

FACTORS INFLUENCING SHOOT PRODUCTION AND MINERAL NUTRIENT LEVELS IN *TYPHA LATIFOLIA*¹

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Abstract. Shoot standing crops for *Typha latifolia* ranged from 423 to 2,252 g dry wt/m². Standing crops were positively correlated with concentrations of dilute acid soluble phosphorus in hydrosols and dissolved phosphorus in the waters. Except for a weak correlation for dissolved calcium, additional site fertility parameters were not correlated with standing crop. Tissue nutrient levels varied considerably, maximum values for most minerals being three or four times as great as the smallest values. Correlations between environmental levels of several nutrients and tissue concentrations were significant, but not very strong. Tissue concentrations of most nutrients were positively correlated with nitrogen content. Despite variations in tissue levels of nutrients, standing crop was the decisive factor determining quantities of nutrients per unit area of stand.

Between site variation in standing crops of certain aquatic vascular plants have been reported (Westlake 1963, Boyd 1968, 1969a), but little is known regarding relationships between site fertility parameters and standing crops. From the limited data available, the nutrient composition of a particular species appears to vary greatly between sites (Boyd 1969a, 1969b). However, stage of maturity influences tissue nutrient levels (Stake 1967, 1968, Boyd 1969a, 1970b) and some of the variation in previous studies may have been due to plant age rather than environmental factors. The nutrient composition of aquatic plants has been reported to increase with increasing environmental nutrient levels (Boyd 1969a), but this relationship is not clear cut and probably differs with both species and individual elements. The present study was initiated to obtain detailed data on variations in shoot standing crop and mineral composition for populations of *Typha latifolia* L. from a large number of sites. Relationships between site fertility and standing crop were also investigated.

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MATERIALS AND METHODS

In order to obtain samples from stands in comparable stages of development, collections were made during a fairly short period (June 8-14, 1969). Stands were located over a fairly large geographic area (Fig. 1). Some of the popula-

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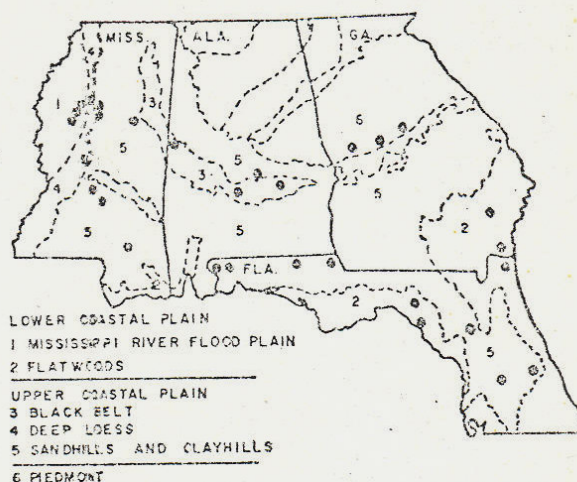


FIG. 1. Physiographic and geographic location of sampling sites for *Typha latifolia*.

tions initiated spring growth earlier than others, so to further insure that the samples were of comparable ages, only flowering populations that were producing pollen were considered. Other criteria for selecting populations were that the communities contained at least 90-95% *Typha* biomass, that density and shoot height was fairly uniform, and that the stands were at least 0.1 ha in size. Several major physiographic regions were represented in the sampling area. Stands were located in farm ponds, vernal ponds, drainage ditches and swamps. Water table depths ranged from about -5 to +76 cm. Such a wide range of habitat types hopefully insured near maximum variability in the characteristics measured.

Three 1-m² quadrats were harvested from the uniform portion of each stand. Shoots were cut at soil level and the wet weight of each quadrat was determined. Two or three shoots from each quadrat were then weighed and placed loosely into

paper bags. The plants rapidly air dried and there was no indication of fermentation. Upon return to the laboratory, the samples were dried at 60°C for 72 hr in a large forced draft oven and reweighed to determine the original dry matter content. These values were used to recalculate quadrat weights to a dry basis. Dried material was pulverized in a Wiley mill and stored for analysis.

