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PHENOTYPIC AND GENOTYPIC COMPONENTS
OF GROWTH AND REPRODUCTION IN *TYPHA LATIFOLIA*:
EXPERIMENTAL STUDIES IN THREE CONTRASTING MARSHES

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James Benjamin Grace

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PHENOTYPIC AND GENOTYPIC COMPONENTS OF GROWTH AND REPRODUCTION IN *TYPHA LATIFOLIA*: EXPERIMENTAL STUDIES IN THREE CONTRASTING MARSHES

By

James Benjamin Grace

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ABSTRACT

PHENOTYPIC AND GENOTYPIC COMPONENTS OF GROWTH AND REPRODUCTION IN *TYPHA LATIFOLIA*: EXPERIMENTAL STUDIES IN THREE CONTRASTING MARSHES

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James Benjamin Grace

The objective of this study was to separate the genotypic and phenotypic variation in biomass allocation for populations of *Typha latifolia* from habitats of differing successional maturity. Field studies revealed that the OPEN marsh population of *T. latifolia* suffered high levels of ramet mortality over winter and had rapid growth in ramet numbers during the growing season. In contrast, the WOODS marsh population suffered predominantly from growing-season mortality with little ramet death over winter. The CATTAIL marsh population was intermediate in mortality patterns to the other two populations. Tissue nutrient analyses and fertilization experiments revealed that *T. latifolia* in the OPEN marsh was principally nutrient limited while *T. latifolia* in the WOODS marsh was light limited. The CATTAIL marsh population was exposed to conditions of nutrients and light intermediate to the other populations.

Field studies of ^{14}C fixation and allocation showed that both sexual and vegetative reproduction consisted of greater percentages of biomass production in the OPEN marsh population than in the CATTAIL or WOODS marsh populations. Ramets in the CATTAIL and WOODS marsh populations allocated a greater percentage of their fixed carbon to growth of the parent ramet. Allocation to roots was greatest in the OPEN marsh population and experiments showed this response to result from low nutrient availability. Leaf biomass was a fixed percentage of the total biomass under all conditions but the leaf volume/leaf weight ratio was greatest in the WOODS marsh population. Experiments revealed that the differences in leaf volume/weight were principally the result of light availability, but that decreased wind exposure also contributed to the high leaf volume/weight ratio.

Differences in biomass allocation under uniform garden conditions indicated biotypic differences among populations such that habitats exposed to high levels of disturbance contained biotypes with high allocation to sexual reproduction. In contrast, the biotype from the habitat with the most intense level of density stress (WOODS-CATTAIL marsh biotype) allocated more biomass to root production, a trait potentially important for competition.

Transplantation of biotypes into natural habitats showed that under nutrient limiting conditions the WOODS-CATTAIL marsh biotype was more productive than the OPEN marsh biotype. This difference resulted from differences in allocation patterns whereby the OPEN biotype allocated a greater percentage of biomass to rhizome storage for sexual reproduction and the WOODS-CATTAIL biotype allocated more to root growth. Under light limiting conditions no differences in productivity between biotypes occurred. It is concluded that both genotypic and phenotypic variation in biomass allocation contribute to the growth and reproduction of _T. latifolia_ over a broad range of habitats differing in successional maturity.

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STATEMENT OF PROBLEM

A central problem of plant population biology is to elucidate the significance of intraspecific variation in morphology, physiology and life history. Numerous studies have dealt with the contribution of intraspecific variation to the growth of a species over a range of environmental conditions, especially over latitudinal and altitudinal gradients (Clausen et al. 1948, McMillan 1960,1969, Mooney and Billings 1961, McNaughton 1966, 1973, 1974). Over the past decade plant ecologists have been especially interested in how intraspecific variation contributes to the ability of a species to persist in a habitat over successional time (Harper and Ogden 1970, Gadgil and Solbrig 1972, Abrahamson and Gadgil 1973, Ogden 1974, Solbrig and Simpson 1974, Abrahamson 1975a,b, Snell and Birch 1975, Holler and Abrahamson 1977, Law et al. 1977, Roos and Quinn 1977, Reader 1978).

One of the principle changes that occurs in a habitat over successional time is an increase in plant density. Concomitant with increasing density is a lowering of available resources per individual, a decrease in plant growth rates and a decrease in average plant size (Harper 1977). In addition to numerical changes in density and plant size, qualitative changes in the growth form of competing species also tend to change from small, short-lived herbaceous species to erect trees and shrubs (depending on the overall environmental constraints)(see Harper 1977 for review). These changes in growth form as well as the interactive effects on soil and micrometerological conditions may result in a shift from water or nutrient limitation to light limitation. The overall effect of these various changes results in a change from conditions that are open to colonization to conditions in which seedling survivorship is very low and most of the mortality in the population results from density effects.

The results of studies of intrapopulation variation across successional habitats show a trend of decreasing sexual reproductive effort (allocation of biomass to sexual reproduction as a percent of total biomass)(Abrahamson and Gadgil 1973, Solbrig and simpson 1974, Abrahamson 1975a, Law et al. 1977, Roos and Quinn 1977, Reader 1978) and/or a longer time to first reproduction (Law et al. 1977, Roos quinn 1977) with increasing successional age. Exceptions to this generalization include cases where allocation to sex is a fixed quantity (Harper and Ogden 1970, Ogden 1974, Holler and Abrahamson 1977) or does not relate to habitat maturity (Hickman 1977). A similar trend also exists for vegetative reproduction (cloning) with a greater allocation occurring in open habitats (Ogden 1974, Abrahamson 1975a, Holler and Abrahamson 1977). Intraspecific variation in morphology and growth form also has been observed. A shift in relative allocation from roots to leaves sometimes accompanies increases in plant density (Abrahamson and Gadgil 1973, Abrahamson 1975a, Holler and Abrahamson 1977). One case exists, however, where the opposite trend was reported for a case where water became more liniting with increasing successional maturity (Reader 1978). Further, studies of photosynthetic adaptation have revealed lower light compensation points, lower light saturation values, and narrower temperature optima for leaves from shaded habitats (Bjorkman and Holmgren 1966, Gauhl 1976, Teramura and Strain 1979).

Intraspecific variation may result from the phenotypic plasticity of a single genotype (within-genotype component) or the differential phenotypic responses of more than one genotype (between-genotype component). These sources of variation are seldom distinguished in studies of intraspecific variation. Studies in which these sources of variation have been distinguished include the work of Solbrig and Simpson (1974,1977) who reported on biotypes of Taraxicum officinale Weber. which differed in their patterns of biomass allocation. Biotypes from highly disturbed habitats possessed short stature and allocated a greater percent of their biomass to sexual reproduction than did biotypes from more successionally mature sites. Competition experiments between these biotypes showed the low-reproductive biotype to be competitively superior to the high-reproduction biotype over a range of conditions. However, when subjected to mowing the high-reproduction biotype lift more offspring than the low-reproduction biotype. Studies by Law et al. (1977) on Poa annua L. showed that genotypes from successionally young habitats had shorter pre-reproductive periods, higher seed output and shorter lives than genotypes from successionally mature habitats. Several authors have shown intraspecific variation in sexual reproductive effort to be entirely due to phenotypic plasticity (Hickman 1975, Snell and Birch 1975, Roos and Quinn 1977, Holler and Abrahamson 1977). Also, in some cases sexual reproductive effert has been found to be a constant percentage of total biomass and quite insensitive to environmental conditions (Harper and Ogden 1970, Ogden 1974).

Studies of the causes of intraspecific variation in vegetative reproduction are few, but to date none have demonstrated genetic variation in the allocation of biomass to vegetative reproduction. (Ogden 1974, Snell and Birch 1975, Holler and Abrahamson 1977). In contrast, studies of intraspecific variation in photosynthetic properties of leaves have revealed genetic variation for light saturation, temperature optima and light compensation levels depending on the degree of shading in the native habitat (Bjorkman and Holmgren 1966, Gauhl 1976, Teramura and Strain 1979).

The purpose of this study was to investigate the magnitude and causes of intraspecific variation in biomass production and allocation, and morphology for *Typha latifolia* L. from three marshes which can be distinguished by their successional maturity. The first stage of investigation was to determine the environmental characteristics of the three marshes and the characteristics of the *T. latifolia* populations. Second, *in situ* studies of ^{14}C fixation and allocation were used to determine the phenotypic variation in biomass production and allocation. Third, populations were sampled for genotypic variation in biomass allocation patterns by comparing growth in controlled garden experiments. Fourth, the growth of different biotypes was compared by transplantation into natural stands of *T. latifolia*. And fifth, the intraspecific variations were considered in terms of their consequences for the persistence of *T. latifolia* in habitats over successional time.

INTRODUCTION

It is of fundamental interest to consider how the morphological and physiological variability of a species determines the range of conditions over which that species can grow and reproduce. For example, how does intraspecific variation in biomass allocation contribute to the persistence of a species in a community that changes with time? MacArthur and Wilson (1967) considered this problem for species colonizing islands and sparked numerous studies which have dealt with the influence of increasing density effects on resource allocation and life history (cf. Stearns 1976, 1977 for review). The general finding for plant communities has been that closed communities with high density levels are characterized by plants that allocate more resources to growth, while open communities consist of plants that allocate more to reproduction. In most cases it is not known how much of the phenotypic variation is the result of genotypic variation (although there are exceptions, e.g. Gadgil and Solbrig 1972, Holler and Abrahamson 1977, Law _et al_. 1977). Indeed, Roughgarden (1974) has pointed out the importance of knowing if a population is polymorphic containing specialists or monomorphic containing one generalist type. The importance of distinguishing the within-genotype variance from the between-genotype variance is that these represent biologically different solutions to a common problem. In plant populations the within-genotype variance is a reflection of the phenotypic plasticity of individuals to their environment while the between-genotype variation reflects genetic variation within the population.

