THE POTENTIAL OF CATTAILS AS AN ENERGY SOURCE

Final Report to the

Minnesota Energy Agency

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Final Report: The Potential of Cattails as an Energy Source

This report describes the research accomplished under a project sponsored by the Minnesota Energy Agency to determine the feasibility of growing cat ails as an energy crop. The report is divided into six sections:

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Acknowledgements

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I. Productivity in Natural Stands

Introduction

The initial estimates of the productive potential of *Typha* spp. in Minnesota were based on studies of the productivity of natural stands. Bray *et al*. (1959) reported that shoot biomass reached 1680 g/m^2 at Cedar Creek Natural History Area, Minnesota. The maximum value reported for the north central region of the United States is 1852 g/m^2 at Theresa Marsh, Wisconsin (Klopatek and Stearns, 1978) while the highest value in the United States (2252 g/m^2) comes from Boyd and Hess's (1971) survey of *Typha latifolia* stands in the southeast. Czechoslovakian *Typha* stands have been reported to be even more productive with 3910 g/m^2 reported for *Typha angustifolia* (Dykyjova, 1971; Dykyjova *et al*., 1971).

There is little available data (Bray *et al*., 1959; Bernard and Bernard, 1973) on the range of *Typha* shoot biomass productivity in Minnesota. Not only would it be useful to have an idea of the variation in *Typha* biomass production to assess its potential as an energy crop, but knowledge of the factors associated with high productivity should suggest possible management methods to increase yields. Nutrient availability has been suggested as one of the most important factors determining natural productivity (Boyd, 1971; Boyd and Hess, 1971) and for this reason tissue element concentration has been compared with shoot biomass in our study. In addition, element concentrations were monitored throughout the growing season in different age leaves in order to provide background data for developing diagnostic sampling methods. Finally, since fertilizer additions have been shown to increase productivity of *Typha* plants grown in pots on a variety of soils (Boyd, 1971) and in artificial paddies (see seedling section), fertilizer was added to a natural stand to observe whether or not the same effect could be observed in a less controlled situation.

Methods

Sampling sites. Since our purpose was to survey the shoot biomass productivity of *Typha* in large stands, fifteen

Table 1. Shoot and environmental data for individual *Typha* stands.

Site	Species	g/m^2	density	symbol	H_2O depth	tissue concentrations % dry weight N	P	K	Ca	Mg	Na	ppm Fe	Mn	Cu	B
Agassiz National Wildlife Refuge (NWR)	H	1516	43	AG	47	1.25	.236	2.37	1.37	.318	.244	27.4	487	3.03	22.0
Carlos Avery Wildlife Management Area (WMA)	H	2052	45	CA	63	1.23	.232	1.15	1.00	.200	.278	44.3	297	1.17	16.9
Eagle Lake WMA	A	2114	67	EA	26	1.49	.267	2.42	1.24	.279	.332	35.5	478	2.88	23.1
Lac Qui Parle WMA	H	1851	66	LQ	32	1.45	.255	2.59	1.00	.337	.492	44.3	716	3.53	39.1
Mille Lacs WMA	L	--[1]	--	ML	--	1.14	.197	1.64	0.77	.230	.126	139.0	639	2.14	21.6
Moose Willow WMA	L	1094	41	MW	33	1.52	.307	2.30	1.30	.276	.393	58.0	657	1.61	50.5
Mud Goose WMA	-	583	18	MG	102	1.27	.188	2.44	1.15	.301	.358	180.8	569	1.10	39.1
Red Lake WMA	A	--[2]	--	RE	--	1.20	.231	1.31	1.26	.308	.517	33.8	414	1.42	31.2
Rice Lake WMA	L	534	27	RI	21	1.37	.312	2.22	0.94	.223	.100	62.1	371	1.22	19.1
Roseau WMA	H	924	50	RO	7	1.47	.220	1.09	1.49	.462	.336	27.2	145	0.91	26.7
Sherburne NWR	H	1602	65	SH	26	1.19	.224	1.77	1.08	.233	.754	67.0	245	2.36	27.3
Talcot Lake WMA N site	H	1032	39	TA-N	0	1.23	.192	1.37	1.25	.277	.353	44.0	626	3.92	18.2
Talcot Lake WMA S site	H	1523	61	TA-S	31	1.29	.246	2.25	1.14	.322	.353	55.7	632	4.37	16.6
Tamarac NWR	H	927	41	TM	41	1.32	.180	2.11	0.98	.407	.216	35.8	201	3.14	19.1
Walnut Lake WMA	A	1229	64	WA	57	1.33	.199	1.25	1.29	.335	.707	48.9	289	1.68	31.2
Whitewater WMA	-	--	--	WW	--	--	--	--	--	--	--	--	--	--	--

[1] Plants were too sparse to be sampled accurately by our methods, approximately 1 shoot/m^2.

[2] Standing crop not measured.

Table 1, continued

Site	Water Analysis ppm $NO_3^- + NO_2^-$	NH_4^+	$PO_4^{\equiv}$	TP*
Agassiz National Wildlife Refuge (NWR)	<0.05	<0.1	<0.01	.045
Carlos Avery Wildlife Management Area (WMA)	"	"	<0.01	.030
Eagle Lake WMA	"	"	0.01	.085
Lac Qui Parle WMA	"	0.250	0.17	.305
Mille Lacs WMA	"	0.1	<0.01	.020
Moose Willow WMA	"	<0.1	0.06	.135
Mud Goose WMA	"	0.1	<0.01	.055
Red Lake WMA	"	<0.1	0.25	.090
Rice Lake WMA	"	<0.1	0.05	.100
Roseau WMA	"	0.1	0.01	.160
Sherburne NWR	"	<0.1	0.01	.110
Talcot Lake WMA N site	"	<0.1	0.155	.225
Talcot Lake WMA S site	"	0.20	<0.01	<0.01
Tamarac NWR	"	<0.1	<0.01	.020
Walnut Lake WMA	6.6	<0.1	0.03	.025
Whitewater WMA	--	--	--	--

* total phosphorus

Figure 1. State and National Wildlife Areas sampled in 1978.

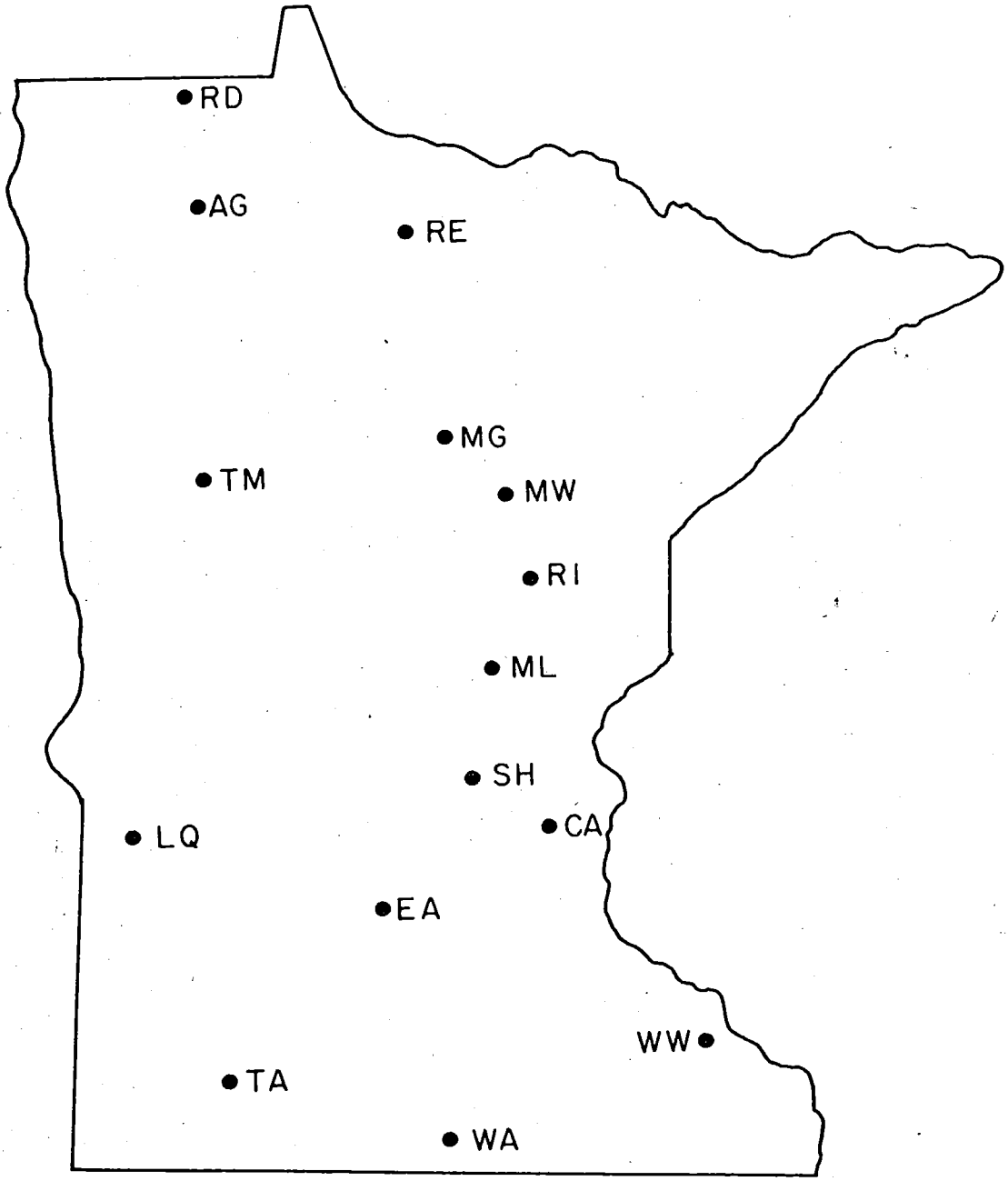
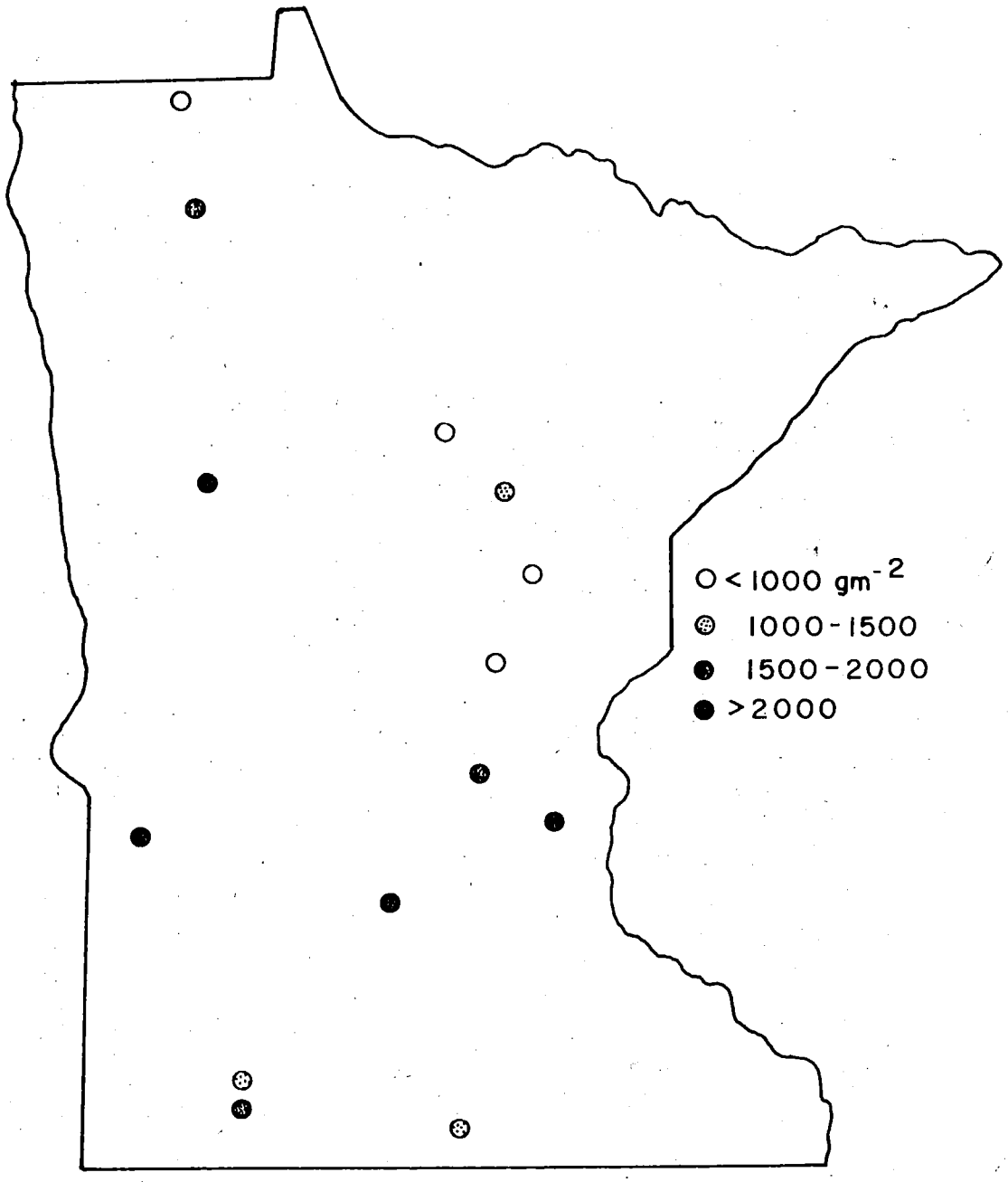

RD
AG
RE
MG
TM
MW
RI
ML
SH
CA
LQ
EA
WW
TA
WA

Figure 2. Shoot biomass for monospecific stands in Minnesota.


O < 1000 gm^{-2}
1000-1500
1500-2000
>2000

state and national wildlife areas (Figure 1, Table 1) were visited between July 20 and August 6, 1978. Management of parts of these lands for waterfowl often also results in large Typha marshes.

Sampling sites were mainly marshes (mostly vegetation and little open water) of 0.5 hectare or larger, although several stands bordered lakes. In one instance (Mud-Goose) the site was a stand in open water in a lake. Typha was estimated to account for more than 95% of the biomass at all sites except Rice Lake and Mille Lacs. Small floating aquatic plants such as Lemna spp. (duckweeds) and Riccia fluitans (aquatic liverworts) were sometimes present in plots but not collected. The term "monospecific" was used in describing these stands to emphasize their uniformity. Sampling occurred following pollen release. At the time of sampling anthers were still present on many spikes at northern locations but the pollen had been released. At southern sites few if any flowering stalks had flowers remaining.

Typha latifolia L., Typha angustifolia L. and a hybrid between those two, Typha x glauca Godr. (Smith, 1967) are found in Minnesota. Eight sample sites were dominated by plants that were clearly hybrid (Table 1). Typha angustifolia or T. latifolia occurred at six sites -- three sites with one species and three with the other. At the Mud-Goose site no inflorescences, which are needed for positive identification of the species, were present. However, the deep water in which they were growing suggested they were the hybrid (Harris and Marshall, 1963).

At Talcot Lake two sites on opposite sides of the access road were sampled. A single site was sampled at all other locations.

Shoot biomass. At each site the live shoots in five plots 1.25 m x 0.25 m were cut at the base and weighed. The dry weight to fresh weight ratio determined from plants taken for tissue element concentration was used to calculate dry weight from the total fresh weight for each plot.

Tissue element analysis. Three large sterile shoots were weighed, placed in paper bags, and allowed to air dry until return to the laboratory where they were dried at 60°C to constant weight. Two young leaf samples, consisting of the two inner exposed leaves from each of five plants, were also collected at each site and dried as described above. After grinding the samples, using a Wiley mill, one gram samples were ashed at 485-500°C. Analysis by inductively coupled plasma spectroscopy was performed by the Research Analytical Laboratory (RAL), Department of Soil Science, University of Minnesota. Analysis for nitrogen using the semi-microKjeldahl method was also performed by RAL.

Water analysis. Two water samples were collected at each site. Mercuric Chloride was added to each sample to form a 0.147 mM solution. Samples were analyzed for nitrate (including nitrate), ammonia, orthophosphate and total phosphate by RAL. Approximate pH was determined, using a set of narrow range pH papers (Duotest, Mackery, Nagel and Co.) with overlapping ranges.

Sampling methods for the determination of the relationship between leaf number and age, and tissue element concentration. Samples were taken from a study area in Carlos Avery Wildlife Management Area used for cutting experiments (Section II). On June 15, 1979 all the plants in a 2 m^2 area were marked with plastic tags. No new offshoots were produced in this area during the rest of the summer. Fifteen flowering shoots and fifteen sterile shoots were collected on June 15th and then at monthly intervals nine flowering and nine sterile shoots were collected from the same area. For each sampling date the leaves from each shoot were separated from one another. The two innermost (youngest) exposed leaves formed a sample, and the two leaves surrounding the leaves of the first sample formed the next sample, and so on. For flowering shoots the flowering stalk comprised the first sample. For each sampling date there were four to six samples

(depending on the number of leaves per shoot) of leaves of increasing age with three replicates of each sample. Preparations and analysis for tissue element concentration were performed as previously described.

Fertilizer additions to a natural stand. The greatest difficulty in adding fertilizer to a natural stand and observing whether or not it has an effect is finding a suitable control stand that is nearly identical to the experimental site. To solve this difficulty, a single isolated stand in a low area at Carlos Avery Wildlife Management Area was divided into two portions, each approximately 600 m^2, by aluminum slashing running north to south across the stand. On June 29, 1978 200 kg/ha nitrogen, 88 kg/ha phosphorus and 166 kg/ha potassium were added to one-half of the stand (the western portion).

Water samples analyzed for ammonia and orthophosphate were used to monitor whether or not the slashing provided an effective barrier to movement of dissolved nutrients. Movement was potentially possible under the barrier as the bottom of the marsh was uneven.

Prior to the addition of fertilizer, three whole shoots were sampled for tissue nutrient analysis. The shoots harvested from five 1.25 x 0.25 m quadrats showed that the shoot biomass of the two portions was similar prior to fertilization. At the end of the first growing season (September 14, 1978) and at the end of the second (September 14, 1979), ten 1.25 m x 0.25 m plots were sampled for shoot biomass, three shoots were selected for the determination of tissue element concentrations and two 0.5 m x 0.5 m quadrats were gathered for the maasurement of below ground biomass from each side of the stand. The material from below ground biomass plots was washed and dead rhizomes and shoot bases separated from living ones. Dead shoot bases and rhizomes were generally soft and were not white in the interior. The live shoot base rhizomes and attached roots were dried to constant weight at 60°C.

Results

Shoot standing crop and density. Shoot biomass for monospecific stands ranged from 583 to 2115 g/m^2 with an average value of 1371 g/m^2 (Figure 2, Tables 1, 2 and 3). Shoot density ranged from 17.9 to 67.2 shoots/m^2 with a mean of 50.0 shoots/m^2, and apparently represented the season's maximum density for most sites. Although shoot diameter and height were observed to vary within stands, all of the shoots appeared to be mature and no recent offshoots were observed with the exception of two sites. One of these sites, Whitewater, was not included in the analysis since the marsh had obviously been inundated by floods known to have occurred in that area earlier in the summer as evidenced by the silt deposit on much of the foliage. The Moose-Willow site also had young shoots though no effects of a major disturbance were evident. Shoot density was significantly correlated with shoot biomass (Table 4). Shoot density did not vary continuously with shoot dry weight. All but two stands either had a density of 39-45 or 61-67 shoots/m^2. These two clusters did not correspond to different species.

Tissue element concentrations. The nutrient with the largest correlation with shoot biomass was phosphorus (correlation coefficient (r) = .50; probability of data giving that coefficient by chance (p) = .05). If the Moose-Willow site, which is perhaps at a different stage of stand development or is disturbed, as suggested by the presence of young shoots late in the season, is deleted from the data, the relationship between tissue phosphorus concentration and shoot biomass is even stronger ($r = 0.84$, $p = .001$). The correlation coefficients of shoot biomass with the tissue concentrations of other elements are not substantially affected by this deletion (Table 4).

Comparison of young leaf with whole shoot samples. The average tissue concentrations of P, K, Mg, Fe, Na, Mn and Cu in whole shoots as compared to young leaves (Table 5) are highly correlated with $r = 0.78$ ($p = 0.001$). The relationship

Table 3. Summary of shoot and environmental data for Minnesota Typha stands.

	Shoot Dry Wt g/m^2	Density Shoots/ m^2	H_2O Depth, cm	% Dry Weight						ppm			
				N	P	K	Ca	Mg	Na	Fe	Mn	Cu	B
Mean, mono-specific stands[1]	1371	50.0	38.7	1.33	0.228	1.88	1.20	0.304	0.410	54.0	443	2.39	26.5
Means, mono-specific even-aged stands[2]	1395	50.8	39.3	1.31	0.221	1.84	1.19	0.306	0.412	53.7	423	2.46	24.5
Range, mono-specific stands[1]	583-2115*	17.9-67.2	0-102	1.19-1.52	.181-.307*	1.09-2.58	0.978-1.49	0.200-.407	.216-.754	27.2-181	145-716	0.91-4.37	16.7-50.5

[1] excludes Mille Lacs and Rice Lake

[2] excludes Mille Lacs, Rice Lake and Moose Willow.

*excluded sites have values outside of the range.

Table 4. Correlation coefficients for shoot density, water level, and tissue element concentrations with shoot biomass for all monospecific *Typha* spp. stands with even-aged shoots.

	Density	H_2O Depth	N	P	K	Ca	Mg	Na	Fe	Mn	Cu	B
Whole shoots monospecific stands	.684 .002*	-.165 .30	.054 .43	.500 .05	.101 .38	-.310 .16	-.428 .08	.089 .39	-.468 .06	.084 .40	.258 .21	-.057 .43
Monospecific even-aged shoots (Moose-Willow site omitted)	.673 .01	-.1809 .30	.170 .31	.846 .001	.1445 .33	-.2832 .20	-.460 .08	.087 .40	-.472 .07	.087 .40	.226 .252	.126 .36
Young leaves monospecific stands	---	---	---	.450 .08	.230 .25	-.085 .40	-.354 .14	-.170 .31	-.405 .11	.274 .21	.158 .32	-.391 .12

*significance

Table 5. Correlation coefficients for tissue element concentrations in whole plants versus young leaves in monospecific stands.

Element	Correlation Coefficient	Significance
N	.4732	.05
P	.785	.001
K	.856	.001
Ca	.470	.05
Mg	.838	.001
Na	.839	.001
Fe	.827	.001
Mn	.946	.001
Cu	.975	.001
B	.558	.02

between tissue element concentration in the young leaves and shoot biomass was similar to that of shoot biomass and tissue element concentrations of whole plants (Table 4). Phosphorus levels in the young leaves, however, were not as highly correlated with shoot biomass ($r = 0.45$, $p = 0.08$) as in the whole shoot samples.

Water analyses. Total phosphorus in water samples ranged from 0.01 to 0.305 ppm. While there was a low correlation between total phosphorus in the water and the phosphorus levels of inner leaves ($r = 0.47$, $p = .06$) there was essentially no correlation between total phosphorus in the water and shoot biomass or phosphorus concentration in whole shoots. Orthophosphate was less than 0.01 ppm for six sites and the maximum value found was 0.170 ppm. Concentrations of nitrate and ammonia were below the lower detection limit of the method of analysis for most samples (Table 1).

Acid mixed stands. The two sites sampled that were not monospecific (Mille Lacs and Rice Lake) both had low pH accompanied by low tissue concentrations of calcium and sodium. The Mille Lacs samples also had low nitrogen concentrations. In comparison to the monospecific stands phosphorus tissue concentrations were high relative to the Typha shoot biomass. The Rice Lake samples in fact had higher phosphorus concentrations than any other site. Total above ground biomass including all species at this site was 756 gm^{-2}.

Tissue element concentration, leaf age and time of sampling. The concentrations of nitrogen, phosphorus, potassium, zinc and copper were significantly higher ($p < .05$) in younger leaves of sterile shoots than in older leaves in June (Figures 3, 4, 5, 6, 7). As the season progressed the concentrations of these elements in all leaves generally declined and the differences between leaves decreased. The concentrations of these same elements showed a similar pattern in the fertile shoots. The concentrations of phosphorus, potassium and zinc were significantly ($p < .05$) higher in the

Figure 3. Concentrations of nitrogen and phosphorus in different aged leaves and the inflorescence in relation to sampling date.

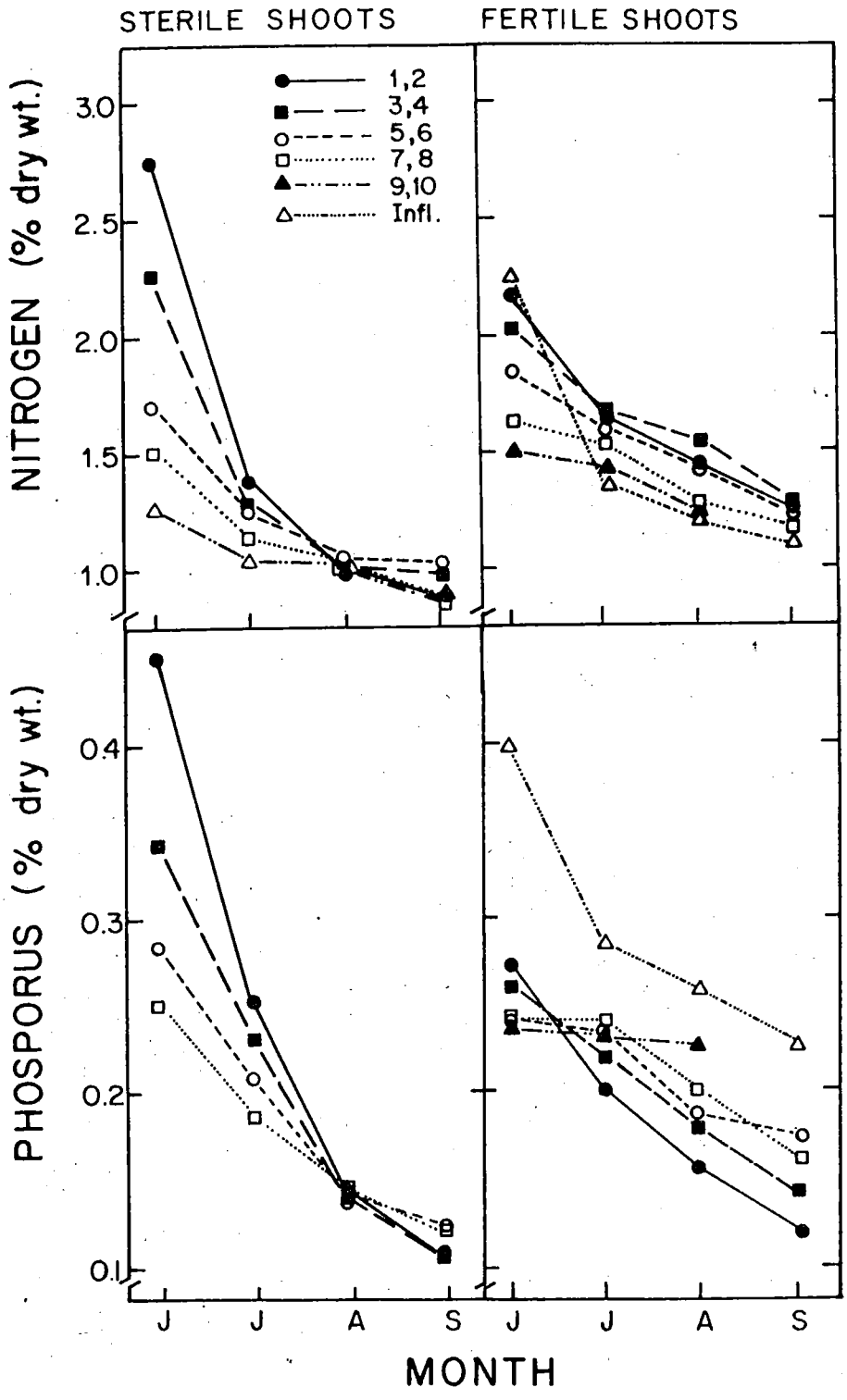

STERILE SHOOTS
FERTILE SHOOTS
1,2
3,4
5,6
7,8
9,10
Infl.
NITROGEN (% dry wt.)
3.0
2.5
2.0
1.5
1.0
PHOSPORUS (% dry wt.)
0.4
0.3
0.2
0.1
J
J
A
S
J
J
A
S
MONTH

Figure 4. Concentrations of sodium and potassium in different aged leaves and the inflorescence in relation to sampling date.