Three soil cores were taken with each quadrat and composited to make a sample. A water sample was obtained from most collecting sites. The soil and water samples were kept on dry ice during transit. The soil samples were dried at 60°C and pulverized with a mortar and pestle. Water samples were stored in a freezer until time for analysis.

Procedures for extracting dilute acid soluble phosphorus and exchangeable cations from soils were reported in Jackson (1958). Phosphorus was measured by the chlorostannous-reduced molybdophosphoric blue method (Jackson 1958). A Perkin-Elmer model 290 atomic absorption spectrophotometer was used to measure exchangeable cations in soil extracts. Soil organic matter was estimated by the Walkley-Black procedure (Allison 1965).

Nitrate and phosphate were determined according to the American Public Health Association (1963). Dissolved cations were measured by atomic absorption spectrophotometry.

Procedures for plant analyses used in the present study have been reported elsewhere (Boyd 1970b).

RESULTS AND DISCUSSION

Variation in standing crop

Standing crop values ranged from 428 to 2,252 g/m² (Avg 951 g/m²). Coefficients of variation for means of the three quadrats from each stand ranged from 4 to 50%, but most coefficients were between 20 and 30%. Within site variation was less for productive sites than for unproductive sites. Samples were taken from the uniform, and usually most productive, area of the stands, so means were considered a good estimate of maximum production for each site. The highest frequency of values was between 500 and 900 g/m² (Fig. 2). The histogram was skewed to the left and 86% of the populations contained less than 1,300 g/m² and 57% were below 900 g/m². McNaughton (1966) reported *Typha* shoot standing crops of 378-1,336 g/m² for five stands located on a north-south transect through the central United States. Bray, Lawrence and Pearson

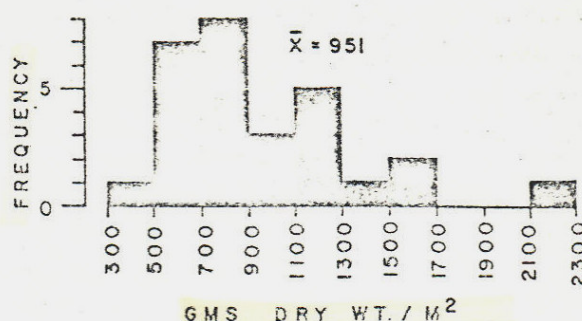


FIG. 2. Frequency distribution histogram for standing crops of *Typha latifolia*. Class intervals are indicated along the base of the histogram.

(1959) have summarized shoot standing crop data for *Typha* ranging from 1,070 g/m² in England to 1,731 g/m² in New England. Bray (1960) reported 1,400 g/m² of shoots in a Minnesota *Typha* stand. These data are in general agreement with those in the present study. McNaughton (1966) found that 50% or more of the total biomass of *Typha* stands was root material. Data in the present study do not allow an estimate of total net production, but labor requirements for root excavation would have limited the study to a few stands.

Individual shoots were not weighed, but it was apparent that standing crop was a function of shoot weight. Most of the productive sites contained less shoots per square meter than unproductive stands, but the shoots in productive populations were taller and more robust.

Site factors and standing crop

Certain physiographic regions had higher standing crops than others. For example, three stands from the Mississippi River flood plain averaged 1,225 g/m², whereas the mean of three stands from the piedmont region of Georgia was 561 g/m². Depth of water had no effect on standing crop. Means for populations from ponds, ditches and swamps were 925, 995 and 875 g/m², respectively.

The sites represented a wide range of soil fertility and water quality (Table 1). Soils varied from sands to heavy clays and from inorganic to highly organic soils. Soil nutrients exhibited a similar range. Waters ranged from very soft to moderately hard. There was a particularly wide range in calcium/magnesium ratios and in sodium concentrations. Nutrient levels in hydrosols and waters were closely related.