The objective of this study has been to separate the phenotypic and genotypic variation in biomass allocation for populations of the cattail, Typha latifolia L., for habitats that differ in their intensity of density effects. Comparison of populations from open and closed communities are assumed to be representative of the changes that would occur within a single community given sufficient time. After examining the causes of variation in biomass allocation the consequences of these variations are considered for the growth and reproduction of T. latifolia in communities ranging from open to closed.

Characteristics which make T. latifolia suitable for my purposes include the following: (1) T. latifolia occurs across a broad range of habitat conditions. (2) Ecotypic differences have been reported for Typha latifolia across latitudinal and altitudinal gradients (McNaughton 1966). (3) Genetic variation in reproductive effort and growth form has been observed for T. latifolia (McNaughton 1966).

T. latifolia is a rhizomatous, herbaceous perennial (Fig. 1). Vegetative reproduction is accomplished by the production of lateral rhizomes which terminate in a system of leaves and flowering structures. The ramet can then be defined as a rhizome and its associated leaves, roots and flowering structures (in contrast, a genet is the entire set of ramets that result from a single seed and are therefore genetically identical). Sexual structures consist of separate male and female inflorescences located terminally on an erect flowering stalk that originates from the basal meristem (Fig. 1). Despite being technically protogynous, self-pollination is highly favored over cross pollination with seed set being as high as 50% in selfed flowers (Krattinger 1975). Fruits are wind dispersed for great distances with the aid of a hydroscopic pappus of fine hairs (Hotchkiss and Dozier 1949). Seed germination is commonly 100% under laboratory conditions but the factors

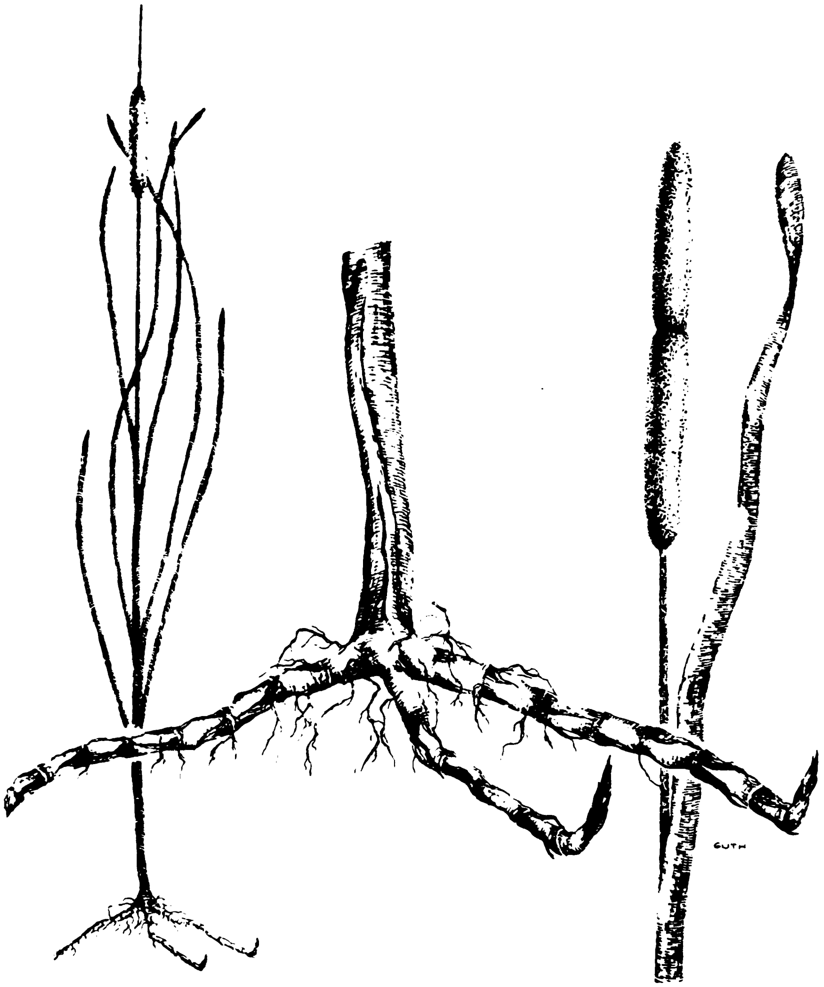

Figure 1. Typha latifolia.

inhibiting germination in the field are somewhat in dispute (McNaughton 1968, Sharma and Gopel 1978). It is clear, however, that seedlings do not contribute significantly to the maintenance of ramet numbers in an established stand and that sexual reproduction serves mainly for dispersal. Ramets which emerge as the first cohort in a season typically die the following year, especially if they flower (a process that largely consumes the apical meristem). As a result, the clone is continually comprised of young ramets. In my excavations of undisturbed stands I have found ramets to be no more than three years old and separation of new ramets from their parent ramets to occur within 2-3 years. Intact rhizome systems are therefore usually comprised only of a single parent rhizome and its attached offspring ramets. This form is not maintained, however, in colonizing populations where clonal growth is very rapid. Consequently, I feel justified in using ramets as a unit of study and assume that emerged ramets behave to a large extent as independent physiological units.

In this paper I present the results of four separate, yet coordinated studies. These studies explore the causes of variations in biomass allocation in _Typha latifolia_ and the consequences of these variations for survival over a range of conditions and include: (1) a description of environmental conditions and population characteristics, (2) experimental determinations of the phenotypic variations in biomass allocation and production, (3) controlled growth studies of the genetic component of biomass allocation patterns, and (4) experimental evaluation of different biotypes under natural conditions.

I. ENVIRONMENTAL CONDITIONS AND POPULATION CHARACTERISTICS

The three populations involved in this study are located adjacent to Lawrence Lake in Barry County, Michigan (Fig. 2, Table 1). The OPEN marsh is dominated by short-statured growth forms and is exposed to prevailing winds and weather from across the lake. I postulated that of the habitats studied, *Typha* of this site would be most subject to mortality by climatic extremes. The CATTAIL marsh consists predominantly of *T. latifolia* in soft, highly organic sediment and is largely sheltered from prevailing winds by the adjacent woods. This habitat represents the "typical" monospecific stand. Contiguous with the CATTAIL marsh is a sharply defined area of aquatic shrubs and trees, the WOODS marsh, which contains a few ramets of *T. latifolia*. In this habitat *T. latifolia* grows on compact, highly organic sediment under a fairly dense canopy. This habitat represents the extreme in competitive stress for *T. latifolia*.

The Lawrence Lake area has been subjected to some human disturbance during the last one hundred and fifty years but the areas included in this study have been largely undisturbed (Rich 1970). The only known exception to this was a brief period around 1930 when attempts to drain the surrounding marshes lowered lake levels significantly for two years. Otherwise these habitats have been unaffected by man and the *T. latifolia* populations are potentially quite old. In this section of the paper I present data on the availability of resources in the various habitats and the dynamics of ramet density through time.

METHODS

Several parameters were measured in order to provide a general characterization of the three habitats (Table 1). Sediment organic matter was measured by combustion of 6 sieved (2-mm mesh), dried sediment samples at 550°C and sediment pH was determined by

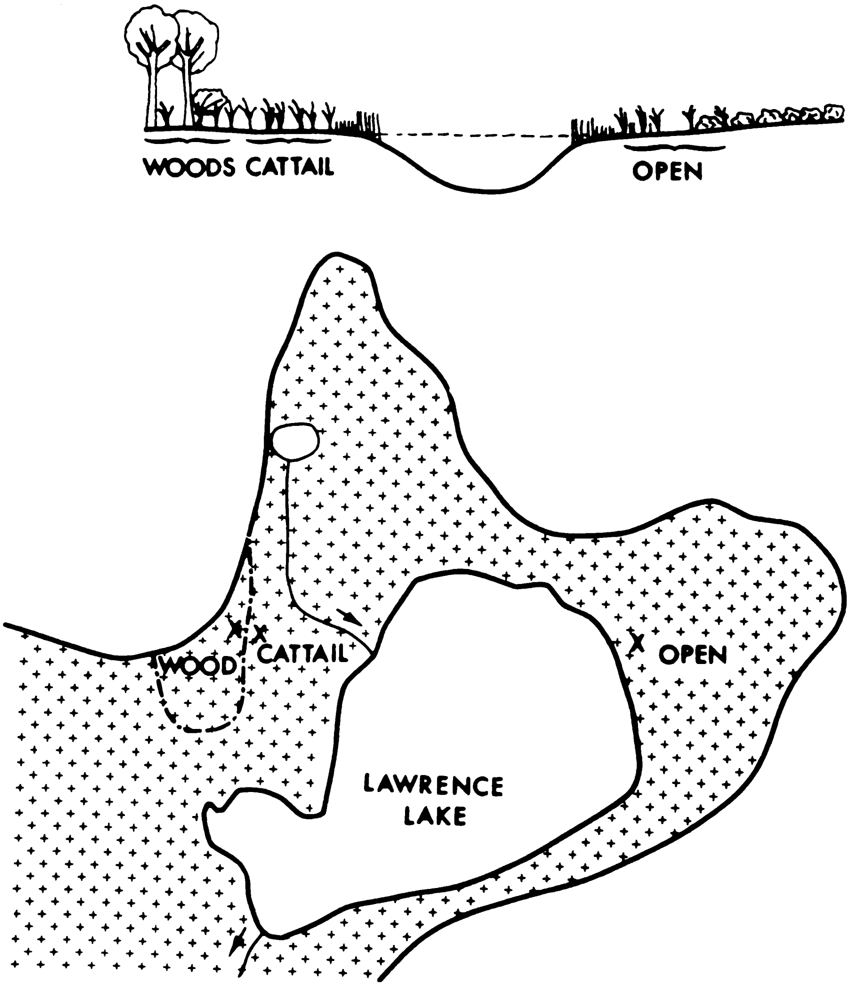

Figure 2. Study sites at Lawrence Lake, Barry County, Michigan.

