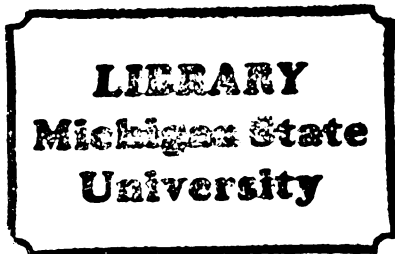


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THE PATTERN AND PROCESS OF CLONAL GROWTH IN A
COMMON CATTAIL (TYPHA LATIFOLIA L.) POPULATION

By

Joyce Ann Dickerman

A DISSERTATION

Submitted to
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ABSTRACT

THE PATTERN AND PROCESS OF CLONAL GROWTH IN A COMMON CATTAIL (*TYPHA LATIFOLIA* L.) POPULATION

By

Joyce Ann Dickerman

A detailed analysis of individually identified *Typha latifolia* shoots quantified the births, deaths, life histories and productivities of the shoots. Three levels of plant structure were addressed: Inter-shoot relationships, individual shoot behavior and leaf dynamics.

Shoots emerged in three major emergence pulses each year, and were grouped by these pulses into three major cohorts. The first cohort emerged in early spring, grew throughout the growing season, and died in late autumn. The second cohort emerged in midsummer; 70 to 80 percent of these shoots died in autumn, while the remainder resumed growth in the following spring. The third cohort emerged in late summer and early autumn; 80 to 90 percent of all third cohort shoots resumed growth the following spring. The number of shoots in each of the three cohorts differed considerably in the two years of the study. In the first year, the pattern of density gradually increased throughout the growing season (from 12.7 to 43.9 shoots/m²), which resulted from an overlapping cohort structure. In the second year, however, a rapid increase in shoot density (to 40.0 shoots/m²) occurred by mid-May; this density was essentially maintained throughout the growing season. The second cohort was so reduced in the second year (only one sixth the size of the first year's second

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cohort) that the second year had a non-overlapping or discrete cohort structure. The differences in cohort structure led to a 60 percent higher maximum aerial biomass in the second year as compared to the first year (833 vs 1318 g/m²).

Conventional hypotheses of effects of abiotic (nutrient and light) or biotic (competitive mediated) factors did not explain the differing density patterns. An intrinsic or self-regulation of density through reallocation of assimilates between shoots and rhizomes did adequately explain the density patterns. This regulation is based on the growth pattern and the differing roles of the cohorts: The first and third cohorts are predominately regenerative, while the second cohort is proliferative, and "fills in" shoot density if, in early spring, density is below a shoot saturation level that apparently effectively holds marsh space.

To Virginia,
from whom I learned my most important lessons.

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CHAPTER 1

INTRODUCTION

The process and pattern of growth in clonal plants is very poorly understood. The first demographic analysis of the longevity and reproductive behavior of ramets and cohorts of ramets in perennial plants growing in a natural habitat was published very recently (Noble et al., 1979). Basic observational studies of clonal plants therefore are needed in order to generate clonal plant theory for hypotheses testing.

Plant population biology is based on noncloning plants despite the widespread occurrence of cloning plants in such habitats as aquatic, forest floor and grassland communities. Several difficult problems associated with the study of cloning plants have probably deterred their investigation. There is a problem of identifying the individual. The functional unit of the clone, the ramet, is only a subunit of the actual genetic individual, or genet. The genet or clonal plant then is the collection of all living ramets that have been derived from the original seedling. Clonal growth progresses as the continued reproduction of ramets. In an established stand of ramets, it is difficult to determine the delineation of the genets. Not only are the ramet linkages frequently subterranean, but these linkages quite often decay in a relatively short time, so that the investigator is left with a disjunct population of ramets of unknown genet heritage.

Productivity is an important aspect of plant population biology that should be combined with demography and population dynamics. Frequent measurements of biomass of individuals and their parts can be used to provide greater ecological insight into growth processes, turnover, and the ways in which resources are allocated. Similarly, most production studies have been done without adequate knowledge of plant demography and population dynamics. The resultant production estimates are often inaccurate because mortality losses and the flux of plant parts are not adequately assessed (Wiegert and Evans, 1964; Valiela et al., 1975). When population dynamics and production measurements are coupled, both aspects are mutually strengthened. Tomlinson (1974) and Bernard and coworkers (1974, 1975, 1977) have emphasized the importance of understanding the growth of individuals in the population in order to accurately determine production.

This study was undertaken to quantify the process and pattern of clonal growth in the common cattail, Typha latifolia L., a highly productive and successful emergent aquatic macrophyte (Fig. 1). Typha latifolia is the second most widely distributed aquatic macrophyte in the world with a range that extends from the Arctic Circle to 30° S latitude (Sculthorpe, 1967). It is a rhizomatous perennial that forms nearly monospecific stands through vigorous vegetative expansion. The unit of vegetative growth, the ramet, is comprised of the submerged rhizome, associated roots and the aerial leaves (shoot) which may or may not have a central flowering spike. The rhizomes are tough and sometimes woody. They usually remain viable from 17 to 22 months (Westlake, 1968). The rhizome linkage between shoots is usually physically maintained for two to three years. Rhizomes function as

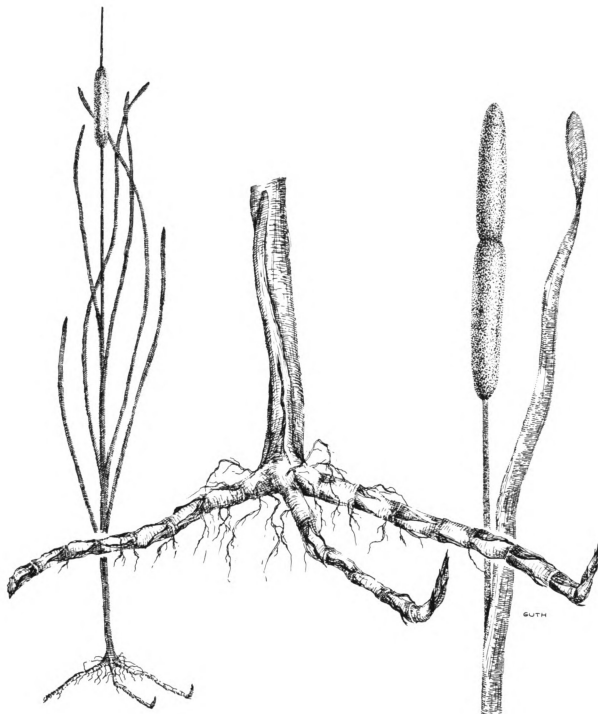


Figure 1. Typha latifolia L., the broad-leaved cattail. Left: General form of the ramet, showing shoot, inflorescence and rhizome system. Center: Rhizome system. Note lateral buds on the rhizomes towards the right. Right: Inflorescence. (From Grace and Wetzel, 1981).

perennating organs (storing carbohydrates) and provide the axis for the lateral growth of the clone. At maximum aboveground biomass, the underground organs comprise approximately half of the total cattail biomass.

In this study, three levels of plant structure were addressed: inter-shoot relations within study plots, individual shoot behavior, and leaf dynamics within individual shoots. Other aspects of this study (to be presented elsewhere) involved interstudy plot analyses, biomass cycling within the marsh habitat, production analysis and techniques comparisons, and decomposition of T. latifolia above- and belowground tissues.

CHAPTER 2

MATERIALS AND METHODS

The study site was a marsh on the western side of Lawrence Lake, a small mesotrophic hardwater lake located in south central Barry County, Michigan. This marsh extends over 7,000 m² and supports a nearly monospecific stand of the common cattail, Typha latifolia. The western marsh has been largely undisturbed for the past 50 years (Rich, 1970), and therefore the Typha stand is potentially that old. The lake and its affiliated watershed have been the site of numerous other studies (cf. Wetzel, 1982). Two small inlet streams, fed by surface runoff and springs, course their way through the marsh and enter Lawrence Lake. In 1978, Grace and Wetzel (1981) examined certain aspects of genotypic and phenotypic variation in biomass allocation for the T. latifolia population in this marsh site, as well as in two other Lawrence Lake marsh sites; data they obtained indicated a western marsh sediment pH of 7.45 and an organic matter content of ca. 71 percent.

Study Plots

The locations of five permanent 1 x 4-m plots (study plots) were randomly selected in the densest area of the Typha stand in April 1978 (Fig. 2). In this area of the marsh Typha comprised over 90% of the peak above ground biomass (dry mass basis). In each plot, all newly emerged Typha shoots were individually identified by loosely-wired

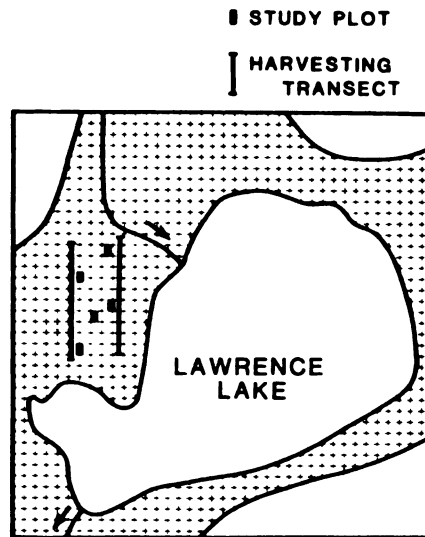


Figure 2. Position of study plots and harvesting transects in the Typha latifolia marsh on the western side of Lawrence Lake, Barry County, Michigan.

numbered aluminum tags around the base of each shoot. On every sampling date, shoots that had emerged since the previous sampling date were similarly tagged. All tagged shoots were examined weekly during the first growing season (end of April to mid-November in 1978; 29 times) and on the average, every two weeks during the 1979 growing season (early April to the end of October; 13 times). Each examination consisted of three measurements: (a) shoot height from the water or sediment level (corrected for fluctuations in water level by comparison to a plot benchmark) to the most distal portion of the shoot's chlorophyllous tissue, (b) the number of leaves per shoot, and (c) the status of each leaf (entirely chlorophyllous, i.e. all green; entirely senesced, i.e. all brown; or in the process of senescing, a combination of green and brown in leaf color).

In year three, all new Typha shoots in four of the five study plots were tagged as members of cohort one if they emerged before 15 June and as cohort two if they emerged after 15 June and before 15 August. These dates were assumed to mark cohort boundaries in the third year because they were the cohort boundaries in the first and second year of this study (see Fig. 3).

Harvesting Transects

At the start of the study, two 50-m "belt" harvesting transects (each 0.5 m wide) were established, one on each side of the five study plots (Fig. 2). The 50-m transects were divided into five 10-m blocks, and the 10-m blocks were further subdivided into 20 0.5 m x 0.5 m plots. A randomized sequence was used to establish the harvesting order for these 20 plots. Each harvest then consisted of cutting all Typha shoots present in each of 10 separate 0.25 m² plots,

one plot from each 10-m block. This analysis resulted in 2.5 m² of Typha being harvested on each sampling date. When all plots along the original belt transect had been harvested, new belt transects were designated parallel to, and one meter from, the original belt transect, and the process was repeated. Harvesting was done biweekly during the first growing season and every three weeks during the second growing season, for a total of 27 times during the study. All T. latifolia shoots were harvested near the sediment-water level; cutting was adjusted to a benchmark in order to compensate for fluctuations in water level. Freshly-harvested shoots were cleaned by rinsing under tap water, and chlorophyllous height (from shoot base to the tallest green tissue on the shoot), total number of leaves and the status of each leaf were recorded as they were in the study plots. All harvested material was dried (105 °C) in forced-air ovens for 24-48 h, and harvested samples were ground in a Wiley-Mill and subsampled for ash content (combusted in ceramic crucibles at 550 °C).

Data Analyses

Data analyses were performed using a Digital Equipment Corporation VAX 11-780 Computer. All computer analyses involved use of P-STAT, a data management and statistical package; more complex statistical procedures were accomplished using the BMDP (Biomedical Computer Programs) statistical software package revised March 1981 for the VAX/VMS system. Copies of P-STAT editor files, as documentation of data manipulation, are available from the author upon request.

A variety of linear and non-linear regression models capable of predicting shoot biomass (ash-free dry mass, AFDM) from field data on live plants were considered. The models included log-log, semilog and

untransformed relationships with various combinations of chlorophyllous height, total numbers of leaves per shoot, and each of the leaf status categories. From these, I selected a non-linear regression predicting shoot AFDM using untransformed data on chlorophyllous height (CH) and total number of leaves per shoot (TNLS). The equation

$$\text{Shoot biomass} = 0.0001404(\text{CH})^{1.791} (\text{TNLS})^{1.13226}$$

provided the best fit to the data for all shoot size classes ($r = 0.916$; $n = 1455$). The residuals between the equation's predicted shoot biomass values and the observed shoot biomass of the harvested shoots were more evenly minimized over all shoot heights. This equation was therefore used to predict shoot biomass throughout the study.

CHAPTER 3

RESULTS

Structural Demography

Shoot Emergence and Cohort Structure

Three major emergence pulses were observed in each year (Fig. 3). Each emergence pulse included a several-week trend of increasing, then decreasing, numbers of emerging shoots. The boundaries between the three major emergence pulses occurred on 15 June and 15 August in each year. A mature stand of T. latifolia in southern Czechoslovakia similarly exhibited three pulses in emergence during a growing season, with pulse boundaries occurring in early June and early September (Fiala, 1971a). Rapidly colonizing two-year old clones in southern Czechoslovakia, however, emerged in four major emergence pulses (Fiala, 1971b).

This pattern of pulsed shoot emergence defined a major cohort structure in which three major cohorts originated in each year. The shoots were grouped into cohorts by their affiliation with a major emergence pulse. Shoots in the first major cohort were further separated into shoots tagged on the first sampling date (I-1a) and those emerging later within the first major cohort of year 1 (I-1b). Nomenclature for these major cohorts is as follows: Roman numerals I, II, or III are used to indicate the major emergence pulse to which a shoot belongs; a 1 or 2 notation following this numeral indicates the growing season whether first or second. This separation results in

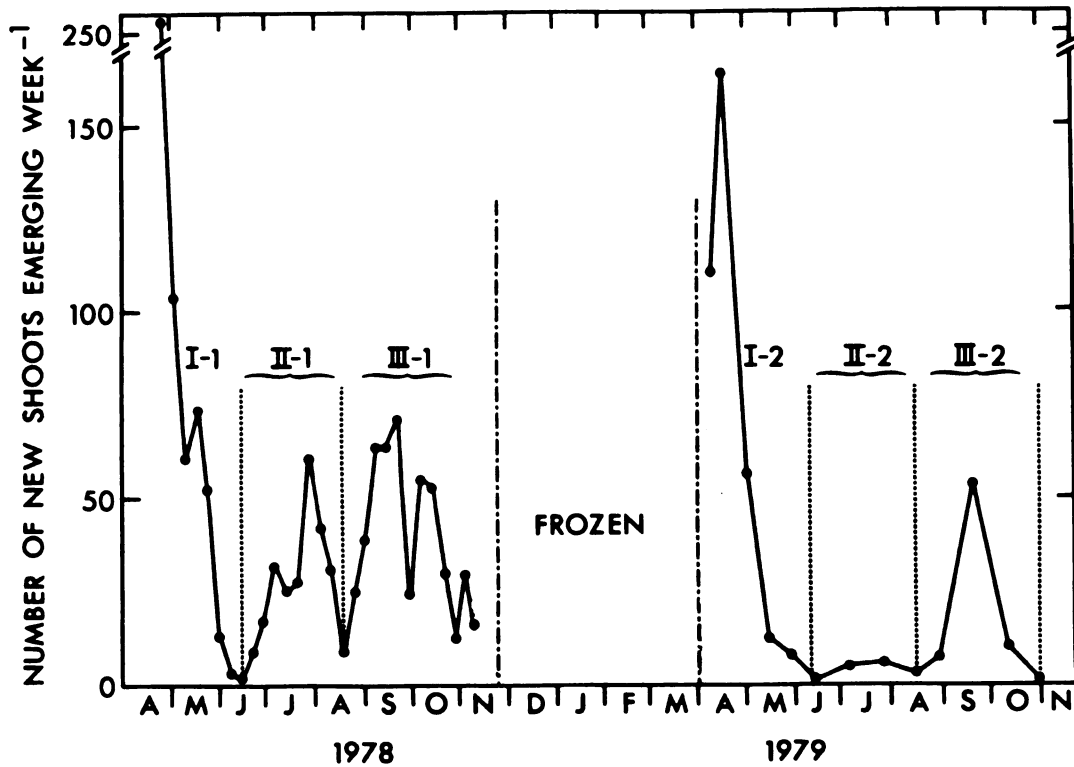


Figure 3. Numbers of newly emerging shoots of *Typha latifolia* in all study plots (20 m²) during 1978 and 1979. "Frozen" indicates the period of winter ice and snow cover when no shoot emergence occurred. Cohort designations are indicated above their respective emergence peaks, and are separated by dotted lines.

the major cohort series. Many analyses were based on these major cohort groupings. All newly emerged shoots of each sampling date have also been grouped into separate cohorts, thereby producing 42 cohorts. Each cohort of this sampling interval cohort series is simply designated by a number, 1-42. The results of many of the sampling interval cohort series analyses (Figs. 8, 9, 15, 18 and 20) further support the validity of the major cohort separations.

As the study progressed, it became clear that the first sampling date (28 April 1978) included many shoots that had emerged during the previous growing season. This condition was ascertained by comparing key relative performance values (e.g. mean heights, Fig. 11; trends in survivorship, Fig. 6; mean mass/shoot, Fig. 17; shoot production, Fig. 20) of the first sampling-period shoots to the performance of the remaining first major cohort shoots, and then comparing these differences to the relative performance values of known overwintering shoots (shoots emerging in year 1 and resuming growth in year 2) in year 2 with major cohort one shoots of year 2. On this basis, it was determined that approximately half of the first sampling date shoots had emerged in the previous growing season. For purposes of some comparisons; therefore, half of the first sampling date shoots were assumed to be newly emerged in year 1.

After excluding half of cohort I-1a shoots (assumed to be 1977 overwintering shoots) from I-1, it was apparent that nearly equal numbers of shoots emerged in the first cohort of year 2 (I-2; 432 shoots) as in year 1 (I-1b; 439 shoots). However, the second and third cohorts of year 1 (II-1 and III-1, with 252 and 482 shoots, respectively) contributed nearly three times as many shoots as their

year 2 counterparts (II-2, 41 shoots; III-2, 208 shoots). The second cohort (II) was the most variable in the two years, and in year 1 the second cohort was six times larger than in year 2. Cohort II contributed only 17 percent to the total number of shoots emerging in year 1 and year 2. The third cohort (III) also exhibited over a two-fold difference in the two years, but together, cohorts III-1 and III-2 accounted for 40 percent of the total number of emerging shoots. Within cohort III-1, there were two one-week periods when numbers of shoots emerging dropped sharply relative to the weeks before and after. The drop at the end of September is most likely the result of an abrupt decline in the mean minimum air temperature (to 6.7 °C, from 15.8 °C during the preceeding four weeks). Mean minimum air temperature for the week following the decline in emergence then increased to 9.4°C.

