After Planting		
N	P	K	22	58	96
0	0	0	9.8(5;2.2;8.0;0)	25.5(4;3.7;8.0;0)	34.9(4;3.6;18.0;2.0)
0	0	7.8	11.5(5;2.3;8.0;0)	22.9(5;3.3;9.6;1.6)	27.7(4;4.4;14.0;2.0)
0	0	23.4	14.4(5;2.2;8.0;0)	25.1(5;4.1;9.6;1.6)	34.8(4;8.3;14.0;2.0)
0	0	41.6	13.5(5;3.2;8.0;0)	27.1(4;1.3;8.0;0)	31.1(4;4.6;14.0;2.0)
0	2.1	0	10.5(5;2.5;8.0;0)	19.6(4;3.9;8.0;0)	27.4(3;7.5;10.7;2.7)
0	2.1	7.8	9.6(5;1.7;8.0;0)	12.9(5;2.6;8.0;0)	23.8(4;2.9;8.0;0)
0	2.1	23.4	11.2(5;1.4;8;0)	21.0(5;2.9;11.2;2.0)	24.7(4;3.7;12.0;2.3)
0	2.1	41.6	12.8(4;0.4;8.0;0)	20.4(4;2.1;8.0;0)	26.8(3;2.7;10.7;2.7)
0	6.2	0	9.5(5;1.1;8.0;0)	14.7(5;0.5;8.0;0)	22.4(4;1.9;12.0;2.3)
0	6.2	7.8	11.4(5;1.2;8.0;0)	19.8(5;3.4;8.0;0)	29.4(4;4.8;8.0;0)
0	6.2	23.4	11.1(5;2.4;8.0;0)	16.4(5;3.9;9.6;1.6)	22.4(4;5.7;10.0;2.0)
0	6.2	41.6	7.3(6;1.1;8.0;0)	12.2(6;1.8;8.0;0)	18.7(5;0.5;9.6;1.6)
0	12.5	0	9.5(4;0.5;8.0;0)	17.3(4;1.4;8.0;0)	22.3(3;2.2;10.7;2.7)
0	12.5	7.8	9.7(5;1.5;8.0;0)	16.6(5;3.4;9.6;1.6)	25.4(3;2.4;13.3;2.7)
0	12.5	23.4	11.1(5;1.4;8.0;0)	19.4(5;1.4;8.0;0)	24.8(4;1.8;8.0;0)
0	12.5	41.6	9.1(5;3.5;8.0;0)	17.7(5;5.3;8.0;0)	19.2(4;4.2;8.0;0)
7.8	0	0	11.6(5;2.1;8.0;0)	75.4(4;16.7;20;4.0)	195(3;32.8;34.7;2.7)
7.8	0	7.8	13.6(5;0.9;8.0;0)	82.2(5;13.2;17.6;4.7)	221(4;14.2;40.0;3.3)
7.8	0	23.4	13.2(5;1.9;8.0;0)	76.4(5;21.3;24.0;2.5)	174(4;52.5;34.0;3.8)
7.8	0	41.6	9.2(5;2.1;8.0;0)	47.2(4;4.6;20.0;4.0)	130(4;3.6;32.0;0)
7.8	2.1	0	10.7(5;1.6;8.0;0)	72.9(5;17.4;14.4;3.9)	142(4;55.2;20.0;5.2)
7.8	2.1	7.8	10.0(5;2.8;8.0;0)	121(5;21.7;28.8;5.4)	244(4;40.9;46.0;6.0)
7.8	2.1	23.4	7.9(5;1.5;8.0;0)	119(4;29.1;22.0;5.0)	273(3;14.8;48.0;4.6)
7.8	2.1	41.6	10.4(5;1.6;8.0;0)	108(5;19.7;25.6;5.3)	244(4;12.4;48.0;4.6)
7.8	6.2	0	10.9(5;2.3;8.0;0)	108(5;13.9;24.0;5.7)	215(4;8.8;40.0;0)
7.8	6.2	7.8	10.2(5;1.1;8.0;0)	139(5;13.8;33.6;4.7)	214(4;9.2;42.0;2.0)
7.8	6.2	23.4	8.5(6;2.1;8.0;0)	130(5;18.8;30.4;3.9)	317(4;108;56.0;11.3)
7.8	6.2	41.6	8.5(5;1.4;8.0;0)	102(5;7.9;32.0;2.5)	222(4;6.8;46.0;3.8)
7.8	12.5	0	13.1(5;2.5;8.0;0)	101(5;15.8;24.0;5.7)	215(4;14.5;46.0;3.8)
7.8	12.5	7.8	13.8(5;3.0;8.0;0)	138(5;13.8;32;3.6)0	240(4;4.5;48.0;3.3)
7.8	12.5	23.4	9.5(5;2.6;8.0;0)	132(5;18.0;32.0;4.4)	238(4;21.1;50.0;7.6)
7.8	12.5	41.6	13.7(5;1.9;8.0;0)	132(5;6.9;35.2;4.1)	206(4;27.1;42.0;7.6)