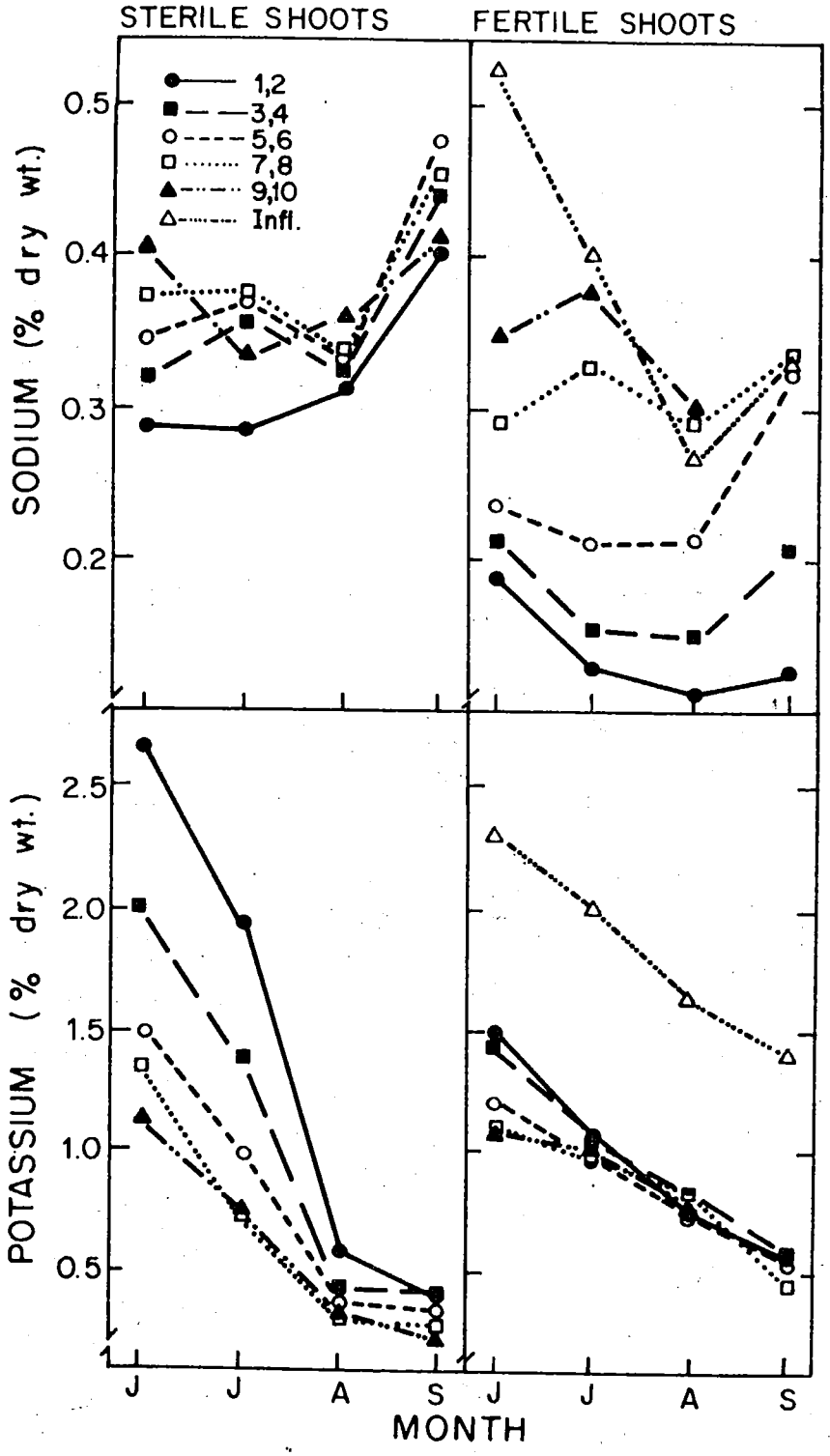

STERILE SHOOTS
FERTILE SHOOTS
1,2
3,4
5,6
7,8
9,10
Infl.
SODIUM (% dry wt.)
0.5
0.4
0.3
0.2
POTASSIUM (% dry wt.)
2.5
2.0
1.5
1.0
0.5
J
J
A
S
J
J
A
S
MONTH

Figure 5. Concentrations of calcium and magnesium in different aged leaves and the inflorescence in relation to sampling date.

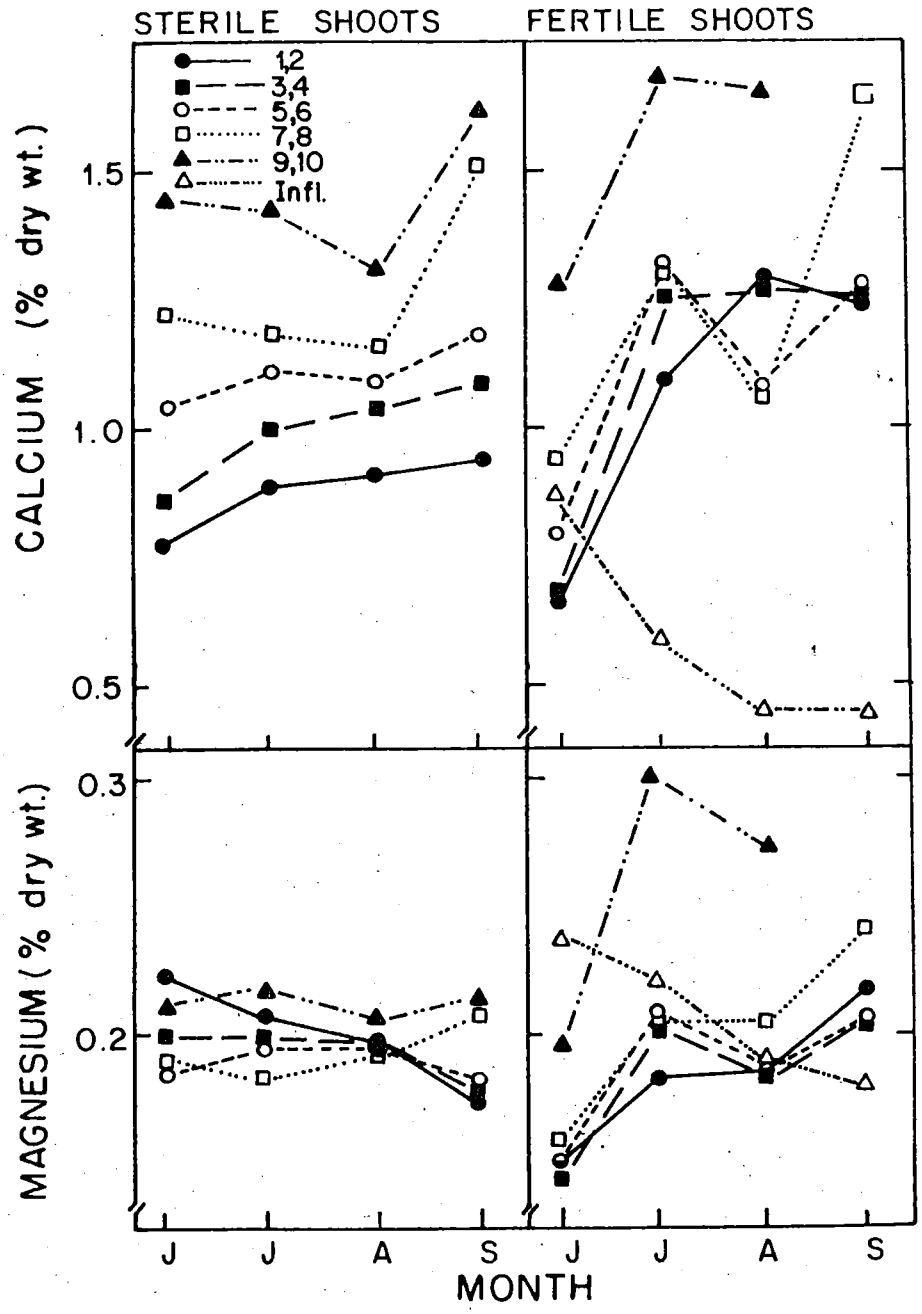

STERILE SHOOTS
FERTILE SHOOTS
1,2
3,4
5,6
7,8
9,10
Infl.
CALCIUM (% dry wt.)
1.5
1.0
0.5
MAGNESIUM (% dry wt.)
0.3
0.2
J
J
A
S
J
J
A
S
MONTH

Figure 6. Concentrations of zinc and iron in different aged leaves and the inflorescence in relation to sampling date.

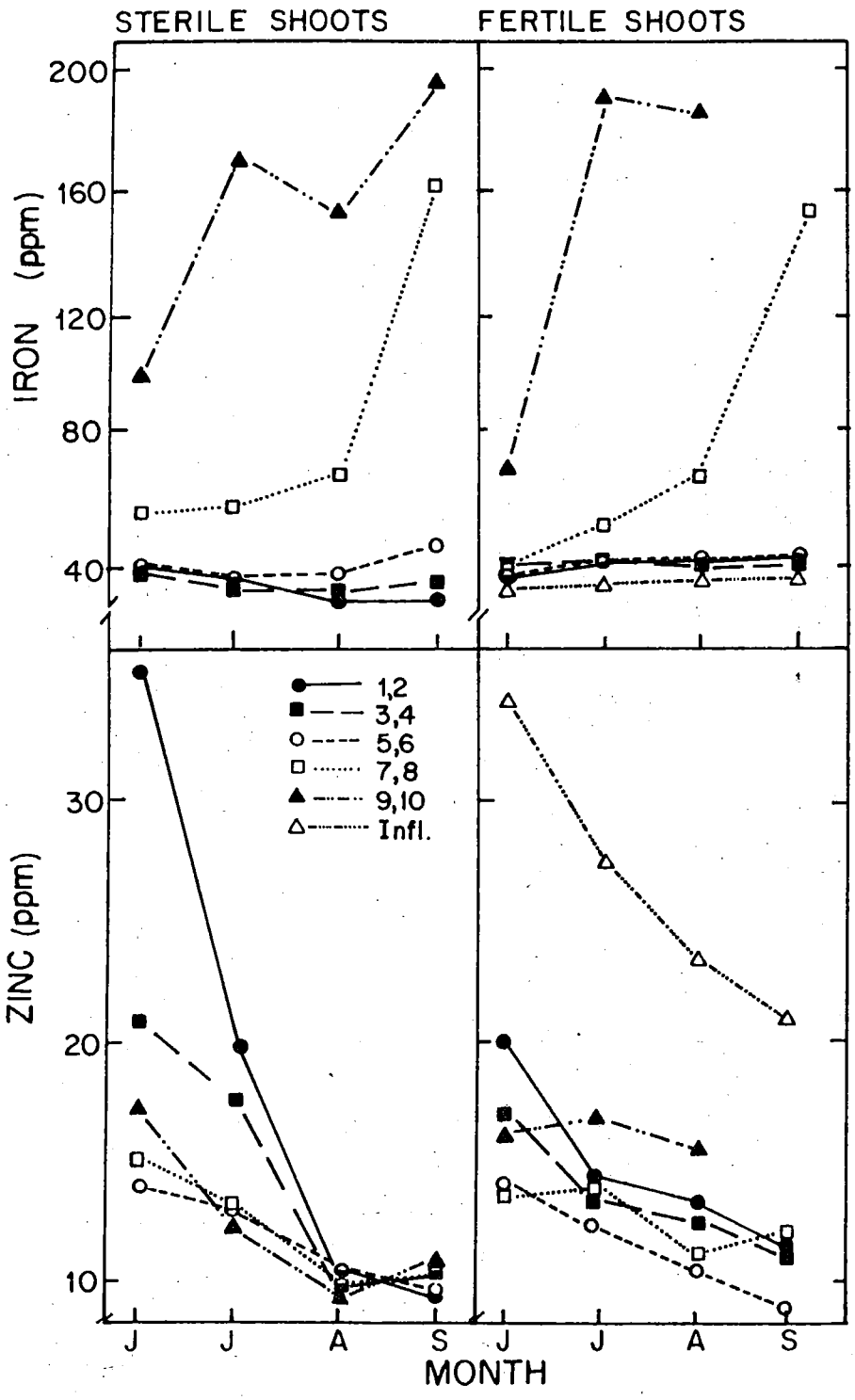
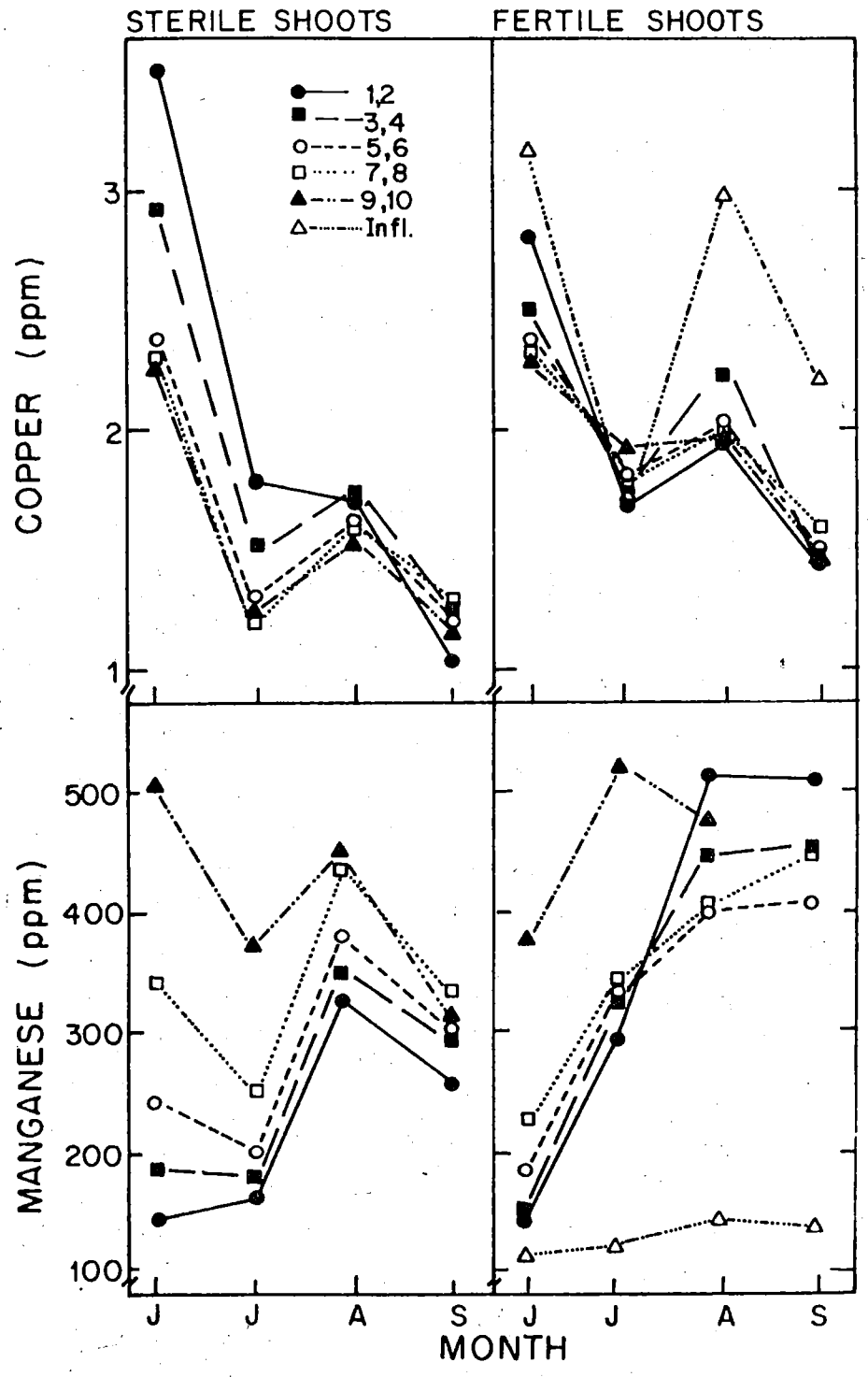

STERILE SHOOTS
FERTILE SHOOTS
IRON (ppm)
200
160
120
80
40
ZINC (ppm)
30
20
10
1,2
3,4
5,6
7,8
9,10
Infl.
J
J
A
S
MONTH

Figure 7. Concentrations of copper and manganese in different aged leaves and the inflorescence in relation to sampling date.


STERILE SHOOTS
FERTILE SHOOTS
1,2
3,4
5,6
7,8
9,10
Infl.
COPPER (ppm)
3
2
1
MANGANESE (ppm)
500
400
300
200
100
J
J
A
S
J
J
A
S
MONTH

inflorescence and its stalk than in the leaves of the fertile shoot.

Sodium, calcium and manganese showed a quite different pattern with older leaves having significantly higher concentrations ($p < .05$) of these elements than the younger leaves (Figures 4, 5, 7). Calcium and manganese concentrations in the inflorescence and its stalk were significantly lower than in the leaves. The concentration of iron was similar in all leaves throughout the season except the outermost leaves (oldest) which had significantly higher concentrations throughout the season (Figure 6). The samples containing the second oldest leaves also contained significantly higher iron concentrations by the end of the season. The concentration of magnesium was similar in leaves of all ages at all times except the oldest leaves of the fertile shoots which had significantly higher concentrations (Figure 5).

Fertilizer addition to a natural site. From water samples taken from the fertilized and control areas (Table 6) it appears that the barrier effectively prevented movement of the applied fertilizer into the control area. At the end of the first season above and below ground biomass in the fertilized area were 11% and 25% higher, respectively, than the control area (Figure 7). Shoot nitrogen and phosphorus levels were also significantly higher ($p = .05$) in the fertilized area. By the end of the second season differences between the fertilized and control areas were even more pronounced. Above ground biomass was 62% higher and below ground biomass was 124% of the control area ($p = .05$). Tissue levels of nitrogen, phosphorus and potassium were also significantly higher ($p = .05$). It should be noted, however, that the 1979 biomass yield from the control area was substantially lower than that of 1978 (Table 7).

Discussion

Shoot biomass. The values of shoot standing crop in the present study fall within the range reported previously for the United States. A wider range though lower mean value of shoot biomass was found in southeastern United States when over twice as many sites in a four state region with several major physiographic regions were sampled (Boyd and Hess, 1971). Our interest in areas with extensive marshes may have resulted in a higher mean shoot biomass than the southeastern study where minimum stand size was one-fifth of our minimum stand size. Our results are consistent with values reported from other northern stands (Bray et al., 1959; McNaughton, 1966; Jervis, 1968; Bernard and Bernard, 1973; Gustafson, 1976; Klopateck and Stearns, 1978).

The results of this study together with those of Boyd and Hess (1971) support McNaughton's (1966) observation that there does not appear to be a correlation between Typha standing crop and latitude within the continental United States.

Seasonal variation in biomass. Typha shoot standing crop increases throughout most of the growing season and then begins to decline before the shoot yellows and dies. In north central United States maximum shoot biomass occurs mid to late August (Andrews and Pratt, 1978; Gustafson, 1976). Thus at the time the sampling was done in this study (late July - early August) shoot biomass had reached approximately 70-80% of its maximum value. By mid-October Gustafson (1976) found shoot biomass had decreased by 26% from the peak value. Most of this decrease was attributed to loss of dead leaves though part may also have been due to transport of nutrients and carbohydrate to the rhizomes.

Shoot standing crop and shoot density. Data on the relationship between density and standing crop from different studies have been contradictory. Boyd and Hess (1971) suggested that their most productive sites had larger shoots

but were less dense than unproductive sites. Supporting this assertion that shoot standing crop was more closely related to shoot weight than density were reports by Boyd (1971) and Klopatek and Stearns (1978). Ondok (1971), however, found the same result supported by the Minnesota data (Table 4), that shoot biomass was closely related to shoot density.

Water depth and shoot density. Harris and Marshall (1963) note that during four years of reflooding following drawdown Typha increased from 16 to 27 shoots/m^2 in water less than 25 cm deep, remained nearly the same in water 25-38 cm deep and decreased in water greater than 38 cm deep. They state, however, that reductions could be attributed almost entirely to T. latifolia dying while the T. glauca seemed unaffected by water depth up to 60 cm. Although water depth (0 to 102 cm) was not correlated with standing shoot crop in this study, such a relationship may exist. As a perennial, Typha growth in any one year is an integration of conditions of the present growing season and those of previous seasons mediated through below ground storage organs. Long term studies such as Harris and Marshall's (1963) may be needed to distinguish optimal conditions not only for water level but other environmental parameters as well.

Tissue element concentrations: 1) Range. Although the shoot biomass range found in Minnesota encompassed most reported values for Typha in North America, the range of tissue element concentrations were generally less than those reported by Boyd and Hess (1971). However, since their sites covered a greater geographic and physiographic range than the present study this was not unexpected.

2) Effect of sampling date. Concentrations of nitrogen, phosphorus, and potassium decline in Typha shoot tissue during the season (Bayly and O'Neill, 1972; Mason and Bryant, 1975). Although the concentrations may decrease throughout the season, because of the increase in biomass the total

amount of an element in the plant increases (Mason and Bryant, 1975).

3) Use of leaves rather than whole shoots for diagnostic sampling. Since in mid-August the concentration of any element except calcium and manganese tends to be equal throughout the sterile shoots, subsamples rather than entire shoots would provide reliable results at that time. Correlations of concentrations of N and Zn between inner leaves and whole shoots were low, however. Whether this is due to the late July - early August sampling or variation in tissue content in leaves at other sites is unknown. Subsamples taken early in the season are less reliable. The data presented here for leaf concentration from shoots of a relatively productive stand will be useful in diagnosing the nutrient status of stands in future studies.

4) Shoot biomass and nutrient concentration. The strong correlation between phosphorus content and standing crop tends to implicate phosphorus as the major nutrient limiting Typha growth in Minnesota marshes. Results of tissue analysis, although suggestive, do not prove that phosphorus is limiting. Low tissue concentrations of elements have been shown to be due to other factors limiting uptake of the element in question (Smith, 1962).

Fertilizer additions to a natural stand. Fertilizer application had a significant effect on biomass yield and tissue nutrient concentration (Table 7). However, the average biomass obtained in the fertilized area above ground (1,359 g/m^2) and below ground (2,965 g/m^2) is often exceeded in natural stands without costly fertilizer additions. In order to minimize energy inputs it may be feasible to site wetland biomass plantations near sewage plants or feedlot facilities. Alternatively, harvesting methods which include an in-field dewatering step would result in the retention of valuable nutrients.

Table 6. Water samples from fertilized site and control site.

Sampling Date	Orthophosphate, ppm		Ammonia, ppm	
	Fertilized Site	Control Site	Fertilized Site	Control Site
6/29/78 (prior to fertilization)	0.01	<0.01	0.02	0.02
7/6/78	0.77	0.01	1.19	0.05
7/18/78	1.27	<0.01	0.45	<0.1
8/14/78	0.16	<0.01	<0.1	<0.1
9/14/78	0.23	0.06	--	--

Table 7. Biomass and Shoot Nutrient Concentrations for Fertilized and

Table 7. Biomass and Shoot Nutrient Concentrations for Fertilized and Control Sites at Carlos Avery (mean ± S.E.).

Date	Biomass, g/m^2			Shoot Nutrient Conc., % dry weight		
	Above Ground	Below Ground	Total	Nitrogen	Phosphorus	Potassium
6/29/78 Prior to fertilizer addn						
Fertilized:	630±70	---	---	2.03±.01	0.471±.04	2.53±.20
Control:	662±106	---	---	2.03±.01	0.471±.04	2.53±.20
9/14/78 End of 1st season						
Fertilized:	1446±163	1270±522	2716	1.35±.07*	0.244±.01*	1.14±.31
Control:	1305±83	1016±44	2321	1.04±.10	0.182±.03	0.94±.24
6/15/79 Beginning of 2nd Season						
Fertilized:	---	---	---	2.39±.20	0.476±.02	3.50±.16
Control:	---	---	---	2.34±.03	0.475±.01	3.19±.33
9/14/79 End of 2nd Season						
Fertilized:	1359±116*	1606±420	2965	1.35±.08*	0.213±.03*	1.46±.20*
Control:	839±104	714±62	1553	1.08±.08	0.183±.02	1.19±.27

*Difference between the means of the fertilized and control areas are significant (.05).

Summary and Recommendations

1. The maximum Typha shoot biomass found in natural stands in late July and early August in Minnesota was 2115 g/m^2 dry weight.

2. Shoot biomass from twelve monospecific stands in Minnesota averaged 1371 g/m^2.

3. Plants should be collected from stands with differing productivity and then grown at a single site in order to observe to what extent yields are due to genetic differences or differences in environmental factors, such as nutrient availability.

4. Tissue element concentrations suggested phosphorus as the nutrient most likely to be limiting shoot biomass.

5. Because of the great variation in below ground to above ground ratio, it is difficult to predict what the range of total biomass in Minnesota stands is. Reliable estimates of below ground biomass are difficult to acquire because of water depth and the cleaning and sorting necessary. However, if sufficient support is available, a survey of total biomass is a logical next step.