Table 1: General comparison of the habitat conditions.

HABITAT	PRINCIPAL VEGETATION	DENSITY OF *T. LATIFOLIA* IN 1978 RAMETS/m^2	DOMINANT GROWTH FORM	AVAILABLE LIGHT AT 0.5 m, % of Full	SEDIMENT ORGANIC MATTER/pH	EXPOSURE TO WIND & WEATHER
"OPEN" Marsh	A mixture of *T. latifolia*, *Potentilla fruticosa*, and various sedges	10.4	short herbs and shrubs	100	7.9%/7.88	exposed
"CATTAIL" Marsh	*T. latifolia*	21.0	intermediate height herbs	-	70.8%/7.45	protected
"WOODS" Marsh	*Cornus stolonifera* and *Salix* spp.	4.8	tall shrubs and trees	19	70.0%/7.25	protected

electrometric methods (Chapman 1976). Light measurements were made at midday at ten locations within a habitat at several heights above the ground using a hemispherical photometer (Rich and Wetzel 1969). The light environment of a *Typha* leaf is very complex in the WOODS marsh and our measurements can only serve as an approximate indicator of the habitat type.

The dynamics of emergence, growth and death of ramets were followed at ten sites within each of the three habitats in 1978. At each site a randomly selected ramet of the first cohort of the season was chosen for detailed study of biomass production and allocation using radiocarbon isotope methods (see below). The neighboring *Typha* ramets within a radius of 2 m in WOODS, 1 m in OPEN, and 0.5 m in CATTAIL marshes were flagged and monitored for height, basal diameter, leaf volume, emergence date, mortality, and distance from the "main" ramets at weekly or biweekly intervals. The resulting sample sizes were: OPEN marsh - 63 ramets, CATTAIL marsh - 53 ramets, and WOODS marsh - 32 ramets. Additionally, ten leaf systems were harvested in each marsh every four weeks to determine the relationship between leaf volume and ash-free dry weight (procedures for ash determinations given in Chapman 1976). These measurements of ramet dynamics were supplemented by the establishment of 5 or 6 plots in each marsh (WOODS - 24 m^2 total, CATTAIL -10 m^2, OPEN - 20 m^2) in September 1978 which were monitored until July 1979. Ramets in these plots were marked with numbered flags and the overwinter mortality of young shoots determined in May of 1979. Because of the possibility of overwinter death in non-emerged leaf buds, 88 ramets were randomly selected from the OPEN and WOODS marshes in fall 1978 and half of the ramets from each marsh were transplanted into each of the two

marshes for determining overwinter mortality. These ramets were checked for survivorship in early June of the following year.

Available nutrients were determined by tissue analyses to avoid the problem of extrapolation from sediment analyses (Fried and Broeshart 1967). Meristem tissues were used for analyses to avoid the complicating effects of variable amounts of structural tissues. Two samples from each "main" ramet (described above) were digested using sulphuric acid and hydrogen peroxide (Allen 1974). Digestion efficiency was determined by comparison to the organic nitrogen and phosphorus standards glutamine and sodium glycerophosphate. Nitrogen was determined by the salicylate method (Verdouw et al. 1978) and phosphorus by the molybdenum-blue method (Allen 1974). Meristem values were compared to leaf values since most authors have reported leaf values only. Meristem values gave similar population means to leaf values but the exact relationship varied from sample to sample.

Field fertilization experiments were used to further evaluate the nature of resource limitation. Twenty randomly selected ramets were collected in both the WOODS and OPEN marshes and transplanted into 55-liter perforated, plastic tubs in November, 1978. Tubs were used to permit the recovery of root material and were planted in the marsh sediments to allow for exchange of interstitial water. At weekly intervals from June 27 to September 5, 1979 five replicate transplants in each marsh were given the following treatments: control- no nutrient additions; (1) phosphorus- 88 mM as KH_2PO_4 (contained 90 mM potassium); (2) nitrogen- 188 mM as NH_4NO_3 (plus 90 mM potassium as KCl); (3) potassium- 90 mM as KCl; (4) nitrogen, phosphorus and potassium- 188 mM N + 88 mMP + 90 mM K. Transplants were harvested in early September

1979, processed for dry weight of all tissues and subsampled for percent ash weight of leaves, rhizomes and roots.

RESULTS AND DISCUSSION

Examination of the three *Typha* populations revealed large differences in ramet dynamics and mortality patterns (Table 2). The WOODS population underwent high ramet mortality during the growing season with most population growth restricted to early summer. The OPEN marsh population was subjected to much more overwinter mortality and showed a considerable increase in ramet numbers throughout the growing season. The greater exposure to weather at the OPEN marsh was also reflected in a three-week delay in leaf emergence. This difference in emergence date was not the result of genetic differences among the *T. latifolia* populations since there were no differences in either overwinter mortality or date of emergence in ramets transplanted into habitats from both WOODS and OPEN marshes.

In order to provide a general representation of ramet dynamics through time, Figure 3 was constructed as a composite of information from several sources. Changes in density from May 1978 to September 1978 were taken from the ten "neighborhood" plots in each marsh while the remaining values were from the larger "fixed" plots in each marsh. Overwinter mortality values were based on *T. latifolia* ramets with emergent leaves 50 cm or less in height as of November 1978 (Table 2). These mortality values were extrapolated to ramets of all heights since my experience showed that ramets with leaves more than 50 cm tall typically replace themselves overwinter through vegetative reproduction. These estimates of overwinter ramet mortality do not include the natural senescence that occurs the following year for ramets with leaves greater

Table 2. Population characteristics for the period May 1978-June 1979.

		MARSH	
	WOODS	CATTAIL	OPEN
Date of Peak Leaf Emergence	April 25	April 25	May 16
Ramet Mortality During Growing Season	15.6%	3.8%	0.0%
Ramet Mortality Overwinter(Nov.-June)			
Based on Ramet Dynamics	10.5%	15.4%	40.0%
Based on Transplants	55%	-	71%
Percent of Population Flowering	0.0%	0.0%	11.1%

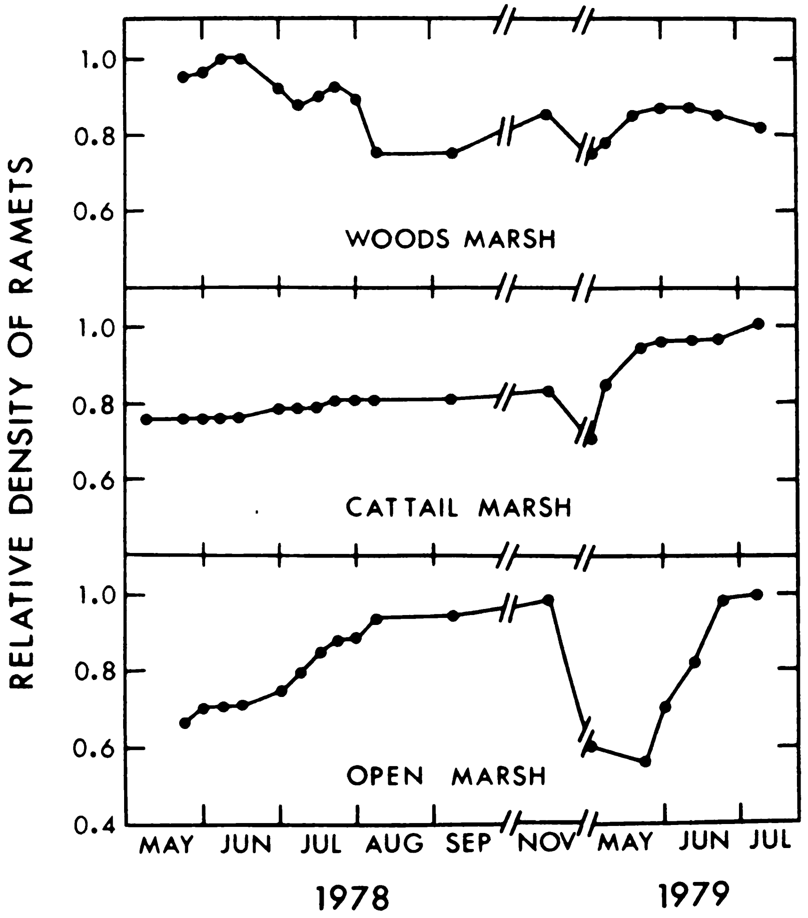

Figure 3. Density of ramets relative to the seasonal maximum for each population at Lawrence Lake.

than 50 cm. Because of these assumptions, the mortality values can only be used for general comparisons among marshes and do not represent absolute values.

In the WOODS marsh increases in ramet numbers were largely restricted to the period May to June (Fig. 3). During the remainder of the year mortality exceeded emergence of new ramets. In the CATTAIL marsh apparent ramet production was also greatest in the spring with a slight increase in density during the 1978 growing season. Despite an estimated 15% mortality overwinter, density in the CATTAIL marsh was 25% greater in spring 1979 than in 1978. In contrast, the OPEN marsh population showed continuous growth in ramet numbers throughout 1978. In spite of heavy mortality overwinter, by late June 1979 the density in the OPEN marsh recovered to values equal to or greater than those in 1978. A portion of the density plots in the OPEN marsh suffered grazing damage by deer (*Odocoileus* spp.) in May 1979. Ramets showing signs of leaf damage were excluded from the analyses.