The timing of cohort emergence was causally related to the developmental status of previously emerged shoots and their attendant rhizomes. Fiala (1971a,b) observed a general seasonal pattern of carbohydrate reserve fluctuation that was consistent from clone to clone despite wide variations in clone age (mature stands or cultivated, rapidly colonizing clones) or environmental conditions (also see Kvet et al., 1969). The seasonal minimum of carbohydrate reserves was found following the initial growth burst of the overwintering and newly emerged cohort I shoots. This period would be the time when numbers of shoots emerging per week declined down to only five shoots for all 20 m² of the study plots over a two week period in year 1 and three shoots during the analogous period in year 2. Exported photosynthate was apparently directly transported to the

sites of new shoot development, so that the second major cohort began emergence shortly after this time. Carbohydrate content of the rhizomes did not start to appreciably increase until late summer and then increased sharply in response to lower night temperatures in the southern Czechoslovakian T. latifolia populations studied. Again a period of reduced emergence in mid-August occurred just after the maximum aerial aboveground biomass (see Fig. 17), followed by the emergence of cohort III. The decline in live aboveground biomass was very likely the result of the major withdrawal of carbohydrates from the senescing tissues. These assimilates along with export of photosynthate from active portions of leaves were undoubtedly transferred into the underground organs for use in formation of cohort III shoots and later, for the formation of the next year's cohort I as well as for generally increasing the carbohydrate rhizome reserves.

Shoot Deaths

The rate of shoot death (= complete shoot senescence, all shoot tissue brown) was more nearly a mirror image of shoot emergence rate, with a large pulse of deaths during the last weeks of the growing season (Fig. 4). The rate of shoot death before the fall peak was just less than 0.5 shoots/m²/week. This rate was small relative to the mean rate of shoot emergence (Fig. 3) and mean live shoot density (Fig. 16). The pattern of shoot death/week was very similar for both years of the study.

The age specific death rate compensates for the fact that larger numbers of shoots are surviving in the younger age classes, and allows direct comparisons of mortality risk at different shoot phases (Fig. 5). The age specific death rate was calculated as the number of

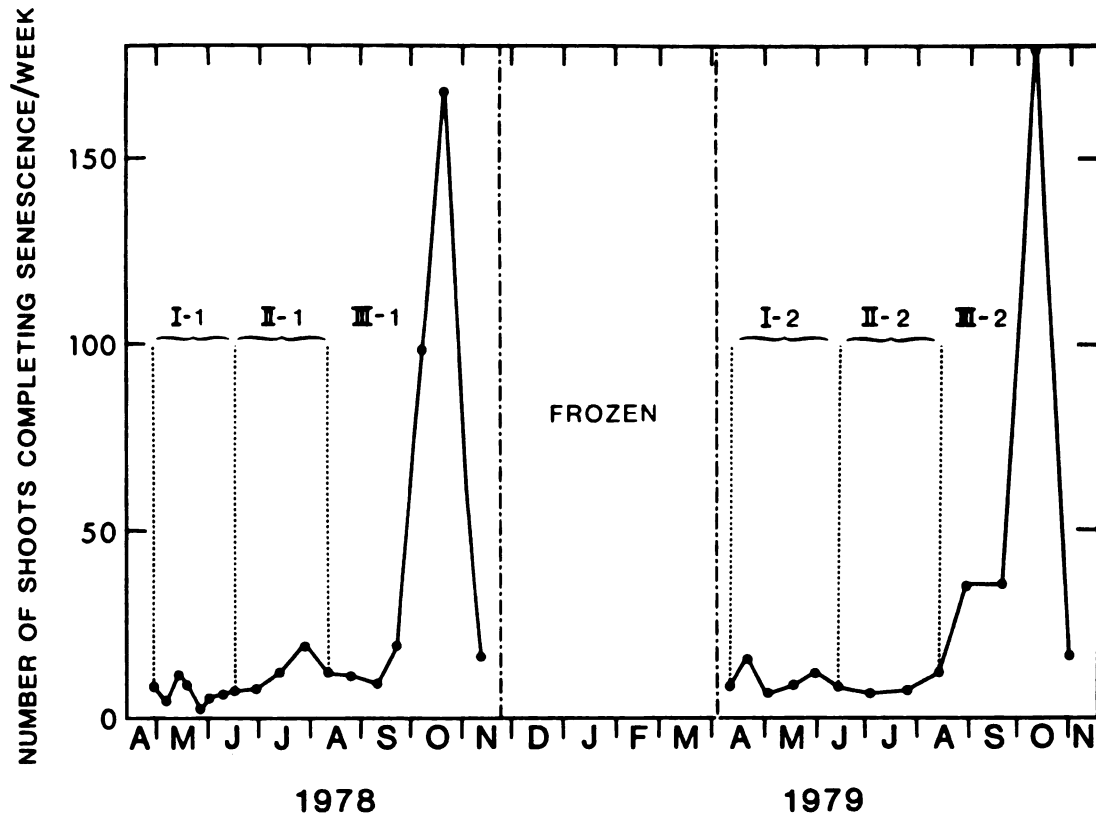


Figure 4. Weekly rates of senescence completion for shoots of *Typha latifolia* (20 m² area) during 1978 and 1979.

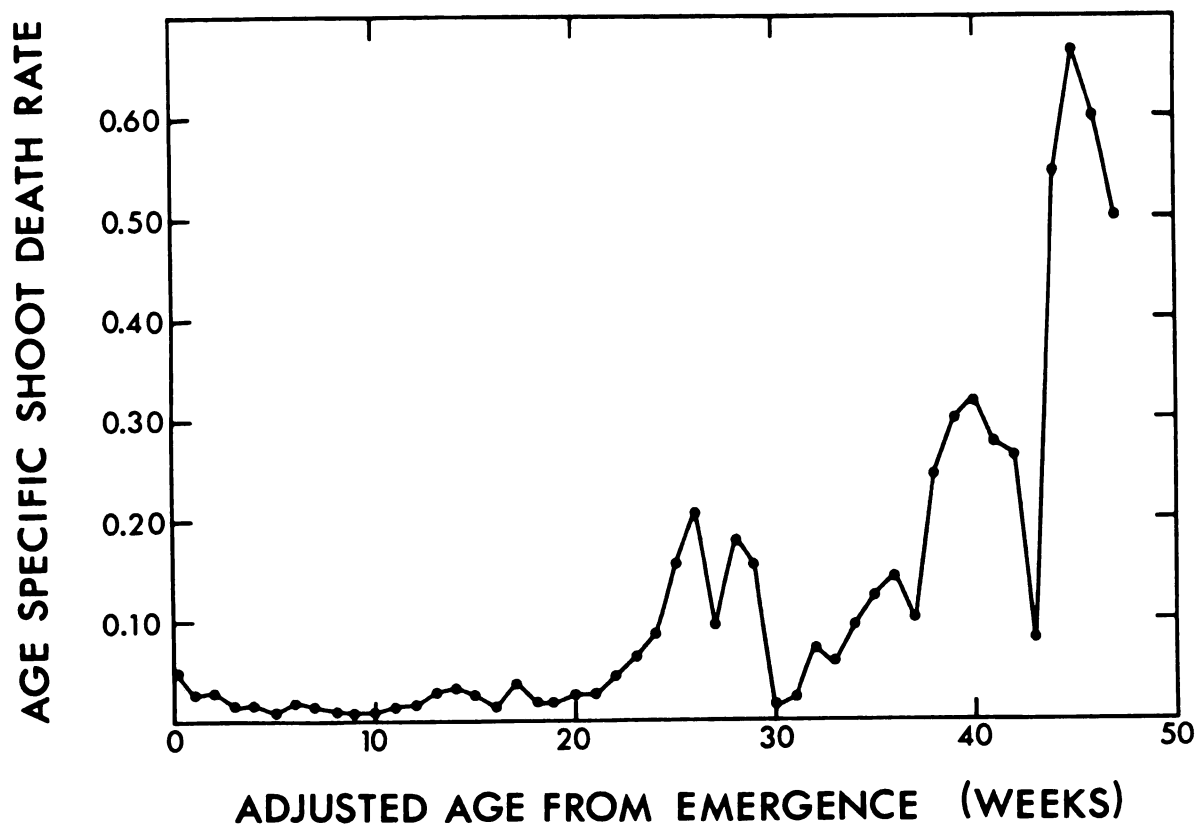


Figure 5. Age specific death rates for Typha latifolia as a function of shoot age (see text for details).

shoots dying in an age class (1-3 week intervals) divided by the number of shoots observed attaining that age. The age classes were adjusted so that only growing season survival was counted. During dormancy (20 weeks in the winter of 1978-1979), no shoot mortality was noted.

The timing of complete senescence for most of the Typha shoots was clearly coincident with the conclusion of the growing season, and indicates an "efficient" pattern of growth. The age at which a shoot dies reflects predominantly the number of weeks available between shoot emergence and the end of the first growing season, if the shoot attains a height of approximately 30 cm or more during the first year of growth. The age at death for shoots achieving less than 30 cm of height during the first year, however, will usually be the number of weeks between emergence and the conclusion of the second growing season, because a winter shoot height-survivorship relationship occurs (see Results section on overwintering-nonoverwintering compromises, Fig. 21).

The risk of mortality during the juvenile phase was clearly minor relative to the senescent shoot phase, and was only slightly greater than the mortality risk experienced by shoots in the adult phase. Early shoot mortality, although slight, was most common in the first week following emergence.

Juvenile shoot mortality was scrutinized by examining those shoots which completed senescence at seven weeks of age or less (Table 1). These shoots were grouped by age in weeks (1 through 7), with a special category being established for newly emerged shoots that were seen only once. Since the sampling interval was weekly during year 1,

Table 1. Juvenile shoot mortality of Typha latifolia: Age in weeks at complete senescence.

<u>Shoot Age Category</u>	1978 (cohorts 2-29) n = 1047		1979 (cohorts 30-39) n = 488	
	<u>Σ shoots</u>	<u>Σ percent</u>	<u>Σ shoots</u>	<u>Σ percent</u>
Shoots alive week #1 but dead by week #2	27	2.6	13	2.7
shoots seen only once	36	3.4	0	0
1 week	63	6.0	13	2.7
2 week	107	10.2	14	2.9
3 week	136	13.0	28	5.7
4 week	150	14.3	30	6.2
5 week	163	15.6	45	9.2
6 week	177	16.9	50	10.3
7 week	190	18.2	63	12.9

this information is useful not only as a quantification of juvenile mortality, but also as an indication of potential early shoot flux missed in studies of similar plants using longer sampling intervals. During year 2 of the study, sampling was at one, two or three-week intervals: therefore, direct week-to-week comparisons of shoot losses in Table 1 are not advisable. Sampling intervals during year 2 did not allow shoots that completed senescence to be assigned to all week intervals. For example, shoots assigned to a four week age at complete senescence may actually have completed senescence at three weeks of age; a two-week sampling interval could not ascertain that age. The lower levels of juvenile mortality in year 2 consequently might represent slight underestimates. Even so, a distinct juvenile mortality difference remained between year 1 and year 2 shoots (see also Figs. 6-8). Thirteen percent (or nearly 7 shoots/m²) of all shoots known to emerge during year 1 (n = 1074) were lost through early mortality (i.e., completed senescence within three weeks of emergence). About half of this early mortality in the year 1 shoot population occurred within the first week following emergence (see also Fig. 5). Less than six percent of all shoots emerging and completing all growth phases during year 2 fell into the early mortality category; this percentage accounted for 1.4 shoots/m². As in year 1, nearly half of the year 2 early mortality occurred within the first week following emergence.

Survivorship

Survivorship curves for the major cohorts closely resembled a stairstep type curve, in which survival rates underwent sharp transitions from one life history stage to the next (Fig. 6). Because

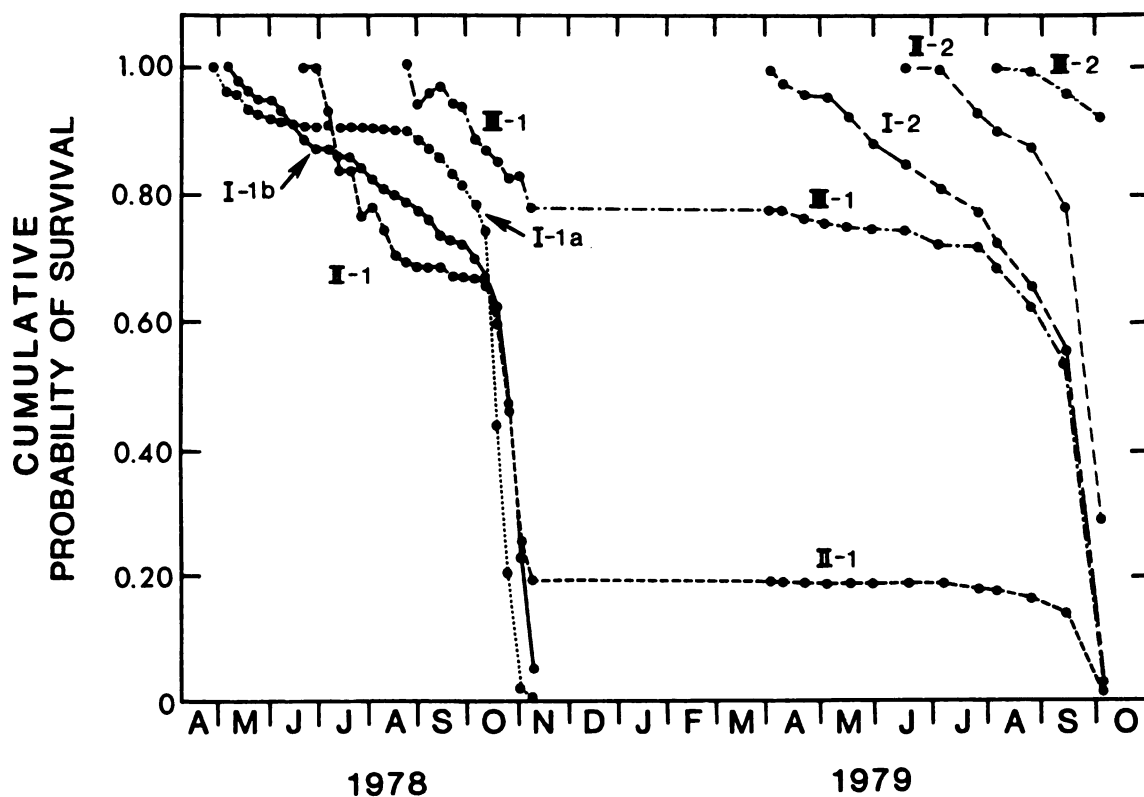


Figure 6. Cumulated probability of survival for major emergence peak cohort shoots of *Typha latifolia* during 1978 and 1979. (See text for explanation of cohort recruitment period treatment).

the major cohort series pooled the emergence of shoots for as many as 12 sampling dates, cohort recruitment continued over the initial survivorship curve period. The probability of survival was cumulated during these periods as cumulated deaths/cumulated cohort recruitment. Hence, it was possible to have increases in probability of survival during these initial periods. The actual curves during these periods may have obscured some flux in deaths and emergences. All survivorship curves revealed an initial juvenile phase of rather low risk of mortality, an adult phase in which risk of death was lowest (in some cases including a span of zero mortality risk; (II-1 in year 2), and finally a senescent phase of extremely high mortality that resulted in the cohort's elimination. In cohort I (I-1b and I-2), however, a separation of juvenile and adult phases would be arbitrary, for mortality risk through these two phases appeared nearly constant. Cohort I survivorship curves completed all phases within one growing season, while the adult phase of cohort II and III survivorship curves extended into a second growing season. A large fraction (80 percent in year 1, 90 percent in year 2) of cohort III shoots survived the winter and resumed growth the following spring; much smaller fractions (20 percent, year 1; 30 percent in year 2) of cohort II shoots successfully overwintered.

Longevity

Longevity was examined for each cohort by determining mean survival time (adjusted longevity index (ALI)) (Fig. 7). Additionally, the success of each of the sampling interval cohorts was assessed by comparing their attained longevity to the maximum longevity possible within the constraints of the growing season (the

portion of the maximum longevity attained (MLA)) (Fig. 8).

The adjusted longevity index (ALI) was calculated for each of the sampling interval cohorts by adjusting the lifespan of each shoot (time of emergence to time of total shoot senescence) so that only growing season survival was counted (Fig. 7). When the marsh was frozen (20 weeks in the winter of 1978-1979 no shoot mortality occurred and no shoot growth was noted. Hence, these 20 weeks were subtracted from the age of any shoot that emerged in year 1 and resumed growth in year 2. The adjusted age of shoot senescence was then multiplied by the relative (percent) contribution of each shoot to the total number of shoots in the cohort. The products derived in this manner were summed for each cohort to yield the ALI. Larger ALI values therefore indicate longer-lived shoots.

Cohort longevity was a function of two factors: primarily the time between shoot emergence and the conclusion of the growing season, but also the shoot mortality suffered during the interim. In each year, the ALI of cohort I decreased down to a minimum longevity value near the first and second cohort boundary. From this boundary, sampling interval cohort longevity increased up to maximal values around the second and third major cohort boundary. Sampling interval longevity within cohort three then declined slightly to the end of the growing season.

Insofar as comparisons between the two years are possible, the same trends in cohort longevity during the two growing seasons were evident. However, longevity was somewhat greater during year 2 largely as a result of a one to two week longer growing season and lower juvenile shoot mortality. The mean longevity for cohort I in

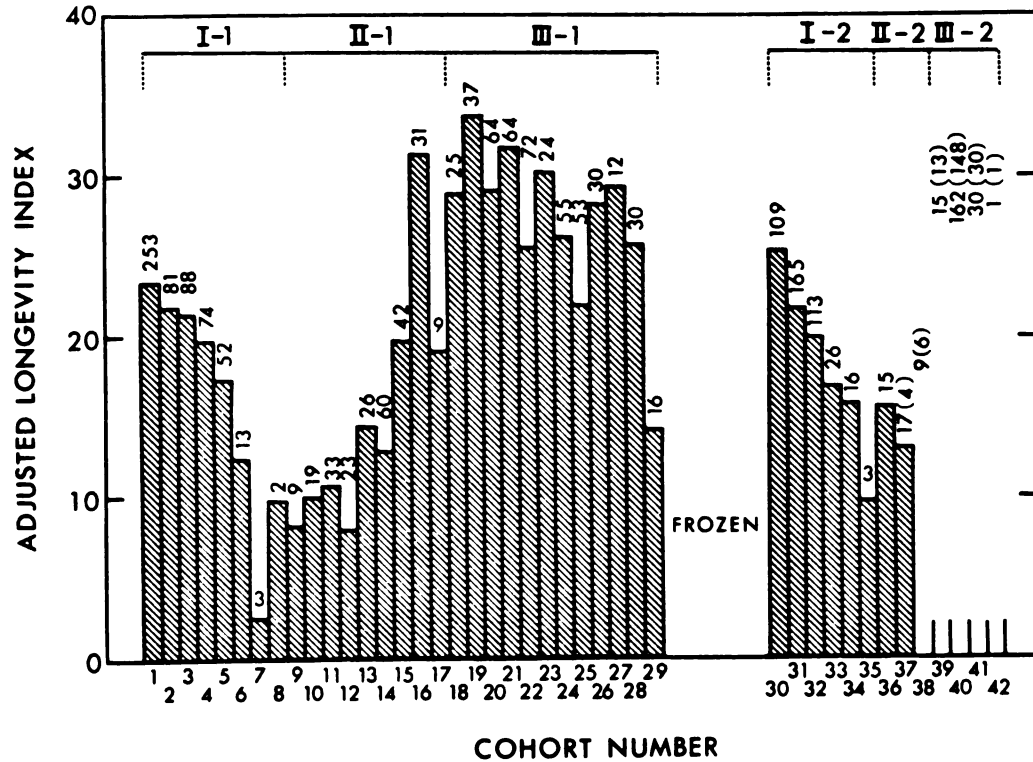


Figure 7. Adjusted longevity (see text for calculation procedure) of *Typha latifolia* shoots during 1978 and 1979. Numbers along the abscissa indicate cohort number (= sampling interval); values above histogram bars designate the number of shoots in each cohort, with shoots still surviving at the end of the study being indicated by values enclosed in parentheses. Major emergence peak cohorts (I-1 through III-2) are shown at the top of the graph.

year 2 was 22 weeks, while longevity for I-1b the previous year was 16 weeks. Longevity for shoots emerging in the latter part of cohort I and the earlier sampling intervals of cohort II in year 1 (cohorts 6-12) was 9.6 weeks, and in year 2 (cohorts 34-36) was 15.2 weeks. Cohort III-1 shoots grew for 27.5 weeks, which was substantially longer than shoots in cohorts I-1b or II-1. Longevity of shoots in cohorts I-1b and II-1 were very similar (16.0 and 15.5 weeks, respectively).