Correlation coefficients between hydrosol fertility parameters and standing crops were: organic matter 0.23, calcium 0.29, magnesium 0.17, potassium 0.12, sodium 0.23 and phosphorus 0.71 ($P < 0.01$). Kjeldahl nitrogen and reserve sul-

TABLE 1. Range of fertility parameters for sites from which *Typha latifolia* was collected

Parameter	Soil		Water	
	Min.	Max.	Min.	Max.
Organic matter (%)	1.60	30.45	—	—
Phosphate (ppm as P)	1.0	116.0	0.02	0.32
Nitrate (ppm as N)	—	—	0.01	0.45
Calcium (ppm)	153.0	6,437.0	2.2	53.0
Magnesium (ppm)	11.0	703.0	0.62	20.61
Potassium (ppm)	14.0	779.0	0.3	31.0
Sodium (ppm)	37.0	472.0	3.4	118.4

fur were not measured since each is a function of soil organic matter (Jackson 1958, Sanford and Lancaster 1962). The highly organic sites undoubtedly had large concentrations of inorganic nitrogen and sulfur since these nutrients are mineralized from organic matter by microbial activity. Soil phosphorus accounted for about 50% of the variation in standing crop. This was a fairly high correlation since the populations were located over a wide range of soil variable, some of which influence phosphorus availability. Much of the available phosphorus had already been absorbed by the plants. An average value for soil weight per unit area to a depth of 15 cm (Jackson 1958) was used to calculate the ppm phosphorus that had been removed from the soil by the plants. When this phosphorus was added to the extractable phosphorus, a correlation of 0.80 ($P < 0.01$) was obtained.

Water samples were obtained from all but five of the stands. Correlation coefficients between dissolved nutrients and standing crop were: nitrate 0.15, phosphorus 0.82 ($P < 0.01$), potassium 0.21, sodium 0.22, calcium 0.45 ($P < 0.05$) and magnesium 0.20. The correlation for calcium accounted for only 20% of the variation in standing crop. Phosphorus was strongly correlated with standing crop and accounted for 67% of the variability. The correlation for dissolved phosphorus was better than the correlation for dilute acid-soluble phosphorus. Dilute acid (0.002N H_2SO_4 buffered with K_2SO_4) extracts phosphorus that is readily available to plants (Jackson 1958), but dilute acid-soluble phosphorus is also correlated with water-soluble phosphorus (Boyd unpublished data). In addition, equilibrium processes between phosphorus in hydrosol and in water occurs at a rapid rate (Hayes and Phillips 1958). In view of these facts, the high correlation for water-soluble phosphorus was not surprising. Dissolved phosphorus is simpler to measure than hydrosol phosphorus and should be used for any subsequent site fertility studies on *T. latifolia*.

Mineral nutrient concentrations in plants

The tissue concentrations of ash and mineral nutrients decline as *Typha* matures (Boyd 1970b). The central Florida stands were undoubtedly older than the others, but with the exception of calcium and magnesium, the marked decreases in nutrient levels occur before fruiting, and all stands in the present study should have been comparable. Some of the variation in composition was probably due to differences in stages of growth, but a considerable amount of the variation was no doubt due to other factors. Means for individual sites were calculated and frequency distribution histograms (Fig. 3) were prepared to illustrate variation in chemical constituents. Ash values were about equally distributed between 4 and 9%, only three samples containing above 9%. Most carbon values were between 45–47%. On a dry weight basis, carbon decreased with ash content ($r = -0.83$; $P < 0.01$). However, on an ash-free dry weight basis, carbon and ash levels were not related ($r = 0.03$). Ash-free carbon ranged from 47.95 to 50.57% (Avg 49.19%). Values for individual mineral nutrients varied greatly. Maximum values for nitrogen, phosphorus, calcium and potassium were three to five times as large as minimum levels, while the greatest levels of sulfur and sodium exceeded the smallest by 10- and 20-fold, respectively. There were statistically significant differences (Avg. ± 2 se did not overlap) between some stands for all constituents. In a study of nutrient levels of 18 species in a single lake (Boyd 1970a), species differences in concentrations of individual macronutrients were very similar in magnitude to the variation reported in *T. latifolia*. Sodium was the most variable constituent in both cases. The variation in the species of a single community appears to be no greater than the variation of a single species from different sites. Distribution of all nutrients except sodium in *T. latifolia* formed a more or less bell shaped curve. In view of the few really extreme values and the obvious peak median frequency for most nutrients, the data probably give a good estimate of the range of variation that can be expected in *T. latifolia*.