The differences in ramet dynamics among sites suggest that the principle cause of mortality varied among populations. In the WOODS marsh most apparent ramet production occurred in the spring when the canopy of trees and shrubs is undeveloped. As the canopy overstory developed, a decreasing rate of new ramet production and an increasing rate of ramet mortality occurred, presumably as a result of competition for light (see below). In addition to the increased interception of light by trees and shrubs during the growing season, a climbing vine *Apios americana* Medic. frequently was observed to cause major structural damage to the leaves of *T. latifolia*. The final cohort of ramets in 1978 emerged in all populations by November but was a greater

percentage of the total ramets in the WOODS marsh than in the other marshes (Fig. 3). Ninety percent of the ramets in this last cohort survived overwinter and contributed to the first cohort of the 1979 populations whose density was 13% lower than in 1978. Therefore, in the WOODS marsh most of the mortality appears to have resulted from competitive interactions, while climate-related mortality overwinter was slight in comparison.

In contrast, the OPEN marsh population exhibited a more protracted period of ramet production during the growing season, especially in 1978. Overwinter mortality was estimated to be 40% in contrast to no mortality during the growing season. Evidence indicates, therefore, that climate-related death was responsible for a much greater share of the mortality in the OPEN marsh than in the WOODS marsh.

The essential difference between climate-related and competition-related mortality is its effect on available resources. When a *T. latifolia* ramet dies from climatic extremes, resources are freed for later recolonization. However, when ramet death results from shading, little if any freeing of resources occurs in relation to the *Typha*. A quantitative separation of the contributions of climate and resource limitation (through competition) to mortality was not possible from my data, but the relative contributions of these two factors to mortality did differ between the populations. As a result, the overall level of total available resources for *T. latifolia* was greater in the OPEN marsh than in the WOODS marsh.

The CATTAIL population was intermediate to the other marshes in rates of mortality and ramet production and densities were comparatively stable. Competition in this marsh was principally intraspecific and the

overall availability of resources appeared to be intermediate to the OPEN and WOODS marshes.

Tissue nutrient analyses and fertilization experiments were used to evaluate more precisely the nature of resource limitation. The nutrient concentrations in tissues were determined for the 10 "main" ramets in the "neighborhood" plots of each marsh. Concentrations of both nitrogen and of phosphorus increased from OPEN to CATTAIL to WOODS marshes (Table 3). It has been suggested that 1.5% tissue nitrogen and 0.15% tissue phosphorus may represent average critical values for submersed plants below which limitation for that nutrient is likely to occur (Gerloff and Krombholz 1966). Based on these criteria phosphorus may be limiting growth in the OPEN marsh and nitrogen may be limiting in both OPEN and CATTAIL marshes. Critical tissue concentrations such as those proposed by Gerloff and Krombholz (1966) are subject to a variety of influences (Fried and Broeshart 1967) and do not provide unequivocal evidence for nutrient limitation. Tissue concentrations do, however, indicate differences in the availability of nutrients from the soil (Fried and Broeshart 1967).

Fertilization experiments in the field were used to more conclusively evaluate resource limitation (Table 4). In the WOODS marsh additions of nitrogen, phosphorus and potassium failed to have any effect on ramet growth. In contrast, in the OPEN marsh there was a suggestion of phosphorus limitation ($p = 0.088$ for the one-tailed test) and a 5-fold increase in growth when phosphorus, nitrogen and potassium were all added. The absence of nutrient enhancement does not conclusively demonstrate that light was the principle limiting factor in the WOODS marsh. However, 27% of the transplants in the WOODS

Table 3. Nutrient concentrations in meristem tissues.

	WOODS		CATTAIL		OPEN
Percent Nitrogen	1.86 ± 0.31	>	1.05 ± 0.08	>	0.56 ± 0.05
Percent Phosphorus	0.34 ± 0.03	=	0.29 ± 0.01	>	0.05 ± 0.004

> signs indicate significant differences at the 0.05 level.

Table 4. Effects of nutrient additions on total biomass.

	WOODS MARSH	OPEN MARSH
Percent Mortality of Transplants	26.9	7.7
Nutrient Additions	†TOTAL BIOMASS, g	
Control	15.0 ± 1.2a	27.1 ± 4.6a
Nitrogen	15.2 ± 5.8a	29.4 ± 5.0a
Phosphorus	17.3 ± 2.9a	48.8 ± 8.1a
Potassium	16.0 ± 5.4a	30.1 ± 1.8a
Nitrogen + Phosphorus	11.3 ± 4.1a	137.8 ± 11.2b

†Means and standard errors.

Means within a marsh followed by the same letter are not significantly different with $p < 0.05$.

population died in mid to late summer despite nutrient additions. Further, ramets transplanted into full sunlight in the OPEN marsh on soil from WOODS marsh (see later section) showed considerably greater ramet growth. These data, then, strongly suggest that light was the main limiting resource for _T. latifolia_ in the WOODS marsh and that nutrients (phosphorus in particular) limited growth in the OPEN. The CATTAIL marsh was presumably intermediate to the OPEN and WOODS marshes in the relative importance of nutrients and light as limiting factors.

In summary, the differing patterns of mortality among populations reflect a greater density stress in WOODS than in OPEN, with CATTAIL being intermediate. Also, _T. latifolia_ was more limited by light in WOODS and by nutrients in OPEN.

II. PHENOTYPIC VARIATIONS IN BIOMASS PRODUCTION AND ALLOCATION

In this section I describe the phenotypic variation in biomass production and allocation among populations _in situ_. In particular, Iexamine per ramet ^{14}C fixation and apportionment into ramet growth, vegetative reproduction (cloning), and sexual reproduction. Further, leaf and rhizome production of the parent ramet are considered as well as total allocation to root growth. Intrapopulation variation in biomass allocation is also examined to facilitate understanding of the factors regulating phenotypic response to environmental conditions within populations. Analysis of growth form and reproductive effort are best handled in the context of biomass allocation and production as long as biomass relates well to the function of a particular structure. It should be kept in mind, however, that morphological constraints may result in relationships not best treated as percent allocation.

METHODS

The ten "main" ramets from the "neighborhood" plots in each habitat were repeatedly labeled during the growing season of 1978 with radiocarbon by exposure to $^{14}CO_2$ gas. At initially weekly and later biweekly intervals entire leaf systems were enclosed in clear, Plexiglas® chambers and exposed to either 10 or 20 μCi $^{14}CO_2$ for one hour at randomly chosen times during the day. Radioactive CO_2 gas was supplied by acidifying $NaH^{14}CO_3$ with phosphoric acid in a glass vial and circulating the released gas by means of a hand-operated peristaltic pump. This treatment provided a dosage of 10 μCi per week throughout the labeling period. Senesced leaves and leaf tips were harvested throughout the season to be included in the final analyses. Harvesting of material began September 1 when the labeled ramets began to senesce. Labeled ramets and their parent and offspring ramets were removed by excavation and separated into leaves and rhizomes. Roots were harvested by removal of sediment from an area around the labeled ramet 40 cm in diameter and 25 cm deep. The recovery of root material was accomplished by washing in a series of screens with minimum mesh size of 3.2 mm. Dried plant material was weighed, ground to pass a 2-mm mesh and subsampled for ^{14}C content. Two replicate subsamples of each sample were combusted to $^{14}CO_2$ using a Packard Tri-Carb Sample Oxidizer (Model 305). Carbon dioxide gas was trapped in ethanolamine and radioassayed by liquid scintillation methods in a Liquid Scintillation Counter (Beckman model 8000). Specific activity was corrected by comparison to glucose standards. Root and rhizome production were calculated by comparing the percent of total isotope in a category to the measured biomass production in leaves. Radiocarbon found in lateral rhizomes or

their leaves is referred to as allocation to vegetative reproduction.

Because of the low number of flowering plants included in the labeling study, nine additional flowering ramets were excavated from the OPEN marsh in August 1979 to determine if allocation to sexual structures was fixed or variable. These ramets were separated into component parts and processed for ash-free dry weight (105°C to constant weight less ash upon combustion at 550°C).

RESULTS AND DISCUSSION

Ramets in the OPEN marsh were more productive on the average than those from the WOODS marsh but variation within a habitat was considerable (Table 5). In addition, biomass production and allocation patterns differed considerably among populations (Fig. 4). WOODS marsh ramets allocated none of their resources into sexual reproduction and a relatively small amount into vegetative reproduction. Instead, WOODS ramets allocated a greater percentage of their photosynthate to ramet growth as rhizome (Fig. 4), although the quantity allocated to the parent rhizomes was not significantly greater than for the other populations (Table 5). The CATTAIL population had patterns of production and allocation that were similar to the WOODS population, the principal difference being for root production which was higher in CATTAIL than in WOODS. In contrast, the OPEN ramets showed a much greater total reproductive effort than did the other populations. Sexual reproductive effort was high in the OPEN ramets that flowered with fruiting structures constituting more than 35% of the fixed carbon (Fig. 4). OPEN ramets that remained vegetative also allocated on the average twice as much to vegetative reproduction as did the other populations. Leaf biomass did not vary significantly among populations

Table 5. Biomass production based on ^{14}C fixation and allocation. Values are means of ten ramets.

	Grams Ash-Free Dry Weight			
	WOODS	CATTAIL	OPEN	P
Sexual Reproduction	0.00	0.00	6.29	**
Fruits Only	0.00	0.00	1.63	**
Vegetative Reproduction	2.27	2.33	7.73	**
Leaf Biomass	33.58	43.67	37.52	NS
Roots	0.36	1.25	2.43	**
Parent Rhizome	4.15	3.21	2.67	NS
Total	40.36	50.46	58.27	*
Leaf Height, cm	227	197	147	**
Leaf Volume/weight, cm^3/g	464	292	223	**

The column labeled "P" indicates whether there are significant differences among means.