6. Reference data has been collected on variation in tissue concentration of ten elements from samples of different geographic origin, different parts of the shoot and different times during the growing season. These data should prove useful in diagnosing the nutrient status of stands in future studies.

7. The application of fertilizer to natural stands can significantly increase yield; however, alternatives to costly fertilizer additions should be considered.

II. Germination Requirements for *Typha* Seed

Introduction

Knowledge of the germination requirements of *Typha* seed is basic to developing the practical aspects of establishing stands with seed. Factors known to affect seed germination include temperature, oxygen concentration and light quality and quantity. Sifton (1959) reported that 30°C was the optimum temperature for the germination of *Typha latifolia* seeds. Later, NcNaughton (1966), who was studying ecotype variation in *Typha*, demonstrated that the optimum temperature for germination increases with increasing latitude.

The germination of many seeds is inhibited by low oxygen levels (Heichel and Day, 1972). However, a number of aquatic plants have been shown to require or germinate better at reduced oxygen levels (Hutchinson, 1975). This is not surprising since terrestrial plant seeds usually germinate in soil which normally has air spaces while aquatic plant seeds germinate in water or mud where the oxygen concentrations are reduced. Moringa (1926) and Sifton (1959) both found that seed germination in *Typha* was enhanced by reduced oxygen concentrations.

Typha seeds also require light for germination (Moringa, 1926a; Sifton, 1959). The light requirement of the seeds has been shown to be a phenomenon mediated by the pigment phytochrome (reviewed by Evenari, 1964; Smith, 1975). Red light promotes germination and far-red light inhibits it. If an alternating sequence of red and far-red light is used the type of light which is last in the sequence is of primary importance. The amount of red light, both intensity and duration, required for germination varies from species to species.

It has been reported that *Typha* seed germination is inhibited by some substrates (McNaughton, 1968; Van der Valk and Davis, 1976, 1978). While autotoxicity has been suggested, the responsible compounds have not been identified (McNaughton, 1968).

The objectives of the experiments on *Typha* seed germination were to (1) determine the effects of temperature on

seed germination, (2) determine the optimal oxygen concentration for germination, (3) determine the nature of the light requirement, and (4) observe the effects of various substrates on seed germination and seedling growth.

Materials and Methods

Seed. The seed used was the same as described under "materials and methods" in Section III

Temperature experiments. For each treatment fifty seeds were placed in a filter paper lined petri dish and 10 ml of distilled water was added. They were placed in growth chambers with continuous fluorescent and incandescent light at the following temperatures: 10°, 15°, 20°, 25°, 30° and 35°C. After seven days the number of the seeds which had germinated were counted.

Basic experimental procedure for oxygen and light requirement experiments. Flasks containing 5 mg of seed (ca. 50 seeds) and 20 ml of distilled water were filled with a gas mixture consisting of three parts nigrogen to two parts air. Where "soaked" seeds were used, the seeds remained in darkness for 12 to 24 hours before receiving a light treatment. There were 3 replicates per treatment.

Light sources. White light was provided by three 12-watt cool white fluorescent lamps. Blue and red light was obtained by using three millimeter thick plexiglas filters. Three green fluorescent lamps shielded by a green plastic filter provided the green light source. The far-red illumination was supplied by five 50 watt infra-red reflector lamps separated by ca. 10 cm of distilled water (to absorb heat) from the three millimeter thick "black" plexiglas filter.

Reduced oxygen concentration. Flasks were filled with one of seven mixtures of air and nitrogen. The ratios used were: 5 parts air to 0 parts nitrogen, 4 to 1, 3 to 2, 1 to 1, 2 to 3, 1 to 4, and 0 to 5. All flasks were placed under red light. At intervals (Figure 2) flasks were examined in red light and the number of seeds with the root tip protruding counted. Thus the time course as well as final percentage of seeds germinated was observed. Following removal of the

flasks from the red light the oxygen concentration was determined using an oxygen electrode. The 0:5 and 5:0 air to nitrogen mixtures were then bubbled with a 2:3 mixture. Two replicates were returned to the red light regime and a third was placed in the dark for another 40 hours.

Soaking and germination. Seeds were placed in distilled water and kept in the dark for periods ranging from 0 to 24 hours before being exposed to red light. Ten hours after the beginning of the red light treatment, and every two hours thereafter, the number of germinated seeds were counted. After 36 hours the experiment was terminated.

Amount of red light needed for germination and far-red light needed for reversal of red effect. After exposure to red light the flasks were placed in the dark or under far-red light for the designated interval (Table 8) and then into the dark. After twenty-four hours the flasks were opened and the number of germinated seeds recorded.

Substrates with different pH. Sphagnum moss (dried), milled peat, a mixture of milled peat and black dirt in equal proportions, black dirt and sand were the substrates tested. Five 9 x 9 cm pots were filled with each substrate to 2 cm below the top of the pot, and placed in a tray. Water was added to the tray until the surfaces were covered by 1 cm of water. Fifty 1977 season Typha seeds were scattered in each pot. The first experiment began on February 22, 1979. The experiment was repeated on July 6, 1979. In the first trial two additional treatments were included. In one the seeds were covered by 1 cm black dirt. In the second the seeds were placed on filter paper in petri dishes as described in the methods for temperature experiments. All experiments were carried out in a greenhouse. During the second trial all but three seedlings were removed from each pot. After two months the height of each seedling was measured. On June 1, 1979 germination on the soil used in the paddies and on soil taken from the Carlos Avery seeding site were tested using the same method.

Table 8. The effect of light quality on percent germination of *Typha* seed with N_2: air ratio of 3:2.

	Blue	Green	Red	Far-red
Percent germination				
mean	15	36	83	0.6
range	10-22	30-39	79-88	0-2

Results

Temperature. The percent germination increased with increasing temperature (Figure 8) for seeds exposed to constant light. The highest germination occurred at 35°C, the maximum temperature tested, while essentially no germination occurred at 10°C. During seven days of darkness at 30°C none of the 1977 and less than 0.5% of the 1978 seeds germinated.

Reduced oxygen concentrations. Maximum germination oxxurred at oxygen concentrations between 2.3 and 4.3 mg/l (Figure 9). Seeds germinated at a slightly faster rate at 3.7 mg/l oxygen than at the other oxygen levels. Seeds inhibited from germination at 1.0 and 7.5 mg/l oxygen readily germinated when the oxygen concentration was changed to 3.7 mg/l.

Light quality. Light quality had a significant effect on germination (Table 8). Percent germination was highest under red light (83%). Germination was significantly lower under blue and green light at 15% and 36%, respectively.

Soaking and photosensitivity. Soaking the seeds in the dark prior to exposure to red light increased the germination rate under red light (Figure 10), and decreased the minimum duration of red light required for germination (Figure 9). Soaking for periods of 1 to 24 hours did not, however, affect the final germination percentage. After 36 hours of light, all treatments resulted in 70-95% germination with no clear relationship between length of imbibition prior to light treatment and total percent germination.

Amount of red light needed for germination. Maximum germination percentage, given the optimal soaking treatment and oxygen level, occurred after 10 hour exposure to red light (Figure 11).

Reversibility of red light effect by far-red light. Germination resulting from up to 4 hours of red light treatment was returned to near control (no illumination) levels by two hours of far-red light whether or not seeds had been

Figure 8. The effect of temperature on the germination of *Typha latifolia* seed.

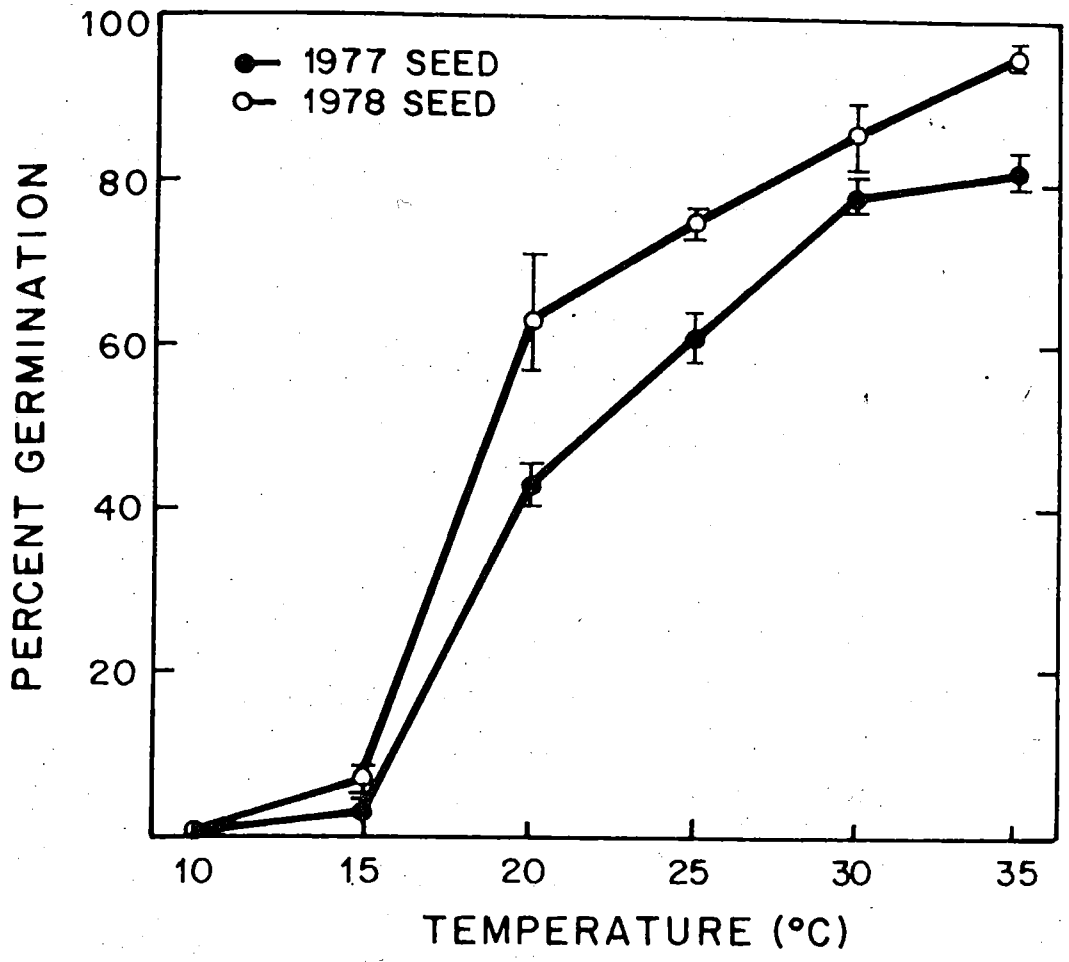

100
80
60
40
20
1977 SEED
1978 SEED
PERCENT GERMINATION
10
15
20
25
30
35
TEMPERATURE (°C)

Figure 9. The effect of oxygen concentration on the germination of Typha seeds under red light. (The bar indicates the range for the samples after 48 hours of light.)

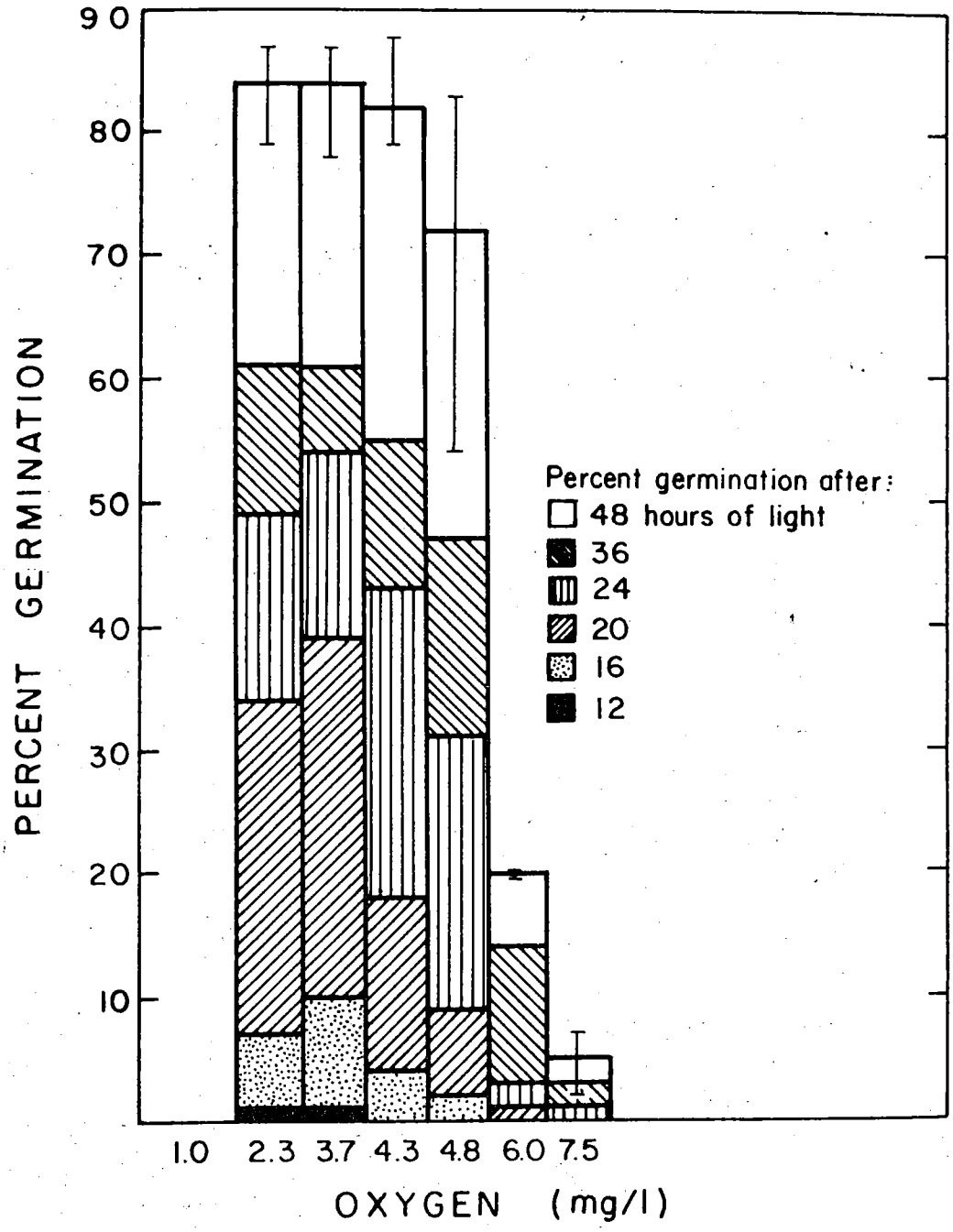

90
80
70
60
50
40
30
20
10
PERCENT GERMINATION
Percent germination after:
48 hours of light
36
24
20
16
12
1.0
2.3
3.7
4.3
4.8
6.0
7.5
OXYGEN (mg/l)

Figure 10. The effect on rate of germination of soaking the seeds prior to their exposure to red light.

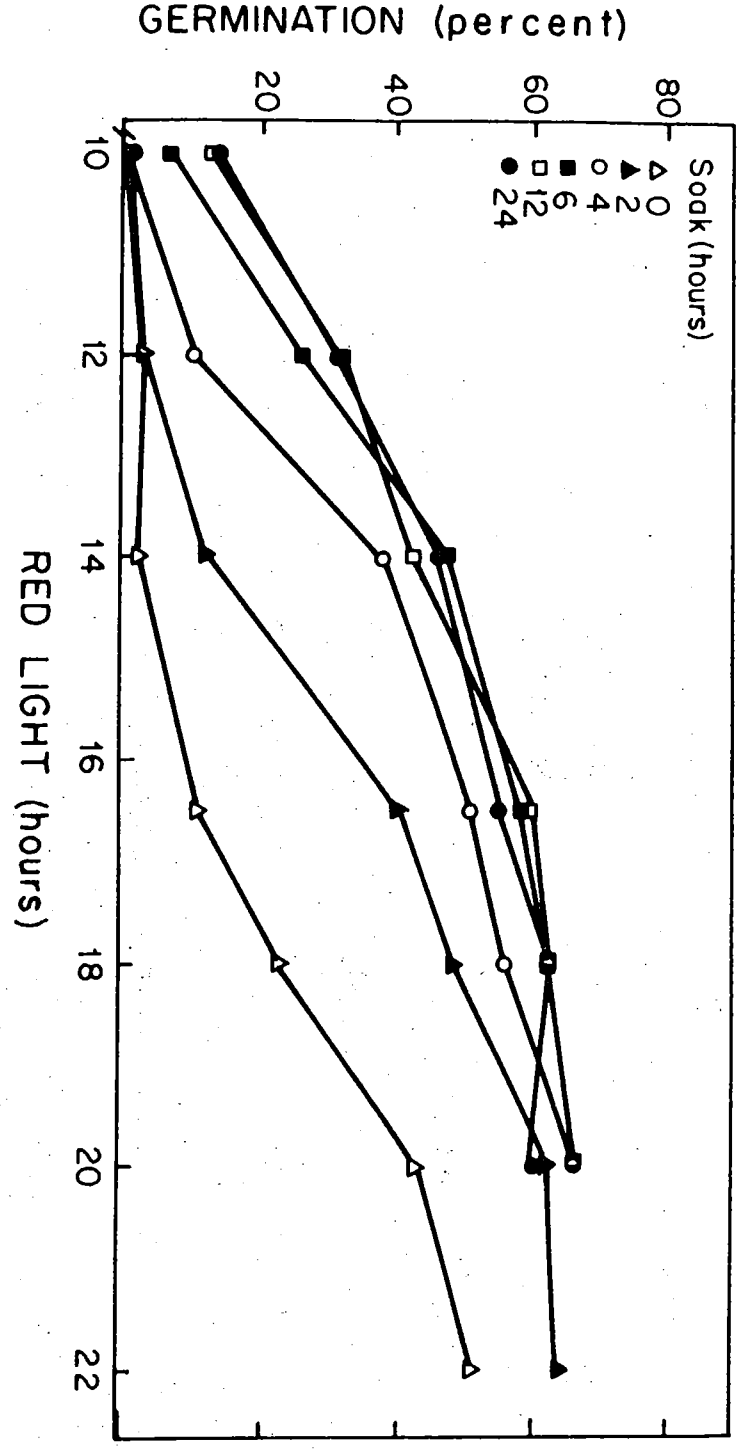
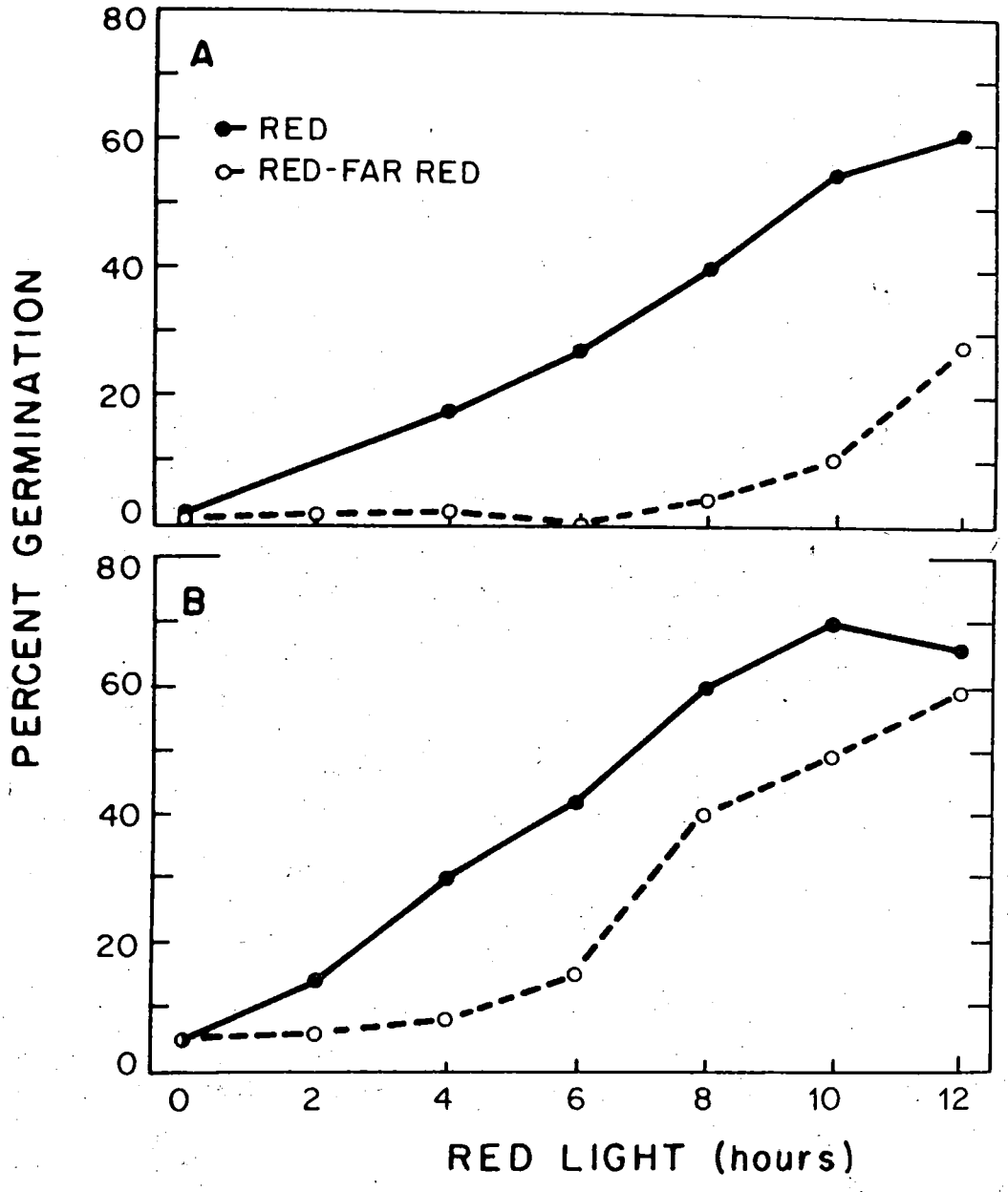

GERMINATION (percent)
20
40
60
80
Soak (hours)
0
2
4
6
12
24
10
12
14
16
18
20
22
RED LIGHT (hours)

Figure 11. Percent germination as affected by hours of red light and hours of red light followed by two hours of far-red light. A. No soaking treatment prior to exposure to red light. B. Nineteen hours of soaking treatment prior to exposure.


A
RED
RED-FAR RED
B
PERCENT GERMINATION
0
20
40
60
80
0
2
4
6
8
10
12
RED LIGHT (hours)

soaked prior to light treatment (Figure 11A and B). After eight hours of red light the germination of seeds which had been given the soaking and far-red treatments increased to nearly 40% (Figure 11B). The red light effect on seeds which had not been soaked was reversible for a longer period than the effect on soaked seeds (Figure 12). Five minutes of far-red light were sufficient to reverse six hours of red light.

When treatments of red light and far-red light were alternated, the last treatment in the sequence determined the nature of the response. However, germination of seeds exposed to two treatments of red interrupted by far-red (R-F-R) was less reversible than seeds exposed to a single treatment of red light (Figure 13).

Substrates with varying pH. Thirty to seventy percent of the seeds germinated in the summer on substrates having pHs ranging from 4.0 to 7.8 (Table 9). Germination rates were higher for the summer experiment probably owing to higher ambient temperatures in the greenhouse. One percent of the seeds covered by one centimeter of black dirt germinated while 35 percent of those not covered germinated. Seedling growth measured as height after 2 months was highest on black dirt and a mixture of black dirt and milled peat.

Discussion

The results of the light experiments on Typha seeds are consistent with the theory that seed germination is mediated by the pigment phytochrome. Germination was promoted by red light, inhibited by far-red light, and showed repeated reversibility.

Under natural conditions both red light and far-red light are present. Red light predominates during the middle of the day while far-red light increases relative to red at sunrise and sunset (Smith, 1973). The significance of the red and far-red effects under natural conditions is uncertain. However, the light requirement probably helps to insure that the seeds will germinate in areas where they are not shaded

Figure 12. The amount of far-red light required to reverse the effect of six hours of red light. A. No soaking treatment. B. Eighteen hours of soaking treatment.

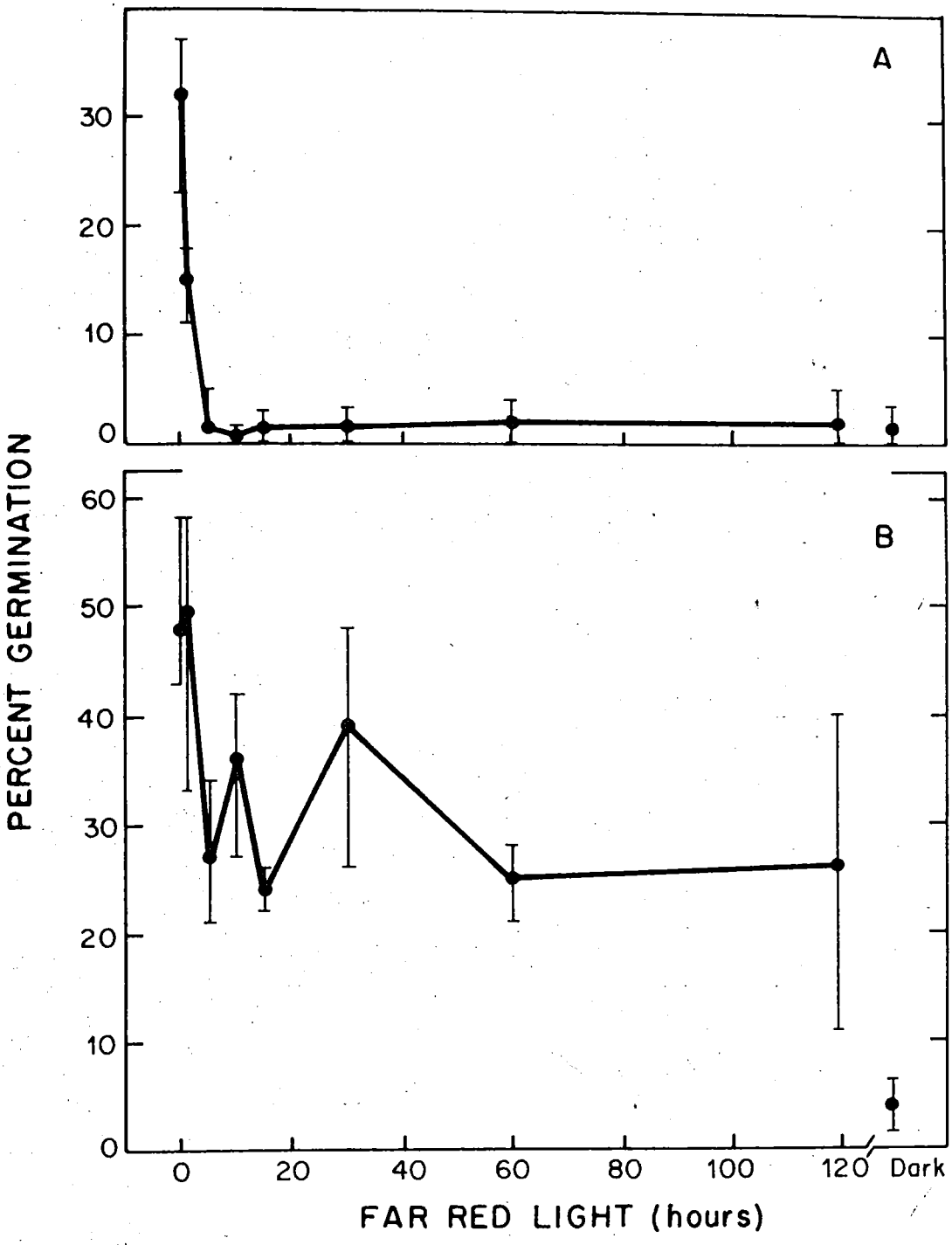

A
B
30
20
10
0
60
50
40
30
20
10
0
0
20
40
60
80
100
120
Dark
PERCENT GERMINATION
FAR RED LIGHT (hours)

Figure 13. The effects of a sequence of exposures to red and far-red light on percent germination.