Table A3 (cont'd.).

Treatment (g m-2) N	P	K	Days After Planting 22	58	96
23.4	0	0	10.3(5;3.1;8.0;0)	46.5(5;11.2;20.8;6.0)	173(4;18.8;32.0;3.3)
23.4	0	7.8	8.8(5;1.7;8.0;0)	71.5(5;13.7;19.2;4.8)	270(4;63.3;44.0;8.3)
23.4	0	23.4	5.8(5;0.9;8.0;0)	45.6(4;13.4;16.0;3.3)	178(3;85.4;29.3;11.6)
23.4	0	41.6	15.0(5;3.0;8.0;0)	117(4;3.4;32.0;4.6)	373(3;56.6;58.7;9.6)
23.4	2.1	0	9.2(5;1.3;8.0;0)	75.7(5;7.5;19.2;3.2)	298(4;34.5;48.0;7.3)
23.4	2.1	7.8	6.5(5;1.4;8.0;0)	94.2(4;17.8;22.0;6.8)	565(4;30.1;76.0;6.9)
23.4	2.1	23.4	11.1(5;1.3;8.0;0)	141(5;16.5;20.8;4.1)	637(4;46.0;86.0;5.0)
23.4	2.1	41.6	8.9(5;2.2;8.0;0)	61.4(5;24.5;17.6;5.9)	482(4;36.9;68.0;10.1)
23.4	6.2	0	9.5(6;2.0;8.0;0)	132(5;12.9;28.8;2.0)	528(4;15.5;66.0;3.8)
23.4	6.2	7.8	7.0(5;1.2;8.0;0)	92.4(5;20.5;22.4;3.9)	505(4;70.3;74.0;8.9)
23.4	6.2	23.4	8.7(4;1.4;8.0;0)	105(4;38.1;26.0;3.8)	469(3;129;74.7;14.1)
23.4	6.2	41.6	10.9(5;1.2;8.0;0)	123(5;20.5;33.6;3.0)	494(4;119;80.0;13.5)
23.4	12.5	0	7.5(5;1.2;8.0;0)	89.9(5;25.5;20.8;3.2)	481(4;69.1;62.0;6.0)
23.4	12.5	7.8	4.4(5;0.6;8.0;0)	69.4(4;12.8;20.0;5.2)	459(3;38.5;69.3;7.1)
23.4	12.5	23.4	11.6(5;2.1;8.0;0)	158(5;27.5;30.4;3.0)	619(4;15.4;82.0;3.8)
23.4	12.5	41.6	7.5(4;1.6;8.0;0)	82.7(4;16.8;22.0;6.0)	640(3;42.4;77.3;7.1)
46.8	0	0	6.2(5;1.2;8.0;0)	41.7(4;1.7;12.0;2.3)	165(4;39.9;36.0;5.2)
46.8	0	7.8	4.8(5;1.4;8.0;0)	26.2(4;7.2;12.0;4.0)	131(3;51.7;29.3;7.1)
46.8	0	23.4	7.0(5;2.0;8.0;0)	40.2(3;21.7;18.7;5.3)	121(2;44.3;28.0;12.0)
46.8	0	41.6	6.7(5;1.8;8.0;0)	30.8(4;10.5;8.0;0)	237(2;92.2;36.0;12.0)
46.8	2.1	0	9.0(5;1.5;8.0;0)	77.9(5;9.3;19.2;3.2)	310(4;52.1;50.0;6.8)
46.8	2.1	7.8	8.9(5;1.9;8.0;0)	81.0(5;21.9;22.4;3.4)	418(4;62.7;62.0;7.6)
46.8	2.1	23.4	8.6(4;4.3;8.0;0)	80.9(3;57.5;16.0;8.0)	502(2;238;68.0;36.0)
46.8	2.1	41.6	5.8(5;0.8;8.0;0)	62.9(4;15.7;16.0;3.3)	406(3;121;48.0;12.2)
46.8	6.2	0	6.3(5;1.3;8.0;0)	70.8(5;21.9;22.4;5.3)	403(4;87.3;66.0;14.4)
46.8	6.2	7.8	6.5(5;1.8;8.0;0)	141(4;55.6;22.0;8.2)	646(3;41.9;80.0;8.0)
46.8	6.2	23.4	4.3(5;1.1;8.0;0)	48.6(5;15.6;20.8;5.4)	456(4;124;62.0;14.4)
46.8	6.2	41.6	8.0(5;2.3;8.0;0)	69.7(4;21.6;22.0;6.0)	525(3;109;72.0;25.7)
46.8	12.5	0	8.1(5;4.2;8.0;0)	99.9(3;50.6;24.0;9.2)	479(1;-;96.0;-)
46.8	12.5	7.8	9.7(5;2.1;8.0;0)	121(5;35.7;25.6;5.9)	604(4;51.9;86.0;10.0)
46.8	12.5	23.4	6.4(5;2.9;8.0;0)	83.5(3;55.7;18.7;10.7)	574(2;329;80.0;48.0)
46.8	12.5	41.6	6.8(5;1.6;8.0;0)	91.5(4;5.8;24.0;3.3)	805(3;13.3;96.0;12.2)

