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Growth and Mortality of Shoots in Three Populations of *Typha glauca* Godr.

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ABSTRACT — A double sampling technique and permanent quadrats were used to monitor seasonal changes in shoot density and aboveground standing crop in three Minnesota *Typha glauca* populations. Shoot growth began several weeks later in stands located in floating mats (Boot Lake and Cedar Creek) relative to a nonfloating stand (Lauderdale). Mortality reduced shoot density by 10.8% at Boot Lake, 6.3% at Cedar Creek, and by 53% at Lauderdale. Shoot death was largely confined to smaller than average shoots at Boot Lake and Cedar Creek. At Lauderdale many relatively large shoots were killed by a lepidopteran stem borer (*Archanara oblonga* Grt.) or a mammalian herbivore. Peak standing crop occurred at different times at the three sites and was 329 g/m^2 at Boot Lake, 645 g/m^2 at Cedar Creek, and 868 g/m^2 at Lauderdale. These values underestimated actual aboveground productivity by 4.9, 0.5, and 6.3% at the three sites, respectively.

Introduction

Populations of many emergent macrophytes, including *Typha* spp., are subject to varying degrees of shoot mortality over the course of a growing season (e.g., 1-6). Shoot mortality can result in a considerable discrepancy between peak aboveground standing crop and actual net aboveground productivity (1, 3, 4). Although *Typha* standing crop has often been assessed (7), few studies (2, 6, 8, 9, 10) account for losses due to shoot mortality. Furthermore, for reasons discussed below, most of these studies probably do not provide an accurate estimate of the impact of mortality on aboveground productivity.

This study determined the effect of shoot mortality on net aboveground productivity in three natural *Typha glauca* Godr. populations. A double sampling technique utilizing permanent quadrats was employed to monitor shoot emergence and mortality. The advantages and disadvantages of this method are discussed.

Methods

Study Sites

All three study sites were located in east-central Minnesota, a region with a midcontinental climate characterized by short, warm summers and cold winters. Lauderdale was a small (0.2 ha) marsh located in Ramsey County (See 7 for exact locations of all sites). The marsh was fringed by a highway and lawns, and was partially shaded by adjacent willows (*Salix babylonica* L.). Water depth ranged from 30-40 cm in the spring to 20 cm below the soil surface in late summer. The site received highway runoff, however, and was subject to periodic flooding throughout the growing season. The marsh substrate was a sandy clay loam with low organic content. The marsh was roughly divided into equal areas dominated by *T. latifolia* L. and *T. glauca*. All sampling was limited to the *T. glauca* stand. Other vascular plants were rare, and except for *Lemna* early in the growing season, had a combined cover value of less than 2%.

The other two study sites were highly organic floating mats located in Anoka County. One site was a small ($400m^2$) stand situated on an extensive mat, which fringes Boot Lake (11). The stand was located about 75m from open water and 10m from where the mat graded abruptly into a nonfloating forested wetland dominated by *Larix laricina* (DuRoi) K. Koch and *Pinus strobus* L.. The pH of mat impounded water was ca. 5.0. The average cover value of vascular plants other than *Typha* was 15%.

The third site was a $500m^2$ stand located in the Cedar Creek Natural History Area. The floating *Typha* mat was bordered by a *Salix-Alnus* carr and a floating *Carex* fen. The pH of mat impounded water was 6.25. The average cover value of vascular plants other than *Typha* was 20%.

Plot Placement and Monitoring

Three $1m^2$ plots were established at each site in the spring of 1980. Initially, all live *Typha* shoots within each plot were marked with numbered tags and measured. Tags were attached loosely to shoots with monofilament line. Shoot height was measured (to the nearest cm) from substrate level to the outstretched tip of the tallest leaf. On subsequent sampling dates the status (live or dead) of all shoots was noted, and all live shoots were measured. Any new shoots were also tagged and measured.

At each stand, and for each sampling date, nonflowering shoots were collected from outside the permanent quadrats. These shoots were taken to the laboratory, measured, dried (at 80 °C), and weighed. Shoot weight-height regression equations were determined and used to calculate the biomass of shoots within the permanent quadrats (1, 9). For each plot, weights of individual shoots were calculated and summed using a BASIC program. The standard error of standing crop estimates was calculated according to Leiffers (9).