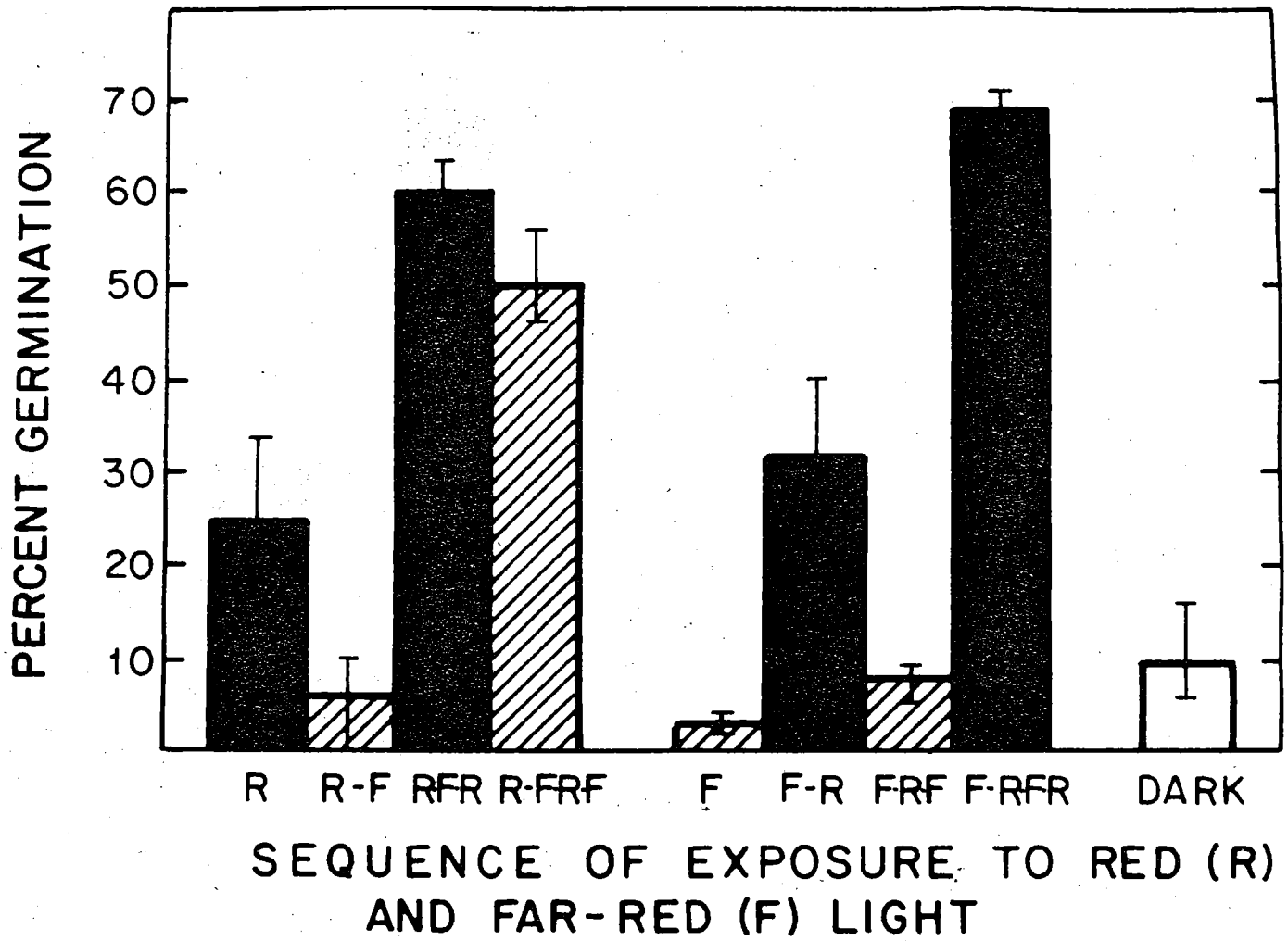

PERCENT GERMINATION
70
60
50
40
30
20
10
R
R-F
RFR
R-FRF
F
F-R
FRF
F-RFR
DARK
SEQUENCE OF EXPOSURE TO RED (R)
AND FAR-RED (F) LIGHT

Table 9. Percent germination on various substrates one month after seeding.

	Sphagnum moss	Milled peat	1/2 milled peat, 1/2 black dirt	Black dirt	Sand	Black dirt; seeds buried 1 cm	Distilled water
Winter experiment							
% germination	54 ± 3*	1 ± .3	32 ± 3	35 ± 3	40 ± 7	1 ± .2	73 ± 7
pH	4.9	4.0	4.7	7.6	8.4	7.6	--
Summer experiments 7/6/79						soil used in paddies	soil from Carlos Avery seedling site
% germination	74 ± 2	55 ± 5	48 ± 2	44 ± 3	48 ± 2	51 ± 7	31 ± 7
pH	4.4	4.0	6.2	7.2	7.8	5.5	5.5
height after 2 mo, cm	3.6 ± .5	<1.0	16 ± 1	12.5 ± 3	<2.0	--	--

*mean of 5 replicates ± the standard error.

by established plants or where the water is too deep.

The high temperature requirement for germination results in a high probability that the seeds will germinate during the appropriate season. The optimum temperature of 35°C found in our study is higher than that reported by Sifton (1959). The difference between the temperature optima of the two studies may be due to the ecotypic differences that McNaughton (1966) demonstrated.

While the germination requirements of Typha are appropriate for insuring survival of many naturally occurring Typha seedlings, they limit the conditions under which areas may be artificially seeded. The light requirement, for example, means that seeds must be soaked and exposed to light immediately prior to seeding if seeding is done under conditions where the seed may be buried. This would happen if seeding was done in shallow water and the substrate was stirred up by the seeding operation. The temperature requirement will minimize the success of early seeding.

Seeds generally germinated quite well on the substrates tested in this study with the exception of milled peat. Van der Valk and Davis (1976) noted lower aquatic plant seed germinated on substrate with high organic content. In particular, Typha seed germination was lower in areas where Typha was already established compared to nearby mudflat areas (Van der Valk and Davis, 1978), and was lower on substrate samples taken from areas where Typha was growing than on substrate taken from open water (Van der Valk and Davis, 1976). Their results support McNaughton's (1968) hypothesis that Typha plants produce autotoxic substances. This implies that seeding may not be an effective method of re-establishing a Typha stand.

Possibilities exist for modifying the germination requirements of Typha seed. Since rupturing the seed coats resulted in Typha seed germination in the dark (Moringa, 1926; Sifton, 1959), treatments which do this to large batches of

seed may eliminate the light requirement. A long range project would be to develop seed with lower temperature requirements so that the growing season would be lengthened. This might be accomplished by crossing northern plants with southern plants whose temperature requirements for seed germination are lower.

Recommendations

1) Seeding should be done after water temperatures reach 20° C for at least part of the day.
2) Seeds should be soaked in the light for 12 hours prior to seeding, if seeds may become buried during seeding. Soaking should be done just prior to seeding since seeds begin to germinate within 24 hours.
3) Because of the possible toxicity of some soils to Typha seeds, when seeding sites are chosen samples of the substrate should be tested, particularly if emergent aquatics have recently been growing at the site.

III. Establishing Stands by Seeding

Introduction

Typha seedlings have been found on mud flats produced when water levels fall in marshes or lakes (Summerhayes and Burrill, 1948; Kadloc, 1960). This happens during years of low rainfall or as a result of a "drawdown" by wildlife managers. Even when a drawdown is planned to optimize wildlife habitat, the resulting vegetation is quite variable depending largely on the types of seed present in the mudflat or "seed bank" (Van der Valk and Davis, 1978). Controlled experiments have examined the effects of water depth (Bedish, 1967; Weller, 1975) and shoot density (Szczepanska and Szczepanska, 1973, 1976) on seedling growth. However these experiments were performed in pots in greenhouses, thus limiting their use for predicting yields under natural conditions.

Outdoor paddies were used for the initial work on establishing stands by seeding. The paddies were large enough (1.5 m^2 individually, 7.5 x 8 m together) to simulate a natural stand, and had several advantages over a natural site: controlled water level, reduced competition and convenient location for observation. The objectives of these experiments were to: (1) determine the biomass produced by seedlings in a single season, (2) determine the effect of different seeding rates, planting dates, and fertilizer application rates on seedling shoot biomass, and (3) determine the biomass and density of two year old plants.

Materials and Methods

Paddies. Plants were grown in 1.5 m^2 paddies consisting of plywood frames lined with black polyethylene. The 40 cm deep paddies were filled with 25 cm of organic soil. Analyses characterizing the substrate were performed by the Research Analytical Laboratory, Department of Soil Science, University of Minnesota (Table 10). Diagnostic testing was done by the Florist Soil Testing Service, Department of Soil Science, University of Minnesota (Table 11). Water was added until the water surface was 10 cm above the soil. In 1978 forty-two

Table 10. Characterization of substrate used for Typha paddies, 1978 and 1979.

NO_3+NO_2 N ppm	NH_4-N ppm	Kjeldahl N %	pH	PO_4 ppm	SO_4 ppm	K ppm	Ca ppm
32.4	10.9	1.16	5.6	11.5	974	40	8178

Mg ppm	Na ppm	Mn ppm	Fe ppm	Mn ppm	Zn ppm	Cu ppm	Pb ppm	Ni ppm
884	13.5	9.8	458	2.9	0.6	0.8	-.23	-.24

Cr ppm	Organic carbon %	Organic matter %
<0.02	19.0	32.7

Table 11. Results of diagnostic testing of substrate before first seeding (May 1978), after growth of seedlings for one year with high fertilizer rate (October 1978) and from additional paddies set up in 1979 (May 1979) compared to the desirable range for most established crops.

	May 1978	October 1978	May 1979	Desirable range
pH	5.8	5.7	5.5	--
Conductivity	61	35	72	30-80
Spurway, ppm:				
Nitrates	3	3	25	50-120
Phosphorus	Trace	Trace	Trace	5-15
Potassium	2	6	7.5	40-80
Calcium	91	94	60	>80
Ammonia	Trace	1	Trace	<8

paddies were constructed in a solid 6 x 7 paddy block. In 1979 two additional rows were added at the southern end of the block.

Seed. During May 1978 and again in October, mature spikes were collected from Typha latifolia L. at Carlos Avery Wildlife Management Area. Spikes collected in May were produced during the 1977 season and those collected in October contained seed from the 1978 season. Seed was separated from the rest of the inflorescence by modifying the procedure used by McNaughton (1968). Spikes wetted by blending in water with a few grains of detergent were stirred in chromatography tanks partially filled with water. Seeds sank to the bottom of the tank while the rest of the inflorescence floated. After the seeds were removed by suction, they were washed with tap water through sieves to remove insect larvae, collected on a 30 mesh sieve, rinsed with distilled water onto "Miracloth", and dried for several hours at 30°C. Seeds from all the spikes obtained at each collection were thoroughly mixed, thus producting two lots of seed -- 1977 seed with 16.7 seeds/mg and 1978 seed with 14.3 seeds/mg. These were stored at room temperature in glass bottles. During 1979 plants grown from the 1977 seed flowered and were identified as T. latifolia.

Seeding rate. In 1978 an experiment to examine the influence of seeding rate on plant density and biomass was set up using four seeding rates: 20, 40, 80 and 160 mg/m^2. After being soaked overnight, the seeds were sprayed in 100 ml water into the paddy with a plastic water bottle. This method insured that seeds sank immediately. If dry seeds are scattered onto the water they tend to float and clump together.

Seed added on May 31, 1978 did not germinate in all boxes. When seed was added again on June 27 to paddies without seedlings, germination occurred in all paddies. This caused an alteration in the experimental design. The result was an early (May 1978) planting with three

replications of the 20 mg/m^2 rate and two replications of the other three rates and a late (June 1978) planting with one paddy seeded at 20 mg/m^2, two at 40 mg/m^2 and three at the other two seeding rates. All seeding rate paddies received the high fertilizer treatment described in the fertilizer section.

Second year shoots. Most of the seeding rate paddies were not sampled below ground at the end of the 1978 season. In the spring of 1979 new shoots were produced from underground buds and rhizomes, and growth continued throughout the 1979 season. During this second growing season fertilizer application was increased by 50% to 60 g/m^2 nitrogen, 13.2 g/m^2 phosphorus, and 60 g/m^2 potassium. One sixth was applied as shoots began growing in the spring (May 16, 1979), one-third three and one-half weeks later, and the remainder after another five weeks.

Rate of fertilizer application. The seedlings in the six paddies seeded June 27, 1978 received either no fertilizer, low fertilizer or high fertilizer. A total of 40 g/m^2 nitrogen, 8.8 g/m^2 phosphorus, and 40 g/m^2 potassium was added in the high fertilizer treatment. One-quarter of this was raked into the soil prior to seeding. Six weeks after germination when the leaves of the seedlings changed from the floating stage to the upright stage another quarter was added. The rest of the fertilizer was added two weeks later. The low fertilizer treated paddies did not receive the final application and hence received a total of 20 g/m^2 nitrogen, 4.4 g/m^2 phosphorus and 20 g/m^2 potassium. The paddies receiving the various fertilizer treatments were in the outer row of the block of paddies -- one on the north and one on the east, two on the west and two on the south.

1979 paddies. In 1979 all new paddies were seeded at a rate of 30 mg/m^2. Eight were seeded on May 23 and two each on June 1 and June 11. Seeding was accomplished in the same manner as in 1978 except that 250 ml of water were used to

apply the seed to each paddy. Although the total amount of fertilizer applied was the same as to seedlings in 1978, the time of application differed. No fertilizer was added prior to seeding. One quarter of the fertilizer was added after 6 weeks from seeding when the leaves changed from floating to upright. The second quarter was added ten days later and the final half after another ten days.

Biomass determinations. Shoots were harvested by cutting all the shoots in each paddy off just above the soil surface. The fresh weights of the entire shoot sample and a subsample of approximately 500 g were recorded. The subsample was placed in a paper bag and dried to constant weight at 70°C. In 1978 the dry/fresh weight ratio of each subsample was used to calculate the dry weight for the shoots in the paddy from which the subsample was taken. In 1979 the means of dry/fresh weight ratios from all the subsamples of seedlings from each row or all subsamples of the second year shoots were used to calculate the dry weight for each paddy.

Below ground biomass (shoot bases, roots and rhizomes) was sampled using a 50 x 50 cm metal frame. This was pushed into the soil in the center of the paddy and all plant material within the frame removed. Clinging soil was washed from the plant material which was then placed in cotton bags and dried at 70°C. Below ground samples were taken from each of the fertilizer treatments and from two early and three late seeding rate paddies. The remainder of the paddies were not sampled below ground so that their growth during a second year could be monitored. In 1979 below ground samples were taken from all new paddies and from fifteen paddies with 2 year old shoots.

Results

Total biomass was 1303 and 583 g/m^2 for May and June 1978 seeded paddies, respectively (Table 12). Seedling biomass from May seeded paddies was similar in 1979 (1226 g/m^2) to that of 1978, however, the distribution of the total

Table 12. Seedling biomass produced by various seeding rates in 1978.

Treatment	Shoot dry$_2$weight g/m	Below ground dry$_2$weight g/m	Total dry$_2$weight g/m	Below ground / Above ground	# of paddies
Seeded May 1978, all	860±67*				9
20 mg/m^2	862±69				3
40	844±119				2
80	852±32				2
160	882±361				2
interior paddies	802±60				7
paddies sampled above and below ground	905±85	398±42	1303±43	.45±.09	2
Seeded June 1978, all	418±33				9
20 mg/m^2	486				1
40	366±63				2
80	480±43				3
160	366±71				3
paddies sampled above and below ground	384±30	199±18	583±46	.52±.03	3

*standard error of the mean.

between above and below ground biomass differed. The below ground to above ground ratio (R/S) in 1978 was 0.45 while it was 0.18 in 1979 (Table 13).

The average seedling shoot biomass was 860 g/m^2 for plots seeded in May 1978 and 583 g/m^2 for plots seeded in June (Table 12). No significant differences ($\alpha = .05$) in shoot dry weight resulted from seedling rates changing from 20 to 160 mg/m^2 for either 1978 seeding date.

Different seeding rates would be expected to produce densities of plants proportional to the seeding rate if the germination rate was constant. Hence any effect of seeding rate would actually be a more direct result of shoot density. However in 1978 the germination rate (as reflected by seedling counts six weeks after seeding) varied from 0.5% to 69% with a mean of 25%. That the resulting shoot densities were quite variable in the seeding rate treatments is indicated by the large standard errors in Table 14, particularly in the June seeding. Since the various seeding rates did not provide treatments which had distinctly different shoot density, the relationship between shoot density and shoot dry weight was examined by computing the correlation coefficient for shoot biomass and density. The low but positive correlation coefficients (Table 14) suggest that little of the variability in shoot biomass was due to the density of the plants. The correlation coefficients were not, however, significant at the 5% level of probability.

Seed germination in 1979, based on seedling counts four weeks after seeding was higher (43%) and less variable (maximum 57%, minimum 36%) than in 1978.

Fertilizer applications resulted in increased biomass of June 1978 seeded paddies from 298 g/m^2 with no fertilizer to 796 g/m^2 with 40 g/m^2 nitrogen (N), 8.8 g/m^2 phosphorus (P) and 40 g/m^2 potassium (K) (Table 15). The below to above ground ratio decreased with increasing amounts of fertilizer. The increasing availability of nutrients was reflected by the increased concentration of nutrients in shoot and below ground

Table 13. Seedling biomass 1979.

Treatment	Shoot dry weight	Below ground dry weight	Total dry weight	Below ground / Above ground	# of paddies
seeded in May	1039±72	187±29	1226±91	.18±.02	4
seeded in June	729±115	116±0.5	844±115	.17±.03	2

Table 14. Density of shoots produced by different seeding rates and correlation between density and shoot biomass.

	density - weeks after seeding #/m^2	density at harvest #/m^2
Seeded May 1978		
20 mg/m^2	62±12*	171±13
40	187±15	297±64
80	322±20	364±23
160	437±424	367±277
r**	0.39	0.56
Seeded June 1978		
20	53	109
40	263±206	122±39
80	429±285	285±36
160	488±73	231±49
r**	0.05	0.53

*Standard error of the mean.

**Correlation coefficient for density and shoot dry weight, not significant at 5% level.

Table 15. Seedling biomass resulting from different amounts of fertilizer, seeded in June 1978.

Treatment (g/m^2 N-P-K)	Shoot dry weight, g/m^2	Below ground dry weight, g/m^2	Total biomass, g/m^2	R/S
No fertilizer	150 ± 33*	148 ± 36	298 ± 69	.99 ± .02
Low fertilizer (20-4.4-20)	363 ± 15	202 ± 10	565 ± 5	.56 ± .05
High fertilizer (40-8.8-40)	562 ± 30	234 ± 34	796 ± 64	.42 ± .03

*standard error of the mean

tissue (Table 16). Concentrations of N, P, K in May 1978 seedlings were lower than in June seedlings. However, because of the greater biomass produced by the seedlings with the longer growing period, the total amount of N, P and K accumulated in the shoots receiving high fertilizer but planted at different times was similar (Tables 17, 18 and 19). Amounts of N, P and K accumulated by plants receiving the high fertilizer rate were, respectively, 5.5, 4.9 and 5.9 times that of plants receiving no fertilizer.

While all the 1978 seedling paddies had the shoots harvested at the end of the season, only a few were sampled below ground. The rest were left in order to follow growth of two year old plants. The number of shoots produced the second year was less than the shoot density at the end of the first year. For plants seeded in May of 1978 shoot density at the beginning of the 1979 season was 40% of the density at the end of 1978; for June 1978 seeded paddies it was only 23% (Table 20). Total biomass of 2 year old plants was 2268 g/m^2 for plants seeded in May 1978. Although June 1978 plants continued to have lower dry weights in their second year compared to May 1978 plants the differences were not significant at the 5% level. Second year shoot dry weight was significantly ($\alpha = .002$) correlated with shoot dry weight of the previous season for May 1978 plants but was not significant at the 5% level of probability for June plants (Table 21).

Since shoot bases and rhizomes are known to live for 17-22 months (Westlake, 1968), part of the below ground biomass harvested from 2 year old plants was produced the previous season. Using the 1978 shoot biomass and the root/shoot ratio of 1978 seedlings, the below ground biomass was calculated for each paddy. By subtracting the estimated 1978 below ground biomass from the total 1979 biomass the net dry weight produced in 1979 was estimated as 1964 g/m^2 for May 1978 plants and 1531 g/m^2 for June 1978 plants (Table 22).

Table 16. Tissue element concentrations (% of dry weight) of shoots receiving different amounts of fertilizer.

Treatment	Nitrogen		Phosphorus		Potassium	
	Shoot	Below ground	Shoot	Below ground	Shoot	Below ground
Seeded June 1978						
No fertilizer	1.50±.06	0.95±.13	0.244±.003	0.283±.005	2.19±.004	1.44±.06
Low fertilizer	1.87±.09	1.36±.07	0.354±.004	0.470±.004	3.60±.24	2.90±.14
High fertilizer	2.58±.005	2.28±.08	0.466±.011	0.523±.022	4.34±.12	2.77±.12
Seeded May 1978						
High fertilizer	1.87±.14	--	0.388±.054	--	3.19±.38	--
Seeded May 1979	1.42±.04	--	0.286±.04	--	3.51±.01	--
Second year shoots (seeded May 1978, sampled Sept. 1979)	1.26±.02	--	0.239±.002	--	2.41±.61	--

Table 17. Amount of nitrogen contained in seedling shoots and below ground organs.

Treatment	Shoots g/m^2	Below Ground g/m^2	Total g/m^2	Amount contained in fertilizer g/m^2
Seeded in May 1978				
No fertilizer	2.23±.41	1.35±.15	3.58±.56	0
Low fertilizer	6.80±.61	2.75±.28	9.55±.33	20
High fertilizer	14.53±.75	5.31±.59	19.83±1.33	40
Seeded in June 1978				
High fertilizer	16.05±1.30	--	--	40

Table 18. Amount of phosphorus contained in seedling shoots and below ground organs.

Treatment	Shoots g/m^2	Below ground g/m^2	Total g/m^2	Amount contained in fertilizer g/m^2
Seeded in May 1978				
No fertilizer	0.37±.08	0.42±.11	0.79±.19	0
Low fertilizer	1.28±.07	0.95±.04	2.23±.03	4.4
High fertilizer	2.62±.02	1.22±.13	3.84±.33	8.8
Seeded in June 1978				
High fertilizer	3.31±.41	--	--	8.8

Table 19. Amount of potassium contained in seedling shoots and below ground organs.

Treatment	Shoots g/m^2	Below ground g/m^2	Total g/m^2	Amount contained in fertilizer
Seeded in May 1978				
No fertilizer	3.29±.73	2.15±.61	5.44±1.3	0
Low fertilizer	13.05±.35	5.88±.57	18.93±0.91	20
High fertilizer	25.45±.68	6.54±1.24	31.99±1.92	40
Seeded in June 1978				
High fertilizer	27.2±2.9	--	--	40

Table 20. The shoot density of seedlings at the end of the first season compared to the density of new shoots produced the following season (# shoots/m^2 on May 29, 1979 ÷ # shoots/m^2 on Sept. , 1978).

Treatment	Mean	Standard error	No. of samples
Seeded in May 1978	.400	±.07	7
Seeded in June 1978	.228	±.02	6

Table 21 . Correlation between shoot biomass produced the first year and that produced the second year by plants grown from seed.

	All paddies	Paddies not sampled below ground in 1978		
		All	Seeded in May	Seeded in June
Correlation coefficient (r)	.515	.615	.811	.470
Significance	.006	.006	.002	.174
Number of values	23	16	10	6

Table 22. Total and net biomass of two year old plants.

Treatment	Shoot dry weight /m^2	Below ground dry weight g/m^2	Total dry weight g/m^2	Below ground / Above ground	Net below ground dry weight g/m^2	Net total dry weight g/m^2
Seeded in May 1978	1448±104(7)*	840±176(6)	2268±168(6)	.57±.09	536±119(6)	1964±178(6)
Seeded in June 1978	1268±151(6)	519±179(3)	1697±391(3)	.41±.09	353±186(3)	1531±386(3)

*Mean ± standard error of (x) values.

During the first year where seedling density was greater than 200 shoots/m^2, density generally decreased during the season. When seedling density was less than 200 shoots/m^2, it increased during the season. During the second year densities between 100 and 200 shoots/m^2 showed little increase in the number of shoots throughout the season. Where initial density was less than 100 shoots/m^2, density increased sharply between June 11 and July 31 (Figure 14). While shoot density did not have a significant effect on total shoot biomass during the first year, total shoot dry weight was significantly (α = .00001) correlated with initial and final shoot density the second year (Table 23).

Plants developing from the very small Typha seed required a month to attain 10 cm in height while the average height of second year shoots was 1 m in mid-June. The rate of height increase of second year shoots decreased during August (Figures 15 and 16). Seedling shoot growth rate remained high in August thus reducing the difference in the average heights between seedling and second year shoots to 48 cm by the beginning of September.

Discussion

Because of the lack of studies on Typha seedlings growing in natural stands, few comparisons between biomass in natural stands and that in paddies are possible. Fiala and Kvet (1971) reported dry weights of one year old Czechoslovakian shoots as 889 g/m^2 and below ground biomass as 496 g/m^2. While their total biomass is similar to that achieved in the paddies, the Czech samples were taken in mid-season and presumably their biomass would have been higher by the end of the season.