Correlation coefficients between nutrient levels in the water and tissue concentrations were; phosphorus 0.44 ($P < 0.05$), calcium 0.35, magnesium 0.18, potassium 0.50 ($P < 0.01$) and sodium 0.56 ($P < 0.01$). Correlation coefficients for soil vs plant nutrient levels were; phosphorus 0.39, calcium 0.18, magnesium 0.46 ($P < 0.01$), potassium 0.20 and sodium 0.53 ($P < 0.01$). None of the correlations accounted for more than 32% of the variability in tissue concentrations of an element.

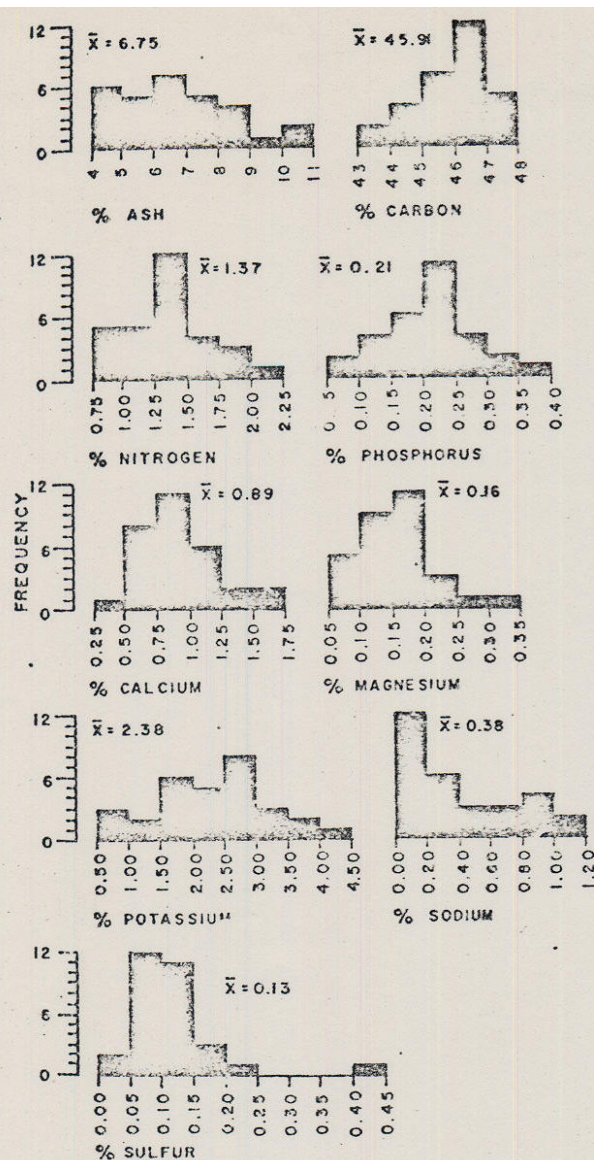


FIG. 3. Frequency distribution histograms for concentrations of various constituents (dry wt. basis) in *Typha latifolia*. Class intervals are indicated by numerals along the base of the histograms.

Studies on native aquatic plants (Boyd and Lawrence 1966, Boyd 1969a) did not reveal high correlations between external and internal nutrient levels. Cultures of aquatic plants (Gerloff and Skoog 1954, 1957, Gerloff and Krombholz 1966) absorbed nutrients in relation to external concentrations. However, the nutrient in question was the only variable. Many interrelationships exist between the concentrations and ratios of ions in the environment and the uptake of these ions by plants (Sutcliffe 1962). Sites for the present study represented a wide range of concentrations of all nutrients and nutrient ratios varied greatly between sites. Environmental factors other than

TABLE 2. Correlation coefficients (r) and regression equations for the relationship between tissue levels of nitrogen (X-variable) and other constituents in *Typha latifolia*

Constituents (y)	r	Regression equation
Ash.....	0.656**	$1.562 + 3.772 X$
Phosphorus.....	0.702**	$-0.019 + 0.166 X$
Sulfur.....	0.592**	$0.004 + 0.032 X$
Calcium.....	-0.052	—
Magnesium.....	0.041	$-0.009 + 0.127 X$
Potassium.....	0.733**	$-0.435 + 2.048 X$
Sodium.....	-0.051	—

**Significant at the 0.01 level of probability.

nutrient regimes also influence nutrient uptake. Therefore, the lack of strong correlations was not surprising.