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Results

Shoot Emergence

The growing season began in mid May at the Lauderdale site and during the first two weeks of June at Cedar Creek and Boot Lake. Patches of ice were present in the floating mats until after June 8 at Cedar Creek and after June 20 at Boot Lake. At all three sites most shoots emerged within the first few weeks of the growing season (Table 1). Only at Boot Lake did shoots emerge after early July. A second cohort emerged in late fall, but consisted entirely of overwintering shoots, and is not considered here.

Shoot Mortality

Shoot mortality was substantially lower at Boot Lake and Cedar Creek (Table 1). At these sites most of the shoots that died were much smaller and thinner than average. No extrinsic cause of death was apparent. At Lauderdale, in addition to the death of smaller shoots, a substantial number of larger shoots died. Many of these shoots were damaged and eventually killed by the lepidopteran stem borer *Archanara oblonga* Grt. (Noctuidae) and/or an unidentified mammalian herbivore. Herbivore and borer damage weakened the bases of shoots and caused lodging. In a few cases weak shoots regrew from the undamaged basal meristem of lodged shoots.

Standing Crop and Productivity

Shoot height and the natural log of shoot weight were linearly related and all regression equations used to estimate shoot biomass were based on this relationship. For all sites, analysis of covariance showed that regression equations for different sampling dates were significantly different. Therefore, separate regression equations were used to calculate *Typha* biomass for each sampling date (7).

Peak standing crop occurred at different times at the three sites and was greatest at Lauderdale and lowest at Boot Lake (Table 2). By September shoot mortality accounted for small reductions in standing crop at Boot Lake (5.4%) and Cedar Creek (0.5%). At Lauderdale, however, mortality reduced standing crop by ca. 40%. Corrected for mortality, net aboveground productivity at Boot Lake, Cedar Creek, and Lauderdale was, respectively, 346, 648, and 926 g/m^2. Peak standing crop underestimated net aboveground productivity by 4.9% at Boot Lake, 0.5% at Cedar Creek, and 6.3% at Lauderdale.

Table 1. Seasonal changes in shoot density, natality, and mortality.

Site / Date	Density	Natality (shoots m^{-2})[a]	Mortality	Mortality (%)
Boot Lake				
June 20	29.3 ± 4.7	—	—	—
June 30	41.3 ± 4.3	12.3 ± 6.3	0.3 ± 0.3	0.7
July 12	44.0 ± 4.6	3.0 ± 1.7	0.3 ± 0.3	1.3
July 25	43.3 ± 4.6	0.6 ± 0.6	1.3 ± 0.9	4.2
Sept. 4	40.6 ± 4.9	0.3 ± 0.3	3.0 ± 1.5	10.8
Cedar Creek				
June 8	30.7 ± 2.2	—	—	—
June 20	36.0 ± 3.8	6.0 ± 2.5	0.7 ± 0.3	1.9
June 30	36.7 ± 4.2	1.3 ± 0.7	0.7 ± 0.7	3.7
July 12	36.3 ± 3.8	0	0.3 ± 0.3	4.5
July 25	36.3 ± 3.8	0	0	4.5
Sept. 4	35.7 ± 3.7	0	0.7 ± 0.3	6.3
Lauderdale				
May 21	68.0 ± 10.1	—	—	—
June 2	84.3 ± 11.7	17.0 ± 3.4	0.7 ±0.5	1.0
June 10	93.5 ± 7.9	12.1 ± 4.8	3.1 ± 0.9	3.6
June 22	93.3 ± 8.5	2.0 ± 1.4	2.3 ± 1.1	6.1
July 1	89.8 ± 7.9	0.3 ± 0.3	3.7 ± 0.8	9.8
July 31	75.3 ± 5.1	0	14.5 ± 2.6	24.4
Sept. 6	47.3 ± 1.4	0	28.0 ± 5.3	53.0

[a] ± one standard error.

Discussion

Shoot Mortality in Typha Populations

Shoot mortality during the growing season has been noted in other *Typha* populations (2, 8, 9, 12, 13). Mortality rates range from about 4% to 50% in these studies. The causes of shoot death in *Typha* stands are obscure. Herbivory by stem boring insects as at Lauderdale (7, 14, 15), muskrat (16, 17), or waterfowl (16) can severely damage natural stands. High water levels (18, 19) and excess salinity (20) have also been implicated in the decline of some stands. Although shoot death may be due to competition in some *T. angustifolia* stands (2), Dickerman and Wetzel (13) found little evidence that competition occurred in a *Typha latifolia* population.