Seedlings of T. latifolia produced 827 g/m^2 of shoot biomass and 730 g/m^2 of below ground biomass when grown in sand cultures (Dykyjova, Veber and Priban, 1971). Second year yields were 3084 g/m^2 of shoot biomass and 2375 g/m^2 of below ground biomass. These higher yields may be due in part to the terraced arrangement of culture tanks which allowed

Figure 14. Shoot density throughout the growing season for 2 year old shoots with differing initial densities (5/15).

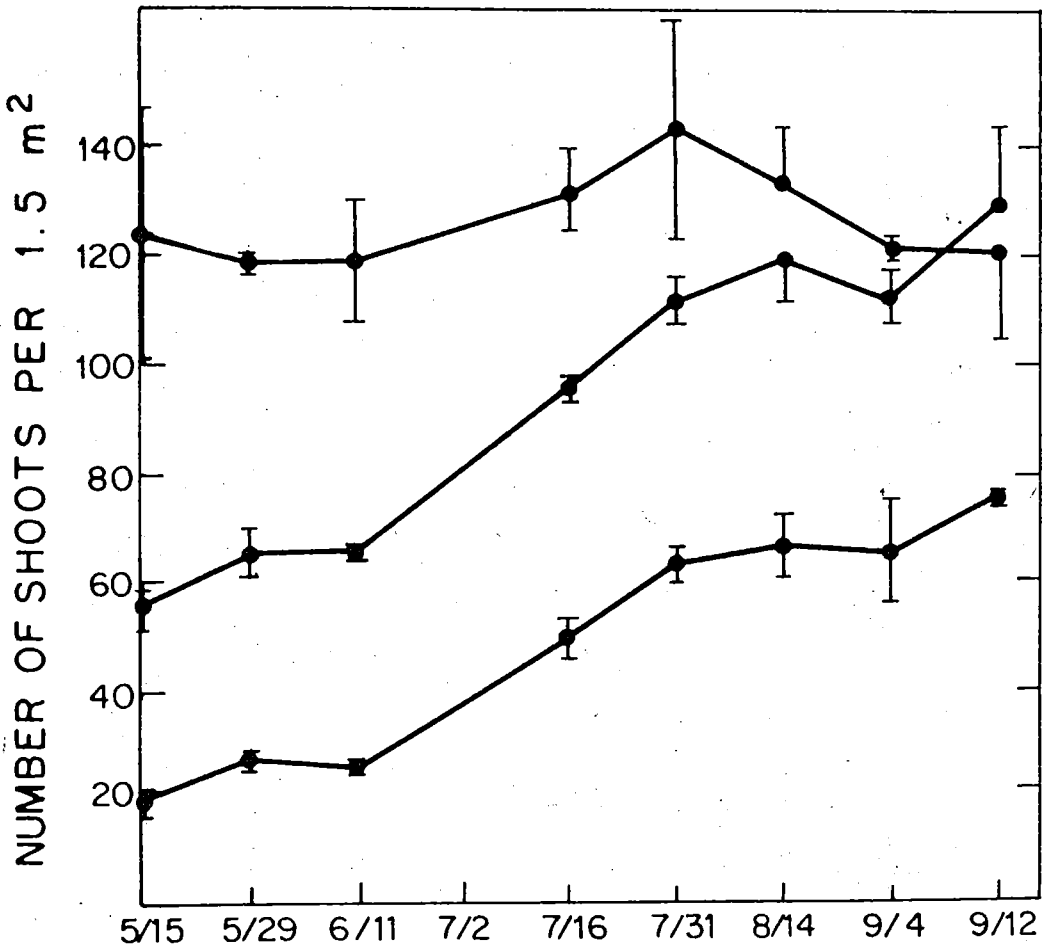

NUMBER OF SHOOTS PER 1.5 m²
140
120
100
80
60
40
20
5/15
5/29
6/11
7/2
7/16
7/31
8/14
9/4
9/12

Table 23. Correlation between second year shoot biomass and shoot density at the beginning (May 29, 1979) and end (September 17, 1979) of the second season.

	May 1979	September 1979
Correlation coefficient	.72	.82
Significance	.00006	.00001
Number of values	23	24

Figure 15. Seedling and second year shoot heights during the 1979 growing season.

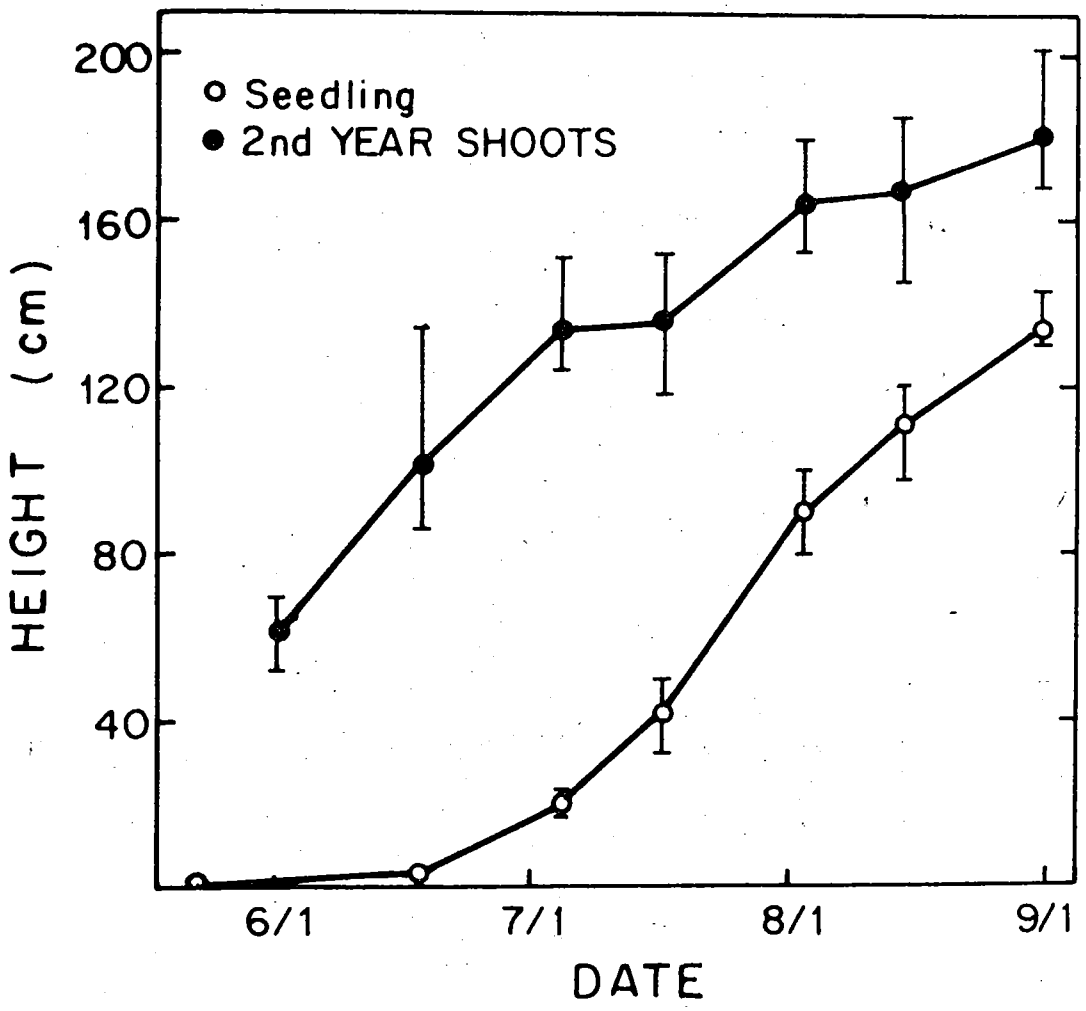
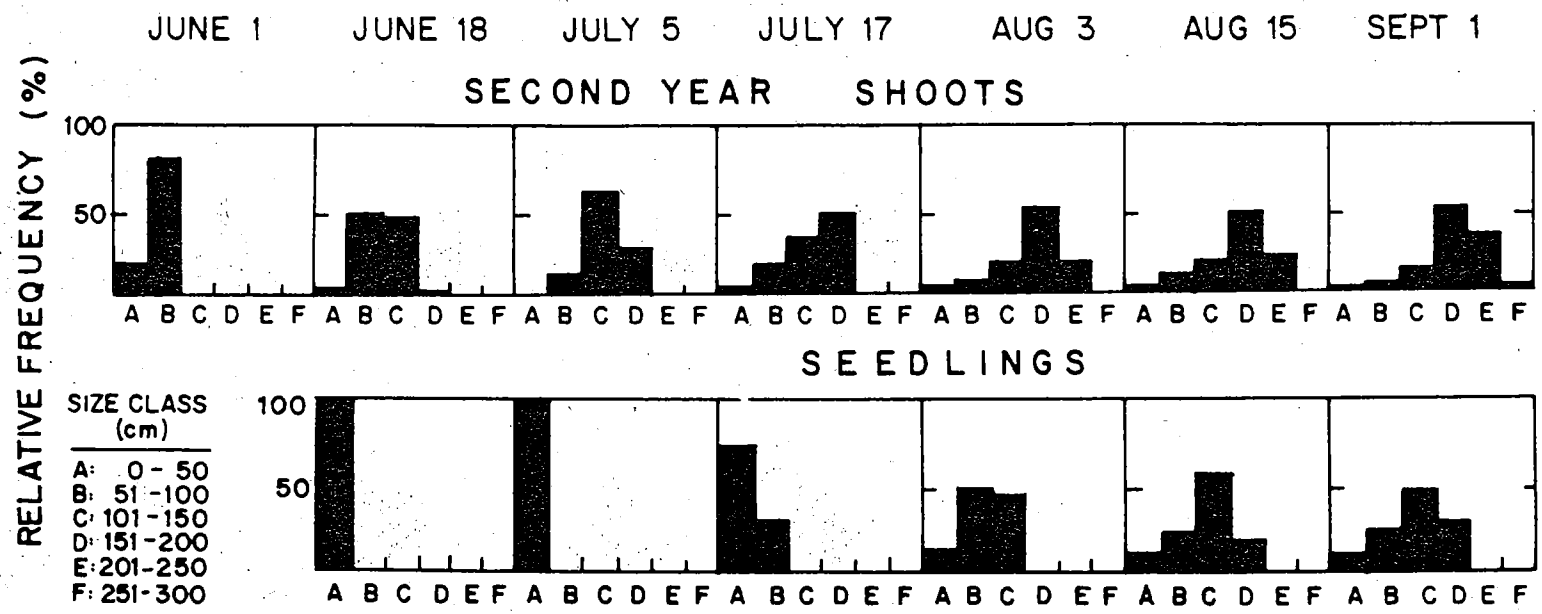

200
160
120
80
40
HEIGHT (cm)
Seedling
2nd YEAR SHOOTS
6/1
7/1
8/1
9/1
DATE

Figure 16. Size class distributions of first and second year shoots.


JUNE 1
JUNE 18
JULY 5
JULY 17
AUG 3
AUG 15
SEPT 1
SECOND YEAR SHOOTS
SEEDLINGS
RELATIVE FREQUENCY (%)
100
50
A B C D E F
SIZE CLASS (cm)
A: 0 - 50
B: 51 - 100
C: 101 - 150
D: 151 - 200
E: 201 - 250
F: 251 - 300

more light to reach the leaves than in the solid stand arrangement of the paddies.

Yields from Typha hybrid plants grown from rhizomes in paddies averaged 2875 g/m^2 in 1977 (Andrews and Pratt, 1978). The lower yields reported in this study are partly the result of the tiny seed, ca. 0.1 mg. As indicated by Figures 15 and 16 the seedlings have attained only 15% of their final height when the second year shoots have reached 75% of theirs. While second year rhizomes were observed to be larger in diameter than those produced by first year seedlings, they were still not as robust as those found in mature natural stands. This suggests that yields may increase as the rhizomes increase in size and thus contain larger reserves from which to renew the shoot growth each spring. This theory is supported by the lower biomass of second year plants and the lower overwintering capacity of buds produced by the June 1978 seeding compared to the May 1978 seeding.

Paddies were seeded at different rates in order to determine what rate of germination could be expected outdoors where conditions were less controlled than in growth chambers or the greenhouse. The result was that the germination rate was quite variable from paddy to paddy. The most consistent germination occurred in 1979 in May when the several days following seeding were mild, calm and sunny. Seed added to a single paddy in late April and early May had very low germination rates, supporting the results of growth chamber experiments on temperature requirements presented in Section II.

By seeding at different rates we also hope to achieve varying density of seedlings and to observe the influence of density on biomass yield. Experiments with T. latifolia seedlings in pots indicated that as densities increased from 10 to 2560 seedlings/m^2 weights of individual shoots decreased and hence the biomass for a given area remained the same (200 g/m^2) Szczepanska and Szczepanska, 1973). The present study

also found biomass little affected by final densities ranging from 100 to 400 shoots/m^2.

The low yields from paddies which were not fertilized reflects the low availability of nutrients in the organic soil that was used as substrate (Tables 10 and 11). Although calculations based on the concentrations of N, P and K in the plant indicate they contained less than 67% of the K, 35% of the P, and 41% of the N added in the fertilizer, the availability of these nutrients was no higher at the end of the season than at the beginning before fertilizer was added (Table 11). The N, P and K added as fertilizer but not accounted for in the Typha tissue may have been incorporated into organic compounds, chelated by compounds in the soil, or in the case of N, lost through denitrification.

The concentrations of N, P and K in shoot tissue of the plants receiving no fertilizer were above the mean shoot tissue concentrations of those same elements in mature stands in Minnesota. The concentrations in the shoot tissue of paddies receiving low fertilizer were greater than maximum concentrations in the Minnesota mature stands (Section I). The concentrations in the plants receiving high fertilizer application were not only greater than the maxima found in Minnesota but larger than any reported values for nitrogen and phosphorus and near the maximum reported value for potassium (Boyd and Hess, 1970). These high values are even more remarkable as they were from samples taken at the end of the season when nitrogen, phosphorus and potassium concentrations are at their lowest (Bayley and O'Neill, 1972; Mason and Bryant, 1975). This suggests that seedlings may require greater concentrations of nutrients for maximum growth than do mature plants.

When water levels varied from one to sixteen inches, germination was found to be highest at a water depth of 1 inch for seeds in pots in the greenhouse (Weller, 1975). Water levels of approximately 10 cm were present during seeding and early seedling growth to lessen the impact of

wind and rain on the loose substrate. Once seedlings appeared to be established water level was allowed to fall in order to encourage upright leaves. Addition of fertilizer often resulted in algal blooms. If seedlings still had floating leaves when algal blooms occurred the plants were shaded and some died. Once the seedlings had upright leaves the algal blooms did not visibly injure the plants.

Recommendations

(1) Seeding rates resulting in 100 plants/m^2 appear to be sufficient for maximum yield where seedlings are harvested on an annual basis. Greater density, however, will not cause reduced yields.

(2) Higher density, ca. 200 seedlings/m^2, may provide higher yields in subsequent years if only shoots are harvested.

(3) Germination rates appear to be highly variable. To achieve high germination rates water temperature should exceed 20°C, at least during the day. Calm sunny weather is preferable. Seeds were soaked for twelve hours in the light prior to seeding in these experiments.

(4) In soils having low N, P and K availability, fertilization rates of 400:88:400 kg/ha are needed for maximum yields of seedlings.

(5) In highly organic soil the seedlings may become uprooted. Good control of water level is necessary so that sufficient water is available to protect seeds and seedlings at early stages. Later water levels need to be lowered to encourage upright leaves and prevent shading by algae and floating plants.

(6) At present the somewhat chancy nature of seeding establishment suggest that rhizome planting, although more labor intensive, is a more certain method of stand establishment. A compromise between the alternatives of seeding and rhizome planting would be to grow seedlings in the greenhouse early in the spring to the stage of upright leaves. Although planting of individual plants would still be necessary, this

would eliminate digging up and sorting rhizomes. It would also lessen the need for precise water control needed for seeds. Complete removal of water for planting, followed by flooding and maintenance of several inches of water would probably suffice. Seedling yields might also be increased, by the increased length of their growing season.

IV. Rhizome Dormancy and Development

Introduction

During the latter part of the growing season, shoot growth in Typha stops and further increases in biomass occur only in the below ground organs (Andrews and Pratt, 1978; Gustafson, 1976). In fact, material appears to be shifted from above to below ground organs (Prentki et al., 1978). As the current season's shoots stop growing, overwintering buds are produced which will rapidly expand the following spring (Fiala, 1971). While this growth pattern has been well documented, the factors favoring cessation of shoot growth, increased bud and rhizome formation, and the induction and period of bud dormancy in Typha have not been.

"True dormancy" is the inability to produce normal growth under any environmental conditions. True dormancy may be preceded by a "predormancy" in which the plant grows but growth occurs under a more limited set of conditions. If predormancy does not develop into true dormancy then the dormancy is known as "relative" or "conditional" dormancy (Vegis, 1964). The cessation of growth and induction of dormancy is known to be affected by such external conditions as temperature, photoperiod, quality of light, temperature during light and dark periods, and nutritive conditions. Generally, short days result in decreased growth and the onset of dormancy. Although often only a single factor is examined at a time, usually several environmental parameters interact in controlling the onset of dormancy.

That Typha undergoes a period of at least relative dormancy was suggested by Dykyjova et al. (1972). They found reduced shoot growth in plants receiving winter cold treatments that were much shorter than usual. Reduced growth of shoots in northern clones under cool thermoperiods suggested temperature as a possible inducer of this dormancy (McNaughton, 1966). By the time growth has ceased natural Typha stands exhibit ratios of below ground to above ground biomass (R/S) varying from 0.67 (Gustafson, 1976) to 2.35 (McNaughton, 1966).

In the experiments on the development and dormancy of Typha rhizomes presented in this report, the objectives were to: (1) determine the nature of dormancy in overwintering plants, (2) determine the amount of cold treatment needed to overcome the dormancy, (3) determine the effects of day length and temperature on growth and formation of overwintering structures, and (4) determine the effects of nutrient availability on the R/S ratio.

Material and Methods

Plant material. Typha latifolia L. seedling rhizomes and shoot bases with attached buds were removed on September 22, 1978 from paddies planted in June 1978 (Section III). After being rinsed in tap water the plant material was placed in plastic bags and stored at 4°C.

Growth chamber environments. Light was provided by fluorescent and incandescent lamps (Koukkari and Johnson, 1979). Irradiance was 1300-1500 foot candles 80 cm below the lights. Plants at 35°C received 15 hours of light each day. Plants at 25°C received either 15 hours of light (long days) or 9 hours of light (short days). The chamber with temperature set at 35°C slowly drifted to 30°C between October and December. Following adjustment it thereafter maintained a constant temperature of 34.5 $\pm$ 0.5°C. The relative humidity in the chambers ranged from 70 to 90%.

The plants which received no storage at 4°C were removed from the ground on October 6, 1978 when the soil temperature was 10°C.

Induction of dormancy. Rhizomes or shoot bases with attached buds were placed individually in sterile soil in 8 x 8 cm pots. All plants were maintained at 25°C with 15 hours of light per day for one month. The plants were then divided into three groups with five replicates per group. Group 1 (short day) received fourteen hours of incandescent and fluorescent light each day. Group 2 (long day) received fourteen hours of incandescent and fluorescent light preceded and followed by a half hour of incandescent light (ca. 95 foot candles at the top of the foliage). Thus the total

period of light was 15 hours. Both of these first two groups remained at 25°C throughout the light and dark periods.

Group 3 (cold night) received the same light treatment as Group 2 but during the dark period the temperature was reduced to 15°C.

On day 77 the light period was reduced to 13 hours for Group 1 (short day). The other two groups continued to receive 15 hours per day of incandescent light but fluorescent lights were on for only 13 hours. One-half gram of 20:10:10 fertilizer was added to each pot on days 32 and 74.

Solution culture plant material. Rhizomes and shoot bases with buds were collected during the fall of 1978 from a Typha x glauca Godr. clone maintained in outdoor plots at the University of Minnesota. This material was stored at 4°C during the winter. The material was removed from storage, washed with tap water and individual pieces trimmed to 40-75 g of living tissue consisting of a young shoot attached to a rhizome or shoot base. These initiating pieces were distributed equitably among all treatments according to weight and type. Three pieces were dried at 70°C to determine the dry/wet weight ratio. Prior to placement in the nutrient solution, the parts of the initiating pieces which would be submerged were soaked in 0.25% sodium hypochlorite for 20 minutes and then rinsed in tap water.

Solution culture treatments. Hoagland's solution (Hoagland and Snyder, 1933) was used as the nutrient solution with ferric tartrate replaced with 0.01 mM Fe-EDTA. The complete solution contained 15 mM nitrogen and 1 mM phosphorus. The eight other treatments consisted of reduced nitrogen or phosphorus solutions that were 1/4, 1/16, 1/64 and 0 times the concentration of nitrogen and phosphorus present in the complete solution. The experiment began on June 17, 1978 and lasted for 16 weeks. Five replicates of each treatment were placed in a randomized block design consisting of five 3 x 3 blocks with one treatment per block. Statistical analyses

were performed on a CDC Cyber 74 computer using the SPSS Version 7.0 statistical package.

The culture method used was the same as used in previous experiments (Bonnewell and Pratt, 1978). The major difference in the present experiment was the increased length of the experiment to allow further development of below ground organs.

Upon termination of the experiment the plant in each bucket was separated into individual shoots, rhizomes, shoot bases, buds, roots, and the piece that visually corresponded to the initiating piece which will be referred to as the "old rhizome".

Results

Duration of storage. Shoot growth was vigorous at 35°C whether or not buds attached to shoot bases and rhizomes received a cold treatment (Figure 16). Growth, measured as increase in shoot height, did not increase at 35°C with longer intervals of prior cold treatment. Shoot development was poor at 25°C for material stored for 1.5 months (Figure 16A). After four months of cold treatment, however, shoot growth for plants at 25° and 35°C was similar (Figure 16B). Although initial shoot growth at 25° and 35°C was similar for plants receiving five months cold storage, mean height for shoots grown at 25°C was 33 cm greater than that of shoots grown at 35°C after 87 days (Figure 16C).

The new rhizomes, produced during the three months the plants were grown, caused the plants growing in a single container to become so intertwined that separation into individual plants was impossible. Hence the total dry weight with no estimate of variability for the plant material was used. Table 24 presents the final shoot number and dry weight for each treatment. Increasing the length of cold treatment did not result in significant increases in dry weight for plants grown at 35°C, but it did result in increases in dry weight for plants grown at 25°C.

Figure 16. The effects of storage time, photoperiod and temperature on shoot growth.

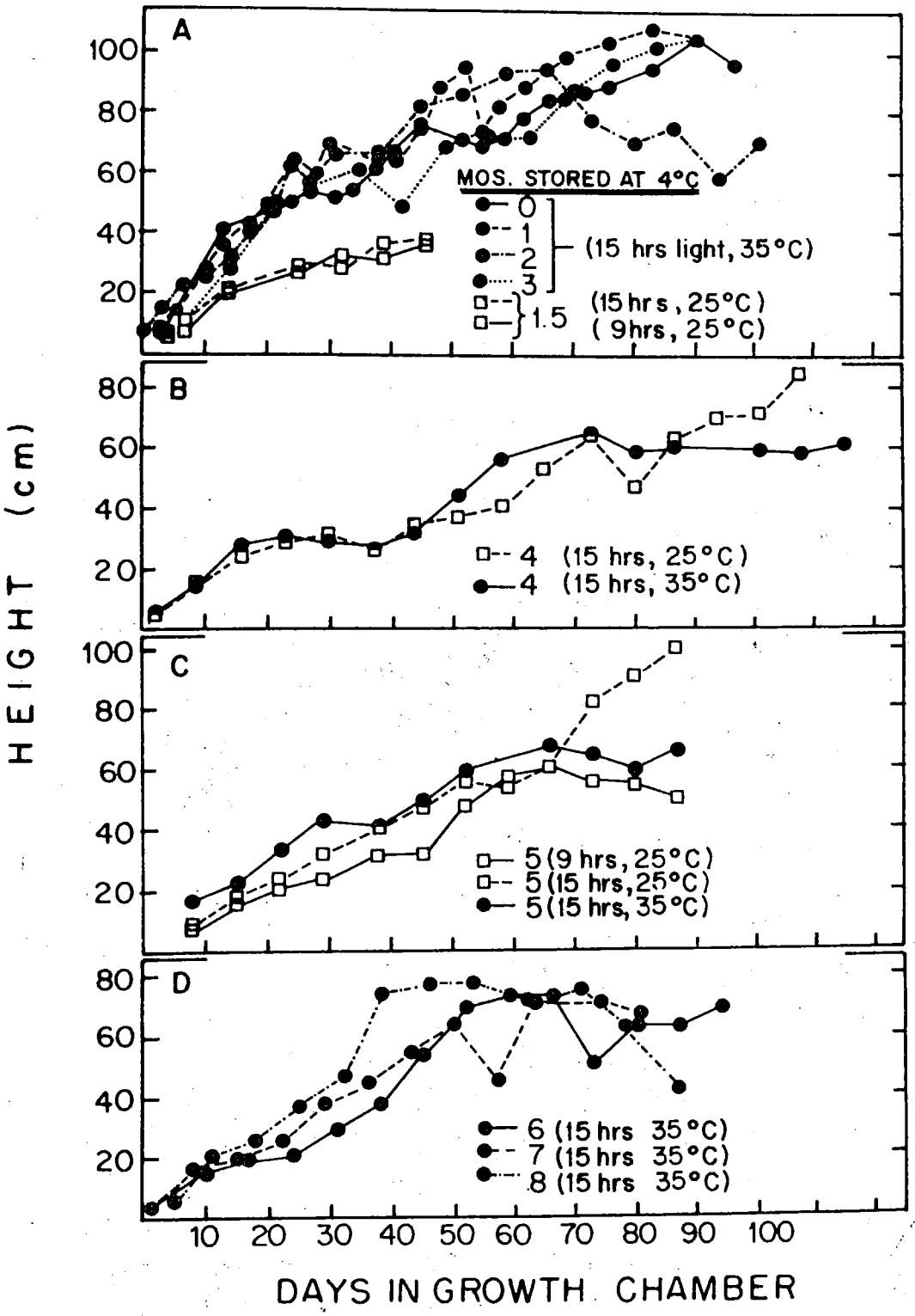

A
B
C
D
HEIGHT (cm)
DAYS IN GROWTH CHAMBER
MOS. STORED AT 4°C
0
1
2
3
(15 hrs light, 35°C)
1.5
(15 hrs, 25°C)
(9 hrs, 25°C)
4 (15 hrs, 25°C)
4 (15 hrs, 35°C)
5 (9 hrs, 25°C)
5 (15 hrs, 25°C)
5 (15 hrs, 35°C)
6 (15 hrs 35°C)
7 (15 hrs 35°C)
8 (15 hrs 35°C)

Table 24. Duration of storage, final number of shoots produced, and total dry weight.