*	probability of error < 0.10
**	probability of error < 0.05
NS	not significantly different

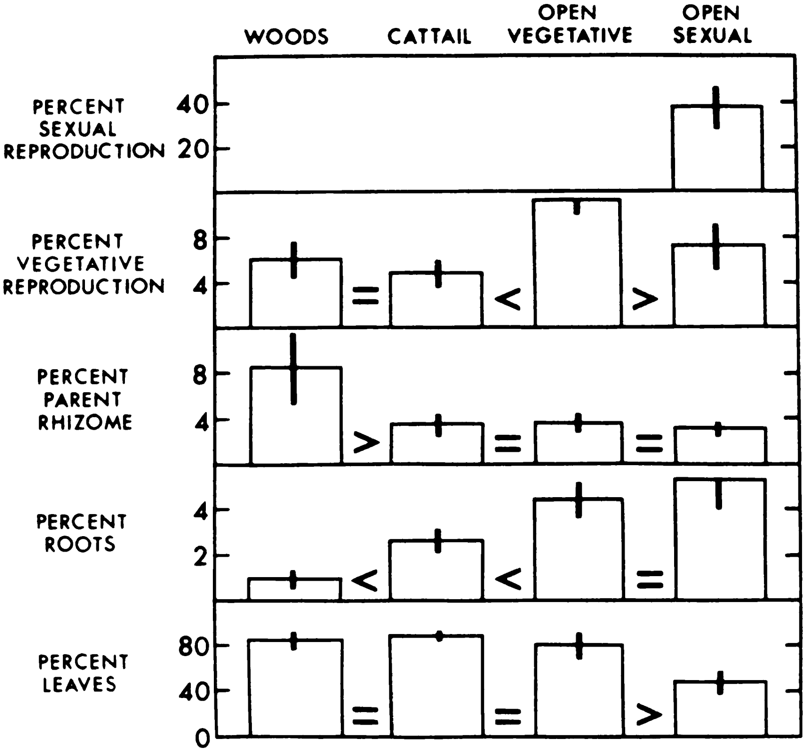

Figure 4. Biomass allocation based on ^{14}C fixation and transport. Vegetative and sexual ramets are considered separately for the OPEN population. Values for each marsh are means of ten ramets except for the OPEN population which consisted of seven vegetative and three sexual ramets. Error bars represent 95% confidence intervals which, for vegetative reproduction, have been adjusted for covariance with total biomass (see Fig. 5).

either in amount or as a percent. However, leaf height and leaf volume/weight were greatest for WOODS ramets, intermediate for CATTAIL ramets, and least for OPEN ramets. Allocation to root growth was low in all populations but highest in OPEN ramets (Table 5, Fig. 4).

Analysis of intrapopulation variation in RA revealed that some of the differences among populations in allocation patterns can be attributed to differences in total production (Fig. 5). Significant correlations existed between vegetative reproduction and total production in all populations. The WOODS and CATTAIL populations showed very similar relationships between total production and vegetative reproduction, and are combined in Figure 5. In the OPEN population, however, the regression equation between total production and vegetative reproduction had a significantly greater slope than in WOODS and CATTAIL populations. This difference between regressions is further reflected in percent allocation to vegetative reproduction. In WOODS and CATTAIL populations allocation to vegetative reproduction was a constant percentage for ramets larger than 20 g total production. In contrast, OPEN marsh ramets showed a strongly increasing allocation to vegetative reproduction with increasing total production. Covariance analysis further showed that differences existed between populations in vegetative reproduction independent of differences in ramet size.

Differences in allocation patterns also existed between flowering and non-flowering ramets in the OPEN marsh (Figs. 4 and 5). Flowering ramets allocated 10 - 15% less to vegetative reproduction than did non-flowering ramets. Analysis revealed that total production during the growing season was not a good predictor of which ramets would flower. Instead, leaf biomass the week prior to flowering was a good predictor

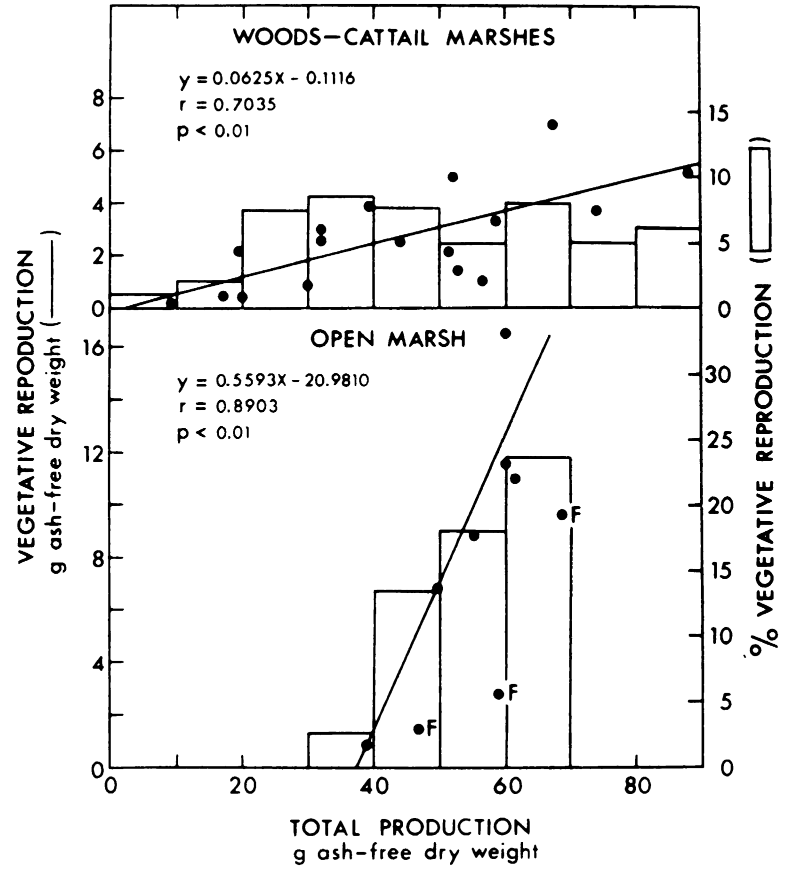

Figure 5. Biomass allocation to vegetative reproduction based on ^{14}C fixation and transport. "F" indicates data from ramets which flowered and these data were excluded from the regression.

of flowering within the OPEN marsh (Fig. 6). At that time only 4 out of 56 non-flowering ramets were as large as the smallest flowering ramet. At the end of the growing season, however, there were 21 non-flowering ramets which were as large as the smallest flowering ramet. This relationship did not apply to the other populations where many ramets were as large as even the largest flowering ramet in the OPEN marsh but failed to flower.

Excavations of unlabeled ramets in the OPEN marsh revealed several features of intrapopulation variation in reproductive effort (Fig. 7). These data are not directly comparable with the biomass production values since these samples represent biomass that may have accumulated over more than one year. Nonetheless, allocation to vegetative reproduction was again an increasing percentage with increasing size. Surprisingly, however, allocation to sexual reproduction was a decreasing percentage with increasing total ramet weight. This relationship results from the fact that an inflorescence of _T. latifolia_ is generally a fixed weight (30 g) (Fig. 7), which is in sharp contrast with the usual situation where sex is either an increasing percentage with increasing plant size (Gadgil and Solbrig 1972, Abrahamson 1975b, Hickman 1975, Snell and Birch 1975, Roos and Quinn 1977) or a fixed percentage (Harper and Ogden 1970, Hickman 1977, Abrahamson and Hershey 1977, Holler and Abrahamson 1977, Andel and Vera 1977). A similar finding has also been reported by Werner and Platt (1976) for goldenrod (_Solidago_) species.

To summarize, there are several main conclusions that can be made about variations in resource allocation within and among the _Typha_ populations. First, the evidence suggests a tradeoff between

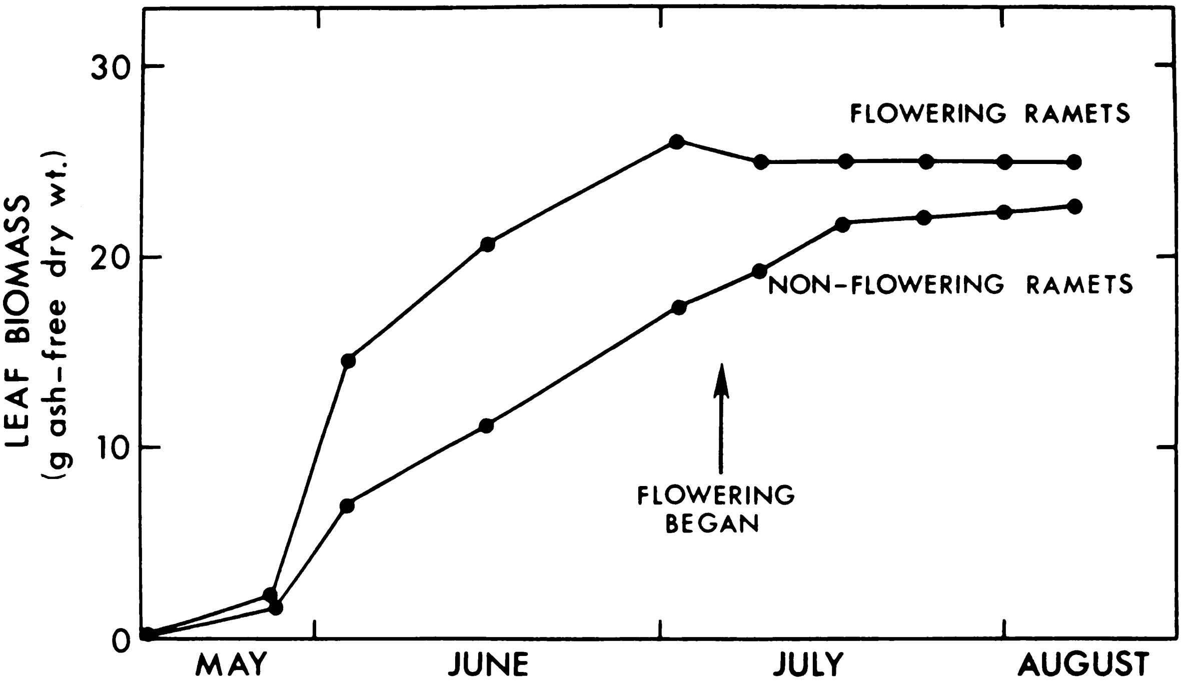

Figure 6. Comparison of seasonal changes in estimated leaf biomass between flowering and non-flowering ramets in the OPEN marsh during 1978.