The high longevity of cohort III shoots resulted from low juvenile mortality, limited growth during the last 11 weeks of the year 1 growing season, and a high probability of shoot survival (ca. 80 percent) over the entire second growing season. For most of these shoots, growth ended with abrupt senescence at the end of the second growing season.

In order to relate the survival success of the Typha shoots to the maximum length of time possible for survival (i.e., to the end of the growing season) and to factor out the ALI trends due only to these differences in time from shoot emergence to the end of the growing season, the portion of maximum longevity attained (MLA) by each of the sampling interval cohorts was determined (Fig. 8). For cohorts 1-14 and 30-37, the maximum possible longevity was considered to be the number of weeks between emergence and the conclusion of the first growing season, at which time all shoots in these cohorts had senesced. For cohorts 15-29, the maximum longevity possible was considered to be the number of weeks between the time of a shoot's emergence and the conclusion of the growing season for year 2. This maximum longevity was arbitrary only in the cases of cohorts 13-16; in

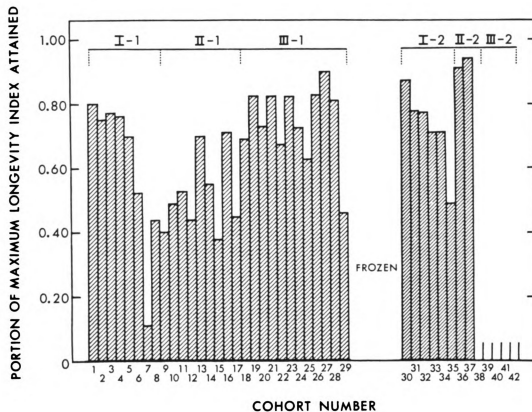


Figure 8. Portion of maximum longevity attained by *Typha latifolia* shoots during 1978 and 1979. Figure notations are the same as those in Figure 7; see text for calculation procedures.

cohorts 13 ($n = 26$) and 14 ($n = 60$), only 2 and 7 shoots respectively survived to continue growth during the second growing season. For these two cohorts, maximum longevity was consequently designated as the end of the first growing season. For cohorts 15 and 16 ($n = 42$ and $n = 31$, respectively), maximum possible longevity was assigned as the end of the second growing season, for in these two cohorts larger numbers of shoots (21 and 5, respectively) resumed growth in year 2.

The general trend within a growing season still shows a declining longevity particularly around the boundary between the first and second major cohorts that could not be accounted for by the reduced time between shoot emergence and the end of the growing season (Fig. 8). Also, the longevity within the second major cohort of year 1 was decidedly reduced relative to the first and third major cohorts. These times of highest early shoot mortality (found in this study) were coincident with the times of lowest carbohydrate reserves in the rhizomes (as determined by the work of Fiala, 1971a,b and Kvet et al., 1969). The very high longevity of the second major cohort of year 2 was a result of very few shoots (one sixth the cohort II-1 shoots) emerging in that cohort, while there were many more adult shoots in the population at that time in year 2 relative to year 1 (see Fig. 16) to export photosynthate. Therefore each emerging shoot probably had a larger supply of photosynthate available. The mean MLA for all shoots is 0.76, or 76 percent of the maximum possible longevity (0.73 in year 1, and 0.80 in year 2). Although no other plant population data exist to which the MLA values can be compared, T. latifolia shoots appear to be impressively successful in terms of survival.

Population Age Structure

When examining the age structure of the T. latifolia shoot population for each month of the two growing seasons (Fig. 9), it is important to recall that the uppermost bar in the year 1 population designates a composite cohort which contains shoots emerging during the 1977 and 1978 growing seasons. This cohort includes shoots ranging in age from 1 to 16 weeks. Although conspicuous emergence peaks (particularly for cohorts I and III) occurred, one could observe a wide range of shoot ages on any given sampling date during the two growing seasons. Because juvenile and adult phases of the shoots in the population experienced low mortality, the shoot emergence pulses (cohorts) could be readily followed through the monthly age structures and on to the conclusion of the growing season. At no time during the study was an even-aged population structure observed.

Population Dynamics

Population Size Structure

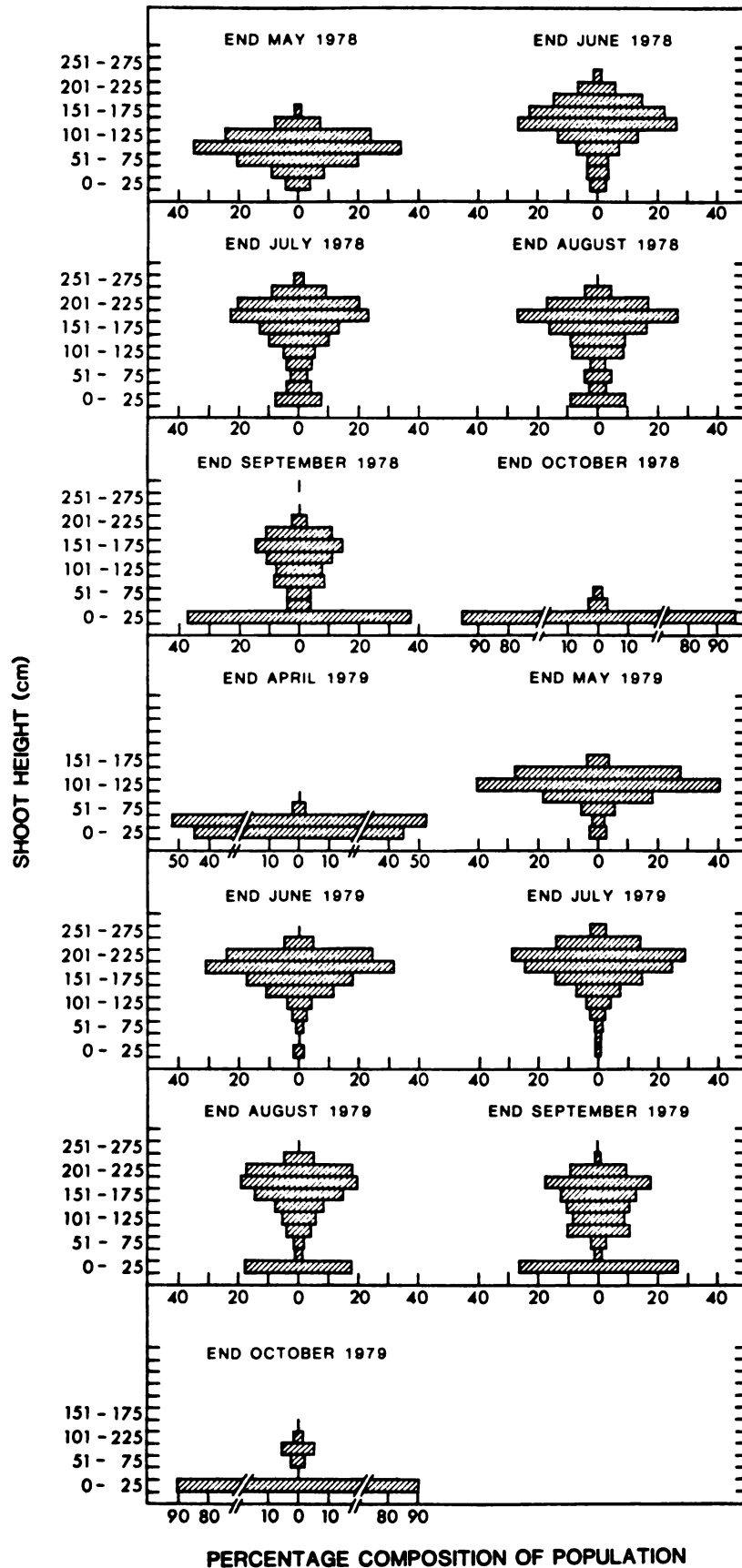
Monthly shoot height structures of the Typha population are shown in Figure 10. Due to the manner in which measurements were made, shoot height values reflect only the development or loss of chlorophyllous tissues. The six major cohorts could readily be identified and followed through the monthly population height structures, just as they could through the monthly population age structures. In both years, an overstory was established by the end of May; the overstory persisted until near the end of September. In year 2, however, the overstory was more extensive due to the greater number of shoots in the same life phase coursing simultaneously through the

Figure 9. Monthly age structures of shoots in a Typha latifolia population for 1978 and 1979.



PERCENTAGE COMPOSITION OF POPULATION

Figure 10. Monthly height distributions of shoots in a Typha latifolia population for 1978 and 1979.



population. When the overstory was maximally developed in year 2, smaller shoot size-classes comprised an even smaller proportion of the total population than they did in year 1. For example, understory shoots (≤ 75 cm in height) at the end of June 1978 comprised 9.6 percent of the population, while understory shoots at the end of June 1979 comprised only 3.3 percent of the population. Due to the domination by overstory shoots, the shoot height structures had negatively skewed distributions during most of the growing seasons in the two years.

The height structures of the T. latifolia population offer no evidence of a hierarchy comprised of a few large, dominating shoots and a large number of short, suppressed shoots. A dichotomous hierarchy of this sort has been suggested to result from a few individuals gaining an early growth advantage over neighboring individuals, thereby suppressing their neighbor's growth more strongly through time (Harper and White, 1974). A positively skewed size distribution is therefore associated with competitive interactions (Koyama and Kira, 1956); by increasing the plant density, the positive skewness of the size distribution can be increased further (Naylor, 1976). The negatively skewed size distributions observed in the Lawrence Lake populations of T. latifolia were the reverse of what one might expect from density-exacerbated competition and simply reflect the process of growth and senescence for the major emergence pulses of shoots.

Mean Shoot Heights

The mean height of each of the major cohorts (with cohort I-1 subdivided into I-1a and I-1b) was calculated for each sampling

interval (Fig. 11). The mean height of a major cohort was also closely linked to its longevity, with the oldest cohorts consistently being tallest at any given time. The oldest major cohorts maintained the highest growth rates up to maximum shoot height. However, the difference in the growth rates between major cohorts diminished with time. The growth rates increased to maximum values in the interval preceding maximum shoot height.

Height of the shoots decreased as senescence occurred because measurements were made only on chlorophyllous tissue. The decline in mean height of the shoots is not the result of a selective loss of tall shoots, but rather a gradual senescing of all individual shoots. The survivorship shoot deaths/week and age specific death graphs (Figs. 4-6) support this observation. The timing of the onset of shoot senescence was very similar in both years for analogous cohorts. The onset of senescence was initiated in a strict order determined by cohort longevity, with the oldest cohorts starting senescence first. Overwintering shoots initiated senescence in late July, followed by cohort I in mid-August; cohorts II and III (in their year of emergence) began senescing simultaneously at the end of August.

The relative performance among cohorts in the same growing season was very similar for the two years. The absolute maximum mean height attained for analogous cohorts, however, was somewhat greater in year 2; the exception to this trend was cohort III-1, which grew taller than III-2 in their respective years of emergence.

Leaf Dynamics

Leaf production, senescence onset, senescence completion and leaf abscission rates were calculated from leaf status information on an

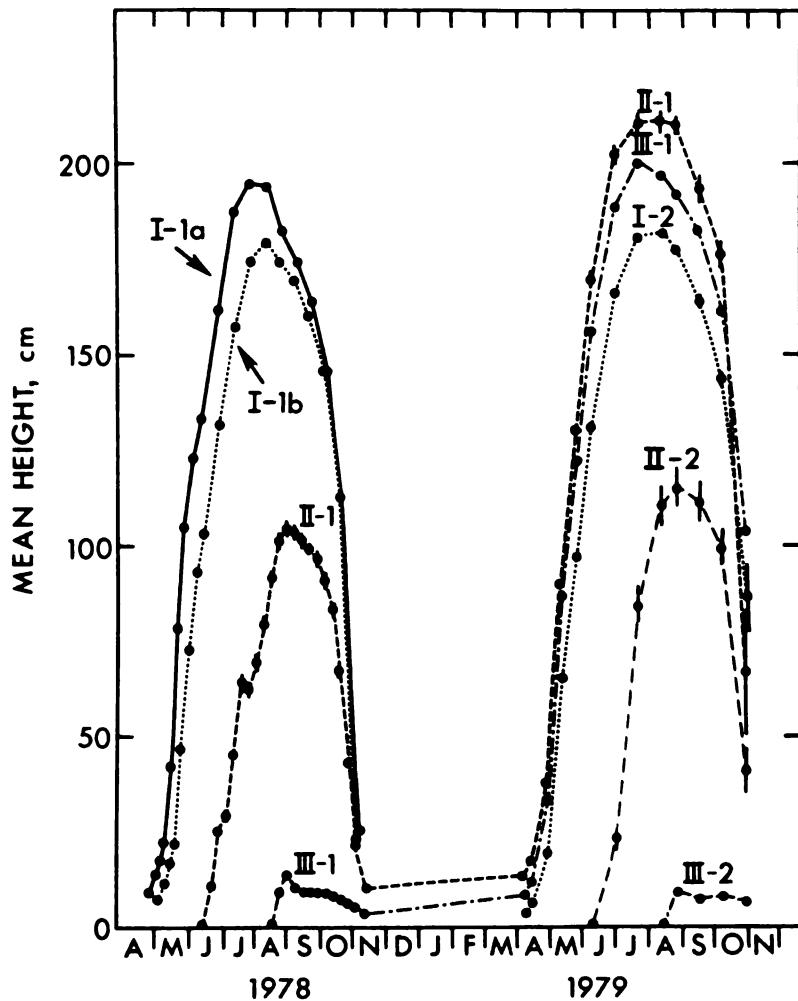


Figure 11. Mean height of major emergence peak cohort shoots of *Typha latifolia* during 1978 and 1979. Error bars designate standard error measurements for all points in which bars would not be obscured by the points themselves.

individual shoot basis for all live shoots in the five study plots. These rates were then grouped into the major cohort series to derive mean values for each leaf status category for all sampling intervals.

Shoots growing from the beginning of the growing season (= main pulse), whether newly emerged (cohort I) or overwintering, exhibited very similar behavior with regards to amplitude and timing of leaf status changes (Fig. 12). This synchronicity of growth in the main pulse shoots was also apparent in the shoot height graph (Fig. 11) and in the shoot biomass graph (see Fig. 17).

Leaf Production

Leaf production in all cohorts was highest during the period just after emergence; rates declined consistently thereafter over the lifespan of the shoot. Overwintering shoots demonstrated a second period of high leaf production when their growth resumed early in the spring. During the spring of year 2, the older the cohort, the greater the initial rate of leaf production. Initial leaf production rates for cohort I in year 1 were higher than for the analogous composite (II-1, III-1 and I-2) in year 2. However, the lower initial leaf production rates in year 2 were sustained for a longer time period. The initial plateau of high leaf production for cohorts II and III in year 1 probably do not indicate real differences in early leaf production patterns for the two years, but more likely indicate differences in sampling intervals.

Senescence Onset

The sharp oscillations in senescence onset rates were not matched by oscillations in rates of senescence completion (Fig. 12). The

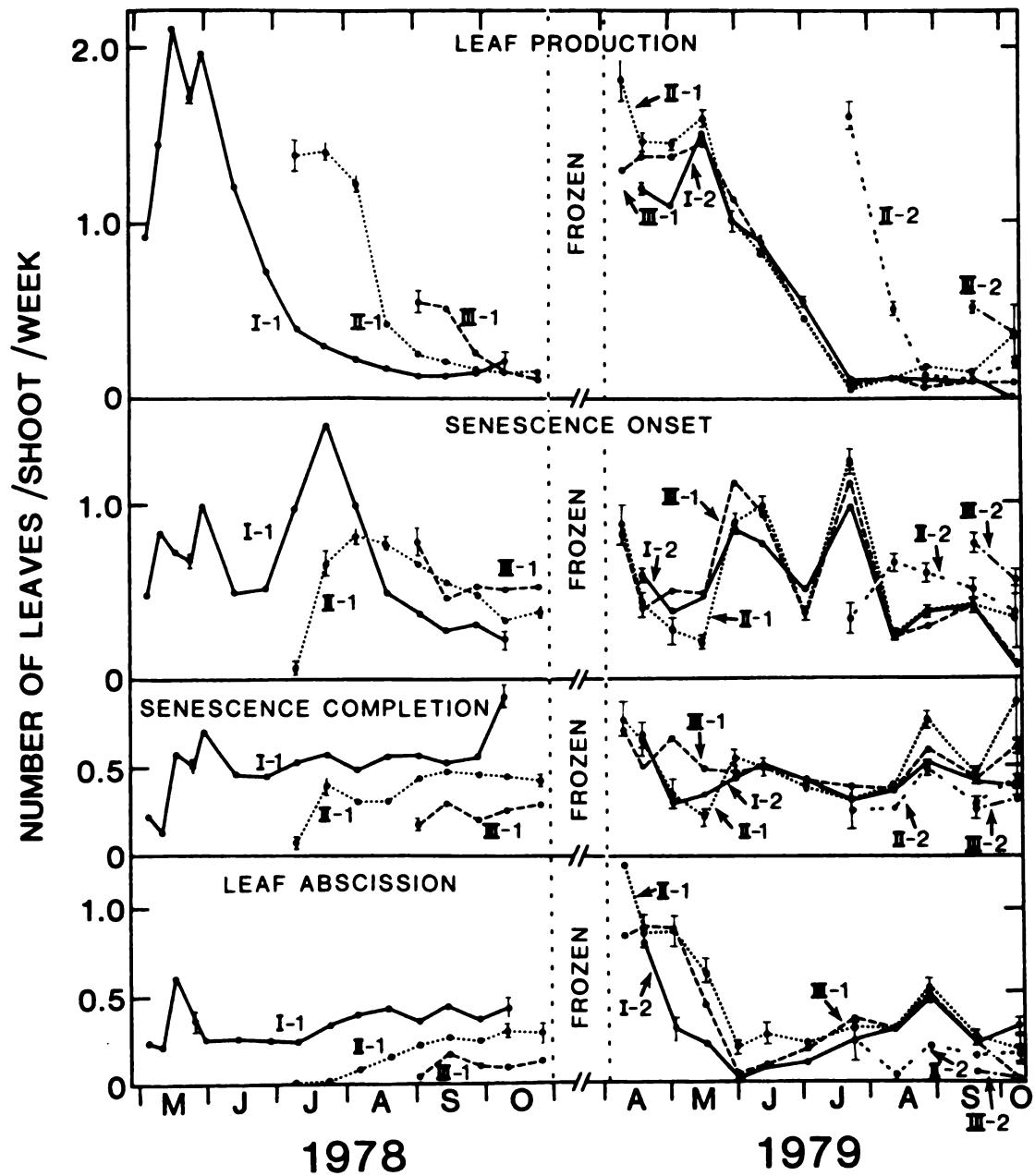


Figure 12. Leaf production and leaf status changes for a *Typha latifolia* population during 1978 and 1979. Error bars designate standard errors whenever they exceed the width of the symbol. Major emergence peak cohorts are indicated by codes I-1 through III-2 (see text).

early increase in the rate of senescence onset observed in all cohorts could be attributed to the loss of sheath leaves. Apart from this early increase, two other peaks were conspicuous in both years for cohort I and the overwintering cohorts. The timing of these two peaks was very similar each year: 1 June 1978 and 31 May 1979; 28 July 1978 and 25 July 1979. The late-July peaks occurred in the sampling interval following the peak aerial biomass for cohort I and the overwintering cohorts. The peak rates of senescence onset for cohort II-2 also occurred in the sampling interval immediately following peak biomass. In the case of cohort II-1, the peak biomass occurred in the second sampling interval subsequent to the peak in rate of senescence onset.