Months at 4°C	Month planted	Temperature °C	Hours of light/day	Final shoot no.	Total dry weight
2	October	35	15	22	86
.5	October	35	15	14	138
1	October	35	15	12	--
2	November	35	15	14	116
3	December	35	15	14	126
4	January	35	15	30	108
4	January	25	15	11	66
5	February	35	15	21	59
5	February	25	15	8	85
5	February	25	9	7	20
6	March	35	15	8	--
7	April	35	15	1	--
8	May	35	15	1	--

After five months storage at 4°C, fewer of the buds attached to the rhizomes or shoot bases developed (Table 24). In May (after eight months of storage) only 11% of the buds on plants kept at 35°C grew while 41% of those at 25°C developed.

Induction of dormancy. Shoots grew equally well under photoperiods of 15 and 14/13 hours (Figure 17) at 25°C. The cool night treatment (25°C day/15°C night) resulted in plants whose mean height was 730 cm less than shoots grown at a constant 25°C. The shoot and rhizome net dry weights were also lower (Table 25). However, shoots subjected to cool nights produced an average of two more buds per plant. None of the differences between treatments were significant ($p = .05$), however.

Nutrient availability. Generally, increasing nitrogen concentration resulted in increased dry weight for individual plants grown in nutrient solutions (Figure 18). However, at the highest concentration (15 mM N) net dry weight was significantly ($p = .05$) lower. The same pattern was observed with increasing phosphorus concentration (Figure 19); however, the decrease in dry weight at the maximum phosphorus concentration (1.0 mM) was less pronounced and was not statistically significant ($p = .05$).

Below ground/above ground dry weight ratio (R/S). The above ground biomass was composed entirely of sterile shoots. The total R/S ratio increased over two-fold between complete solution and the 0 phosphorus treatments, and four-fold between complete solution and 0 nitrogen treatments (Figure 20). Since the initiating piece was composed primarily of rhizome, a net R/S ratio was obtained by subtracting the initial dry weight from the total below ground dry weight. When this was done the ratios still decreased significantly with increasing nitrogen and phosphorus concentrations although not as dramatically (Figure 21).

Figure 17. The effects of photoperiod and temperature on shoot growth for rhizomes stored at 4°C for 8 months.

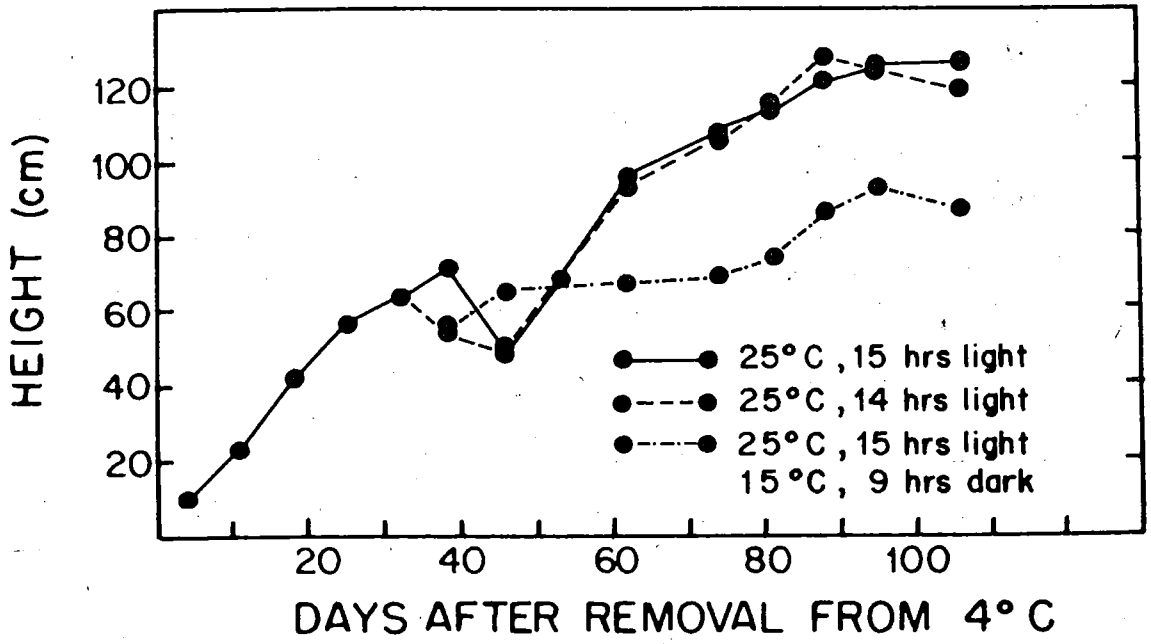

HEIGHT (cm)
120
100
80
60
40
20
20
40
60
80
100
DAYS AFTER REMOVAL FROM 4° C
25° C , 15 hrs light
25° C , 14 hrs light
25° C , 15 hrs light
15 °C , 9 hrs dark

Table 25 The effect of short days and cool nights on *Typha* growth.

Treatment	No. of buds per plant	Shoot dry weight	Rhizome net dry weight	Total net dry weight	R/S
15 hours of light 25°C day and night	4.3±1.0*	18.9±3.9	21.2±4.0	40.1±5.0	1.2±.2
14/13 hours of light 25°C day and night	5.0±0.5	20.4±2.8	17.5±2.3	38.0±5.0	0.9±.1
15 hours of light 25°C day/15° night	7.1±1.0	13.6±3.3	16.0±4.9	29.6±8.1	1.1±.1

*The mean of five replicates ± standard error of the mean.

Figure 18. The effect of increasing nitrogen concentration on net dry weight.

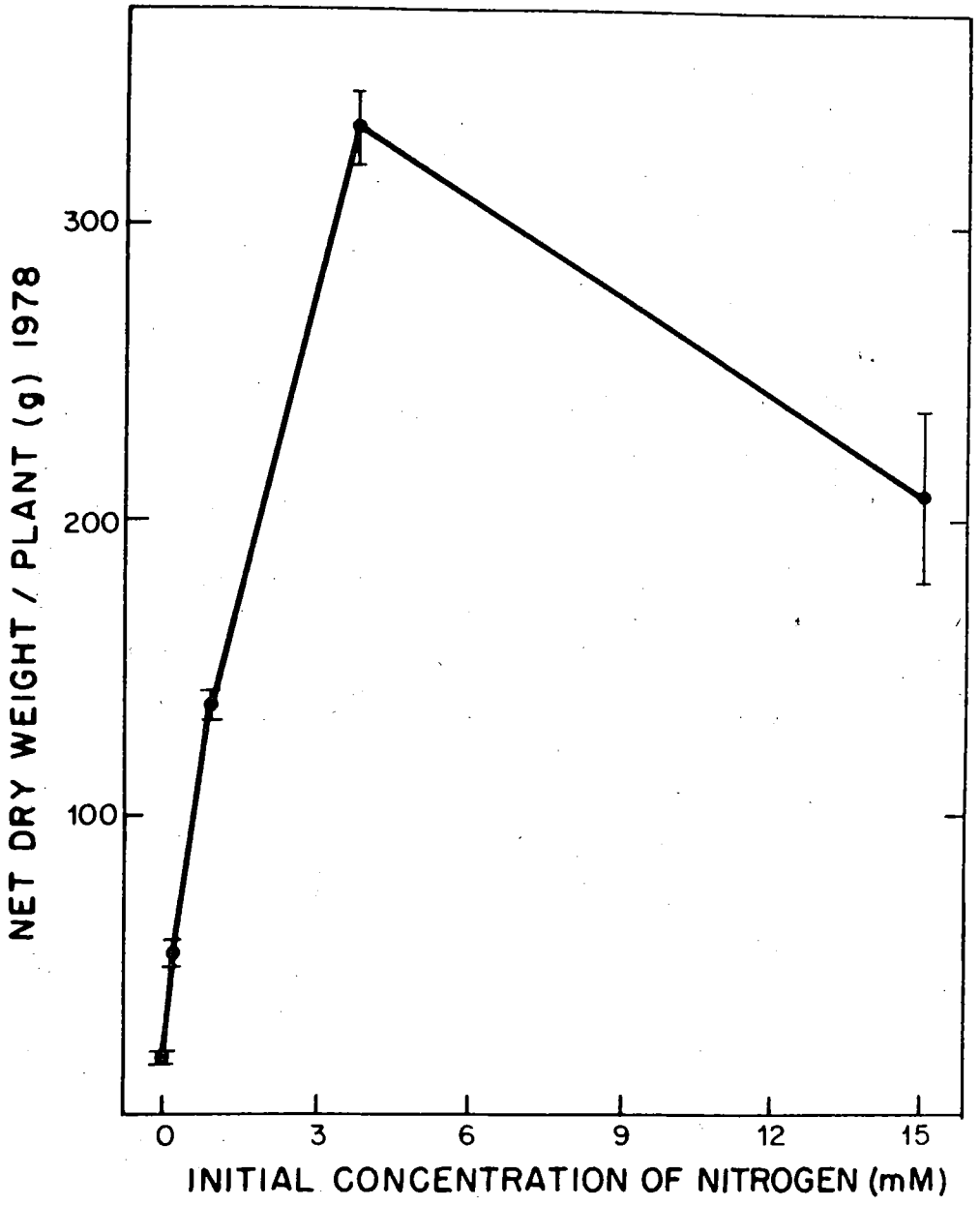

NET DRY WEIGHT / PLANT (g) 1978
300
200
100
0
3
6
9
12
15
INITIAL CONCENTRATION OF NITROGEN (mM)

Figure 19. The effect of increasing phosphorus concentration on net dry weight.

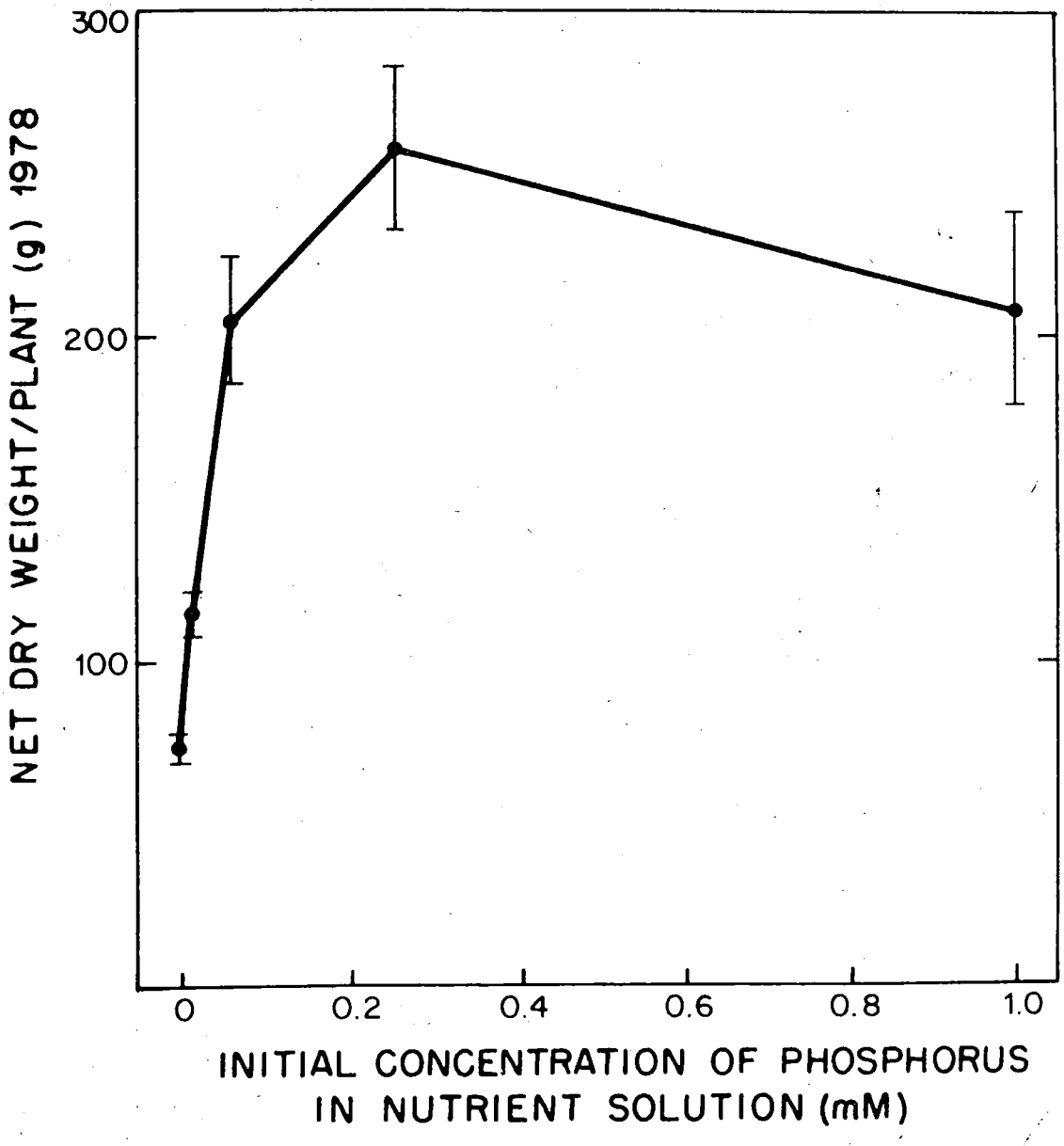

300
200
100
NET DRY WEIGHT/PLANT (g) 1978
0
0.2
0.4
0.6
0.8
1.0
INITIAL CONCENTRATION OF PHOSPHORUS
IN NUTRIENT SOLUTION (mM)

Figure 20. The effects of phosphorus and nitrogen concentration on the ratio of total below ground to above ground dry weight.

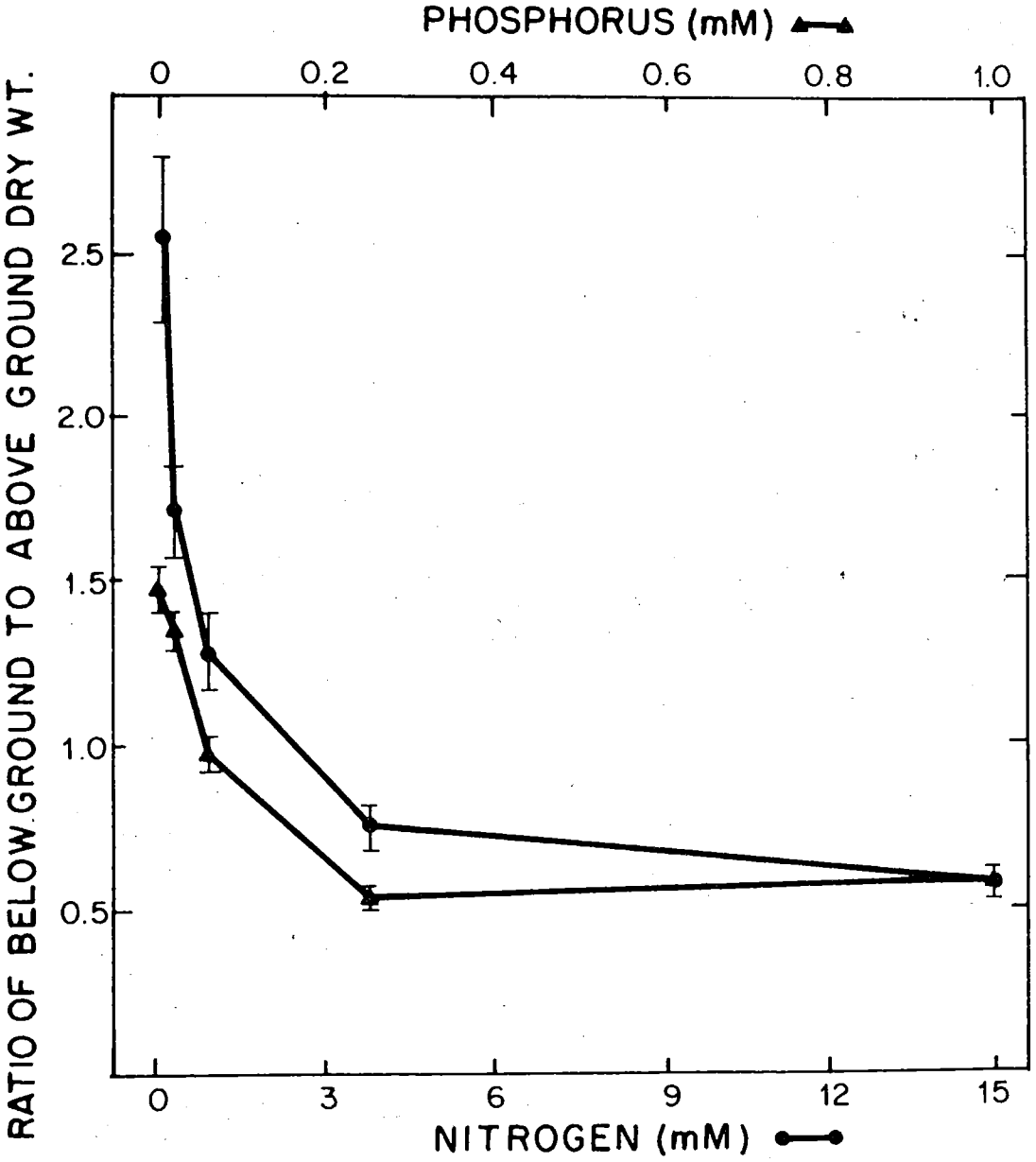
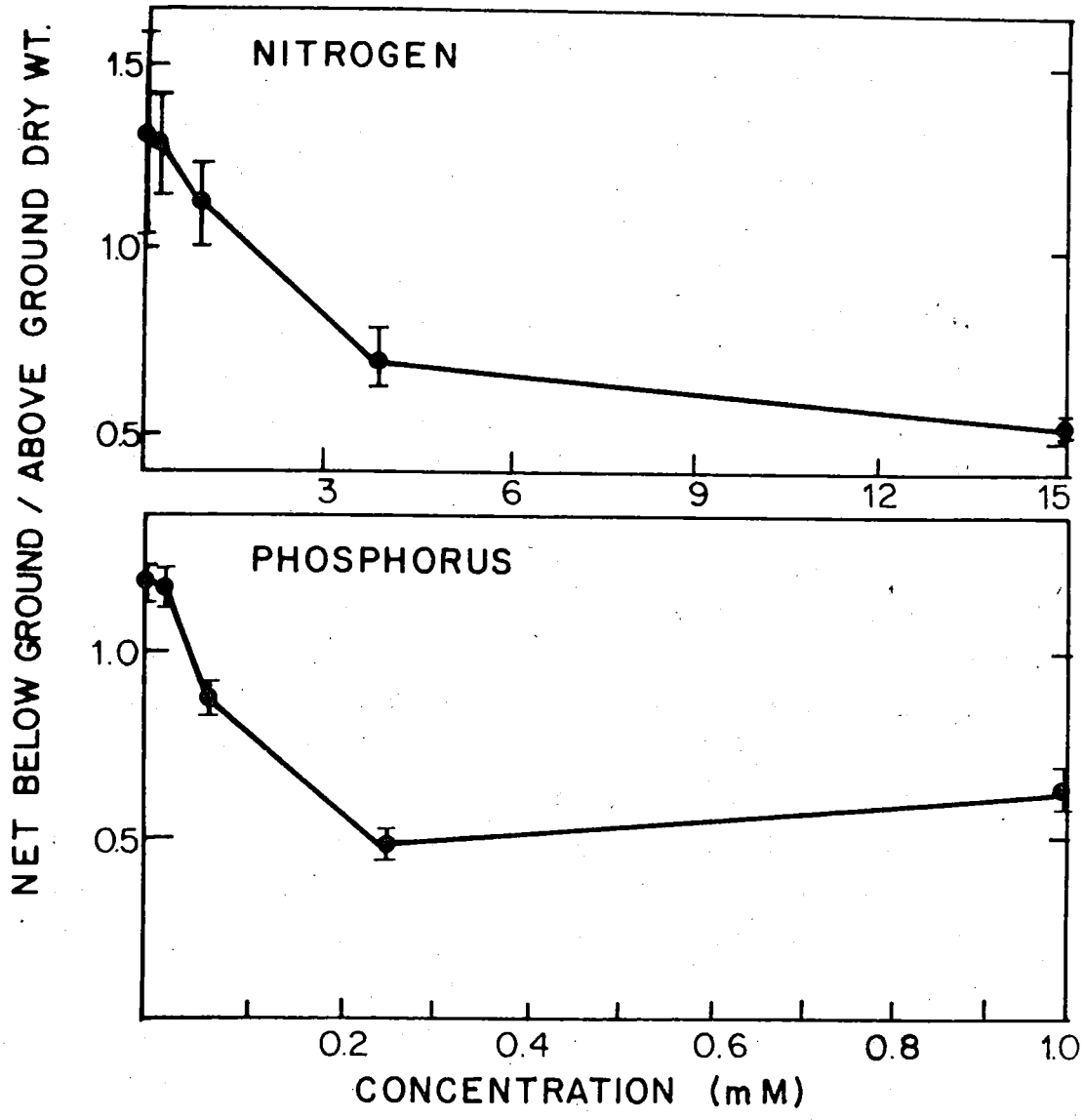

PHOSPHORUS (mM)
0
0.2
0.4
0.6
0.8
1.0
RATIO OF BELOW GROUND TO ABOVE GROUND DRY WT.
2.5
2.0
1.5
1.0
0.5
0
3
6
9
12
15
NITROGEN (mM)

Figure 21. The effect of phosphorus and nitrogen concentrations on the ratio of net below ground to above ground dry weight.


NET BELOW GROUND / ABOVE GROUND DRY WT.
NITROGEN
1.5
1.0
0.5
3
6
9
12
15
PHOSPHORUS
1.0
0.5
0.2
0.4
0.6
0.8
1.0
CONCENTRATION (mM)

The inverse relationship between total R/S ratio and nutrient supply was in part due to the relationship between root development and nutrient supply. The root percentage of total dry weight decreased significantly ($p = .05$) from 14% to 6% for phosphorus and from 28% to 6% for nitrogen (Figure 22). Old rhizomes were the second major contributor to the dimunition of total R/S ratio with increasing nutrient supply. In comparison to complete solutions for both nutrients, lower concentrations resulted in significantly higher proportions of the total biomass contained in the old rhizomes.

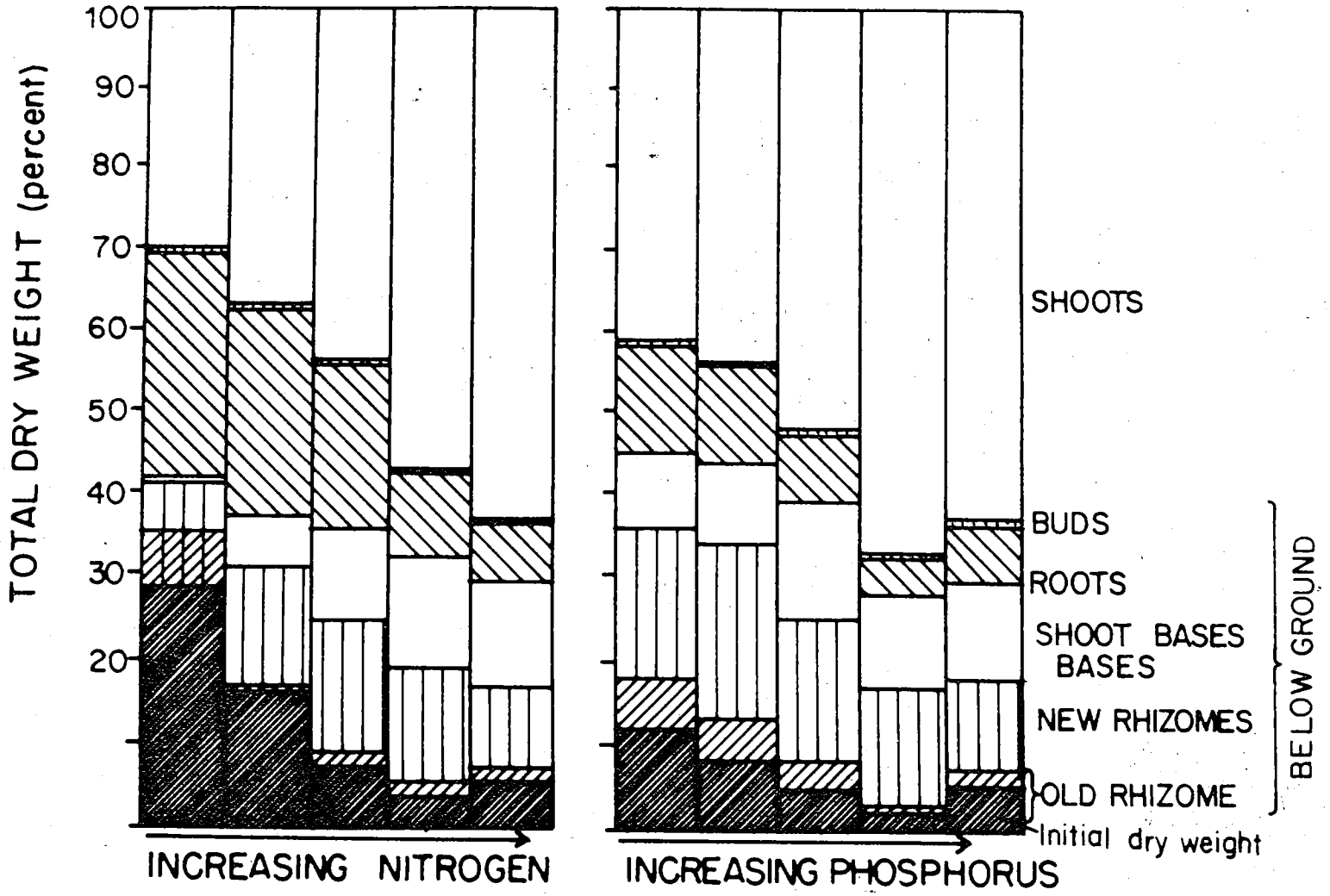
The net dry weight of all storage organs (new rhizomes, old rhizomes, shoot bases) of the 0.06 mM phosphorus treatment was larger than that of the 0.25 mM treatment although the 0.25 mM phosphorus treatment had greater net biomass. However, neither the differences in the dry weight of the total storage organs nor net dry weights of the entire plants were significant ($p = .05$).