Table A4. 1981 T. latifolia aboveground dry weight (g m-2) estimates from regressions. Numbers in parentheses represent number of replicates; standard error of the mean; average number of shoots per m2; and standard error of the mean for the number of shoots, respectively.

Treatment (g m-2) N	P	K	Days After Planting 22	58	96
0	0	0	26.3(5;5.8;8.0;0)	37.1(5;4.1;11.2;2.0)	51.1(4;3.9;12.0;2.3)
0	0	7.8	21.1(5;5.9;8.0;0)	56.2(5;14.3;9.6;1.6)	65.1(4;21.4;12.0;2.3)
0	0	23.4	24.3(5;4.6;8.0;0)	40.1(5;14.3;9.6;1.6)	79.3(4;11.9;12.0;2.3)
0	0	41.6	21.6(5;4.4;8.0;0)	52.6(5;9.7;8.0;0)	64.2(4;15.3;14.0;2.0)
0	2.1	0	19.5(5;3.7;9.6;1.6)	44.9(5;8.6;9.6;1.6)	53.4(4;9.2;10.0;2.0)
0	2.1	7.8	28.6(5;3.2;8.0;0)	54.1(5;12.2;8.0;0)	53.6(4;4.7;12.0;2.3)
0	2.1	23.4	25.8(5;5.1;12.8;3.2)	71.3(5;10.5;11.2;2.0)	91.6(4;15.0;16.0;3.3)
0	2.1	41.6	28.4(5;2.1;8.0;0)	66.5(4;29.4;8.0;0)	69.8(3;33.9;8.0;0)
0	6.2	0	32.5(5;8.0;8.0;0)	43.6(5;8.3;16.0;4.4)	59.8(4;11.4;14.0;2.0)
0	6.2	7.8	19.6(5;2.2;8.0;0)	45.4(4;15.3;8.0;0)	58.8(3;15.0;13.3;2.7)
0	6.2	23.4	17.8(5;2.9;8.0;0)	38.1(4;8.0;14.0;6.0)	42.0(4;9.2;14.0;3.8)
0	6.2	41.6	38.6(5;9.0;8.0;0)	60.6(5;6.7;9.6;1.6)	72.9(4;10.6;10.0;2.0)
0	12.5	0	21.3(6;5.4;8.0;0)	56.9(4;15.7;8.0;0)	70.0(3;12.1;8.0;0)
0	12.5	7.8	29.8(6;4.0;8.0;0)	68.9(6;18.1;8.0;0)	59.7(5;9.6;9.6;1.6)
0	12.5	23.4	20.5(5;3.7;8.0;0)	50.0(3;13.4;8.0;0)	29.1(2;19.7;8.0;0)
0	12.5	41.6	23.7(5;7.3;8.0;0)	37.7(5;8.1;9.6;1.6)	62.1(4;9.3;12.0;2.3)
7.8	0	0	23.9(5;6.5;8.0;0)	112(5;30.5;11.2;3.2)	273(4;20.4;22.0;5.0)
7.8	0	7.8	21.4(5;5.8;8.0;0)	154(5;37.7;12.8;3.2)	314(4;27.1;26.0;6.0)
7.8	0	23.4	16.5(5;2.8;8.0;0)	125(5;18.2;8.0;C)	199(4;14.3;18.0;2.0)
7.8	0	41.6	15.9(5;3.9;8.0;0)	107(5;25.8;14.4;3.0)	283(4;17.3;22.0;6.0)
7.8	2.1	0	22.6(5;3.2;8.0;0)	161(5;42.1;14.4;1.6)	293(4;48.3;20.0;2.3)
7.8	2.1	7.8	12.6(5;2.3;8.0;0)	187(5;55.3;14.4;4.7)	320(4;20.3;22.0;2.0)
7.8	2.1	23.4	25.7(5;4.7;8.0;0)	211(5;48.6;20.8;3.2)	326(4;28.1;26.0;3.8)
7.8	2.1	41.6	23.3(6;7.0;8.0;0)	172(6;52.8;20.0;4.5)	299(5;57.6;30.4;1.6)
7.8	6.2	0	17.4(5;4.1;8.0;0)	120(5;34.8;9.6;1.6)	229(4;40.4;24.0;4.6)
7.8	6.2	7.8	10.6(5;2.3;8.0;0)	178(4;43.8;12.0;4.0)	290(3;47.9;26.7;5.3)
7.8	6.2	23.4	24.3(5;6.6;8.0;0)	187(5;37.6;14.4;4.7)	305(4;75.6;28.0;5.2)
7.8	6.2	41.6	24.6(4;3.9;8.0;0)	173(4;42.9;18.0;6.0)	293(3;75.3;34.7;7.1)
7.8	12.5	0	25.9(5;4.3;8.0;0)	130(5;39.4;14.4;4.7)	263(4;53.6;30.0;6.0)
7.8	12.5	7.8	24.1(5;7.5;8.0;0)	138(5;31.3;17.6;3.9)	303(4;20.4;24.0;3.3)
7.8	12.5	23.4	31.4(5;8.7;8.0;0)	111(5;21.3;14.4;3.0)	268(4;53.2;26.0;3.8)
7.8	12.5	41.6	14.1(4;1.8;8.0;0)	135(4;28.6;14.0;2.0)	321(3;31.2;24.0;0)

Table A4 (cont'd.).