Significantly, in both years the peaks in rates of senescence onset preceded the second cohort's emergence by two weeks, and the second peak preceded the third cohort's emergence by three weeks. A coincidence of leaf senescence on parent rosettes and establishment of daughter ramets was observed in a study of Ranunculus repens plant populations (Lovett-Doust, 1981). The events of peak rates of senescence onset, peak biomass and subsequent shoot emergence appeared to be causally related. The June 1 rate of senescence onset peak must have represented the first major withdrawal of assimilates from the main pulse shoots. These assimilates were very likely being directed to the formation of the second cohort shoots that emerged two weeks after the June 1 peak. In year 2, the analogous peak was more pronounced despite a reduced cohort II-2, one sixth the cohort II-1 size. The large peak in rate of senescence onset reflected an innate synchronicity that was directed primarily in this second year to the

buildup of rhizome carbohydrate reserves rather than new shoot formation. The late-July peak of senescence onset rate must have represented the major assimilate withdrawal associated with the formation of cohort III, which emerged three weeks later. Decreasing vigor of the main pulse of shoots may explain why an additional week was required for the emergence of cohort III shoots as compared to shoots from cohort II. The late-July peak of senescence onset rate marked the beginning of the senescent life phase for the main pulse shoots; leaf production in these shoots was less than 0.1 leaves per shoot per week and their chlorophyllous height rapidly declined from late July (for the overwinter shoots) and mid-August (for the cohort I shoots).

Senescence Completion

The senescence completion rates exhibited little fluctuation relative to the other leaf status change rates (Fig. 12). Only slight increases associated with sheath leaf loss and autumnal leaf loss were evident; a slow, gradual senescing of leaves occurred throughout the growing season.

Leaf Abscission

Leaf abscission rates did not increase markedly towards the end of the growing season (Fig. 12). The only notable increase in rate of leaf abscission was in May of year 1 and in April and May during year 2. The increase in leaf abscission rates during the spring of these two years reflected the loss of sheath leaves and the loss of other outer leaves damaged during winter.

Leaf Status per Shoot

The mean number of leaves in each leaf status category (chlorophyllous, senescing and senescent) and the total mean number of leaves for all living T. latifolia shoots (Fig. 13) are the products of the leaf status change rates seen in Figure 12. The timing of the maximum mean total number of leaves per shoot was coincident with the mean maximum number of chlorophyllous leaves per shoot for both years. These mean maxima were recorded on the same sampling period in each of the two years (30 June 1978 and 3 July 1979). The mean maximum total number of leaves per shoot was greater in year 2 (13.6 leaves per shoot) than in year 1 (12.3 leaves per shoot). By contrast, the mean maximum number of chlorophyllous leaves per shoot was lower in year 2 than it was in year 1 (7.5 and 9.1, respectively). The curves depicting the mean number of chlorophyllous leaves per shoot were distinctly similar to their corresponding leaf production curves (Fig. 12) for cohort I-1 and its year 2 analog. In year 2, the peak in mean number of chlorophyllous leaves per shoot persisted two weeks longer than the leaf production curve. This two-week lag between the decline in rate of leaf production and the decline in the actual mean numbers of green leaves per shoot indicates that, in year 2, leaves were growing more slowly than they were in year 1.

The maxima in the total number of leaves per shoot and the number of chlorophyllous leaves per shoot occurred approximately four weeks before the seasonal peak aerial biomass (see Fig. 17) in each of the two years. Since the growth of leaves is most often determinant (Harper, 1977), it is plausible that the four-week delay to seasonal peak aerial biomass indicates a four-week (or ca. 28-day) life span

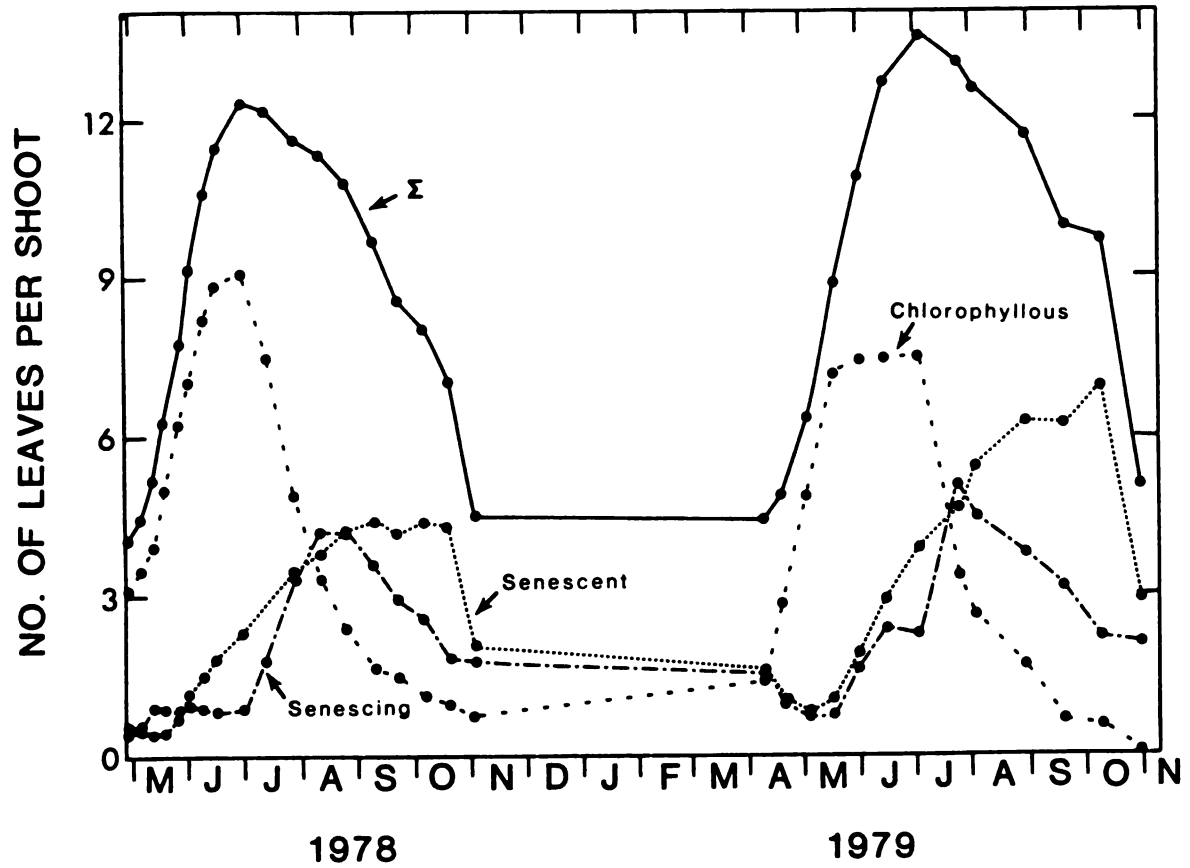


Figure 13. The mean number of total leaves, and the number of leaves in three status categories for shoots of *Typha latifolia* during 1978 and 1979.

for leaves of T. latifolia, inasmuch as the greatest rate of senescence onset occurred just following the peak biomass. This leaf life span closely agrees with the 26-day life span for T. angustifolia in a Wisconsin marsh (Linde et al., 1976).

Total leaf production, mean numbers of leaves per shoot and leaf turnover rates (see Fig. 16) were compared for those shoots that completed all life phases within one growing season (cohorts 2-14 in year 1 and cohorts 30-36 in year 2, but no significant differences in any of these parameters were found between the two years.

Maximum Number of Leaves per Shoot

Shoots that completed all life phases during the study (cohorts 1-35) were analyzed to determine their greatest number of leaves at any given time. These shoots were then grouped according to their affiliation with a major emergence pulse (i.e., cohorts I-1 through I-2). Most notable was the strong clustering of shoots bearing a maximum of 14 leaves, except in the case of cohort II-1 (Fig. 14). Nearly half (42 percent) of all Typha shoots had a maximum number of leaves between 13 and 16, and only 1.7 percent (= 29 of the 1,704 shoots) accrued more than 19 leaves. Shoots in the one- to six-leaf per shoot maximum category (16 percent of all shoots) were primarily shoots that had completely senesced in the juvenile shoot phase (cf. Table 1), for 16.2 percent of the entire T. latifolia population completely senesced before six weeks of age. Fourteen leaves per shoot could be an optimum number, perhaps in terms of maximizing photosynthetic efficiency while minimizing effects of self-shading and costs of leaf maintenance.

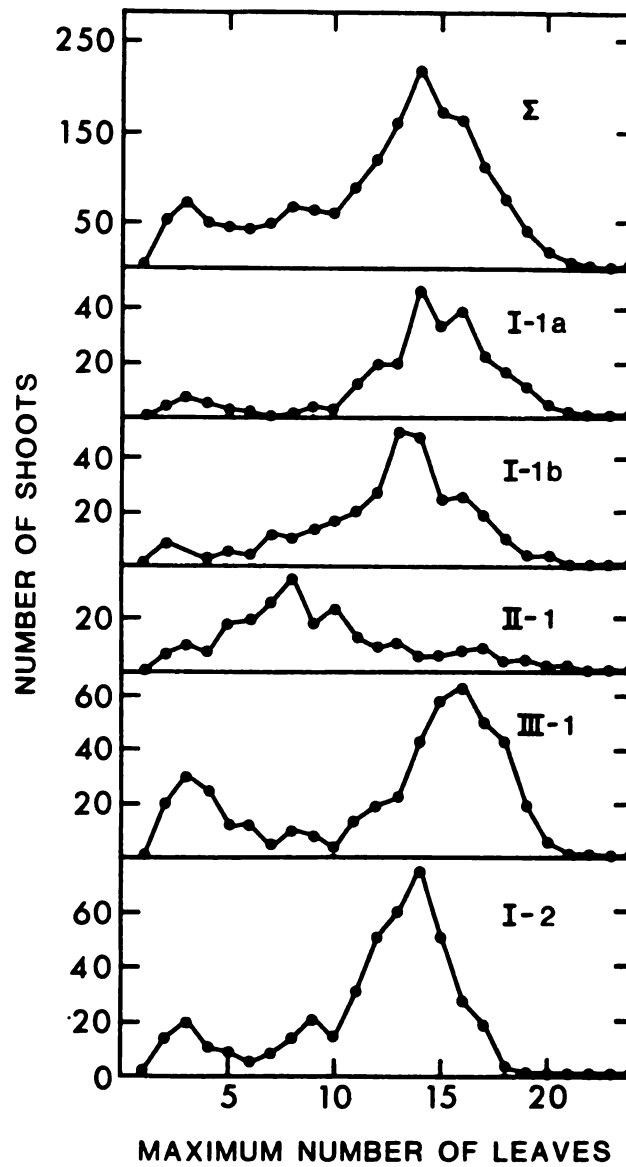


Figure 14. Maximum numbers of leaves per shoot of *Typha latifolia* in different major emergence peak cohorts. The uppermost panel shows the distribution of maximum number of leaves in the total shoot population (cohort I-1 through I-2).

Modal maximum numbers of leaves per shoot for cohorts that completed all shoot phases in one growing season were 13 for cohort I-1b, 8 for cohort II-1, and 14 for cohort I-2. Overwintering cohorts had slightly higher leaf maxima. Cohort I-1a was bimodal, with peaks in leaf maxima modes at 14 and 16. In this cohort, the maximum of 14 leaves was very likely from the 1977 cohort III shoots, while the 16 leaf maximum probably originated from the 1977 cohort II contribution to cohort I-1a. Shoots in the overwintering cohort III-1 had a leaf maximum mode at 16, while overwintering shoots in cohort II-1 had 17 leaves per shoot as a mode. Modes for the year 1 shoots were all lower than modes for leaf maxima in year 2 cohorts.

Leaf Turnover

Leaf turnover was calculated for each of the sampling interval series cohorts completing their life phases during the study (Fig. 15). Total leaf production (the sum of the initial number of leaves plus leaf production for each subsequent interval) was divided by the mean number of leaves per shoot (as determined from two-week intervals for both years) to obtain the leaf turnover values. Calculating leaf turnover provided a way to assess and compare the numbers of leaves produced and lost on a shoot during the shoot's life span. Leaf turnover ranged from no turnover (1.00) to 1.93, the latter value indicating nearly one complete turnover of leaves over a shoot's life span. Cohorts dominated by overwintering shoots (cohorts 15-29) demonstrated a higher leaf turnover (1.61) compared to mean leaf turnover values of nonoverwintering shoots (cohorts 2-14 and 30-36), which had means of 1.29 and 1.27, respectively; this difference was highly significant ($t = 6.38$, $p < 0.001$). Overwintering shoots

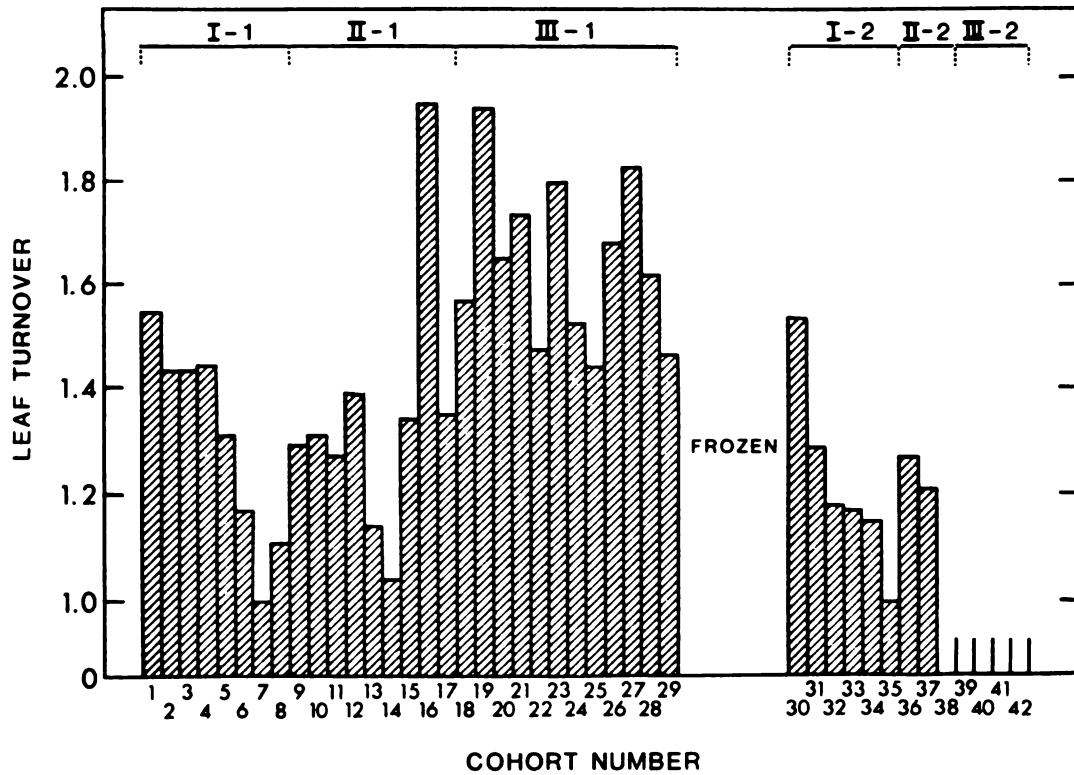


Figure 15. Leaf turnover in *Typha latifolia* shoots during 1978 and 1979. Numbers along the abscissa indicate cohort number (= sampling interval) to which the shoots belong; major emergence peak cohorts (I-1 through III-2) are shown at the top of the graph (see text for calculation procedure).

sustained leaf losses in addition to the sheath leaf loss and late spring frost leaf damage that most other shoots also experienced. The replacement of these leaves by overwintering shoots resulted in the higher leaf turnover values.

Shoot Density

Total live shoot density and density of live shoots in each of the major cohorts (I-1 through III-2) are shown in Figure 16. The ranges in live shoot density were very similar for the two years: 12.7 to 43.9 shoots/m² in year 1 vs 11.2 to 41.9 shoots/m² in year 2. However, the Typha population achieved the two comparable live shoot density ranges via two very different routes. In year 1, total live shoot density increased continuously from 12.7 shoots/m² to a maximum of 44.6 by mid-October. In striking contrast, a high live shoot density was established early in the second growing season (40.1 shoots per m² by mid-May), and this density was largely maintained throughout the growing season.