Discussion

Induction of dormancy. The temperatures and daylengths used in this study were chosen to represent the natural environment in mid-August when shoot biomass reaches its peak (Andrews and Pratt, 1978). Daylength (sunrise to sunset) is 14 hours in mid-August and by early September has decreased to 13 hours. The average August maximum daily temperature is 27°C and the minimum is 16°C for Minneapolis, MN. While low night temperatures resulted in reduced growth both in the plants studed here and those from northern clones observed by McNaughton (1966), the induction of characteristics associated with overwintering by either thermal or photoperiodic treatments was not clear.

McNaughton (1966) observed the effects of twelve combinations of daylength and temperature. Because his study was designed to study trends associated with latitudinal ecotypes where samples from as many different populations as possible were desirable, the number of replications from each site was small (2). Thus little can be deduced from the

Figure 22. The effects of increasing nitrogen and phosphorus concentrations on the dry weight of individual plant parts.


TOTAL DRY WEIGHT (percent)
100
90
80
70
60
50
40
30
20
INCREASING NITROGEN
INCREASING PHOSPHORUS
SHOOTS
BUDS
ROOTS
SHOOT BASES
BASES
NEW RHIZOMES
OLD RHIZOME
Initial dry weight
BELOW GROUND

clones originating from the same latitude as the material used in our study, particularly since no indication of the variability of the duplicates is given. With this reservation in mind, if his data for mid-continent sites corresponding to latitudes encompassing Minnesota are examined, a possible trend of increasing R/S ratio with decreasing temperature can be observed. There was not a clear relationship between dry weights, R/S ratio or percent starch and photoperiod.

The lack of clear evidence for induction of overwintering characteristics in both studies may not necessarily indicate the proper environmental cues for eliciting them were absent. The variability in the data may have been too great to distinguish the effects of treatments at an acceptable level of significance. Or, the shoots may not have been at the proper developmental stage to respond to the cues. Finally, the plants may respond to additional factors in the natural environment, all of which are needed for overwintering characteristics to develop.

The nature and length of dormancy. Typha dormancy appeared to be a relative dormancy. Although shoots did not develop at temperatures which would normally be encountered in spring (or autumn warm periods), they did not grow at exceptionally high temperatures either. Such narrowing of the range by raising the minimum temperature at which growth occurs is often found in plants of regions subject to long periods of cold (Vegis, 1964). It is possible that the relative dormancy observed was actually predormancy and that rhizomes were harvested before the conditions resulting in true dormancy occurred. Unless freezing temperature is the condition needed for this, it seems unlikely since material harvested when soil temperatures had dropped to nearly the storage temperature grew well.

Dykyjova et al. (1972) found when rhizomes were planted at monthly intervals from November to January in 15° or 20°C greenhouse that those receiving longer cold treatments grew better. All rhizomes began growing in March, hence those treatments having the shortest cold treatment also had the longest exposure to raised temperatures prior to growth. As the rhizomes are living, though not growing, higher temperatures may have increased the respiration rate thus reducing the reserves available for growth.

After five months storage the viability of the rhizomes and shoot bases appeared to decrease, as indicated by declining numbers of shoots (Table 24). This may have been a result of changing conditions for optimum growth. However, since the shoots which did survive showed growth patterns similar to those with less storage, this seems unlikely. With increasing period of storage more and more of the stored material was found to be unusable (rhizomes and buds were grayish and soft as opposed to white and firm), suggesting that bacterial and/or fungal growth was damaging the material. High temperatures (35°C) apparently contributed to susceptibility to pathogens. This is not to suggest that rhizomes cannot be stored successfully for long periods of time. Mature rhizomes stored at 4°C in peat, dirt, or in trays which allowed greater evaporation of excess water remained healthy for 12 months and in some cases two years.

Summary and Recommendations

(1) Where forced plants are desired during the winter months, four months of cold treatment appears to be sufficient for growth where temperatures can be maintained at 25°C. If 35°C can be maintained, then no cold treatment seems necessary.

(2) Storage of rhizomes at 4°C for long periods has been most successful when rhizomes have been kept moist in plastic bags either with or without packing material (i.e., peat or soil). However, excess standing water in the plastic bags was associated with an increased rate of deterioration.

(3) Shoot growth appears more sensitive to cool temperatures than decreasing daylength. Whether or not rhizomes and dormant buds are also induced by cool temperatures is not clear.

(4) Ratios of below ground to above ground biomass decrease with increasing nutrient availability during a single growing season. The applicability of these results to perennial stands is unclear.

V. Harvesting and Stand Establishment

Introduction

Although some work has been carried out in natural stands (Sections I and III), most of our work has taken place in the greenhouse and in artificial paddies. Several small scale experiments were set up at Carlos Avery Wildlife Management Area to see what problems we are likely to encounter when working under less controlled conditions.

Materials and Methods

Study Site. The study sites for all field trials were located within the Carlos Avery State Wildlife Management Area. Mature stands of Typha x glauca along the northern and southern edges of pool 16 were used for the harvesting trials. For the seedling and rhizome establishment studies an area near pool 6 where water levels could be easily controlled was selected. In late May the water level was drawn down to expose a mudflat for the establishment studies.

Total Harvest. To study the regeneration and productivity of Typha following the removal of both above and below ground biomass we harvested six large areas in mid-October 1978 using a dragline. Three of these areas were approximately 3.5 m x 10 m and two were approximately 7.5 m x 10 m. In each area all of the plant material was removed along with 20-40 cm of fibrous peat. Metal stakes were used to mark the boundaries of each area and growth was photographically documented throughout the 1979 growing season. Water level was maintained at 70-80 cm throughout the 1979 growing season.

Above Ground Harvest. These experiments were designed to answer the following questions: (1) What is the effect of the time of cutting on productivity and regeneration? (2) Can the shoots be harvested more than once per season? (3) What effect will harvesting have on productivity the following season? To look at the effects of time of harvest on yield and regrowth, trial plots were cut in June, July, August and September 1978. In June and July 12 plots, 1.25 m x .25 m, were harvested by cutting the shoots off 5 cm above the water

level (partial harvest). (It has been reported that Typha can be eliminated by cutting the shoots off belowwater level.) A sample plot of shoots cut off at soil level was also collected to estimate the amount of standing biomass remaining below the water. In August 12 plots were harvested by cutting the shoots off at the soil surface (total shoot). In September 10 plots were harvested, five with the partial harvest method and five with the total shoot method. To determine whether shoots can be harvested more than once per season, we recut the June and July plots in September (Table 25). In September 1979, at the end of the second growing season, the trial plots were harvested using the total shoot method. Five randomly selected control plots from areas in the stand which had not been disturbed were also harvested to serve as controls.

Seeding and Rhizome Establishment. For the seeding experiment a 4 x 8 plot grid was laid out using 6 inch aluminum edging to enclose each plot. The plots were 1.3 m x 1 m giving a total area of 10.4 x 4 m. The experimental design consisted of 4 randomized blocks with 2 treatments and 4 replicates per block. The treatments were seeded (S) and unseeded (US). Seed was added on May 15, 1979 at a rate of 60 mg per plot. On June 21, 1979 we counted the number of Typha seedlings in each plot and on September 13, 1979 half of the plots were harvested by cutting off shoots at the soil surface. All material was then taken to the laboratory where plants were identified, counted and weighed. Subsamples of each species were dried to constant weight at 70°C. The remaining plots will be sampled at the end of the 1980 growing season.

For the rhizome establishment study planting material was collected from a mature Typha x glauca stand near pool 6 in Carlos Avery and from paddies on the St. Paul Campus which contained second year rhizomes as described in Section III. Seven 1 m^2 plots were established on the existing mudflat and the following treatments were randomly assigned:

Table 25. Harvesting Trials Summary.

1 cutting/season	Yield 1st cutting gm^{-2}	Yield 2nd cutting gm^{-2}	Total yield 1978 gm^{-2}	Regrowth Sept. 1979 gm^{-2}	Regrowth % of control area
Total shoot Aug.	1452		1452	21	2
Sept.	1615		1615	159	10
Partial harvest* Sept.	872		872	1041	66
2 cuttings/season					
Partial harvest* June-Sept.	579	90	669	679	43
July-Sept.	845	57	902	293	19

*Partial harvest: Shoots were cut off 5 cm above H_2O level; yields represent approximately 54% of the total standing crop. Water levels range from 60 to 80 cm.

2 control plots, 2 mature rhizome plots (Carlos Avery material) and 3 "seedling rhizome" plots. Each of the rhizome plots was planted with 25 rhizome pieces. The rhizome material for each plot was weighed and a sample was dried to 70°C to obtain a dry to fresh weight ratio. On September 13, 1979 the above ground material in all 7 plots was harvested. Shoot density and fresh weight were recorded and a subsample was dried as previously described. These plots will be monitored during the 1980 growing season.

Results and Discussion

Total Harvest. There was no visible revegetation in the dredged areas during the 1979 growing season. Figures 23 and 24 show two of the trial plots; these pictures were taken in June and there were not any perceptible changes by September. This was probably due to the high water level (70-80 cm) which was maintained throughout the growing season. High water levels are often used as a management technique to keep emergent aquatics from taking over wildlife areas (Weller, 1975; Harris and Marshall, 1963). Growth in these plots will be monitored throughout the 1980 growing season.

Above Ground Harvest. Table 25 presents a summary of the data from the above ground harvesting trials. It appears that only 1 cutting per season is feasible, at least in north temperate regions. Harvesting the total shoot results in maximum yield for that particular season and minimum regrowth the following season. Regrowth, measured as standing crop at the end of the second season, was 2% with an August cutting and 10% with a September cutting as compared to the control plots that had never been harvested. Regrowth in plots where shoots were cut off 5 cm above the water line (partial harvest) ranged from 19-66% of the controls. Maximum regrowth (66%) occurred in plots cut once in mid-September. Because of the high water levels (60-80 cm) only 54% of the total standing crop could be harvested. With lower water levels more of the above ground material would be available for harvest and regrowth would probably be increased.

Figures 23 and 24. Dredged areas at Carlos Avery, June 1979.

Seedling Establishment. Table 26 presents Typha shoot density per plot for June and September. The mean survival between the two sampling dates was 28%, though individual shoots were not tagged so that the September density also includes shoots that appeared after June 21st. The mean shoot density for the seeded (S) and not seeded (US) plots were 23 and 12, respectively, but differences were not significant (Table 27). Differences between the 4 blocks were not significant either. Shoot densities were much lower by September with a mean of 5 shoots in the seeded plots and 2 shoots in the unseeded plots. This establishment rate is very low particularly when compared to the paddy studies (Section III). Competition from other species was the most important factor. Table 28 presents a list of the species harvested from the plots along with the mean dry weight, shoot density and frequency of each species. Alisma Plantago-aquatica (water plantain) was the most dominant plant with respect to dry weight and frequency. In fact, Typha is 13th of the list with respect to mean dry weight per plot.

As described in the methods section, 16 of the plots were not harvested in September. They will be monitored during the 1980 growing season. It will be valuable to see how well Typha is able to compete, particularly under conditions where the water level fluctuates.

Rhizome Establishment. Table 29 presents a summary of the rhizome establishment trials. The mature rhizomes were the most successful; shoot density increased from the original 25 shoot buds on the rhizomes to a mean of 68 shoots/m^2 for the two plots. Mean above ground dry weight was 586 g/m^2, far below the yields from adjacent natural stands. Mortality was high in the seedling rhizome plots; shoot density decreased throughout the season resulting in a mean density of only 18 shoots/m^2 by September. The control plots contained the species listed in Table 28; only 3 Typha seedlings were found.

Table 26. *Typha* shoot density in June and September.

Treatment	Plot No.	*Typha* density/plot: June 21	Sept. 13
Seeded	1-2	56	1
	1-3	26	9
	1-4	29	0
	1-6	1	
	2-1	96	6
	2-3	39	22
	2-5	13	
	2-6	6	
	3-4	18	2
	3-5	0	
	3-7	42	
	3-8	28	
	4-1	6	0
	4-4	2	0
	4-5	0	
	4-8	12	
Not Seeded	1-1	36	5
	1-5	1	
	1-7	34	
	1-8	16	
	2-2	4	5
	2-4	6	0
	2-7	16	
	2-8	5	
	3-1	8	3
	3-2	1	4
	3-3	0	1
	3-6	5	
	4-2	0	0
	4-3	0	0
	4-6	23	
	4-7	44	

Table 27. Summary of *Typha* shoot density in June and September.

Treatment	June 21*	Sept. 13*
Seeded (S)		
Number of plots	16	8
Mean shoot density/ plot	23	5
Stand deviation	25.7	7.6
Unseeded (US)		
Number of plots	16	8
Mean shoot density/ plot	12	2
Stand deviation	14.4	2.2

*Differences between treatments are not significant at the .05 level.

Table 28. Species list from seedling establishment experiment.

Species	Mean Dry Weight, g/m^2	Shoot Density/m^2	Frequency, %
Alisma Plantago-aquatica L.	27	9.3	100
Sium suave Walt.	17	5.9	81
Polygonum sagittatum L.	12		50
Polygonum pensylvanicum var. *laevigatum* forma *pallescens* Stanford	9		62
Bidens connata var. *petiolata* (Nutt.) Fairwell	8	3.2	62
Polygonum natans forma *Hartwrightii* (Gray) Stanford	7		88
Sagittaria latifolia Willd.	7	6.1	94
Crucifer sp.	3	5.6	75
Carex sp.	3	12.1	69
Scutellaria sp.	3	17.2	69
Scirpus sp.	2	2.5	37
Cicuta bulbifera L.	1	4.4	100
Typha sp.	1	2.8	38
Galium trifidium L.	1		44
Lycopus americanus Muhl.	2	1.2	38
Miscellaneous	.8	4.2	

Table 29. Summary of rhizome establishment results.

	Planting Density Rhizomes/m^2	Dry Weight of Planting Material, g/m^2	Shoots/ m^2 Sept.	Shoot Dry Weight Sept. g/m^2
Mature Rhizomes				
(1)	25	887	67	621
(2)	25	942	69	551
mean			68	586
Seedling Rhizomes				
(1)	25	37	12	25
(2)	25	40	18	30
(3)	25	40	24	73
mean			18	43
Control Plots				
(1)	0		3	3
(2)	0		0	

Recommendations

(1) More extensive harvesting trials are needed; larger areas should be harvested using commercially available or specially designed equipment.

(2) Water level is a critical factor in the amount of material that can be harvested (partial harvest) and in subsequent regrowth; studies should be carried out in areas with good water control systems.

(3) More extensive seeding studies are needed; having control of the water level is essential.

(4) Rhizome planting appears to be the most reliable method; a small pilot project will be carried out in 1980.

(5) Competition from other species is a major problem particularly if seeds rather than rhizomes are used. Water level manipulation and the use of herbicides to control competition should be investigated.

(6) Rhizomes should be planted as early as possible; the feasibility of planting in the fall should be investigated.

(7) The effects of fertilizer additions on both seed and rhizome establishment should be studied.

VI. Analysis of Canopy Structure and Radiation Profiles in a Natural Typha x glauca Community.

Introduction

The potential of Minnesota wetlands to produce energy crops has been the focus of several research programs at the University of Minnesota. Alnus spp., Salix spp. (Farnham, 1978), Typha spp. (Fox, 1975; Moss, 1977; Pratt, 1978; Andrews and Pratt, 1978; Bonnewell and Pratt, 1978), Phragmites communis, Carex spp. and Phalaris arundinacea are all being considered as potential biomass crops. Typha spp. is the most productive of these species with above ground standing crops often exceeding 15 tons/hectare (van der Valk & Davis, 1978) and with total biomass often exceeding 40 tons/hectare (Fox, 1975; Andrews and Pratt, 1978). The efficiency of Typha as a solar collector is due to the following factors:

(1) Water is not a limiting factor.

(2) Nutrient availability from run-off and decomposition is high (Pearsall, 1954; Boyd and Hess, 1970; Boyd, 1971).

(3) Owing to its perennial habit the canopy expands rapidly in early spring at the expense of carbohydrates stored the previous season (Bray et al., 1959; Bray, 1960; Jervis, 1969; Linde et al., 1976; Gustafson, 1976).

(4) A canopy structure which optimizes both leaf area and the penetration of light throughout the canopy.

Many investigators have analyzed canopy structures and radiation profiles for crop plants (Monsi and Saeki, 1953; Nichiporovich, 1961; de Wit, 1965; Duncan et al., 1967; Loomis et al., 1968; Duncan, 1971; Monsi et al., 1973; Turitzin, 1978). Particularly, Kvet et al. (1969) and Dykyjova (1971a and b) have analyzed the canopy structure of the Typha community and emphasized the received radiation efficiency. Fox (1975) and Gustafson (1976) have recognized the importance of leaf inclination and orientation on dry matter production in Typha but did not analyze it in detail.

The purpose of the present study was to present a detailed analysis of the canopy structure and resultant radiation profiles of a natural Typha community in Minnesota.

Material and Methods

Study Area. The study area, located in the Carlos Avery Wildlife Management Area, was a large (ca. 2 hectares) homogeneous stand of Typha x glauca surrounded by lowland forest. The water level was artificially maintained at approximately 20 cm throughout the season.

Sampling Dates. All samples and measurements were taken on the following dates: May 25, June 4, June 21, July 19, August 27 and September 13, 1979. Owing to overcast conditions light readings were not taken on sampling dates 1 and 2.

Growth Analysis. To analyze the seasonal growth pattern of the canopy, seven .5 m x .5 m quadrats of above ground material were harvested on each sampling date. Shoots were clipped off at the soil surface, placed in plastic bags, and taken to the laboratory where each shoot was washed, cut off at 20 cm (H_2O level) and then cut into successive 40 cm segments. The material from each 40 cm segment or layer was then subdivided into the following categories: (1) leaves, (2) stems and leaf sheaths, (3) reproductive structures and (4) dead material. Leaf area was then measured for each stratum using a Hayaski Denko AAM-5 automatic leaf area meter. All material was then dried to constant weight at 70°C.

Light Distribution. The vertical distribution of light intensity was determined using a Licor model LI-185A Photometer and a LI-190X Quantum Sensor (PAR). A grid was established on each sampling date by running string horizontally between two stakes. Starting at water level strings were placed at 20 cm intervals and light intensity was recorded at each level within the canopy with above canopy readings serving as the controls (Figure 24). All light measurements were taken in the time interval 30 minutes before and 30 minutes after 12 noon on clear, calm days.

Leaf Orientation and Inclination. To describe leaf configuration within the canopy, leaf orientation for each interval was determined using a compass and a large plexiglas plate marked off at 15° intervals. The orientation of the

Figure 24. The study area with reference grid.

apices of at least 70 leaves for each interval were recorded. Leaf inclination, the angle of the leaf lamina to a horizontal plane, was measured using a plexiglas plate marked off at 5° intervals and a plumb line. Thirty leaf angles were determined for each 40 cm interval. All measurements of leaf orientation and inclination were made during periods when there was little or no detectable air movement.

Results and Discussion

Shoot Biomass. In 1979 the overwintering shoots began to expand in mid-May. Figure 25 presents the seasonal distribution of biomass in stems, leaves, reproductive structures, total shoot and dead material. The maximum average shoot dry weight, 1690 gm/m^2, and average stem dry weight, 960 gm/m^2, were obtained in late August while maximum leaf dry weight, 663 gm/m^2, occurred in mid-July. Dead material, most of which was leaves, was first noticed in mid-July and gradually increased to 44% of the total leaf biomass and 22% of the stem biomass in the final September 13 sampling date. The male and female reproductive structures were first observed on July 21 after which total dry weight increased to an average dry weight of 88 gm/m^2 by September 13. The decline in total shoot biomass after the seasonal maximum in late August can be attributed to the following factors: (1) the loss of leaves (Penfound, 1956; Boyd, 1971; Dykyjova, 1971b; Gustafson, 1976), (2) translocation of photosynthate to reproductive structures (Linde et al., 1976), and (3) translocation of photosynthate from shoots to rhizomes (Andrews and Pratt, 1978).

Leaf Area. Figure 26 presents the seasonal change in the leaf area index (LAI) which is a measure of the surface area of leaves/ground area (m^2/m^2). The maximum average LAI occurred in mid-July, was sustained through late August and then diminished. Thus for Typha the maximum canopy coverage is maintained over an interval of approximately 50 days. This is an important characteristic of perennial herbaceous

Figure 25. The seasonal distribution of above ground biomass.

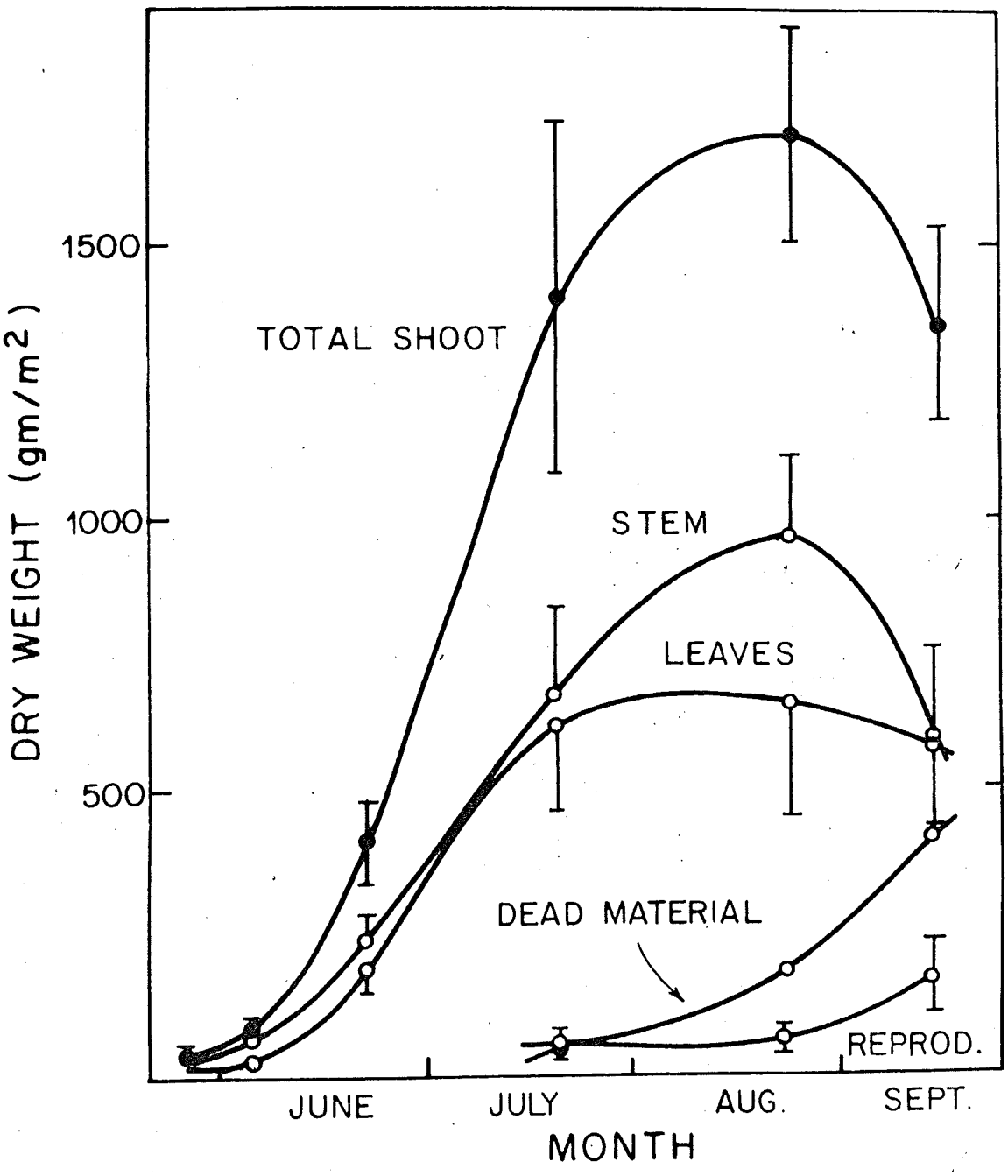
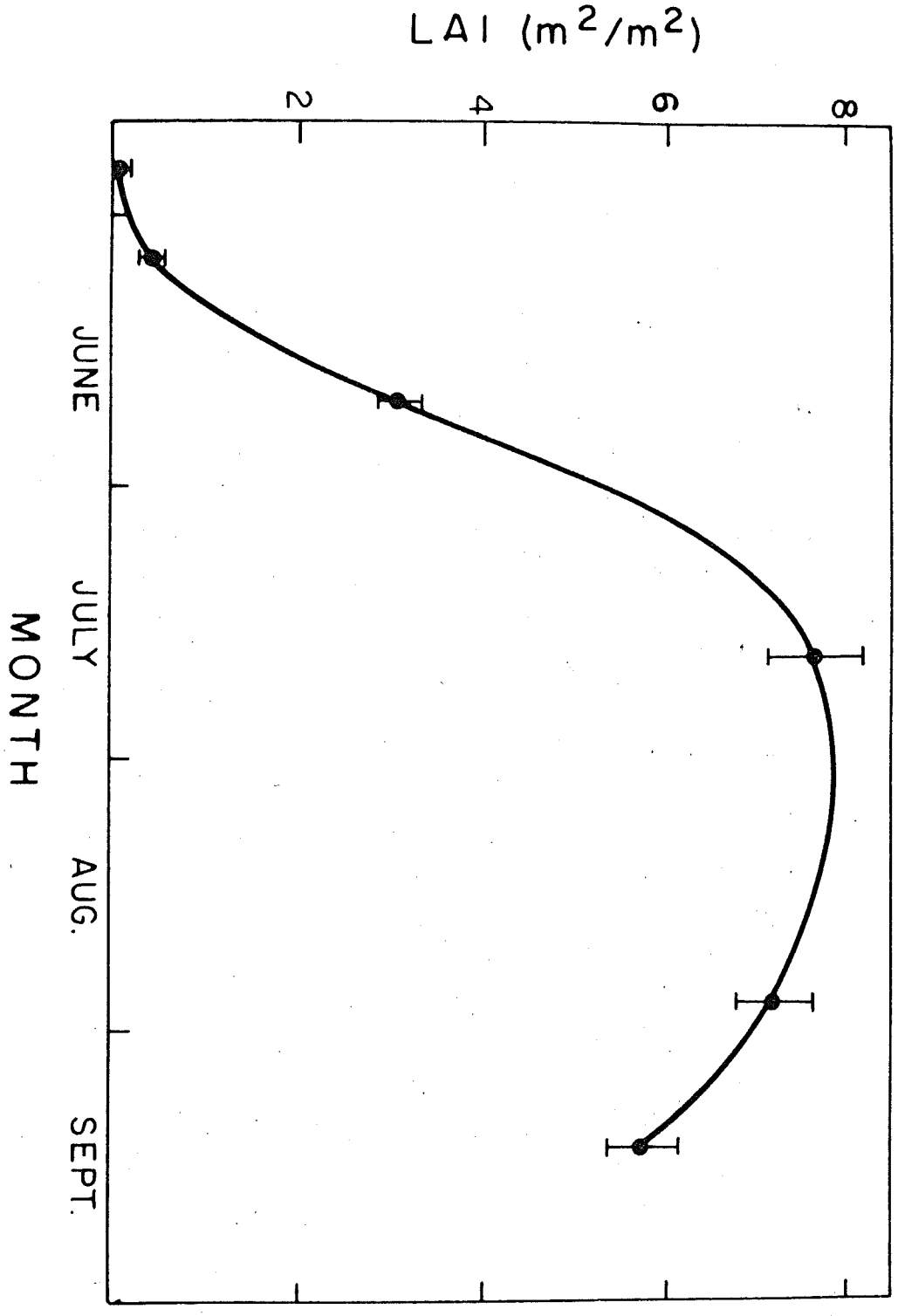

1500
1000
500
DRY WEIGHT (gm/m²)
TOTAL SHOOT
STEM
LEAVES
DEAD MATERIAL
REPROD.
JUNE
JULY
AUG.
SEPT.
MONTH

Figure 26. Seasonal changes in leaf area index (LAI) for the Typha canopy.