Treatment (g m) N	P	K	Days After Planting 22	58	96
23.4	0	0	16.2(5;5.1;1.7;0)	96.8(5;28.9;12.8;3.2)	233(4;54.8;16.0;3.3)
23.4	0	7.8	19.4(4;1.8;8.0;0)	64.9(4;29.9;10.0;2.0)	174(3;17.8;16.0;0)
23.4	0	23.4	13.7(5;2.5;8.0;0)	86.4(4;15.1;8.0;0)	301(3;50.8;21.3;2.7)
23.4	0	41.6	17.2(5;4.4;8.0;0)	87.8(5;42.9;9.6;1.6)	259(4;48.3;18.0;3.8)
23.4	2.1	0	17.4(5;3.8;8.0;0)	150(5;40.6;11.2;2.0)	380(4;95.7;30.0;2.0)
23.4	2.1	7.8	25.4(5;8.2;8.0;0)	212(5;60.7;16.0;2.5)	664(3;93.2;29.3;2.7)
23.4	2.1	23.4	19.2(5;5.4;8.0;0)	237(5;56.2;16.0;4.4)	704(4;72.6;42.0;8.9)
23.4	2.1	41.6	18.0(5;3.2;8.0;0)	148(5;40.9;8.0;0)	655(4;117;32.0;3.3)
23.4	6.2	0	12.4(5;4.1;8.0;0)	95.1(3;9.0;18.7;5.3)	559(2;19.9;32.0;0)
23.4	6.2	7.8	11.9(4;4.9;8.0;0)	70.0(3;4.3;10.7;2.7)	191(2;141;20.0;12.0)
23.4	6.2	23.4	22.8(5;7.6;8.0;0)	134(4;25.8;18.0;6.0)	575(3;149;37.3;2.7)
23.4	6.2	41.6	16.2(5;3.5;8.0;0)	250(5;46.9;14.4;3.0)	863(4;70.2;38.0;2.0)
23.4	12.5	0	14.1(5;4.7;8.0;0)	170(5;37.2;12.8;4.8)	640(4;52.9;44.0;7.7)
23.4	12.5	7.8	16.3(5;2.7;8.0;0)	154(4;41.7;12.0;2.3)	731(3;48.2;42.7;2.7)
23.4	12.5	23.4	9.6(5;2.1;8.0;0)	184(3;106;8.0;0)	651(3;257;26.7;9.6)
23.4	12.5	41.6	14.0(5;3.2;8.0;0)	218(4;63.3;18.0;3.8)	926(3;124;42.7;11.6)
46.8	0	0	16.0(5;3.2;8.0;0)	62.1(5;16.3;8.0;0)	275(3;39.818.7;2.7)
46.8	0	7.8	12.9(5;3.9;8.0;0)	41.2(4;6.7;8.0;0)	164(3;36.2;13.3;2.7)
46.8	0	23.4	17.8(5;3.4;8.0;0)	54.0(5;10.1;9.6;1.6)	196(4;28.4;16.0;0)
46.8	0	41.6	20.9(5;5.7;8.0;0)	84.3(5;31.4;12.8;3.2)	193(4;78.3;20.0;4.0)
46.8	2.1	0	9.5(4;2.9;8.0;0)	41.0(3;18.9;8.0;0)	327(3;84.6;18.7;5.3)
46.8	2.1	7.8	22.1(5;6.2,8.0;0)	147(5;35.0;12.8;3.2)	575(4;67.6;26.0;2.0)
46.8	2.1	23.4	23.2(5;10.8;8.0;0)	139(4;57.5;12.0;2.3)	503(3;241;26.7;9.7)
46.8	2.1	41.6	11.6(5;1.9;8.0;0)	46.1(5;14.1;11.2;2.0)	404(4;113;28.0;4.0)
46.8	6.2	0	13.7(5;5.8;8.0;0)	79.1(4;27.5;10.0;2.0)	545(3;199;29.3;7.1)
46.8	6.2	7.8	11.0(5;3.5;8.0;0)	121(3;49.8;10.7;2.7)	703(3;107;32.0;8.0)
46.8	6.2	23.4	11.1(6;2.0;8.0;0)	97.9(4;38.8;14.0;3.8)	817(3;220;40.0;8.0)
46.8	6.2	41.6	11.8(5;2.5;8.0;0)	88.4(3;29.6;16.0;4.6)	414(2;340;16.0;0)
46.8	12.5	0	13.7(5;6.3;8.0;0)	84.1(2;56.7;20.0;12.0)	593(2;164;36.0;12.0)
46.8	12.5	7.8	16.5(4;2.2;8.0;0)	94.4(4;15.1;12.0;2.3)	593(3;12.9;26.7;5.3)
46.8	12.5	23.4	8.0(5;1.6;8.0;0)	69.3(3;36.8;10.7;2.7)	869(2;420;36.0;12.0)
46.8	12.5	41.6	13.4(8;3.8;8.0;0)	70.7(3;21.2;10.7;2.7)	790(3;118;40.0;8.0)

Table A5. 1982 P. australis aboveground dry weight (g m-2) estimates from regressions. Numbers in parentheses represent number of replicates; standard errors of the means; average number of shoots per m2; and standard error of the mean for the number of shoots, respectively.