The very rapid and early establishment of the high shoot density in year 2 was undoubtedly the consequence of the large number of overwintering shoots from cohorts II-1 and III-1, which together accounted for 50 percent (21.6 shoots/m²) of the total number of shoots (43.2 shoots/m²) comprising the main pulse of shoots in the year 2 growing season. In year 1, however, overwintering shoots from cohort I-1a were estimated to account for only 6.4 shoots/m² of the total main pulse density of 22.0 shoots/m². In year 1, the second cohort added 12.6 shoots/m² to this relatively low density of the Typha population. In year 2, however, the early establishment of high density resulted in a very much smaller contribution (only 2.1

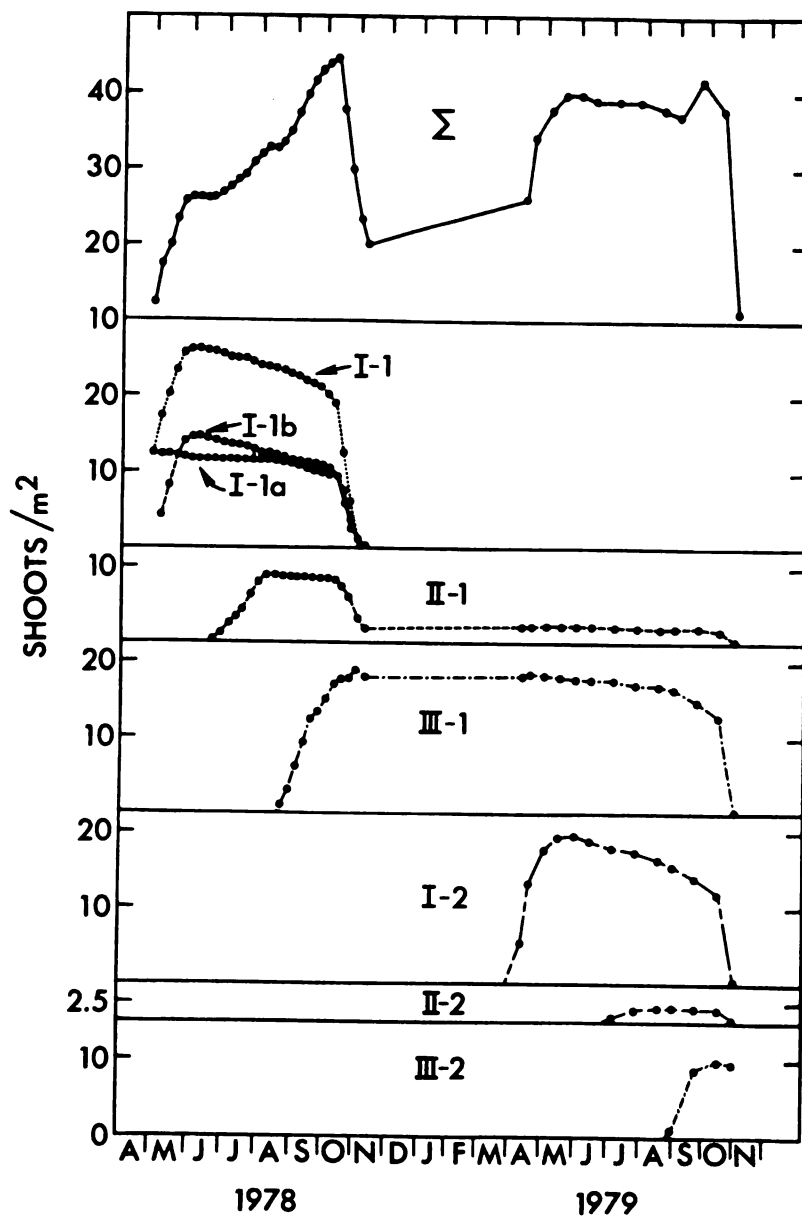


Figure 16. Live shoot density of *Typha latifolia* in different major emergence peak cohorts during 1978 and 1979. The uppermost panel shows total live shoot density.

shoots/m²) to overall density by the second cohort. The different means through which maximal live shoot density was achieved by the T. latifolia population in the two years had far-reaching consequences in terms of total production (see Fig. 18) and patterns of shoot recruitment (see Table 2).

Biomass and Production

Live Shoot Biomass

Total living shoot biomass values (g/m², ash-free dry mass (AFDM)) and living shoot biomass values for each of the major cohorts (with cohort I-1 being separated into I-1a and I-1b) are shown in Figure 17. The timing of peak biomass was very similar in the two years: Cohorts I-1a and I-1b peaked on 28 July 1978, and their analogous cohorts peaked simultaneously on 25 July 1979. The total living shoot biomass peak in year 2 was coincident with the main pulse cohorts (II-1, III-1 and I-2). In year 1, however, total living biomass peaked two weeks later on 11 August, primarily due to the influence of the relatively large biomass contribution of the second cohort in that year.

Peak biomass values for year 1 and year 2 were substantially different, with maximum total biomass in year 2 being 60 percent greater than in year 1 (833 g/m² vs 1318 g/m²). In year 2, the biomass of the main pulse shoots accounted for over 99 percent of that total peak biomass value. These differences clearly underscore the important effect that differences in the pattern of shoot density (early establishment vs a gradual seasonal increase) have on annual production. Establishment of high shoot density early in the growing season by Typha was similar to precocious seed production by other

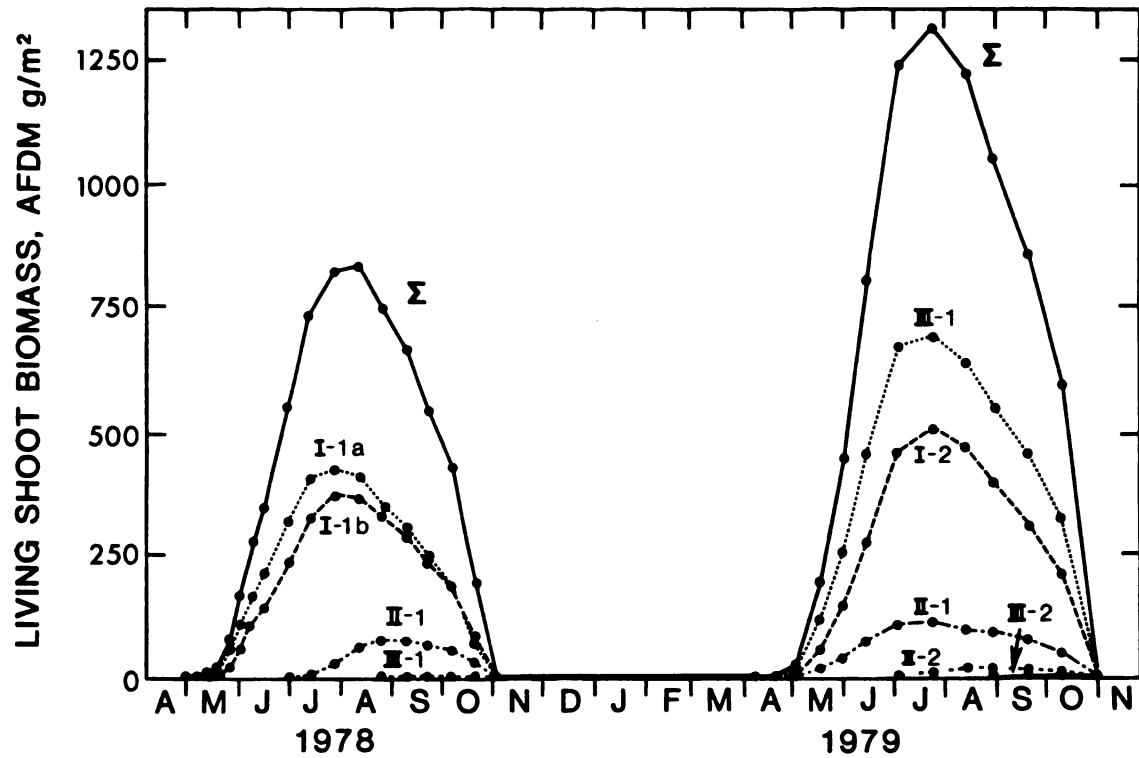


Figure 17. Living shoot biomass of *Typha latifolia* during 1978 and 1979, with contributions by major emergence peak cohorts being designated by codes I-1a through III-2. Total live shoot biomass is also shown.

species: Both strategies yield surprisingly large dividends.

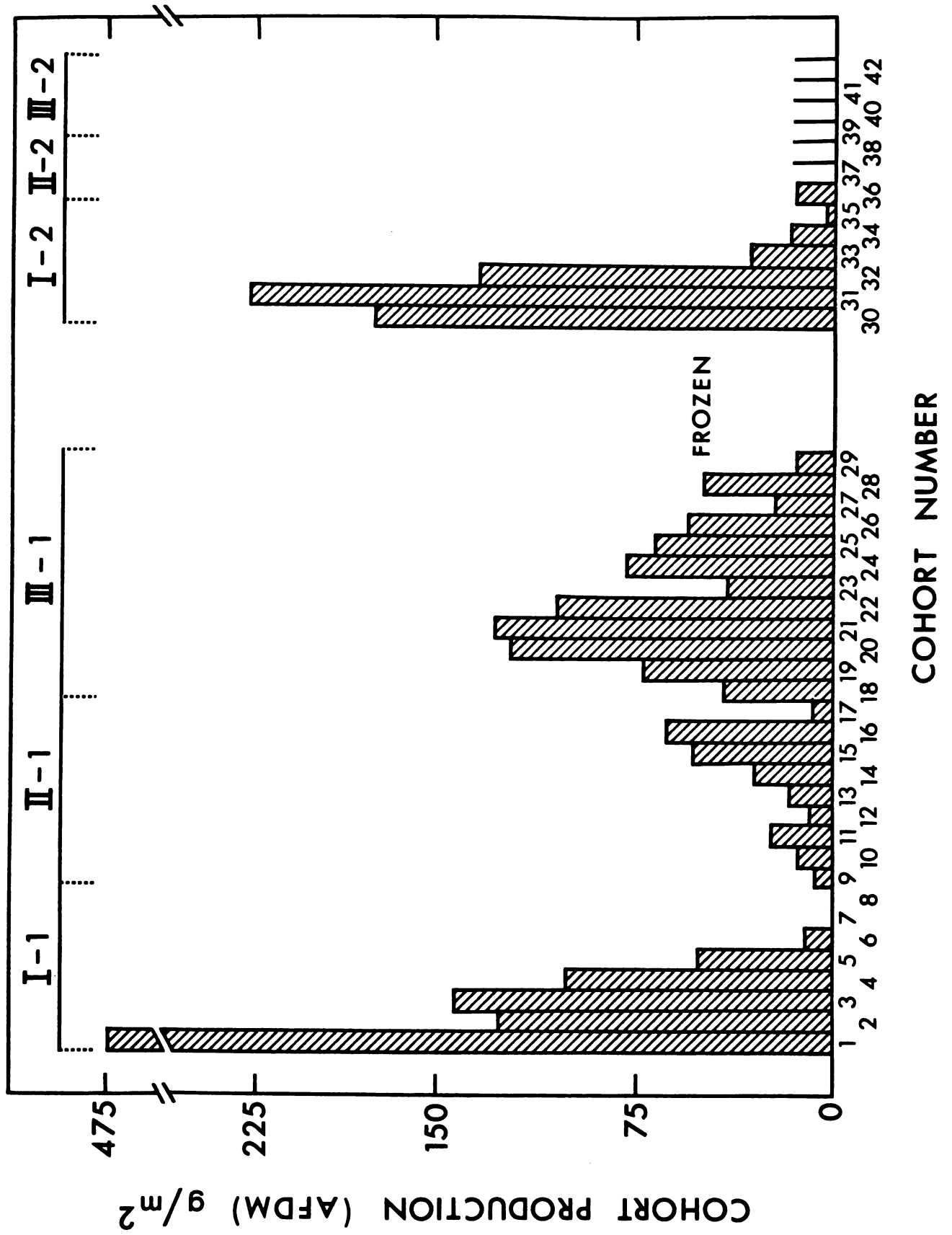
In both years, overwintering cohorts contributed heavily to the total peak biomass of the population. Collective contributions by overwintering cohorts to the total peak biomass were 51 percent in year 1 and 61 percent in year 2.

Cohort Production

Cohort production was calculated for the first 36 of the 42 cohorts (Fig. 18). Production by cohorts 37 through 42 could not be calculated simply because many shoots in these cohorts were still living at the end of the study. Within a cohort, all shoots were grouped into classes according to their age at death (complete senescence). A mean maximum mass (g AFDM) attained by the living shoots in each senescence age class was then determined, and this mean was multiplied by the number of shoots in the senescence age class. These products were summed and expressed on an areal basis to determine the cohorts' production.

Cohort production closely followed the number of shoots in each of the 42 cohorts. In a comparison based on the rankings of number of shoots in a cohort and the rankings of production by that cohort, cohorts belonging to the second major emergence pulse of year 2 were the most consistent. These cohorts also ranked very slightly higher than would be expected based on numbers of shoots alone (+0.3 ranks, on the average). Cohorts belonging to the first major cohort in year 1 and year 2 were the most variable and ranked lower (-0.8 and -1.0 ranks, respectively) for production than for numbers of shoots.

Figure 18. Production (AFDM g/m²) for sampling interval cohorts of Typha latifolia shoots completing senescence during 1978 and 1979. Major emergence peak cohort codes (I-1 through III-2) are shown at the top of the figure.



Biomass-Density Relations

The course of growth of the Typha population for the two years was graphed as a function of mean shoot mass and shoot density (Fig. 19). The most conspicuous feature observed was the variation in pattern of growth from year to year.

The year 1 shoot population showed a more circular succession of density and shoot weight than the year 2 population due primarily to the larger contribution by cohort II shoots during midsummer of the former year. As a result, shoot generations in year 1 demonstrated considerable overlap, whereas generations in year 2 appeared more discrete. The cyclic relationship between mean shoot mass and shoot density was classified by Hutchings (1979) as class B within ramet populations of clonal perennial herbs. The maximum mass per shoot in year 1 was 27.3 g, and this maximum occurred one week before the peak aerial biomass maxima for cohorts I-1a and I-1b and three weeks before the total living shoot aerial biomass.

The year 2 shoot population exhibited little change in density over the growing season. Because in this year there were few cohort II shoots, the population succession was most like ramet populations having discrete cohort generations. The year 2 Typha population consequently appeared to be a class A clonal perennial population (Hutchings, 1979). In this population, maximum mass per shoot was 34.0 g, or 24 percent more mass than in year 1. The more massive shoots in year 2 were observed despite the much greater density of shoots (more than 10 shoots/m²) during the year 2 growing season. In the year 2 season, peak total living shoot aerial biomass, peak main pulse biomass (cohorts II-1, III-1 and I-2), and maximum mass per

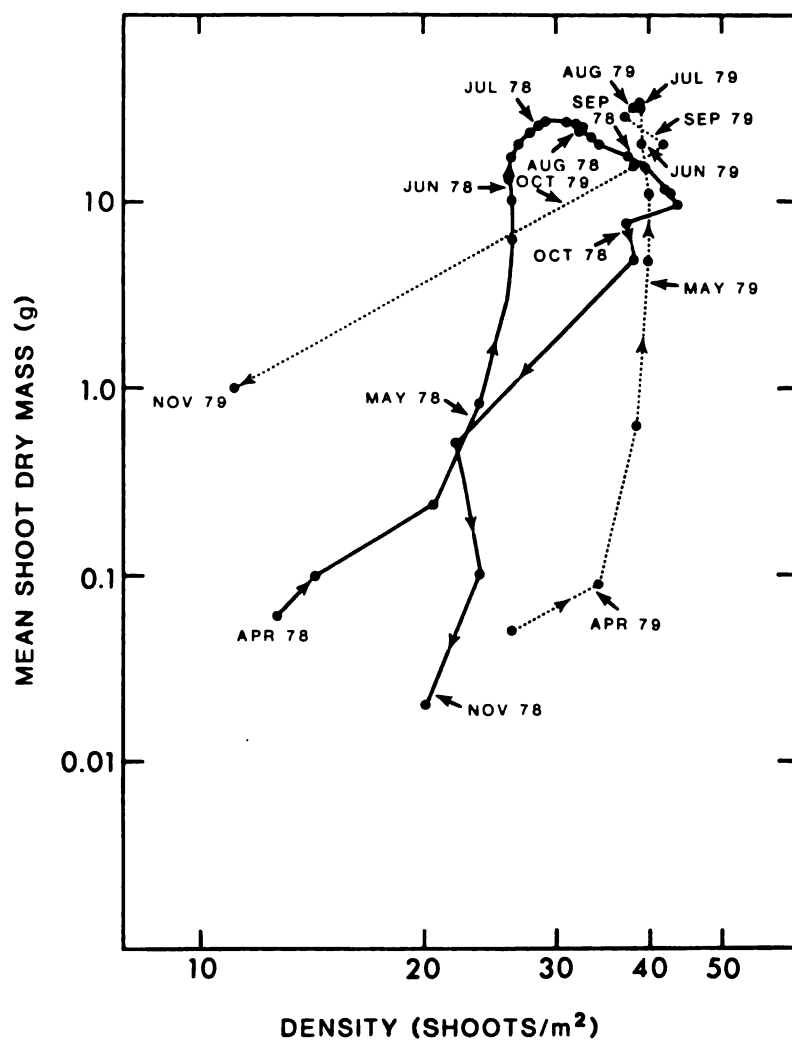


Figure 19. Density-mean shoot dry mass relationships for *Typha latifolia* shoots growing during 1978 and 1979. Arrows show seasonal direction of changes. Indicated dates are placed at midmonth.

shoot were coincident on 25 July, as would be expected in a discrete cohort generation population.

Shoot Production

Data on cohort production was presented earlier (Fig. 18). In production analyses examined on a per-shoot basis for the sampling interval cohorts, shoot production was calculated similarly to cohort production, with the exception that the number of shoots in the senescence age class was divided by the total number of shoots in the cohort before multiplying the mean maximum live mass of each senescence age class (Fig. 20).