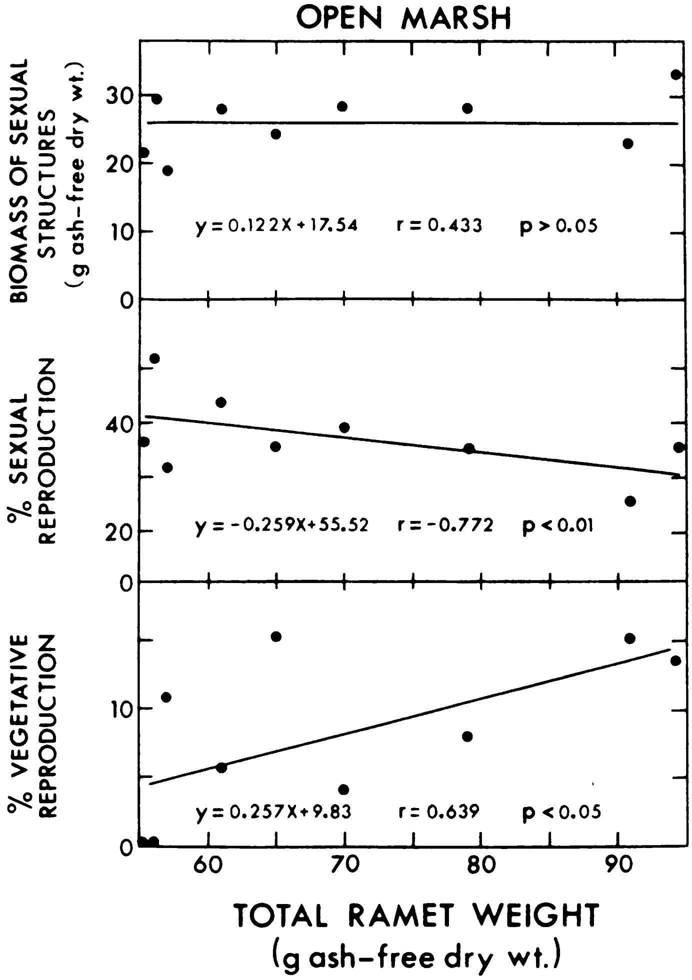

Figure 7. Biomass allocation to reproductive structures for flowering ramets from the OPEN marsh in 1979.

reproduction and growth. WOODS marsh ramets allocated a total of 93.8% of their biomass into ramet growth as leaves, roots and rhizome storage while non-flowering OPEN marsh ramets allocated 88.3% and flowering OPEN marsh ramets only 53.4%. Both sexual and vegetative reproduction were greatest at the OPEN marsh with flowering ramets being rare or nonexistant in the CATTAIL and WOODS marshes. Second, within the total reproductive effort there is evidence of a physiological tradeoff between sexual and vegetative reproduction. Ramets which flowered showed a marked reduction in vegetative reproduction of 10 to 15% (Figs. 4 and 5). Third, ramet growth rate is a reasonably good predictor of vegetative reproduction within populations but this relationship is not consistent among populations. Fourth, whether a ramet flowers or not appears to correlate with its size and/or growth rate just prior to flowering. Finally, a tradeoff occurs whereby allocation to roots is greater where nutrients are limiting. However, light limitation has little if any effect on resource allocation to leaves since _T. latifolia_ has the ability to expand its leaf surface/weight ratio considerably.

III. GENOTYPIC VARIATION IN BIOMASS PRODUCTION AND ALLOCATION

In recent years the possibility of genetic population differentiation on a very local scale has come to be appreciated (Wilken 1977, Hancock and Bringhurst 1979, Turkington and Harper 1979). Ecotypes of _Typha latifolia_ have been described across both latitudinal and altitudinal gradients based on growth under uniform garden conditions (McNaughton 1966). Extensive electrophoretic studies, however, have failed to reveal genotypic variation for _T. latifolia_ on a more local scale, probably due to the inability of electrophoretic

techniques to reveal variation in regulatory genes (Suda _et_ _al_. 1977, Marshburn _et_ _al_. 1978).

In order to determine the genotypic similarity of plants from the different marshes I compared the growth of transplants from the Lawrence Lake populations under uniform conditions. Two other habitats with known histories (ROADSIDE and MANAGED POND) were also sampled for _T. latifolia_ to broaden the comparison. These two additional populations are characterized by high levels of disturbance. Sampling was performed irrespective of the clonal nature of the population and the term "biotype" used to represent only a sample of the genetic population.

METHODS

Since the WOODS marsh population is a narrow zone where the CATTAIL population interfaces with aquatic trees and shrubs, it was assumed that these two "populations" could be sampled as one population in the genetic sense. Six replicate samples were collected randomly within each of the study areas and transplanted into large (35-liter) tubs of topsoil (pH = 7.5) in experimental gardens. Small rhizome pieces (5 gdw as compared to final weights in excess of 200 gdw) were used to minimize historical effects. Transplants were monitored for leaf emergence, leaf height, and ramet number at weekly intervals throughout 1978. Transplants were harvested in September 1978 and processed for ash-free dry weight.

RESULTS AND DISCUSSION

The equal total production among populations suggests, among other things, that historical effects from the natural habitats on the rhizome pieces were insignificant (Table 6). Additionally, there were no

Table 6. Summary of genetic studies.

	POPULATIONS						
	WOODS-CATTAIL		OPEN		ROADSIDE		MANAGED POND
Habitat Description							
Approximate Age of Population	> 50 yrs		> 50 yrs		unknown		ca. 10 yrs
Frequency of Disturbance	Infrequent		Infrequent		Yearly		Yearly
Percentage of Population Flowering	ca. 0.0%		11.1%		13.3%		28.0%
Growth Under Uniform Conditions							
Total Production, g AFDW	207.2	=	206.3	=	201.6	=	213.4
Number of Emerged Ramets	5.83	=	5.33	=	5.50	=	5.83
Leaf Height, cm	159	=	159	=	143	=	144
Leaf Production, g AFDW	103.3	=	100.4	=	91.8	=	101.4
Root Production, g AFDW	42.7	>	35.3	=	31.2	=	33.4
Rhizome Production, g AFDW	61.2	<	70.6	=	78.6	=	78.7
Average Rhizome Size, g AFDW	10.5	<	13.2	=	14.3	=	13.5

significant differences in the average number of emerged ramets, average leaf height, or leaf production. Differences did exist, however, in root and rhizome production, and average rhizome size (Table 6). Overall, the data indicate a tradeoff between root biomass and individual rhizome size with all other traits being equal (Fig. 8). WOODS and CATTAIL ramets had the smallest rhizomes and the greatest amount of root biomass, OPEN ramets were intermediate for both traits and both ROADSIDE and MANAGED POND ramets had the largest rhizomes and least root biomass.

The significance of the observed tradeoff between root and rhizome production depends on the interpretation of variations in average rhizome size. Average rhizome size would seem not to be related to vegetative reproduction since the number of ramets was not different among populations (Table 6). Neither does rhizome size appear to be related to the average leaf biomass of each ramet since this did not vary. The most logical interpretation is that rhizome size is related to flowering since an average of almost 30 grams dry weight must be stored in the rhizome in order to produce an inflorescence (Fig. 7). The fact that most of the biomass for producing an inflorescence comes from rhizome storage is reflected in the observation that a ramet typically shifts from vegetative to fully flowering in as little as three days. This interpretation of rhizome size as allocation to sexual reproduction is consistent with the amount of flowering in the natural populations (Table 6). It is reasonable to assume also that variations in root biomass relate to nutrient uptake potential since root biomass correlates approximately with surface area.

As already mentioned, the interpretation that the OPEN, ROADSIDE

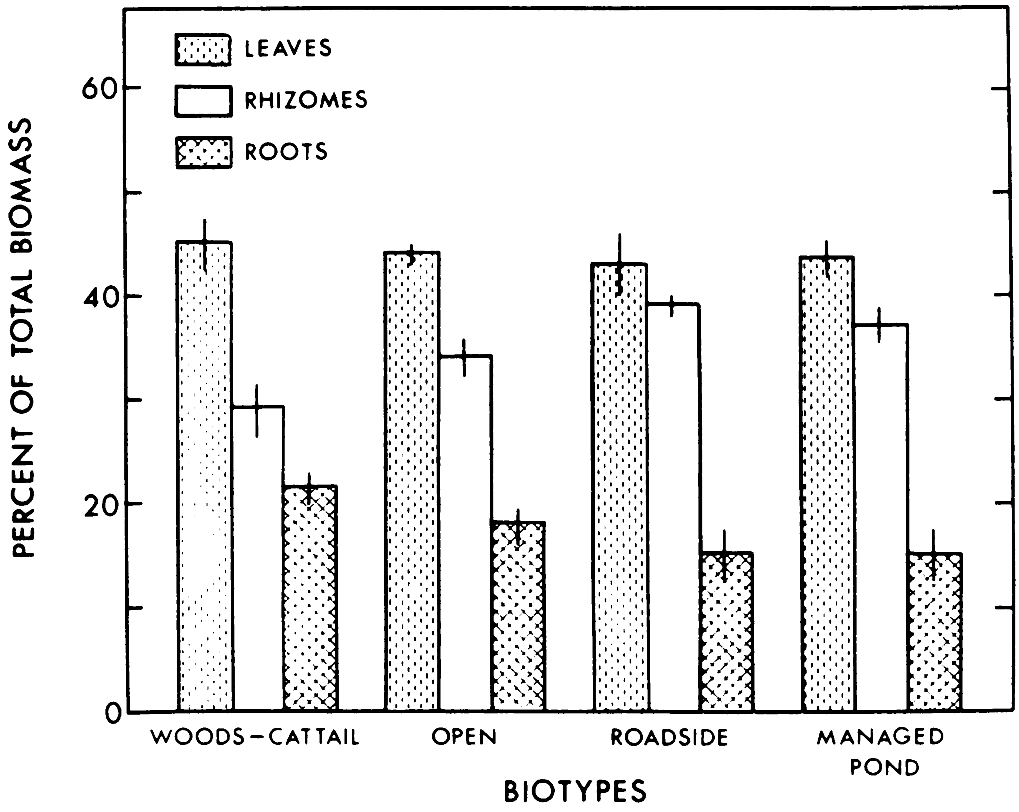

Figure 8. Biotype comparisons of percent biomass allocation under controlled experimental conditions. Rhizomes include both parents and laterals.