Treatment (g m-2) N	P	Days After Planting 30	55	80
0	25.0	3.2(5;0.5;11.2;1.9)	2.7(5;0.4;25.6;3.0)	26.1(5;9.0;30.4;4.7)
7.8	25.0	3.4(5;0.3;12.8;3.2)	9.7(5;4.5;28.8;7.4)	106(5;32.8;70.4;19.5)
23.4	25.0	3.8(5;0.4;11.2;2.0)	11.5(5;2.5;44.8;13.0)	272(5;73.6;146;28.5)
46.8	12.5	4.8(5;0.6;19.2;4.1)	14.3(5;2.4;54.4;4.7)	428(5;102;163;12.0)
46.8	25.0	3.5(5;0.3;12.8;4.8)	16.0(5;6.5;40.0;6.2)	386(5;16.2;128;12.1)
93.6	0	4.2(5;0.7;20.8;4.1)	6.9(5;1.9;30.4;6.9)	102(4;43.9;64.0;8.0)
93.6	2.1	4.2(4;0.3;12.0;2.3)	15.6(4;5.1;28.0;8.3)	184(4;28.1;86.0;6.)
93.6	6.3	4.0(4;0.5;16.0;4.6)	17.5(4;3.3;54.0;14.4)	346(6;55.6;148;20.8)
93.6	12.5	4.0(5;0.9;12.8;4.8)	10.0(5;4.0;43.2;10.3)	338(5;35.1;113;23.9)
93.6	25.0	3.8(5;0.4;17.6;4.9)	10.2(5;1.8;46.4;7.8)	329(5;3.2;158;24.1)

Table A6. 1982 _T. angustifolia_ aboveground dry weight (g m-2) estimates from regressions. Numbers in parentheses represent number of replicates; standard errors of the means; average number of shoots per m2; and standard error of the mean for the number of shoots, respectively.

Treatment (g m-2)		Days After Planting		
N	P	30	55	80
0	25.0	28.1(5;5.6;8.0;0)	13.6(5;1.4;14.4;1.6)	38.1(5;3.2;17.6;1.6)
7.8	25.0	27.8(5;7.3;8.0;0)	83.7(5;9.9;36.8;4.1)	226(5;22.5;41.6;3.9)
23.4	25.0	26.3(5;6.6;8.0;0)	73.5(5;31.3;30.4;6.9)	488(5;72.4;70.4;11.1)
46.8	12.5	23.7(5;8.5;9.6;1.6)	47.8(5;22.7;30.4;9.3)	438(5;105;76.8;21.4)
46.8	25.0	26.1(5;4.7;8.0;0)	54.1(5;5.9;28.8;5.4)	615(5;78.7;92.8;11.5)
93.6	0	14.6(5;3.2;8.0;0)	16.8(5;4.6;14.4;3.0)	119(5;31.8;25.6;3.0)