Comparisons of shoot production revealed that the single most productive cohort was 16 ($\bar{x}$ maximum mass of 38.7 g/shoot), from the cohort II-1 group. However, high shoot production by cohort II-1 was not the rule, for as a group, shoots from this major cohort were short-lived and had very low and extremely variable production ($\bar{x}$ = 16.5 g/shoot, CV = 60.5 percent). The second, third and fourth most productive of the sampling interval cohorts all belonged to the cohort III group that emerged in year 1. As a group, cohort III shoots were most consistently productive ($\bar{x}$ = 31.2 g/shoot, CV = 20.8 percent). Shoots from cohort I-1b were considerably more productive and more variable ($\bar{x}$ = 25.8 g/shoot, CV = 74.4 percent) than shoots from the cohort II-1 group. Shoots from cohort I-2 had the second best consistency ($\bar{x}$ = 25.6 g/shoot, CV = 23.2 percent). Shoots in cohort II-2 that completed their life phases during the study originated from only one cohort of the sampling interval cohort series (cohort 36), and the shoot production values for these shoots was 18.0 g/shoot,

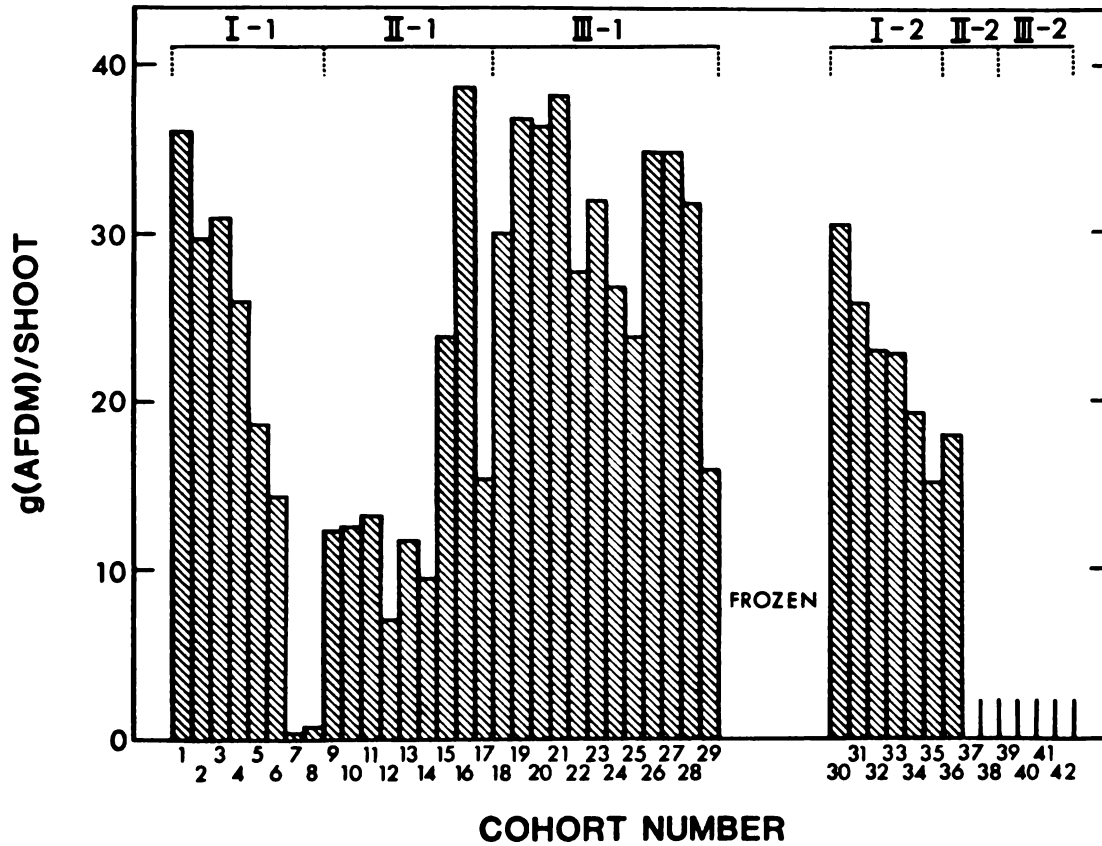


Figure 20. Shoot production (see text for calculation procedure) for sampling interval cohorts of *Typha latifolia* during 1978 and 1979. Major emergence peak cohorts (I-1 through III-2) are indicated at the top of the figure.

considerably higher than shoots from the analogous first three cohorts in the year 1 cohort II group ($\bar{x} = 12.8$ g/shoot). Overall trends in shoot production were most similar to shoot longevity (see Fig. 7) within the sampling interval cohort series.

Overwintering-Nonoverwintering Tradeoffs

Analyses and comparisons of being a nonoverwintering or an overwintering shoot were based on an individual shoot perspective. The comparisons were drawn between year 1 overwintering shoots (cohorts 15-29) and the year 2 nonoverwintering shoots (cohorts 30-36), since these shoots developed during the same growing season.

Shoot Carryover

The phenomenon of overwintering shoots that emerged in one growing season and resumed growth during the next growing season was designated as shoot carryover. Shoot carryover was determined for the years 1977 through 1980 in the Typha population, as well as the contribution to carryover by each of the major cohorts (Table 2). The 1977 carryover value (6.4 shoots/m²) was based upon half the numbers of shoots in cohort I-1a. Only ten percent of the year 1 living shoot population originated from 1977 overwintering shoot. In year 1, shoot carryover into year 2 was over three times as large (21.6 shoots/m²), and accounted for nearly 40 percent of the live shoots in the year 2 Typha population. In year 1, the main pulse of shoots was relatively sparse, which allowed cohorts II and III to develop more extensively; increases in cohorts II and III then resulted in higher carryover into year 2. Carryover from year 2 into year 3 was lower again with only 10.1 shoots/m². This low carryover was a consequence of the high

Table 2. Cohort contributions[†] to aerial density (shoots/m²) and shoot carryover (shoots/m²) for Typha latifolia in the Lawrence Lake marsh.

Year	Cohort I		Cohort II		Cohort III		Total carried over
	gross	(net)	gross	(net)	gross	(net)	
1977	---	---	---	---	---	---	6.4
1978	22.0	(20.2)	12.6	(8.9)	24.1	(18.1)	21.0
1979	21.6	(18.8)	2.1	(2.0)	10.4	(9.6)	10.1
1980*	---	(26.6)	---	(3.3)	---	---	---

[†] Boxed cohorts designate cohorts contributing carryover shoots; the number of shoots carried over (shoots/m²) by each cohort are indicated by circled numbers.

* 1980 totals are net numbers of shoots/m², since for this year, mortality losses were unknown. All net values were calculated for shoots using end-of-cohort dates of June 15, August 15 and mid-November/end of October for the different years (see text for details).

shoot density prevailing in the marsh when cohorts II and III were emerging during the year 2 growing season. Cohort II was very responsive to differences in live shoot density from year to year, and its density values ranged by a factor of six over the course of the study; ranges in density for cohort III varied 2.3-fold by comparison.

The number of shoots that emerged as members of cohort II were fewer than those that emerged as members of cohort III in any given growing season. However, year-to-year fluctuations were large, so that cohort II in year 1 had more shoots (12.6 shoots/m^2) than cohort III did in year 2 (10.4 shoots/m^2).

Overwinter Survival

In an attempt to establish what factors might be important in determining which shoots of cohort II-1 and III-1 successfully overwintered, the maximum height attained by individuals in these two cohorts in the year of their emergence was examined and plotted as a function of probability of survival during the second year (Fig. 21). It was apparent that no shoot growing taller than 100 cm during the year 1 growing season survived to grow during the year 2 growing season. Additionally, the probability of successfully overwintering was inversely related to the maximum height a shoot attained, even though all overwintering shoots senesced down to five or ten cm at the end of their season of growth.

Shoot Production and Longevity

Mean cohort longevity and mean shoot production for the two shoot categories (overwintering, nonoverwintering) were satisfactorily described with linear relationships (nonoverwintering: $r = 0.94$, $p <$

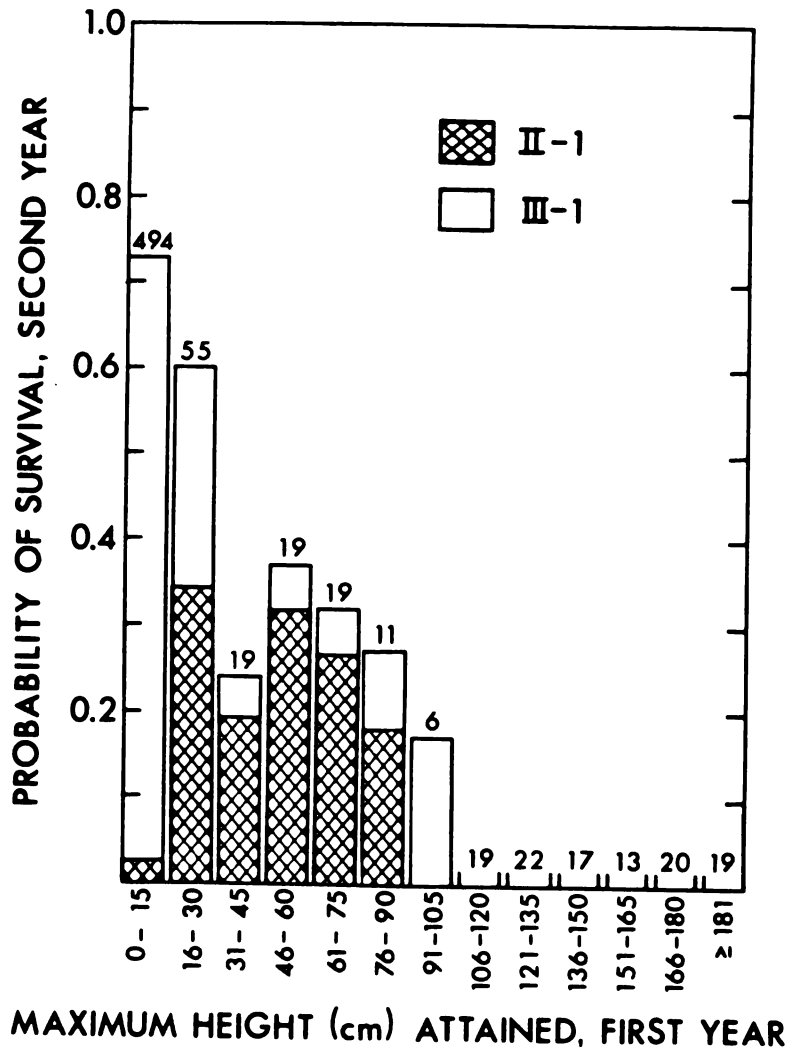


Figure 21. Survival probability of *Typha latifolia* shoots as a function of shoot height attained the previous growing season. Abscissa indicates maximum shoot height attained (cm) during the first growing season. Hatched areas of each histogram bar represent the contribution by cohort II-1, while the open portion of each bar designates the contribution by cohort III-1. Numbers above the bars indicate the number of shoots in each height class.

0.001; see Fig. 22). The slopes of the two relationships were 1.426 and 1.292, respectively. When compared in the region of shoot production overlap, it was clear that overwintering shoots required 2.5 to 2.6 weeks of additional time to match the same level of shoot production as a nonoverwintering cohort.

Total Leaf Production and Longevity

Total leaf production for each of the sampling interval cohorts was plotted against the mean shoot longevity after the cohorts had been grouped into overwintering (cohorts 15-29) and nonoverwintering (cohorts 2-14 in year 1 and cohorts 30-36 in year 2) categories (Fig. 23). The results clearly showed that overwintering shoots had a greater longevity and produced more leaves over their life spans compared to nonoverwintering shoots. As a group, overwintering shoots produced 17.0 leaves per shoot, which was significantly greater ($t = 4.76$, $p < 0.001$) than the 12.4 leaves per shoot produced by cohorts growing only during the year 2 growing season. There was also a slight but nonsignificant ($t = 0.41$) difference in total shoot production for nonoverwintering shoots between year 1 and year 2 (12.8 and 12.4 leaves per shoot for the two years, respectively).

For both shoot categories (overwintering and nonoverwintering), a plot of total leaf production per shoot vs cohort longevity revealed a two-part trend. The first portion of the trend consisted of a clustering of points around a mean leaf production value (11.5 leaves per shoot for the two nonoverwintering groups and 15.2 leaves per shoot for shoots affiliated with overwintering cohorts). Secondly, there was an upward turn after a certain longevity threshold value had been attained. The threshold value varied: 15 and 20 weeks of

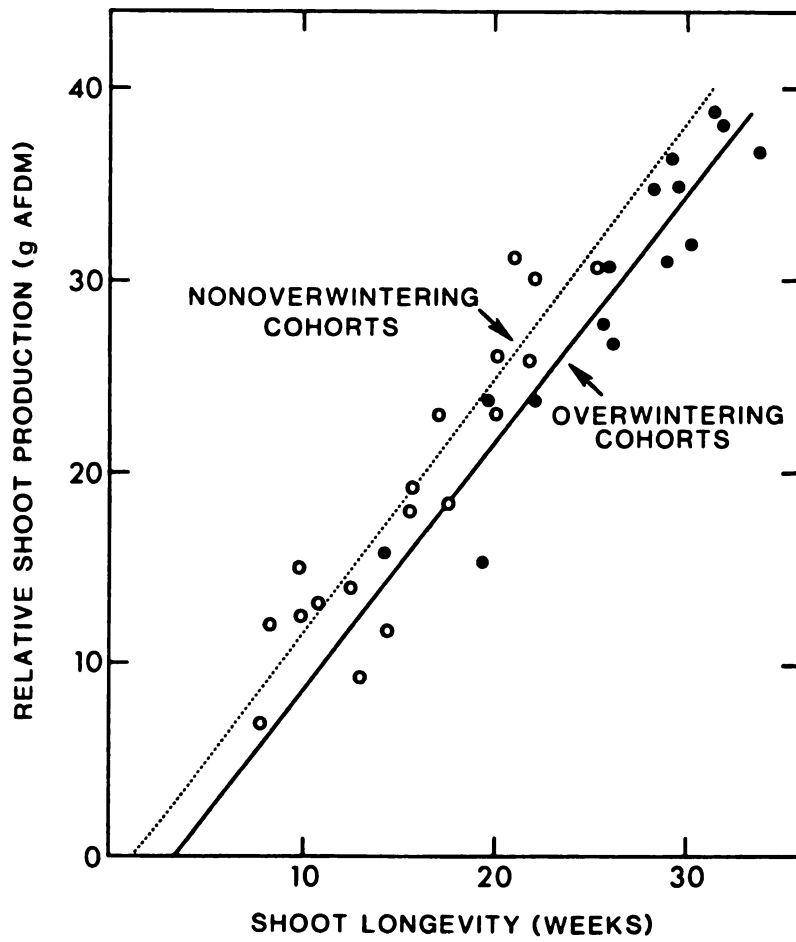


Figure 22. A comparison of shoot production and shoot longevity for Typha latifolia shoots of nonoverwintering and overwintering sampling interval cohorts.

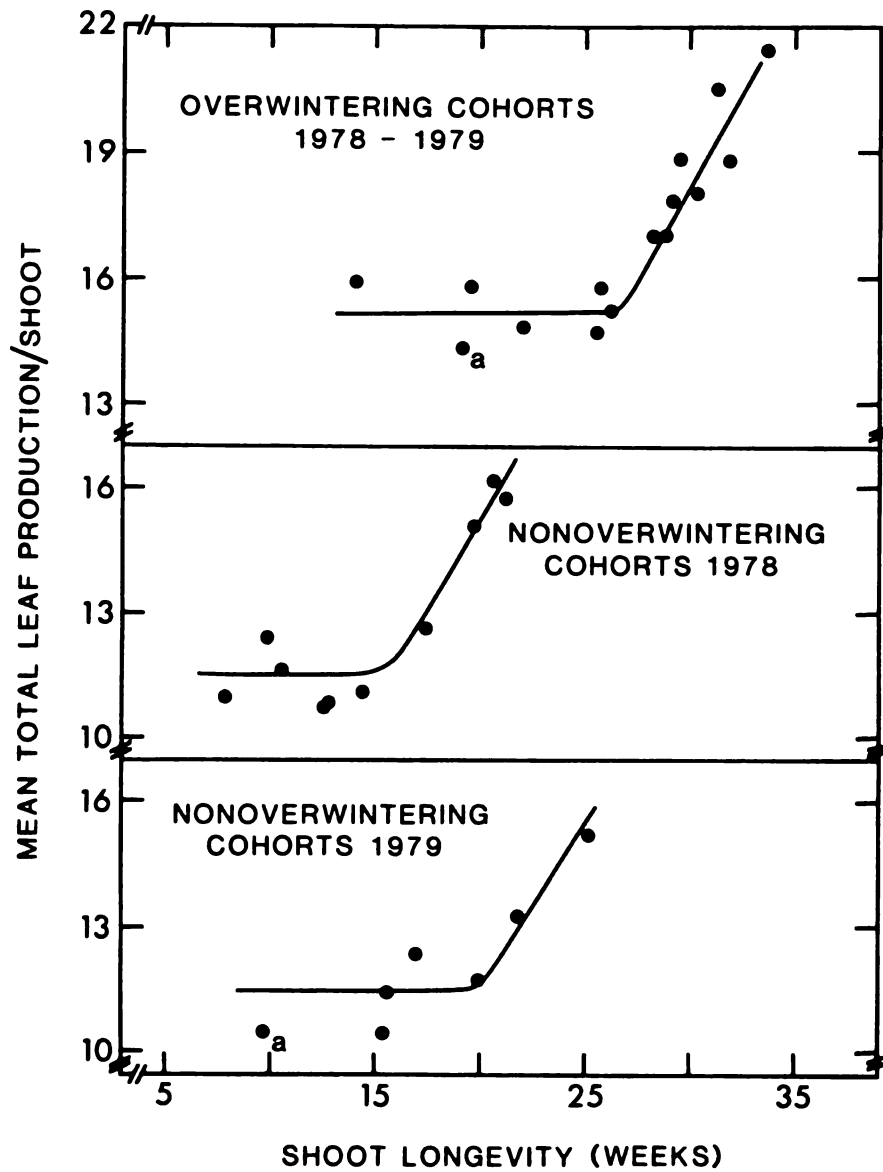


Figure 23. Relationships between mean total leaf production and shoot longevity for overwintering (top panel) and 1978 and 1979 nonoverwintering (lower two panels, respectively) shoots of *Typha latifolia*. Each point represents one of the sampling interval cohorts; "a" subscripts show cohorts containing 9 or fewer shoots. Cohorts 7 and 8 are not included because they had very few shoots and extremely poor longevity.

longevity for the two nonoverwintering groups of shoots, and 26 weeks for the group of overwintering shoots. Beyond the longevity threshold value, mean leaf production increased steadily at a rate of approximately one leaf per week for each additional week of longevity.

Characteristics for each of the major cohorts are summarized in Table 3.

Table 3. Summary characteristics of major emergence pulse cohorts.

Characteristic	Cohort						
	I-1a	I-1b	II-1	III-1	I-2	II-2	III-2
No. of shoots contributed/m ²	6.4	22.0	12.6	24.1	21.6	2.1	10.4
Percent early shoot mortality ¹	6.7 ²	7.6	26.8	12.7	7.6	9.8	--- ³
Mean adjusted longevity ⁴	23.1 ²	19.6	15.5	27.5	21.6	--- ⁵	--- ⁵
Percent of maximum longevity attained	80.0 ²	74.5	62.1	73.8	79.1	--- ⁵	--- ⁵
Cohort product-g/shoot ⁷	456 ⁶	410	208	753	554	--- ⁵	--- ⁵
Leaf turnover ⁸	1.54 ²	1.38	1.31	1.61	1.30	1.30 ⁹	1.23 ⁹

1. For the first three weeks of the growing season; expressed as a percent of all shoots in the cohort.
2. Cohort I-1a is comprised of shoots emerging in 1977; some degree of inaccuracy is present in the indicated values.
3. Value unavailable due to the conclusion of the study in October 1979.
4. Weeks of growing season; adjusted to a per shoot basis (see Fig. 7).
5. Data unavailable: Some shoots were still alive at the end of the study.
6. Based on the maximum weight of each shoot (see Fig. 18).
7. Mean based on numbers of shoots in the cohort (see Fig. 20).
8. Total no. of leaves/mean no. of leaves (see Fig. 15).
9. Underestimates, since some shoots were still alive at the end of the study.

CHAPTER 4

DISCUSSION

SHOOT DENSITY REGULATION

In this section Typha latifolia shoots exhibited recognizably distinct forms of shoot density fluctuations from one year to the next. The observed density changes indicate that T. latifolia is self-regulating, and that the ramet structure of the monospecific stand was the consequence of traits that enhanced genet fitness by integrating inter-ramet relationships. These variations were not adequately explained by conventional hypotheses of abiotic regulation (nutrient or light limitation) or biotic regulation through the generally expected effects of intraspecific competition at higher shoot densities.