and MANAGED POND biotypes allocate more to sexual reproduction than does the WOODS-CATTAIL biotype is reflected in the amount of flowering in the natural populations. However, the greater allocation to vegetative reproduction in the OPEN marsh was not reflected in the differences between OPEN and WOODS-CATTAIL biotypes. Further, intra-population correlations between total production and allocation to vegetative reproduction (Fig. 9) reveal no differences between biotypes. It is recognized that the absence of differences between biotypes in vegetative reproduction may only relate to the particular conditions of the experimental gardens. The fixed percentage of biomass as leaves in the biotype studies is consistent with the lack of variation in the natural populations and points to the highly plastic response whereby leaf surface varies independently of biomass (Table 5). In contrast, allocation to roots is reversed in the biotype studies from that in the natural populations (a further indication that historical effects of the transplants were negligible). In summary, differences in growth form and reproductive effort under uniform garden conditions indicate biotypic differences among populations such that habitats exposed to high levels of disturbance contain biotypes with high allocation to sexual reproduction. In contrast, the biotype from the habitat with the most intense level of competition (WOODS-CATTAIL) appears to allocate more resources to nutrient acquisition, a trait potentially important for exploitative competition.

IV. EXPERIMENTAL EVALUATION OF BIOTYPES UNDER NATURAL CONDITIONS

As summarized in the previous section, biotypic differences under uniform garden conditions suggest a genetic contribution to niche width (i.e. morphological and physiological variability). This

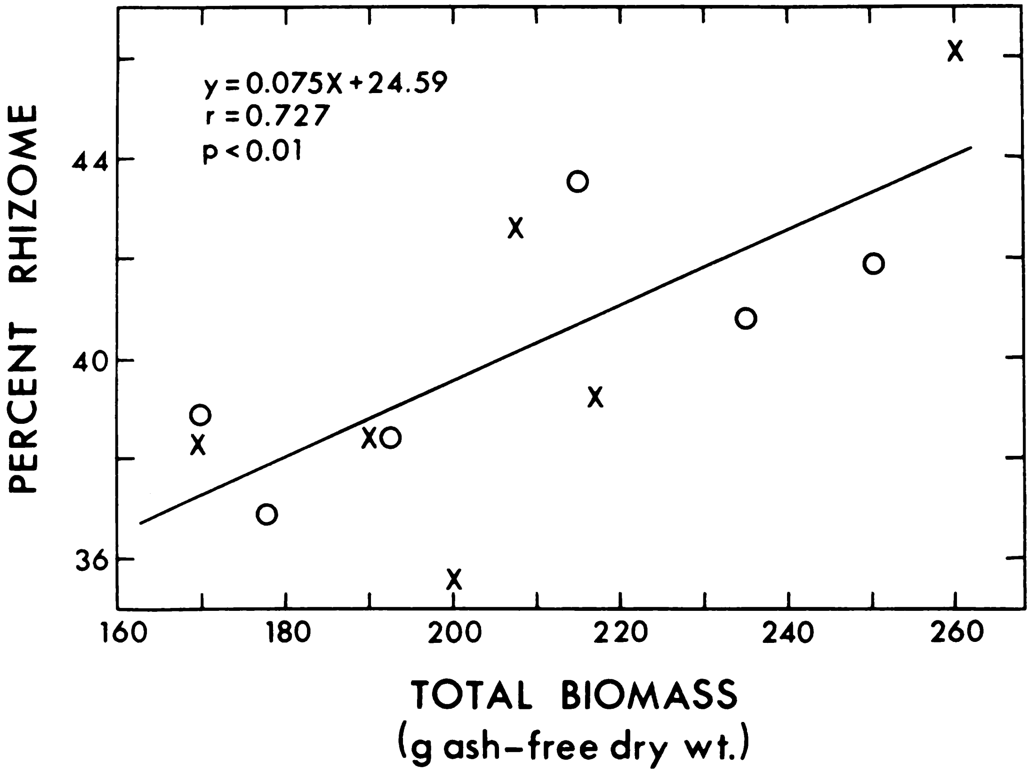

Figure 9. Correlation between total biomass and percent rhizome (a measure of vegetative reproduction in transplants) for the WOODS-CATTAIL (X) and OPEN (O) biotypes. Values have been adjusted by covariance analyses to remove the effect of difference in average rhizome size between biotypes (cf. Table 6).

interpretation, however, depends critically on the assumption that the biotypic differences observed under experimental conditions are maintained in the natural habitat. In this section I test my interpretation of the OPEN and WOODS-CATTAIL biotypes against alternate hypotheses by comparing the production and allocation of biomass between transplanted biotypes in the OPEN and WOODS marshes.

If my morphological interpretation is correct, the OPEN biotype exhibits greater dispersal through sexual reproduction and the WOODS-CATTAIL biotype grows better under limiting nutrient conditions and I would expect the following: (1) the WOODS-CATTAIL biotype should be more productive than the OPEN biotype under nutrient limited conditions, and (2) there should be no differences in total biomass production between biotypes under light limited conditions (unless flowering occurs in which case the OPEN biotype would be less productive). An alternate possibility for biotype differences would be that there are physiological differences that override the morphological differences and the OPEN biotype is better able to grow in the OPEN marsh and, the WOODS-CATTAIL biotype is better able to grow in the WOODS and CATTAIL marshes (alternate adaptive hypothesis). This alternative would imply that other traits, such as nutrient uptake kinetics or the photosynthetic response to low light intensities, were more important in determining growth. A third possible outcome is that biotypes would grow equally well in all marshes (non-adaptative hypothesis) if the differences expressed under uniform conditions were either not expressed or inconsequential under natural conditions.

METHODS

The OPEN and WOODS marshes were chosen to represent habitats

limited by nutrients and light, respectively. The biotypes were grown under uniform conditions of soil and light (described in previous section) for one year prior to transplantation into the field. Six replicate rhizome pieces (average 3.3 g dry weight) were grown in individual perforated tubs (35-liter) which were planted in the ground for each treatment. The experimental design was a complete factoral with the factors of interest being marsh, biotype, and soil. Treatments were randomly assigned to tubs in the field and plants allowed to grow from May through August, 1979. Transplants were harvested in early September 1979 and processed for ash-free dry weight of all tissues. The weight of the starting rhizome fragment was subtracted from the rhizome of the resulting ramet. An additional experiment was conducted to determine the influence of exposure to wind on leaf morphology (specific leaf height per gram dry weight). Six rhizome fragments were grown in planted, 35-liter tubs in the OPEN marsh during 1979. These plants were protected from the prevailing south-west winds by a three sided, clear polyethylene barrier. The height of the barrier was increased over time to keep pace with the increase in leaf height and to minimize the possibility of light shading and air stagnation.

RESULTS AND DISCUSSION

Statistical analyses revealed several significant sources of variation in both total biomass and allocation patterns (Table 7). The comparison of most interest, between biotypes, revealed that twice as much biomass was produced by the WOODS-CATTAIL biotype than by the OPEN biotype in the OPEN marsh (Fig. 10). This difference disappeared when the natural soil was replaced by WOODS soil in the OPEN marsh. The only difference in allocation patterns between biotypes was for the OPEN

Table 7. Selected statistical comparisons for biotype experiments (see Fig. 10).