LAI (m^2/m^2)
2
4
6
8
JUNE
JULY
AUG.
SEPT.
MONTH

plants which accumulate carbohydrate reserves in overwintering underground storage organs and then use these reserves to establish the canopy the following season. The maximum LAI obtained in this study, 7.6, is substantially less than the range reported in the literature, 9.3-17.4 (Jervis, 1969; Dykyjova, 1971; Moss et al., 1977; Andrews and Pratt, 1978). This discrepancy may be due in part to the various methods used to measure LAI (Gustafson, 1976) since the maximum total shoot biomass obtained in this study (1630 gm/m^2) equals or exceeds those reported in the articles cited above.

Specific leaf area (SLA), leaf area per unit leaf dry weight (cm^2/g), with height for four of the sampling dates is depicted in Figure 27. In each curve the SLA above about 100 cm is directly proportional to shoot height while below 100 cm it is inversely proportional to shoot height. This relationship is due to the structure of the Typha leaf lamina which is much thicker at the base. This and other aspects of leaf structure and orientation which contribute to Typha's efficiency as a solar collector will be discussed in subsequent sections. The leftward shift of the SLA curves as the season progresses is due to leaf elongation as the stand reaches its maximum height.

Leaf Orientation and Inclination

Figure 28 presents leaf azimuth orientation with the Typha canopy for four of the sampling dates. In the earlier stages of canopy development the leaves tended to be oriented to the south and northwest (June 21) and north and south (July 19). This pattern appears to be due to the alternate production of leaves as shown by Linde et al. (1976). As the season progressed leaf orientation appeared to be randomly distributed (August 29, September 13). This uniform spatial arrangement of the leaves within the canopy allows for maximum interception of incident radiation per unit area.

The leaf inclination data are presented in Figure 29. The lines within each canopy layer depict the mean angle of the leaves from the horizontal. The frequency distribution

Figure 27. Specific leaf area (SLA) within the *Typha* canopy.

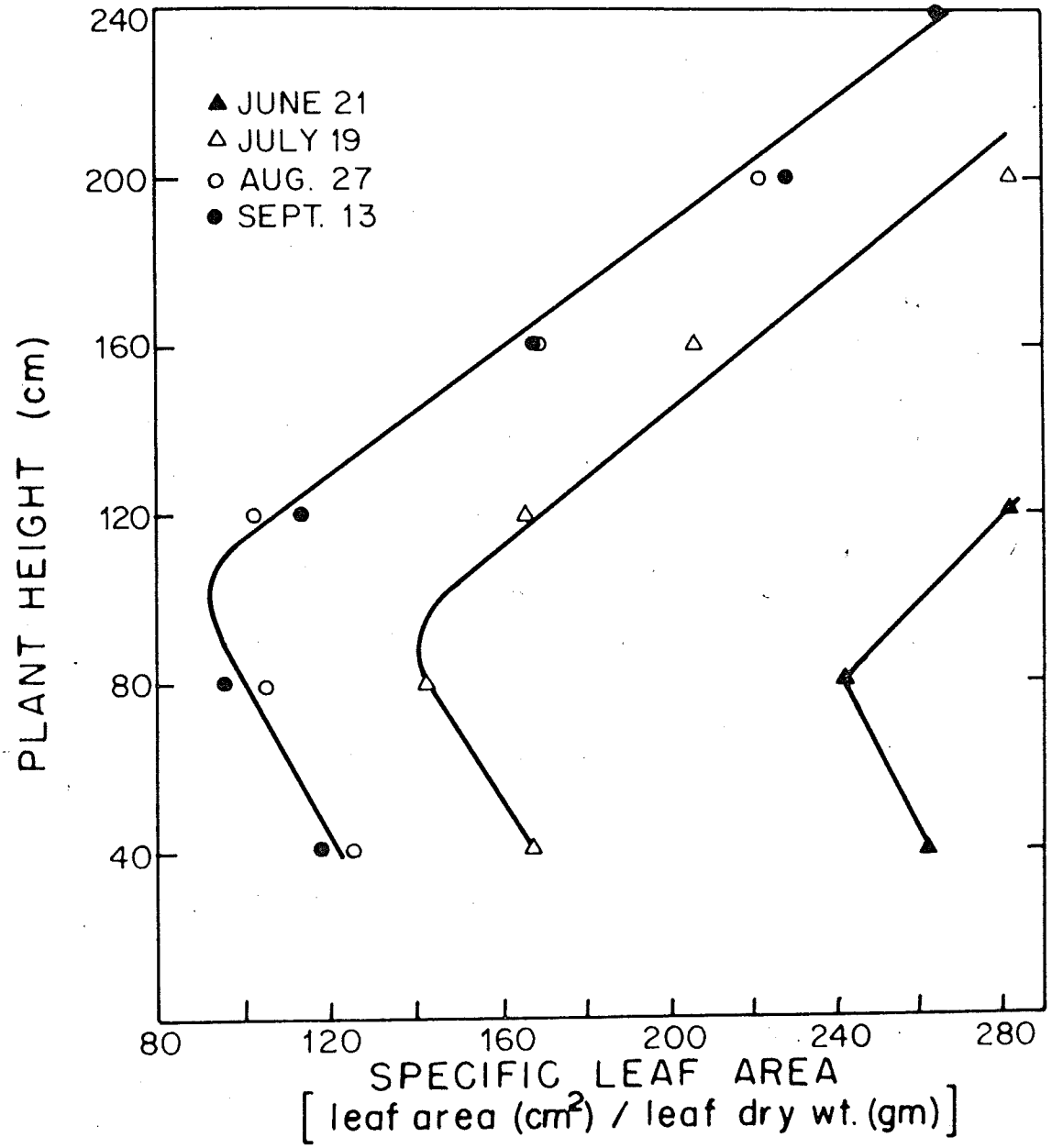

240
200
160
120
80
40
PLANT HEIGHT (cm)
▲ JUNE 21
△ JULY 19
o AUG. 27
● SEPT. 13
80
120
160
200
240
280
SPECIFIC LEAF AREA
[leaf area (cm²) / leaf dry wt. (gm)]

Figure 28. Leaf azimuth orientation within the Typha canopy.

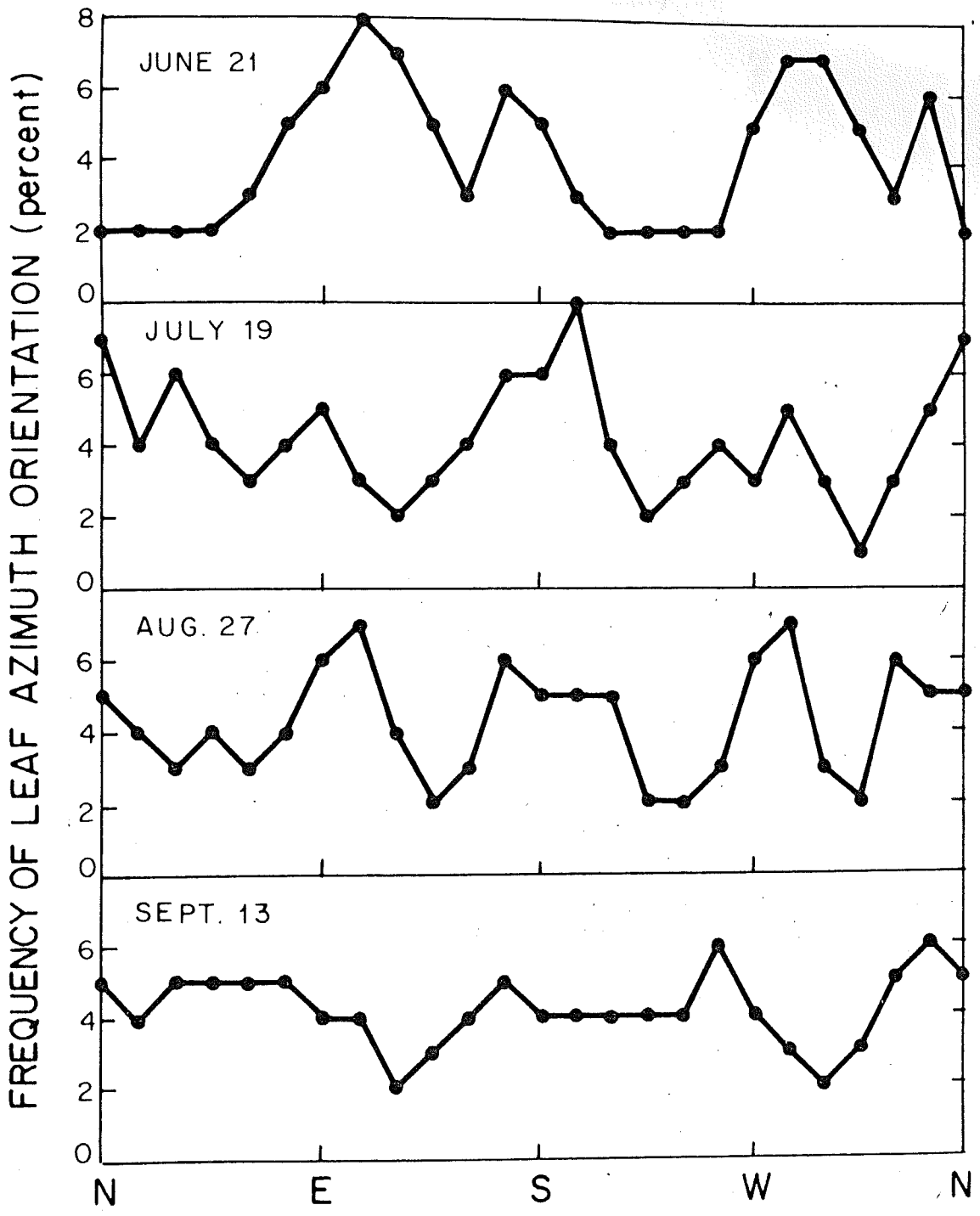
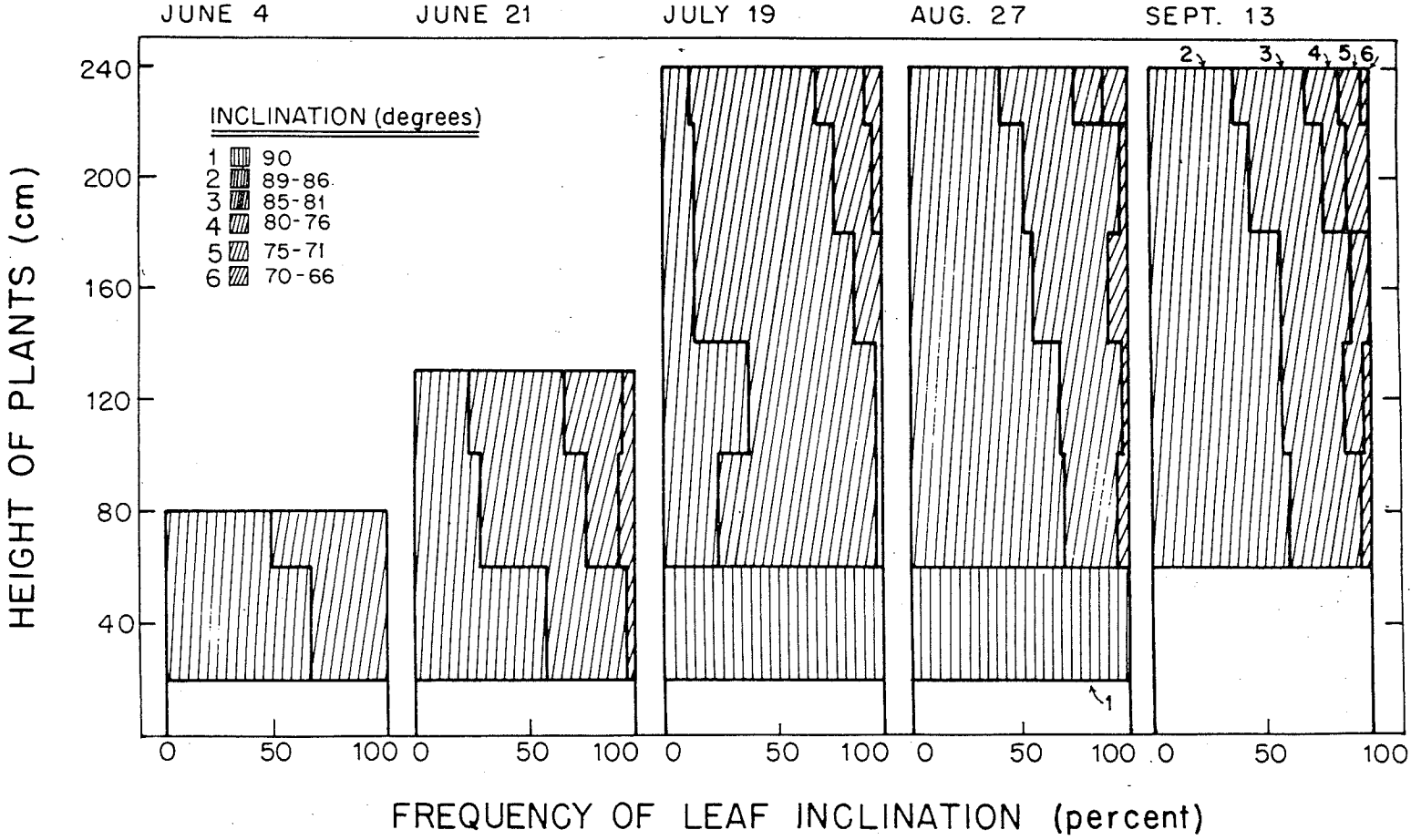

FREQUENCY OF LEAF AZIMUTH ORIENTATION (percent)
JUNE 21
JULY 19
AUG. 27
SEPT. 13
0
2
4
6
8
N
E
S
W
N

Figure 29. Frequency of leaf inclination throughout the *Typha* canopy for 5 sampling dates.


JUNE 4
JUNE 21
JULY 19
AUG. 27
SEPT. 13
INCLINATION (degrees)
1 90
2 89-86
3 85-81
4 80-76
5 75-71
6 70-66
240
200
160
120
80
40
HEIGHT OF PLANTS (cm)
0
50
100
FREQUENCY OF LEAF INCLINATION (percent)

of leaf inclination varied with plant height as well as leaf age. The Typha canopy is dominated by long narrow spiralling leaves ("ribbonlike") with high leaf angles. Thus, leaf shading is kept to a minimum while light penetration into the lower layers of the canopy is maximized. Near-vertical leaves were abundant in the lower and middle layers of the canopy, while the upper layer contained a minor subset of low-angle leaves which increased as the season progressed.

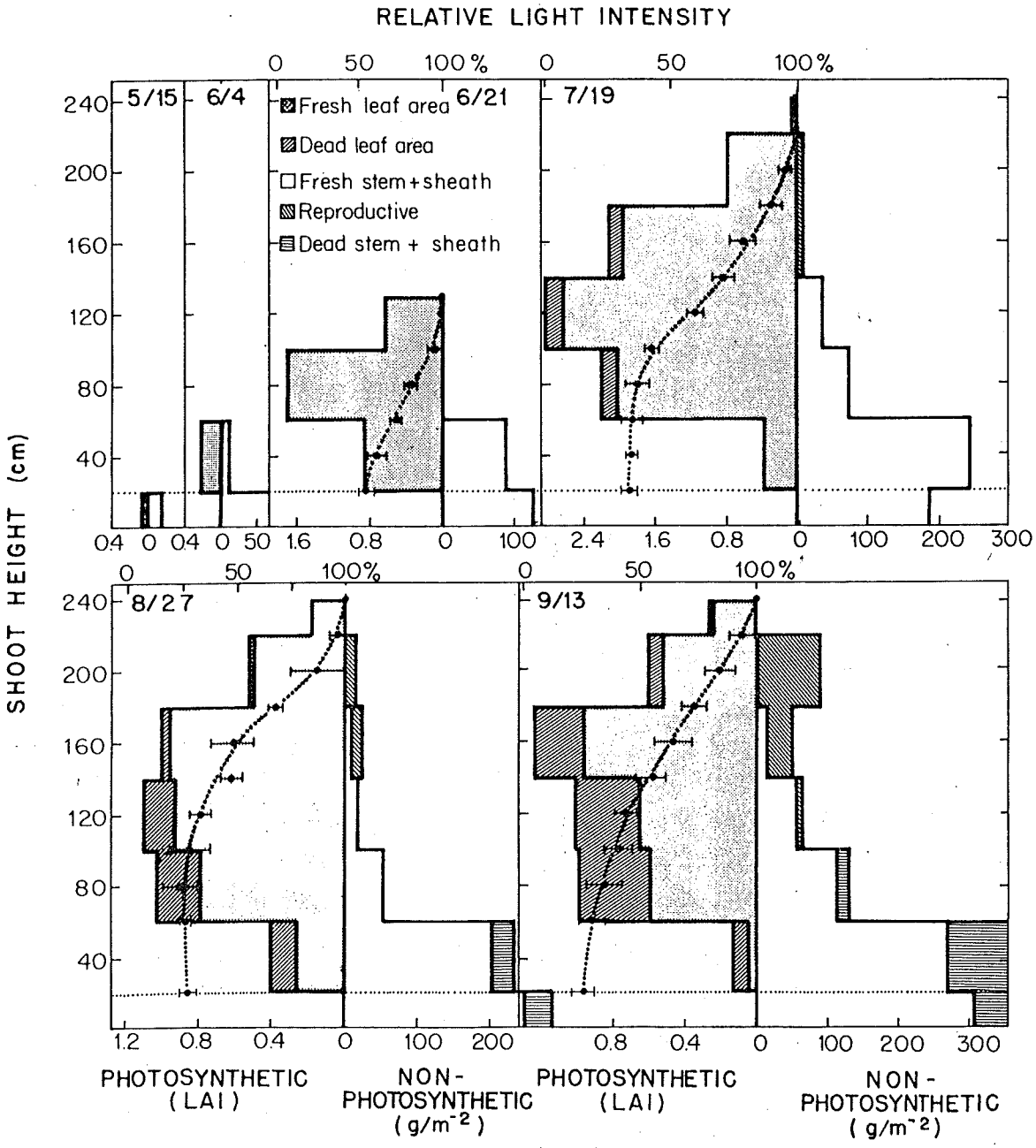
The leaf angles of Typha are higher than those reported for wheat (Nichiporovich, 1961), corn (Loomis et al., 1968), or sugar cane (Hodanova, 1972). The architecture of the Typha canopy is classified as "erectophile" (de Wit, 1965) owing to the high percentage of high-angle or vertically oriented leaves. Duncan et al. (1967) reported that plant productivity is directly related to leaf angle for many plant communities. The vertical distribution of mean leaf inclination in the Typha canopy approaches the theoretically most efficient canopy structure for maximum productivity described by Kuroiwa (1970) and Duncan (1971).

Productive Structure and Vertical Light Distribution

The productive structure of the Typha community is characterized by the narrow leaf type (Monsi and Saeki, 1953) and substantial leaf area in the middle and lower strata of the canopy (Fig. 30). In a mature stand the green leaf area is distributed vertically between 60-240 cm. Figure 30 presents the radiation profiles within the canopy along with leaf area for several sampling dates through the season. Radiation profiles, the vertical distribution of light intensity within the canopy, show exponential attenuation from full sunlight above the canopy to the surface of the water (20 cm). The relative radiation intensities at water level were 53.3, 32.5, 34.0 and 25.4% on June 21, July 19, August 29 and September 13, respectively.

Gustafson (1976) reported that saturation radiation intensity for gross photosynthesis with Typha was 600-800 $\mu Em^{-2}S^{-1}$. In this study the photosynthetically active

Figure 30. Radiation profiles and leaf area within the canopy.


RELATIVE LIGHT INTENSITY
0 50 100%
5/15
6/4
6/21
7/19
8/27
9/13
Fresh leaf area
Dead leaf area
Fresh stem+sheath
Reproductive
Dead stem + sheath
SHOOT HEIGHT (cm)
240
200
160
120
80
40
0.4 0 0.4 0 50
1.6 0.8 0 100
2.4 1.6 0.8 0 100 200 300
1.2 0.8 0.4 0 100 200
0.8 0.4 0 100 200 300
PHOTOSYNTHETIC (LAI)
NON-PHOTOSYNTHETIC (g/m⁻²)
PHOTOSYNTHETIC (LAI)
NON-PHOTOSYNTHETIC (g/m⁻²)

radiation (400-600 nm) at noon was measured at 2000 $\mu Em^{-2}S^{-1}$. It is assumed, therefore, that all of the leaves within the Typha canopy are light saturated at noon on clear days. The quantitative analysis of the vertical productive structure and the radiation distributions reported here are similar to those described by Kvet et al. (1969) and Dykyjova (1971a, 1971b) for natural Typha communities in Czechoslovakia.

The radiation profile for the canopy is closely related to the vertical distribution of leaf area. The structure of the upper layer of the canopy is the most critical in determining radiation penetration. To assess the efficiency of received ratiation, the relationship between LAI and vertical radiation penetration was determined using the Bouger-Lambert law:

$$I = I_o e^{-KL}$$

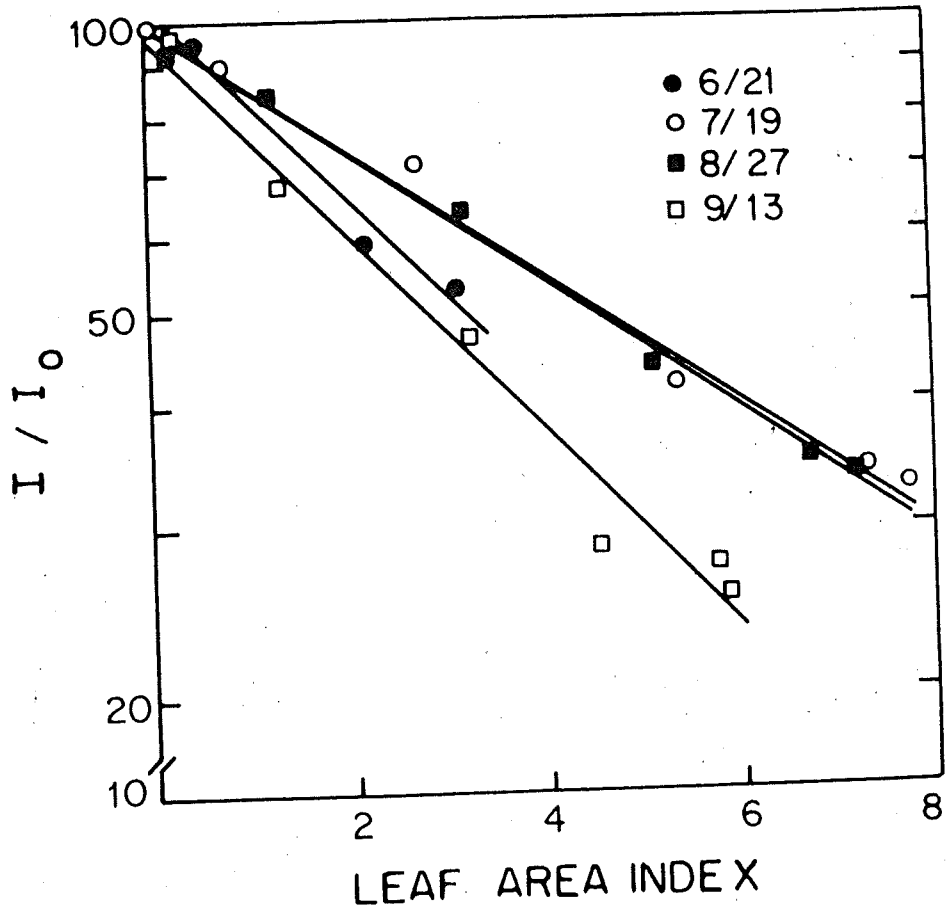
where, I and I_o refer to radiation intensities on a horizontal surface within and above the canopy;

L is the leaf area index;

K is the extinction coefficient.

The extinction coefficient (K) is a constant determined by leaf angle, leaf thickness, reflectivity and chlorophyll content of a particular species. Despite the limitations of this formula (Anderson, 1966) it is well adapted for use with the Typha canopy structure. Radiation interception profiles (Fig. 30) were characterized using the log of the relative radiation intensity (log I/I_o) and the cumulative LAI starting from the top of the canopy (Fig. 31). The extinction coefficients (K) derived from the data were .2033, .1173, .1231, and .2032 on June 21, July 19, August 29 and September 13, respectively. The K for Typha is close to that for Miscanthus sacchariflorus (Monsi and Saeki, 1953) but less than those reported for corn (Loomis et al., 1968), barley (Udagawa and Uchijima, 1969), or sugar beet (Hodanova, 1972). The maximum average daily rate of photosynthesis in a Typha community is approximately 8 gCm^{-2} (Gustafson, 1976) which is less than half the maximum rates reported for corn (Loomis et al., 1967). In spite of this the annual biomass yield from corn

Figure 31. Radiation interception profiles for the Typha canopy on 4 sampling dates.


100
50
20
10
I / I o
2
4
6
8
LEAF AREA INDEX
● 6/21
○ 7/19
■ 8/27
□ 9/13

is often only half that of Typha (Pratt and Andrews, 1980). Typha's high productivity can be attributed to its efficient canopy structure including the uniform leaf azimuth orientation, high leaf angles and the vertical leaf distribution.

Recommendations

Before an extensive plant breeding program can be established, those characters which contribute most to overall yields must be analyzed. Clonal material from the most productive natural stands should be collected and grown under uniform conditions. Detailed analyses of canopy architecture should be carried out.

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