Shoot Density Patterns

In the Lawrence Lake marsh T. latifolia population, year 1 and year 2 ranges in live shoot densities were large and similar (12.7 to 43.9 in year 1, and 11.2 to 41.9 in year 2; Fig. 16). These ranges compared favorably to shoot densities recorded for other mature stands of T. latifolia: 15 to 25 shoots/m² in southern Czechoslovakia (Květ et al., 1969), 17 shoots/m² in a Wisconsin marsh (Klopatek and Stears, 1978), 17 to 41 shoots/m² in different southern Czechoslovakian stands near peak aerial biomass (Fiala, 1971a), and 21 to 32 shoots/m² during peak aerial biomass in South Carolina marshes (Boyd, 1971). However,

much greater densities (108 shoots/m²) were reported for Typha stands surrounding routinely-fertilized fish ponds in southern Czechoslovakia (Dykyjová, 1971). The similarity of these density ranges masked the population structure, however, because in the Lawrence Lake marsh population, the nearly equal year 1 and year 2 density ranges were achieved via very different routes. Mid-May main pulse shoot density was 25.0 shoots/m² in year 1, and 40.0 shoots/m² in year 2. In year 1, six times as many cohort II shoots emerged as in year 2. The net result was a year 1 population whose cohort structure was comprised of strongly overlapping shoot generations, while the year 2 (and year 3) population was much more like a nonoverlapping generation of shoot cohorts. The year 1 and year 2 population dynamics approximated the two poles of the gradient of cohort structure that can occur as a result of population self-regulation.

Self-Regulation: Securing Space Through Shoot Saturation

Shoot density is the most important factor determining the sizes of the major emergence pulse cohorts. If the main pulse of live shoots is less than about 42 shoots/m² (the apparent carrying capacity of T. latifolia shoots in Lawrence Lake marsh), a second cohort will be produced to adjust live shoot density towards this limit. In the highly productive marsh environment, it is important for Typha to maintain a dense stand in order to prevent the acquisition of space by other species of marsh emergent macrophytes. The limit density of ca. 42 shoots/m² was a level of shoot saturation that apparently effectively secured the Lawrence Lake marsh.

The extent to which the main pulse of shoots can acquire and hold space by producing offshoots is clearly a function of their individual

shoot productivities. The shoots must export to rhizomes quantities of photosynthate sufficient to support the development and early growth of the cohort II shoots, and still not jeopardize their capacity to produce offshoots and associated carbohydrate reserves required for the continuation of the clone in the next growing season.

After about mid-August during the growing season, the probability of a potential competitor establishing itself in the marsh habitat was quite remote. Increases in live shoot density caused by the emergence of cohort II shoots were clearly not ecologically equivalent to shoot density increases caused by emergence of the third cohort. After mid-August, securing space in the marsh for the present year was of less importance, and cohort III shoots could not contribute substantially to offshoot formation or underground reserves during the year of its emergence. Offshoots continued to be produced after mid-August as long as shoots in the main shoot pulse could continue to export sufficient photosynthate.

The process of offshooting involves both the formation of the hibernating bud and the accumulation of sufficient carbohydrate reserves into the bud's associated rhizome. Only some of the newly formed buds will elongate to emerge above the water surface and become cohort III shoots. Those that do not emerge immediately (perhaps those formed later in the season) will emerge in the spring of the following year as cohort I shoots. In late summer and throughout the fall, it is important for the main pulse shoots to regenerate themselves through the production of offshoots so that the main pulse during the following year will be as close to the shoot saturation limit as early in the growing season as possible. The density of the

main pulse of shoots is then the decisive factor and the driving force of the population's ability to self-regulate.

In most years, T. latifolia would be expected to have a discrete cohort generation structure (see Fig. 24). This type of cohort structure would be very effective in securing marsh space, because the main shoot pulse is close to shoot saturation early in the spring. A smaller cohort II is produced with this structure, which may translate into a redirection of photosynthate to increase midsummer rhizomatous carbohydrate reserves. With larger numbers of shoots exporting photosynthate towards the formation of cohort III and cohort I offshoots, the rhizomes can accumulate greater amounts of carbohydrate reserves per unit length. Larger rhizome reserves in turn contribute to lower rates of shoot mortality and a more rapid growth of young subsidized shoots. Early establishment of a shoot-saturated stand of Typha latifolia is the net result.

The occurrence of an overlapping cohort generation structure may indicate a recent disturbance. The low density of the main pulse of shoots in an overlapping cohort generation structure could result from arresting the process of offshoot formation during the previous autumn, or from high mortality of offshoots following a normal bud-formation phase. An unusually early freeze or winter onset could result in the premature deaths of main pulse shoots responsible for the production of cohort III (and the following year's cohort I) shoots. Alternatively, an exceptionally mild winter could result in greater rates of utilization of the reserves by the rhizomes, while flooding might decrease oxygen supply to the rhizome and its attendant buds, thereby resulting in damage to the underground tissues.

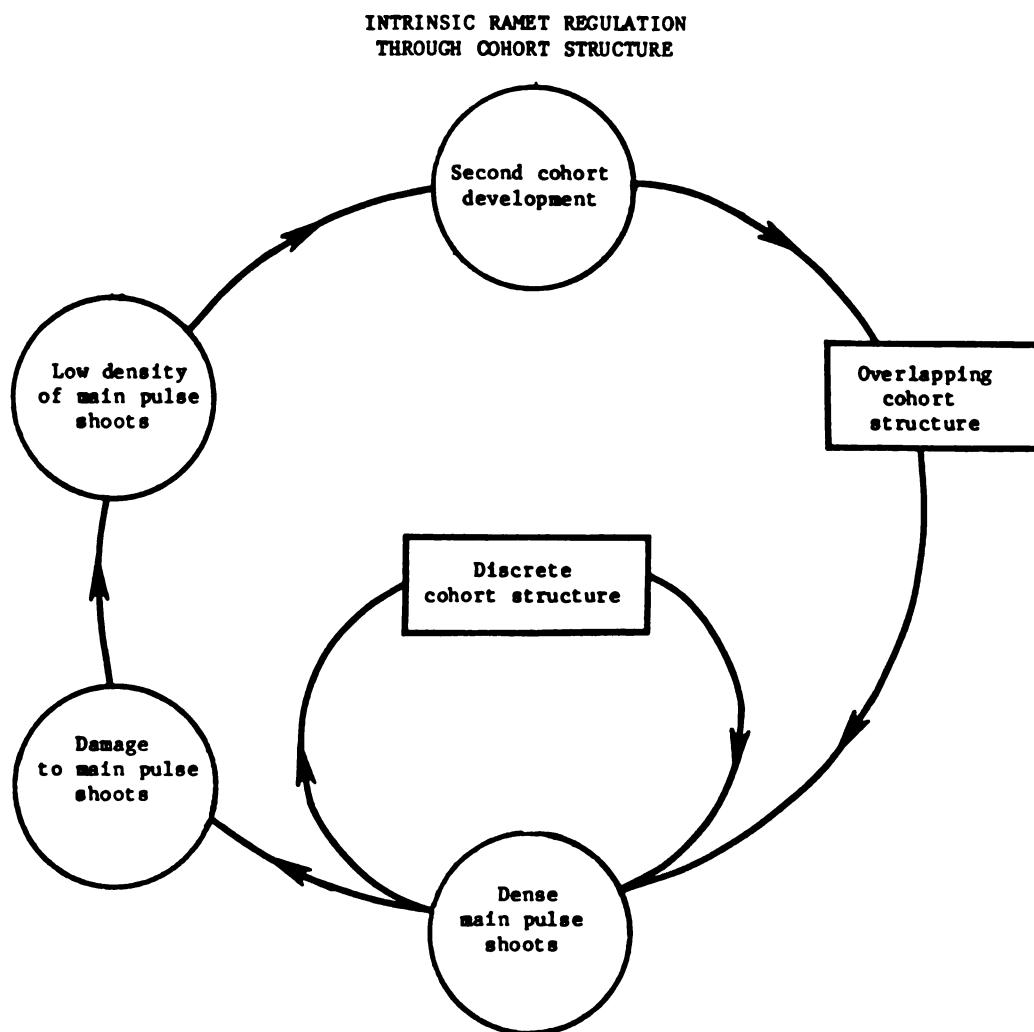


Figure 24. Diagrammatic representation of the proposed intrinsic ramet regulation scheme through cohort structure.

Finally, hard frosts late in the spring could substantially increase shoot mortality of the main pulse shoots.

Biotic Regulation Through Competition

Competitive mediated density effects are expected to adjust populations through any combination of the following: 1) increasing the mortality risk of individuals or their parts, 2) reducing the births of individuals or their parts, or 3) reducing growth rates, delaying maturity, or delaying reproduction (Harper, 1977). Density effects do not affect all parts equally, however, because the size of plant parts is much less plastic than are numbers of plant parts. When density effects increase risk of mortality to whole plants and their parts, the rate of mortality is expected to become a function of the growth rates of the survivors. In a dense Typha stand, one should see less mass per individual as a result. Dense populations tend to form a hierarchy of dominant and suppressed individuals; the frequency distribution of plant size becomes log-normal or skewed because smaller individuals are more abundant than larger ones (Koyama and Kira, 1956). The mortality risk then focuses upon these smaller, suppressed individuals. Additionally, the mortality of individuals within a dense monospecific stand (self-thinning) might be expected to follow a $-3/2$ power equation that relates mean mass per individual to the density of survivors (Yoda et al., 1963).

Because shoot density was relatively high in the year 2 Lawrence Lake Typha population (40 shoots/m²) and density patterns were quite distinct in the two years, evidence of competitive-mediated density regulation can be examined in terms of each of these expected outcomes. Density effects in the Typha stand can also be assessed

during the course of stand development in year 2.

Early shoot mortality risks (within three weeks of emergence) for the year 2 major emergence pulse cohorts were equal to (cohort I) or lower (cohort II) than mortality risks for analogous cohorts in year 1 (see Table 3). The survivorship curves similarly showed very comparable values for analogous cohorts (Fig. 6). Survival of overwintering shoots in cohorts III and II was 90 and 30 percent, respectively, in year 2, and 80 and 20 percent in year 1. The portion of the maximum longevity attained (MLA) for the year 2 cohort I shoots was slightly greater than for cohort I shoots in year 1; MLA values for cohort II shoots, however, were much greater in year 2 than they were in year 1. The best indicators available for leaf mortality are the rates of leaf senescence onset (Fig. 12) and the numbers of leaves per shoot in each leaf status category (Fig. 13). If comparisons are based on cohort I-1b and cohort I-2 so as to remove the overwintering bias, no significant differences in number of leaves per shoot can be found. Within the leaf status categories, there was a higher leaf senescence onset rate in the first peak in year 2, but a lower rate in the second peak, relative to comparable year 1 cohorts. The data clearly showed that shoots in year 2 had a lower risk of death than shoots in year 1, although year 2 density levels were greater. Leaf mortality may have been slightly higher in year 2, but there was no trend for leaf mortality to increase as aboveground biomass increased.

Leaf production rates (Fig. 12) attained higher values in year 1, but the slightly lower year 2 rates were sustained for a longer period of time. These two factors apparently cancelled to some extent, for there was no significant difference in total leaf production for

cohort I shoots between the two years. The numbers of new shoots per week were greater in year 2 when cohort I shoots were emerging (cf. Fig. 3). Emergence rates for shoots in cohorts II and III, however, were much lower in year 2 than they were in year 1. It is apparent that the lower rates of emergence for cohorts II and III during year 2 were due to self-regulation of shoot density rather than to competitive interactions between shoots.

The timing of the offshooting of the second and third cohorts was the same in both years, although the growing season started ca. two and a half weeks earlier in year 2 (it also ended about one and a half weeks earlier; see Fig. 3). This pattern indicates that the general course of development was very similar for the two years; at most, development could have been about two weeks slower in year 2, at least up to mid-June.

There was no significant difference in mean mass per shoot between the two years (25.8 vs 25.6 g/shoot for shoots in cohorts I-1b and I-2, respectively; see Table 3). The percentage differences in main pulse density and maximum aboveground biomass between year 2 and year 1 were both 60 percent which also indicates a relatively uniform mass per shoot in this Typha stand.

No evidence was found for a hierarchy of dominant and suppressed shoots in the Lawrence Lake Typha populations. The monthly shoot size distributions were not positively skewed, and indeed were negatively skewed most of the time. The distributions simply reflected the progression of the major emergence pulse shoots through the monthly age structures.

The relationships between mean shoot dry mass and shoot density in the first and second years did not follow a $-3/2$ slope (Fig. 19). According to Hutchings (1979), these relationships can be classified as type B (overlapping cohort generations) in year 1, and type A (discrete or nonoverlapping generation cohorts) in year 2. The Typha latifolia data support those of Hutchings (1979), who concluded that ramets growing in natural stands do not self-thin according to the $-3/2$ power equation. For most clonal perennial species, shoot density scarcely changed during the growing season; shoot death generally occurred after progress towards an "ultimate" thinning line had stopped.

Overall, competitive-mediated density effects were not obvious. See Table 4 for a summary of the expected and observed competitive-mediated density effects. There were only two indications of potential density effects. Only the slightly slower leaf production rate for shoots during the second year is explained more adequately on a competitive effects basis. This slower leaf production rate could also have been the result of lower carbohydrate reserves in the rhizomes, for this has been shown to affect particularly the rate of early spring shoot growth (Fiala, 1971a). It was concluded that in mature stands of T. latifolia, shoot populations are not routinely regulated via competitive mediated density relationships.

Abiotic Regulation Through Resource Limitation

Since shoot density was substantially higher in year 2, evidence of abiotic regulation through availability of light or nutrients was examined. One indication that a rate of resource supply has become

Table 4. Competitive mediated density regulation.

Expected result in year 2 relative to year 1	Observed result in year 2 relative to year 1
Increased shoot mortality	● Decreased early shoot mortality ● Greater longevity
Increased leaf mortality	● No significant difference in total leaf production ● No significant difference in leaf turnover between analogous cohorts
Reduced emergence of shoots	● Did not occur in I-2 ○ Reduced II-2 (but also expected result for intrinsic regulation)
Reduced leaf production	● No significant difference in leaf production
Reduced growth rates	● No difference in overall growth of shoots (mass or height) in the 2 years ○ Lower rate of leaf production was sustained for a longer time period
Delayed maturity of reproduction	● Timing of major emergence pulses were same in 2 years ● Timing of shoot senescence similar in 2 years
Positively skewed size distribution	● Negatively skewed size distribution
Follows the $-3/2$ thinning power equation	● Did not

limiting to shoot growth is the uncoupling of biomass yield and shoot density at higher shoot density values. Further growth is then dependent upon the rate of supply of the limiting resource (cf. Kira et al., 1953; Shinosaki and Kira, 1956).

Biomass yields of cohort I shoots for year 1 and year 2 were almost identical (25.8 g/shoot for Cohort I-1b, and 25.6 g/shoot for Cohort I-2, respectively). In order to compare biomass yields for overwintering shoots in each of the two years, it was first assumed that all green shoots observed in the study plots on the first sampling date in year 1 (i.e., cohort I-1a) were overwintering shoots. This number was obviously the maximum possible number of overwintering shoots; it was certain that some of these were in fact shoots that had newly emerged that spring. Cohort I-1a shoots had a mean mass of 35.9 g/shoot, and the mean mass of the 419 shoots that successfully overwintered into the second year was 41.7 g/shoot. If one assumed a 50:50 mixture of overwintering and cohort I shoots in the initial I-1a cohort, overwintering shoots in the two years had equal weights as well. If the assumption that most of cohort I-1a shoots were overwintering shoots is correct, then shoots that overwintered into year 2, the year of high shoot density, were heavier than their year 1 counterparts.

In this Typha stand, aerial aboveground biomass was clearly dependent on shoot density over all densities observed, indicating that availability of external resources was not limiting growth. Rate of supply of external resources, however, may have influenced shoot growth.

What could be interpreted as a light compensation response in the T. latifolia populations was observed. Bazzaz and Harper (1977) noted that reduced light intensity caused leaf production to continue longer at a reduced rate in cultivated plots of Linum usitatissimum. This response was viewed as a compensation for lower light intensities. In year 2, the main pulse of Typha shoots exhibited this same pattern, but it is unclear whether this was a compensating response due strictly to lower light intensities. A Typha latifolia stand in southern Czechoslovakia had a shoot density nearly three times the density found in the Lawrence Lake marsh (108 vs 40 shoots/m²). However, the per shoot mass at peak biomass for the Czechoslovakian population was 33 g/shoot, which was very close to the value found for the Lawrence Lake shoots. The differences in shoot densities and similarities in shoot weights for these two Typha stands are indications of how much light compensation is possible in fertilized, mature stands of T. latifolia.

The rates of carbon assimilation for eight stands of T. latifolia were found to be identical and, although photosynthesis proceeds by the typical Calvin (C₃) cycle in this species, it loses only minor amounts to photorespiration (McNaughton and Fullem, 1970; McNaughton, 1974). Rates of carbon assimilation by Typha are comparable to those of some tropical C₄ grasses, and this level of efficiency may allow the plant to operate essentially with an excess carbon budget (McNaughton, 1974). Typha latifolia appears to be morphologically plastic with respect to the way in which leaf biomass can be allocated, which allows a more uniform efficiency of light utilization over a range of light intensities (cf. Grace and Wetzel, 1981). For

these reasons, it is unlikely that the Lawrence Lake population of T. latifolia was regulated by decreases in light intensity resulting from the greater density of shoots in year 2.

Finally, five different Typha populations growing on sites with similar fertility demonstrated variations in aboveground biomass primarily attributable to factors other than environmental nutrient levels; wide fluctuations in shoot standing crop of T. latifolia can occur within local areas where soil fertility levels are essentially uniform (Boyd, 1971).

CONSEQUENCES OF TYPHA SELF-REGULATION TO PRODUCTION

Tomlinson (1974) argued that, in seagrasses, one must understand the growth of the individual modules in order to fully understand population productivity. In a series of studies of populations of Carex lacustris, Bernard and coworkers similarly emphasized the importance of knowing the life history of the population, because life history events influence primary production and must be assessed before a complete picture of community functioning can emerge (Bernard and MacDonald, 1974; Bernard, 1975; Bernard and Solsky, 1977). In the Lawrence Lake marsh Typha population, changes in production from one year to the next (833 vs 1318 g/m² maximum standing crop) were fully explainable on the basis of the internal dynamics of cohort structure.

The large difference in peak aerial aboveground biomass (60 percent) that was found between year 1 and year 2 was a consequence of differences in the way in which shoot density of the Typha population developed. In year 1, the overlapping cohort structure occurred because shoot density in the main pulse of shoots was relatively low (25 shoots/m²). This density was supplemented by cohort II shoots to

nearly 32 shoots/m². In year 2, however, the main pulse of shoots had a substantially higher initial live shoot density (40 shoots/m²). The contribution of live shoots by cohort II was therefore low (only 2 shoots/m²), which led to a more discrete or nonoverlapping cohort structure and the 60 percent increase in production. In years in which a discrete cohort structure occurred, production was higher because most of the shoots were in the main pulse of shoots, and they could grow for a relatively long time. If the Typha population had an overlapping cohort structure in a particular year, the density of live shoots in the main pulse of shoots would require supplementation by shoots from cohort II. The overlapping cohort structure that resulted tended to lower overall production because fewer shoots were present over the entire growing season to accrue biomass.