93.6	2.1	11.7(5;3.7;8.0;0)	28.2(4;14.2;18.0;6.0)	144(4;56.9;34.0;10.5)
93.6	6.3	11.6(5;4.6;8.0;0)	10.2(4;3.7;12.0;4.0)	78.8(4;44.1;24.0;8.6)
93.6	12.5	4.5(5;0.5;8.0;0)	8.4(5;3.2;8.0;0)	87.9(4;18.9;26.0;2.0)
93.6	25.0	14.4(4;2.0;8.0;0)	41.8(3;19.6;24.0;4.6)	263(3;11.6;53.3;5.3)

Table A7. 1982 T. latifolia aboveground dry weight (g m-2) estimates from regressions. Numbers in parentheses represent number of replicates; standard errors of the means; average number of shoots per m2; and standard error of the mean for the number of shoots, respectively.

Treatment (g m-2)		Days After Planting		
N	P	30	55	80
0	25.0	21.6(5;3.1;8.0;0)	8.1(4;2.0;14.0;3.8)	32.7(4;12.7;10.0;2.0)
7.8	25.0	39.4(5;39.4;11.2;3.2)	42.9(5;13.3;19.2;5.4)	257(5;55.7;25.6;5.9)
23.4	25.0	17.0(5;7.4;8.0;0)	23.0(4;16.6;14.0;3.8)	523(3;151;29.3;2.7)
46.8	12.5	16.8(5;4.8;9.6;1.6)	49.0(5;30.2;11.2;3.2)	457(5;155;25.6;6.4)
46.8	25.0	28.6(5;9.4;8.0;0)	84.1(4;40.6;16.0;5.7)	747(4;111;40.0;9.8)
93.6	0	19.3(5;4.0;9.6;1.6)	9.3(4;2.6;8.0;0)	84.4(4;20.4;14.0;3.8)
93.6	2.1	14.4(5;5.6;8.0;0)	34.2(2;14.9;20.0;4.0)	329(2;190;32.0;8.0)
93.6	6.3	11.2(5;1.5;8.0;0)	6.3(3;4.7;8.0;0)	43.5(2;19.7;12.0;4.0)
93.6	12.5	7.0(5;2.0;9.6;1.6)	4.9(4;3.7;8.0;0)	131(4;103;12.0;4.0)
93.6	25.0	16.7(5;8.0;8.0;0)	28.8(4;16.7;12.0;2.3)	251(4;148;22.0;6.8)

Table A8. 1982 S. eurycarpum aboveground dry weight (g m-2) estimates from regressions. Numbers in parentheses represent number of replicates; standard errors of the means; average number of shoots per m2; and standard error of the mean for the number of shoots, respectively.