Relationships between tissue concentrations of nutrients were considered to ascertain if the level of any one nutrient could be used to predict other nutrient levels. Correlation coefficients between nitrogen and other constituents except calcium and sodium were significant (Table 2). Although nitrogen content was strongly correlated with the accumulation of several nutrients, no correlation existed between nitrogen content and standing crop. There was a significant correlation between tissue phosphorus and standing crop ($r = 0.45$, $P < 0.05$).

Another possible source of variation in nutrient and standing crop values

In addition to environmentally induced variation, information regarding the systematic status of *Typha latifolia* may have a bearing upon the interpretation of data for plant nutrient levels and dry matter standing crop. According to Smith (1967), *T. latifolia* and *T. domingensis* are sympatric in southern Georgia and in Florida and *T. domingensis* is the more frequently occurring species of *Typha* in this area. The authors examined the populations very carefully and sampled only those populations that based on field characteristics were easily recognized as *T. latifolia*. However, hybrids of *T. domingensis* and *T. latifolia* are common in areas where the two species are sympatric (Smith 1967), and some of the populations may have been intermediates of the two species. Information on standing crop and mineral nutrient levels in *T. domingensis* are not available. In view of results for other closely related species (Boyd 1968, 1970a), the two species would be expected to differ to some extent with respect to these parameters. The influence of possible *T. latifolia* \times *T. domingensis* intermediates upon the data is not expected to be great. How-

ever, one must be careful in attributing the variation in standing crop and nutrient levels entirely to environmental factors and to possible ecotypic variation between the *T. latifolia* populations.

Quantities of constituents in the stands

Preparation of nutrient budgets for freshwater ecosystems necessitate information on standing crops of organisms and their chemical composition. Equations, based on dry matter standing crops, for calculation of quantities of nutrients contained per unit area of stand for a particular species would be very helpful. In view of the wide variation in nutrient content (Fig. 3), such equations might not appear possible. However, tissue concentrations for productive populations were higher than those for unproductive populations. This relationship did not hold for intermediate standing crops. Correlation coefficients and regression equations for the relationship between standing crops and grams nutrient per square meter are given in Table 3. All *r* values are highly significant. In the cases of ash, carbon, phosphorus, nitrogen, calcium and sodium standing crop ac-

TABLE 3. Correlation coefficients (*r*) and regression equations for the relationship between standing crop (X-variable) and g/m² of ash and nutrients in *Typha latifolia* stands

Constituent (y)	<i>r</i>	Regression equation
Carbon.....	0.99**	-9.09+0.46 X
Ash.....	0.67**	24.41+0.04 X
Nitrogen.....	0.76**	-0.22+0.01 X
Phosphorus.....	0.69**	3.09+0.01 X
Sulfur.....	0.50**	0.28+0.001 X
Calcium.....	0.79**	0.64+0.008 X
Magnesium.....	0.54**	0.60+0.001 X
Potassium.....	0.52**	8.31+0.01 X
Sodium.....	0.68**	-2.90+0.007 X

**Significant at the 0.01 level of probability.

counted for 50% or more of the variation on grams nutrient per square meter. Nutrient inputs for natural systems are usually impossible to ascertain with a high degree of precision, so estimates of these six constituents in *Typha* stands from standing crop data should be sufficient for most nutrient budget studies. Similar data are needed for additional aquatic and terrestrial species. Although different species vary in nutrient content, it may be possible to use standing crop to estimate quantities of nutrients even in mixed stands without separating the component species.

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