The proportion of overwintering shoots in the main pulse of shoots also contributed to year-to-year differences in production, but was a more secondary factor. As the proportion of overwintering shoots increased, shoot aerial biomass increased as well, largely because overwintering cohorts contained shoots that were, on the average, more massive (35.9 g/shoot in cohort I-1a, and 31.2 g/shoot in cohort III-1; see Fig. 20 and Table 3). Nonoverwintering cohort I shoots contributed, on the average, only 25.8 g/shoot (year 1) and 25.6 g/shoot (year 2). Consequently, overwintering shoots produced approximately 25 percent more biomass than shoots that emerged in the spring.

Some controversy exists as to whether it is individual shoot mass or shoot density that is the more decisive factor in determining aerial biomass (cf. Klopatek and Stearns, 1978; Boyd and Hess, 1970).

In the Lawrence Lake marsh Typha population, production was a product of shoot density and individual shoot mass, but live shoot density was the more important of these two factors in determining aboveground production. For the two years, the ratio of mean shoot density in the main pulse of shoots was 60 percent greater in year 2 (40 shoots/m²) than year 1 (25 shoots/m²); this was matched by the 60 percent greater maximum aerial biomass for year 2 (1318 g AFDM/m²) than year 1 (833 g AFDM/m²). Ondok (1971) similarly found shoot density to be more closely related to aboveground production than was shoot height for the narrow-leaved cattail, Typha angustifolia. Density and individual biomass values obviously both contribute to primary production, and in order to understand the productivity of a population, both factors must be assessed.

INTEGRATION OF THE TYPHA PLANT: THE CLONAL PERSPECTIVE

Ramets are units that are clearly subordinate to the genet. Very few ramets occurred in sampling-interval cohorts that demonstrated greatest values of longevity or productivity, and in the mature stand studied, sexual reproduction was extremely rare; only three of the 1779 shoots completing all shoot phases during the study actually flowered. Ramets in the main pulse of shoots attained a peak in rate of leaf senescence onset as early as the beginning of June, probably because large exports of photosynthate were being allocated towards offshoot formation (cohort II) or for carbohydrate storage in the rhizomes. The second and last peaks in rate of leaf senescence onset occurred in late July; these peaks were again associated with the formation of offshoots (cohorts III and next year's cohort I) and accumulation of carbohydrate reserves. Declining shoot vigor (from

late July until senescence was complete) almost certainly resulted from a continual export of photosynthate into underground organs with no apparent investment in the maintenance of the shoot (leaf production rates were less than 0.1 leaves/week; Fig. 12). No clear ramet strategy was apparent when one examines individual ramets simply because the ramets are at a level subordinate to the level from which "strategy" originates--i.e., the genet. Adaptive population traits for this species only clearly emerge as characteristics of the ramet collective.

At the genet level, ramet integration leads to a highly successful plant capable of dynamic growth through space and time. Rapid early shoot growth is possible through the rhizome carbohydrate reserves, and this assures an early occupation of space in the marsh. The branching rhizomes of colonizing genets facilitate a rapid lateral expansion by proliferative offshooting (Fiala, 1971a). By self-regulating ramet density primarily by regenerative offshooting, the genet can maintain shoot saturation of the marsh space (this study). It is consequently no surprise that Typha and other reedswamp dominants such as Phragmites, Glyceria and Carex show negative associations when growing in mature stands (Sculthorpe, 1967). The efficiency with which marsh space is secured by these plants would frequently terminate in exclusion. The rhizome is the longest lived Typha structure; it survives up to two years (Westlake, 1965). The ephemeral nature of the plant parts, when combined with the proliferative capabilities of the offshooting process, afford Typha a dynamic, wandering character. Marsh habitats may well have the most dynamic boundaries circumscribing any seasonally permanent habitat. A

successful genet could move in concert with marsh boundary fluctuations without sacrificing local phenotypic fitness to sexual recombination.

Most inter-ramet interactions occur within the genet, because only peripheral ramets of a clone will have interactions with other genotypes. As the clone enlarges, the proportion of interactions between ramets of different genotypes becomes an increasingly smaller fraction of all ramet-ramet interactions. If the ramet or more likely a small cluster of ramets in the case of Typha remain the ecologically vulnerable unit (White, 1979)--and this is the case in mature stands, where ramet clusters are physically disjunct¹--what does this mean when the evolutionarily vulnerable unit, the genet, is the collection of physically disjunct ramet clusters? Competitive traits are not evident in inter-ramet interactions because competitive traits if expressed would primarily affect ramets of the same genotype. Those other affected ramets would also be expressing the same competitive traits being of the same genotype. The consequence of the competition within the genet would lead to the breakdown of the clonal phlanx structure, thereby reducing the ability of the genet to effectively hold the marsh space through shoot saturation. The traits that were apparent among the Typha shoots revealed inter-ramet interactions characterized by integration and coordination in which a phlanx structure successfully secured the marsh space.

1. When seeds of a clonal grass (Lolium perenne) were sown at four densities, the rate of elimination of genets (but not ramets) was related to the rate of growth of the survivors according to the $-3/2$ power equation (Kays and Harper, 1974). In this case, the genet is the ecologically and evolutionarily vulnerable unit, because the 20-week old survivors must have remained physically intact and therefore behaved like other noncloning plants.

Nobel et al. (1979) suggest that when selection pressures are dominated by light, the tendency is towards growth forms with a persistent vertical axis that maintains the physical integrity of the genotype; when natural selection pressures are dominated by limited water or nutrient reserves, or by grazing or burning, lateral branching of clonal plants, generally with fragmentation of the genet, is instead favored. In the marsh habitat, water and nutrients are generally not in short supply. Similarly, burning rarely occurs, and grazing is mainly restricted to point-source damage (e.g. muskrats). Light is very likely the dominating selection pressure, but two considerations preclude marsh plants from assuming a persistent vertical growth form and attendant intact genet. First, marsh sediments are physically soft and flocculant, and are highly reducing. Sediment texture would necessitate a deep, massive underground structure to adequately anchor the aboveground plant portions; the underground tissues, in turn, require an adequate supply of oxygen, and the larger the underground structure, the more oxygen would be required. The problem is exacerbated because gaseous diffusion through water (or waterlogged sediment) is many times slower than through air (or well-aerated soils) (cf. Wetzel, 1982). Secondly, for the area encompassed, marsh habitats are far less permanent than other seasonally persistent habitats. A marsh plant that heavily invested in supporting tissues (both above- and belowground) might be unable to complete its life cycle because the marsh boundaries had fluctuated sufficiently to leave the plant in a now inappropriate habitat. The rhizomatous lateral branching of Typha and other successful marsh macrophytes allows not only the capability of tracking slow

fluctuations of the marsh boundaries, but permits a minimization of the respiratory burden resulting from underground tissues, as well. Finally, because they branch laterally, cloning emergent macrophytes can form closed stands, thereby securing their marsh space from the sediment upwards.

Several examples of clonal ramet integration have recently been reported. Hutchings (1979) observed that ramet populations of clonal perennial herbs in natural stands failed to conform to the $-3/2$ power equation, and suggested the lack of self-thinning to be one important aspect of an efficient system of utilization and re-distribution patterns of photosynthate within the whole plant. The Typha latifolia data similarly fail to fit the $-3/2$ slope, and the reasons for this discrepancy (the utilization and re-distribution patterns of photosynthate between shoots and rhizomes) were discussed earlier. Kays and Harper (1974) noted that the result of tillering, tiller death and genet death in their seeded plots was to adjust the number of tillers to a density that was "extraordinarily similar" despite wide variations in sowing rate and light intensity. These similar densities can be viewed as the product of intrinsic regulation, like the self-regulation described for the Lawrence Lake Typha stand. Studies by Bell (1974) and Smith and Palmer (1976) revealed an integration of rhizome patterns that resulted in predictable shoot positioning. A pattern of regenerative shoot placement (cohort III and cohort I) near parent shoots, and proliferative placement (cohort II) farther from the parent shoots was also reported in this study.

Because rhizomes maintain viability for 17 to 22 months (Westlake, 1968), they provide a living link between the parent and

offspring shoots for at least two generations. This link provides the basis for feedback from one growing season to the next. Rhizomes originally formed in conjunction with the parent shoot can, and do, receive some photosynthate exported from offspring shoots when carbohydrate reserves are accumulating in the rhizome (Fiala, 1971a). The amounts of carbohydrate reserves and/or the rates of photosynthate export to viable rhizomes are possible means by which shoot production (and thereby density) could be assessed. A large amount of carbohydrate reserve or a rapid rate of export in early June might, for example, release an inhibitor of offshoot development, suppressing the development of the second cohort for that year. Whatever mechanism that does regulate cohort structure must surely be based in the rhizome, the longest-lived part of the Typha plant.

OVERWINTERING-NONOVERWINTERING TRADE-OFFS: THE RAMET PERSPECTIVE

An evaluation of the costs and benefits of being a nonoverwintering or an overwintering shoot can be addressed using analyses and comparisons based on an individual shoot perspective. Comparisons are drawn between year 1 overwintering shoots (cohorts 15-29) and the year 2 nonoverwintering shoots (cohorts 30-36), since these shoots developed during the same growing season.

In terms of longevity, the average overwintering shoot lived 17 percent (= 4.6 growing season weeks) longer than the average nonoverwintering shoot. The difference in longevity was due primarily to time added from shoot emergence to the close of the first growing season, and assured that overwintering shoots would be first up in the developing canopy in the following spring.

Mortality associated with overwintering was extremely low; of 419 shoots that were chlorophyllous at the end of the year 1 growing season, only six (= 1.4 percent) failed to survive at least four weeks into the following growing season. These six shoots also survived the winter, but all died three weeks into the growing season.

During spring and summer growth periods, growth rates were greater for overwintering shoots than they were for shoots that had emerged in spring. The greater rate of growth was reflected in the mean shoot heights, so that older shoots were consistently taller than their nonoverwintering counterparts. The translation of greater growth rates into greater shoot heights probably did not, however, bestow a significant advantage to taller shoots in terms of light competition, for main pulse shoot density was not nearly as high as in another study, in which the photosynthetically most active stratum of the Typha stand was found closest to the ground (Dykyjová, 1971).

In situations where early uptake of nutrients could confer a competitive edge to early emerging shoots, the process of overwintering might be more advantageous. However, in the case of clonal rhizomatous plants, mobile nutrients might be shared via viable rhizome linkages (see discussion section on self-regulation and consequences to genet survival). The greater growth rates of overwintering shoots compared to shoots that first emerged during the spring are likely the result of two factors. First, a larger quantity of carbohydrate reserves may be available in rhizomes associated with overwintering shoots, perhaps because earlier formation of cohort III offshoots allows additional time for carbohydrate storage before the close of the first growing season. Secondly, since they are formed

earlier, overwintering shoots possess a greater level of tissue differentiation relative to nonoverwintering shoots. The latter factor would allow a more direct translation of rhizome carbohydrates into upward growth of the shoot in early spring.

Largely because of their more rapid initial growth rates, overwintering shoots were the most productive on an individual shoot basis. They may have become self-sufficient more rapidly and reinvested net assimilates into additional leaf production (beyond replacement of leaf losses suffered while overwintering) even before the main pulse of shoots synchronously began export of net assimilates to the underground system in early June. Shoots in the overwintering cohorts were 22 percent more productive on a per shoot basis than were shoots from cohort I-2 (30.9 g/shoot vs 25.4 g/shoot), even though they shared the same main growing season. The average 5.5 gram per shoot difference and the attendant more rapid rate of growth in early spring represented benefits of overwintering.

Mean cohort longevity and mean shoot production for the two shoot categories were examined. When compared in the region of shoot production overlap, it was clear that overwintering shoots required 2.5 to 2.6 weeks of additional time to match the same level of shoot production as a nonoverwintering cohort. This extra time could be envisioned as an overwintering cost.

Average total leaf production for overwintering shoots was 17 leaves per shoot, which was 3.3 leaves per shoot greater than leaf production values for nonoverwintering shoots. The 3.3 average leaf difference may have represented the number of leaves required for replacement of leaves lost during fall senescence of the first growing

season. All overwintering shoots, regardless of height attained in the year of their emergence, senesced down to 5 to 10 cm of chlorophyllous tissue with the onset of winter. The 3.3 leaf difference may have also included additional leaves the overwintering shoots were able to produce due to their more rapid growth and the greater total length of time available for growth before the onset of shoot senescence at the close of the second growing season.

Leaf turnover in overwintering shoots was significantly higher than for nonoverwintering shoots (1.61 vs 1.25; $p > 0.001$). The greater leaf turnover value was again probably the result of fall leaf senescence. Apparently the senesced leaves must be replaced to maintain an optimal leaf number. The resulting increase in leaf turnover is another form of the same overwintering cost borne by those shoots that emerged late in the fall and continued growth the next year.

INTEGRATION OF THE TYPHA PLANT: OVERWINTERING SURVIVAL

A Hypothesis to Explain Cohort III Emergence in Autumn

Cohort III shoots emerged late in the season and grew to a mean height of 15 cm before winter terminated growth (Fig. 12). With the onset of winter, these shoots senesced down to 5 cm. It would seem safer to remain submerged, yet fully developed, and wait for the warmer weather of spring. Several explanations are possible. Well-developed shoots may be physiologically incapable of surviving overwinter under water. Alternatively, the shoots may be unable to detect the water surface level, or of predicting water level fluctuations that will expose them to severe cold during the winter. A third possibility exists that provides a benefit for autumnal shoot

emergence which might offset early emergence costs (see Discussion section on overwintering-non-overwintering trade-offs).

Dacey (1980) reported a diffusive or forced ventilation of gases caused by thermally-induced changes in pressure in the yellow water lily, Nuphar luteum. Although gaseous diffusion can occur through fully senesced Typha shoots (cf. Linde et al., 1969), rhizomes of T. latifolia are intolerant of oxygen deprivation (Sale and Wetzel, 1982) and may therefore require a more active means to assure an adequate supply of oxygen. The rhizomes and roots are submersed in a highly reducing environment, and the persistence of the clone depends upon their continued survival over winter via slow respiration of carbohydrate reserves. A flux of oxygen to the underground organs of Typha throughout the winter could be maintained by slight pressurization of gases within the tissues of the cohort III shoots, with a concomitant efflux of respiratory products through the taller, fully-senesced shoots of cohorts I and II from the previous summer. This possibility agrees with the findings of McDonald (1955), who attributed a die-off of T. latifolia in Lake Erie marshes to the lack of oxygen caused by submergence of dormant shoots during the winter.

CHAPTER 5

SUMMARY

A major cohort structure for a south central Michigan population of Typha latifolia shoots was established on the basis of the pattern of pulsed shoot emergence. The three pulses of shoot emergence were found to be identically timed in both years of the study. The boundaries between the shoot emergence pulses were in mid-June and mid-August. The first shoot cohort emerged in early spring, grew throughout the summer, and completely senesced in late autumn. The second shoot cohort emerged in midsummer; 70 percent (year 1) to 80 percent (year 2) of these shoots completely senesced in autumn, while the remainder resumed growth in the following spring. The third cohort emerged in late summer and early autumn; 80 percent (year 1) to 90 percent (year 2) of all third cohort shoots resumed growth the following spring. The longevity of each of these major cohorts then was primarily the time from shoot emergence until the conclusion of their first or second growing season. The main pulse of shoots that grew in the Typha stand was therefore comprised of overwintering shoots in their second year of growth and newly emerged first cohort shoots.

Information on rhizome dynamics (primarily from the work of Fiala) was integrated with the shoot dynamics to explain the identical timing of the three major shoot cohorts through redistribution patterns of photosynthate between the shoots and rhizomes. Timing of

the highest rates of leaf senescence onset always preceded major cohort emergence by two to three weeks. These peak rates of senescence onset were interpreted as indicating a major assimilate withdrawal from the shoots to the underground rhizomes for new shoot formation and for accumulation of carbohydrate reserves. The cohort differences in the minor early shoot mortality (13 percent year 1; 6 percent year 2) were satisfactorily explained by the amount of carbohydrate reserve in the viable rhizomes at the time of each cohort's emergence. The emergence of the third cohort just before winter was attributed to the maintenance of a forced gaseous ventilation system. This type of ventilation system could insure an adequate oxygen supply to the underground organ complex which has been shown to be intolerant of oxygen deprivation.

The density of shoots in each of the three cohorts differed considerably in the two years of the study. In year 1, the pattern of density gradually increased throughout the growing season (from 12.7 to 43.9 shoots/m²), which resulted from an overlapping cohort structure. In year 2, however, a rapid increase in shoot density to 40.0 shoots/m² occurred by mid-May and was maintained throughout the growing season. The second cohort was so reduced in year 2 (one sixth the size of the year 1 second cohort) that year 2 had a discrete or nonoverlapping cohort structure. The density of the main pulse of shoots was 60 percent greater in year 2 (40 shoots/m²). The difference in main pulse shoot density accounted for the 60 percent higher maximum aerial biomass in year 2 as compared to year 1 (833 vs 1318 g/m²).

An intrinsic or self-regulation of density through reallocation of assimilates between shoots and rhizomes satisfactorily accounted for the differing density patterns. This regulation is based on the growth pattern and the differing roles of the cohorts. The first and third cohorts are offshoots on rhizomes that are thick and short and therefore emerge close to the parent shoot. In this way, the first and third cohorts regenerate the Typha stand shoot pattern by replacing the parent shoots. The second cohort, however, is more proliferative and is formed on longer, thinner rhizomes that emerge farther away from the parent shoot. If in early spring the main pulse density is relatively low, a second shoot cohort is produced that helps "fill in" the marsh space. An overlapping cohort structure in a mature Typha stand indicates that recent damage to the main pulse shoots has occurred (presumably due to climatic density independent factors). In most years, a discrete cohort structure would occur as this density pattern results in an earlier, denser shoot establishment.

Because the density of shoots was 60 percent greater in year 2 than year 1 for the main pulse shoots, evidence for increased competitive effects in year 2 shoots relative to year 1 shoots was examined. The evidence clearly did not support a competitive-mediated density regulation of the shoot population (see Table 4).

The ramet, the shoot and its associated rhizome, is the functional unit of the clone, but the ramet is clearly subordinate to the entire collection of ramets that constitute the genetic individual (genet), even though clusters of ramets are physically disjunct. Competitive traits are not apparent in inter-ramet interactions

presumably because their expression would decrease the fitness of genets by reducing their efficiency at holding marsh space. The traits that were apparent among the Typha ramets revealed inter-ramet interactions characterized by integration and coordination. At the genet level, ramet integration leads to a highly successful plant capable of dynamic growth through space and time.

Marsh habitats may well have the most dynamic boundaries circumscribing any seasonally permanent habitat. A successful genet could move via its growth pattern of vegetative offshooting with the marsh boundaries as they fluctuate through time, without sacrificing local phenotypic fitness to sexual recombination.

A cost-benefit analysis of being an overwintering shoot vs a nonoverwintering shoot revealed that overwintering shoots live ca. 4.6 growing season weeks longer, have higher growth rates in spring, attain a 25 percent greater maximum aerial biomass per shoot, and produce 3.3 more leaves per shoot, but have a significantly higher leaf turnover (1.61 vs. 1.25) and require 2.5 additional weeks of growth to match the same shoot production as nonoverwintering shoots.

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