Treatment (g m-2) N	P	Days After Planting 30	55	80
0	0	5.6(7;0.7;8.0;0)	2.4(7;0.7;16.0;3.5)	9.7(7;4.1;19.4;4.9)
0	2.1	6.8(7;0.7;8.0;0)	2.4(7;0.2;14.9;2.1)	18.9(8;10.9;25.0;10.2)
0	6.3	7.0(7;1.6;8.0;0)	3.8(7;0.9;19.4;1.6)	8.7(7;0.8;24.0;4.3)
0	12.5	6.3(7;1.3;10.3;2.3)	2.1(7;0.4;18.3;3.4)	7.0(7;1.3;19.4;2.4)
0	25.0	7.4(7;1.7;8.0;0)	3.6(7;1.0;16.0;2.5)	7.2(7;2.1;18.3;2.3)
7.8	0	14.6(7;2.4;9.1;1.1)	13.1(7;5.5;25.1;2.1)	50.1(7;11.6;28.6;3.8)
7.8	2.1	15.4(6;1.8;13.3;2.7)	25.5(7;2.1;52.6;3.0)	127(6;11.3;77.3;5.7)
7.8	6.3	23.1(7;3.0;21.7;2.9)	41.1(7;10.9;58.3;5.7)	99.5(6;5.4;80;6.5)
7.8	12.5	16.9(7;2.0;17.1;2.1)	53.1(7;12.8;44.6;3.4)	82.2(7;6.6;73.1;4.1)
7.8	25.0	18.1(7;3.5;16.0;3.5)	30.8(7;6.6;49.1;3.2)	87.6(7;9.4;74.3;3.8)
23.4	0	8.3(7;1.8;10.3;1.5)	5.3(7;1.0;22.9;3.7)	40.5(7;10.5;32.0;7.4)
23.4	2.1	6.5(6;2.2;10.7;1.7)	14.7(6;5.9;33.3;6.0)	158(7;22.5;78.9;7.3)
23.4	6.3	13.3(7;1.4;12.6;2.4)	34.7(7;7.0;48.0;4.6)	281(7;11.2;107;6.5)
23.4	12.5	13.4(7;4.6;9.1;1.1)	49.4(7;16.5;42.3;6.9)	253(7;13.9;103;6.9)
23.4	25.0	20.1(7;2.6;17.1;3.2)	47.8(7;18.3;65.1;6.6)	216(8;30.3;113;4.4)
46.8	0	9.1(5;4.4;8.0;0)	6.9(7;2.6;26.3;4.5)	30.8(7;6.8;29.7;3.8)
46.8	2.1	7.4(6;2.7;10.7;1.7)	12.4(6;3.9;32.0;5.1)	130(6;13.9;73.3;3.2)
46.8	6.3	6.4(6;0.8;9.3;1.3)	14.8(6;6.4;30.7;5.6)	217(6;41.4;92.0;14.1)
46.8	12.5	5.4(7;1.4;8.0;0)	19.4(6;7.2;36;6.1)	341(6;39.3;119;11)
46.8	25.0	6.0(7;1.1;9.1;1.1)	22.5(7;7.6;40.0;7.0)	362(7;36.4;122;13.4)
93.6	0	1.9(2;0.2;8.0;0)	0.0(1;-;8.0;-)	1.6(2;1.1;8.0;0)
93.6	2.1	0.7(1;-;8.0;-)	- (-)	- (-)
93.6	6.3	2.0(4;0.7;8.0;0)	1.3(2;1.2;12.0;4.0)	28.1(3;26.0;18.7;10.7)
93.6	12.5	1.9(2;1.6;8.0;0)	0.1(1;-;8.0;-)	3.0(1;-;8.0;-)
93.6	25.0	2.6(1;-;8.0;-)	0.6(2;0.5;12.0;8.0;0)	47.1(1;-;32.0;-)