SOURCE OF VARIATION	TRAIT	NATURE OF EFFECT	STATISTICAL RESULTS
Marsh	-Total biomass	OPEN > WOODS	** F=121.8
	-%roots	OPEN > WOODS	** F= 71.3
	-%rhizome, corrected for covariance with size	OPEN = WOODS	NS
	-%leaves, corrected for covariance with size	WOODS > OPEN	** F= 13.0
Soil	-Total biomass in OPEN marsh	WOODS > OPEN	** F= 38.3
	-%roots in OPEN marsh	OPEN > WOODS	* F= 4.8
	-All traits, taken individually, in WOODS marsh	OPEN = WOODS	NS
Biotype	OPEN soil, OPEN marsh		
	-Total biomass	WOODS-CATTAIL > OPEN	** F= 8.2
	-%roots	WOODS-CATTAIL > OPEN	* F= 5.1
	-%rhizome	OPEN > WOODS-CATTAIL	* F= 4.7
	-%leaves	OPEN = WOODS-CATTAIL	NS
	-ave. rhizome size	OPEN > WOODS-CATTAIL	* F= 7.0
	-ave. leaf height/wt.	OPEN = WOODS-CATTAIL	NS
	-# of ramets	OPEN = WOODS-CATTAIL	NS

* probability of error < 0.05

** probability of error < 0.01

NS not significantly different

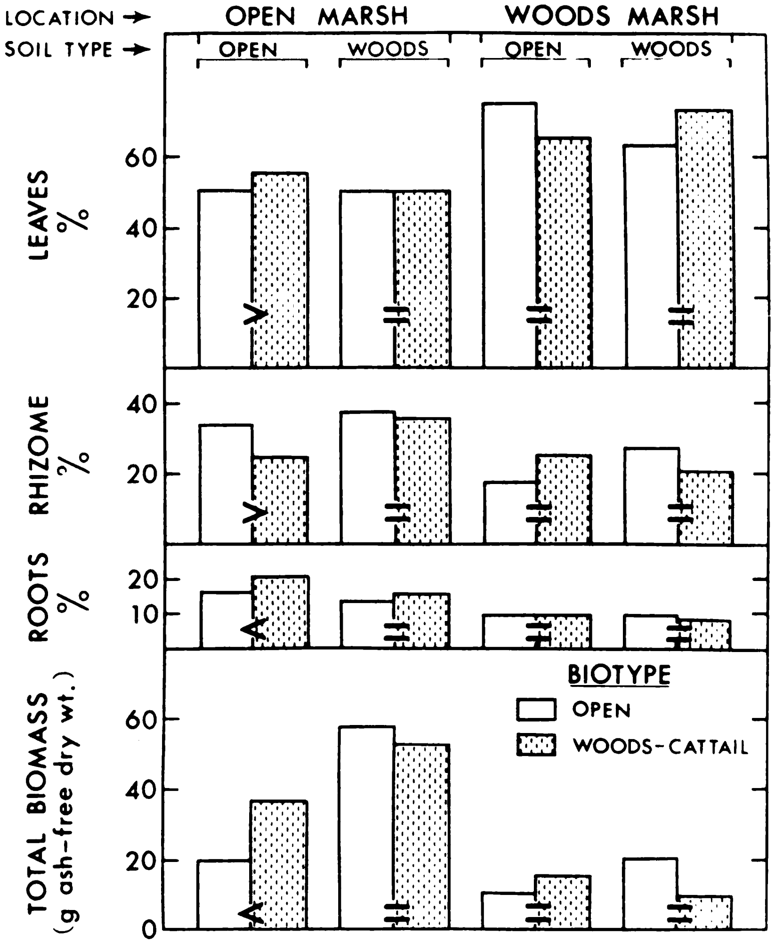

Figure 10. Results from a complete factoral transplant experiment under natural conditions at Lawrence Lake. Factors considered in this experiment were location, soil type and biotype. Data are arranged to allow comparisons between biotypes. Inequality symbols represent significant differences with $p < 0.05$. Effects of location and soil type are presented in Table 7.

marsh - OPEN soil combination (Fig. 10, Table 7) where a tradeoff was observed between rhizome size and root allocation.

Soil type also had a significant effect on total biomass and allocation to roots. Replacement of the natural soil in the OPEN marsh with WOODS soil caused a doubling of total biomass and a decrease in root allocation from 18.4% to 14.3% (Fig. 10, Table 7). In the WOODS marsh soil type no effect on any trait measured was observed.

A significant marsh effect occurred in both total biomass and allocation patterns (Table 7), presumably as a result of different limiting factors. Plants in the WOODS marsh allocated more to leaves and less to rhizomes or roots than did plants in the OPEN marsh. A large portion of this effect was the result of covariance between total biomass and the ratio of leaves to rhizomes. Larger plants allocated more to vegetative reproduction (cf. Fig. 8) which can confound comparisons among different sized plants. Covariance analysis removed the differences in rhizome allocation between marshes but a significant difference between marshes was maintained for leaf allocation despite the removal of 46% of the variation by covariance with total biomass.

Sheltering _T. latifolia_ from the wind in the OPEN marsh caused an increase in the ratio of leaf volume/weight of 48%. This result indicates that wind stress contributed to the low volume/weight ratio found in the natural populations (Table 5), probably by inducing a greater production of structural tissues within the leaves. Nonetheless, the shaded _T. latifolia_ had a greater leaf volume/weight than the sheltered ramets indicating the overriding importance of light intensity in determining leaf volume/weight.

In summary, the WOODS-CATTAIL biotype was more productive than the

OPEN biotype under nutrient limiting conditions. This difference was correlated with a tradeoff in root allocation and rhizome size whereby the greater root biomass of the WOODS-CATTAIL biotype is believed to have resulted in the higher growth rate. When the nutrient-poor soil of the OPEN marsh was replaced by the more fertile soil of the WOODS marsh, the differences between biotypes in both production and allocation disappeared due to plastic responses. Differences between biotypes were also unapparent when plants were grown under the light limiting conditions of the WOODS marsh. In general, these results support the hypothesis posed in the preceding section that the OPEN biotype is better adapted for dispersal (through rhizome storage for sexual reproduction) and the WOODS-CATTAIL biotype is better adapted for nutrient acquisition. These results, however, do not argue that the presence of the WOODS-CATTAIL biotype is adaptive in the WOODS marsh. As stated previously, the WOODS marsh is apparently maintained primarily by vegetative reproduction from the CATTAIL marsh rather than by seed germination. Thus, I have considered Typha of the WOODS and CATTAIL marshes to be one true "population" in the genetic sense. Assuming the interpretation of tissue nutrient concentrations is correct, Typha of the CATTAIL marsh is at least partially limited by nutrients (nitrogen) and the WOODS-CATTAIL biotype would likely be more productive in that marsh than would the OPEN biotype.

CONCLUSIONS AND IMPLICATIONS

Based on my findings, biotypic differences between populations contributed significantly to the differences in biomass allocation patterns. The OPEN biotype stored a greater percentage of its biomass in the parent rhizome and was induced to flower at a lower size/growth

rate than the WOODS-CATTAIL biotype. Under conditions favoring root growth, the WOODS-CATTAIL biotype allocated a greater percentage of its biomass to root growth. However, these traits also had a strong component of developmental plasticity in both biotypes. Sexual reproduction was related to size/growth rate at some period prior to flowering (see also Werner 1975) while vegetative reproduction was highly correlated with growing-season production. Allocation to root biomass was highly responsive to nutrient availability although allocation to leaves was a fixed percentage under the conditions studied. Leaf volume per unit leaf weight increased with decreasing available light and decreasing wind exposure.

Sampling from four contrasting populations of T. latifolia revealed a strong correlation between the frequency of disturbance of a site and the proportion of ramets that flowered. Controlled transplant experiments indicated a genetic basis for these differences. From these results I would infer that the distribution of biotypes among habitats is related to the dispersal and colonization ability of the various biotypes. The more recently disturbed sites are likely to be more open to colonization and perhaps also more subject to the extinction of genotypes.

The consequences of these variations in biomass allocation may be considered in terms of their contributions to niche width as growth and reproduction over a range of conditions from open to closed communities. This range of conditions may occur in space or over time within a community. If only the WOODS-CATTAIL biotype existed, T. latifolia would occur in many fewer habitats because of its lower rate of dispersal. It is also likely that the abundance of T. latifolia would

be less in some of the habitats colonized since arriving later could affect the balance of competition with other species. If only the OPEN biotype existed, there would be little effect on the presence of T. latifolia in marshes such as CATTAIL since competition is largely monospecific and either biotype could probably predominate over the other species. However, the lower productivity of the OPEN biotype under nutrient limited conditions would result in reducing the boundaries of the population if the lower abundance related to reduced competitive ability.

Overall, the range of plastic responses by a single biotype (the within-type component of niche width) would allow T. latifolia to exist over a wide range of open and closed communities. The different biotypes (the between-type component) would have their greatest effect on increasing the number of sites colonized with a lesser effect on abundance in the colonized sites.

A complete understanding of the relative contributions of within-type and between-type variance to growth in successional environments depends heavily on an adequate sampling of the variation. In perhaps the best studied case, Solbrig and Simpson (1974, 1977) have clearly shown the selective value of Taraxicum biotypes which presumably contribute to niche width in a way similar to that described here for Typha latifolia. Law et al. (1977) have also shown a strong genetic component to the ability of Poa annua to grow over a range of successional environments but the contribution of plasticity was not elucidated.

The within-type component has been studied in a number of systems (e.g. Harper and Ogden 1970, Ogden 1974, Abrahamson 1975a,b, Hickman

1975, Snell and Birch 1975, Roos and Quinn 1977, Reader 1978). The general pattern is for reproduction to be greater in open sites. This response may result from either an increasing or a constant percentage allocation to reproduction with increasing plant size/growth rate. Exceptions to this general pattern have been reported by Hickman (1977). It is likely that the life history type (annual, biennial, perennial) and hierarcy of allocation can have a major effect on these plastic responses. For *Typha latifolia* the first priority is for competitive structures (as expected for a perennial), the second priority is for vegetative reproduction, and flowering occurs only when extra resources are available. This allocation hierarchy seems fitting for a species that is replaced successionally only on a very long time scale. A similar allocation hierarchy may occur for *Rubus* (Abrahamson 1975a,b) but the smaller minimum allocation to sex could allow for the variable allocation to sex. I might speculate that since a species such as *Frageria virginiana* (wild strawberry) has a fixed allocation to sex and variable allocation to vegetative reproduction (Holler and Abrahamson 1977), there might be a higher priority for sex than in *Rubus*. It would be interesting to know how this difference might correspond to the persistence of local populations. Interestingly, the annual composite *Senecio vulgaris* has consistently high sexual reproductive effort irrespective of density (Harper and Ogden 1970); and Wibur *et al*. (1974) have suggested that this may contribute to its survival in unpredictable successional environments.

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