In this study, in the absence of herbivory, shoot death seems largely confined to small shoots. Excavations of genets suggest that, in some stands at least, these shoots may be primarily derived from small, secondarily produced rhizomes (7). These shoots may be poorly developed because of internal (within ramet) competition for nutrients and carbohydrates with the larger shoot produced by the primary rhizome. Similar internal competition for resources may also occur in *Phragmites* (21).

Phenology

Shoot growth at Boot Lake and Cedar Creek began later than at Lauderdale and other nonfloating stands in the north-central United States (e.g., 12, 13, 22). Shoot emergence at Boot Lake and Cedar Creek was probably delayed because heavy litter cover caused these sites to remain frozen longer. At both sites plant communities located on the same floating mat, but with relatively little litter cover, thawed and commenced growth several weeks earlier than the nearby *Typha* stands. Other studies indicate that litter removal can allow marsh soils to thaw earlier and increase the length of the growing season (6).

At all three sites shoots emerged in a single pulse. Most (>98%) emerged within one month after the start of the growing season. Bernard and Fits (8) similarily noted no new shoot emergence after early summer in a New York *T. glauca* stand. In *T. latifolia* stands, however, an early to midsummer cohort may emerge (e.g., 9, 13, 22).

Standing Crop and Productivity

This study demonstrates that peak aboveground standing crop cannot always be considered an adequate measure of aboveground productivity in *T. glauca* populations. While peak standing crop was nearly identical to actual productivity at Cedar Creek, peak standing crop underestimated productivity by 4.9% at Boot Lake and 6.3% at Lauderdale. In a similar study, Lieffers (9) found that peak *T. latifolia* standing crop underestimated actual productivity by less than 4%. Other studies have found that peak *Typha* standing crop can underestimate productivity by 9 to 23% (2, 6, 8). These studies, however, may overestimate losses due to mortality since they assume that the mean weight of dead shoots is the population mean for the sample collected prior to shoot death. This was clearly not the case in this study (or in 9) where the shoots that eventually died were much smaller than average.

Table 2. Shoot growth and losses due to mortality.

Site/Date	Height (cm)	Weight (g/shoot)	Standing Crop (g/m^2)[a]	Growth Rate (g/m^2/day)	Mortality (g/m^2)[a]	Cumulative Loss (%)[b]
Boot Lake						
June 20	42	0.8	24 ± 12	—	—	—
June 30	81	2.7	112 ± 35	8.8	0.3 ± 0.5	0.3
July 12	115	5.0	218 ± 80	8.8	0.1 ± 0.3	0.2
July 25	140	7.6	329 ± 72	8.5	3.2 ± 2.3	1.0
Sept. 4	158	7.2	292 ± 41	-0.9	13.0 ± 7.0	5.4
Cedar Creek						
June 8	34	0.6	20 ± 2	—	—	—
June 20	72	1.9	69 ± 5	4.1	0.2 ± 0.3	0.3
June 30	119	4.5	164 ± 4	8.6	0.5 ± 0.6	0.4
July 12	172	8.4	306 ± 21	11.8	0.2 ± 0.4	0.3
July 25	198	16.8	610 ± 98	23.4	0	0.1
Sept. 4	208	18.1	645 ± 137	0.9	2.2 ± 1.8	0.5
Lauderdale						
May 21	15	0.2	12 ± 4	—	—	—
June 2	62	1.4	122 ± 42	8.5	0.1 ± 0.1	0.1
June 10	100	3.8	351 ± 62	28.6	2.0 ± 1.4	0.6
June 22	133	6.5	611 ± 63	21.7	7.0 ± 3.6	1.5
July 1	157	9.7	868 ± 69	25.7	9.3 ± 3.5	2.1
July 31	184	10.6	799 ± 30	-2.3	105 ± 22	13.4
Sept. 6	197	12.0	569 ± 60	-6.2	234 ± 48	38.6

[a] ± one standard error.

[b] cumulative loss of biomass due to mortality expressed as a percent of current standing crop + the cumulative loss.

Midsummer standing crop at the Lauderdale site was somewhat less than the average for nonfloating Minnesota *T. glauca* stands (1036 m^2; 7, 23). Peak aboveground standing crop at Cedar Creek was, however, similar to that of a floating *T. glauca* stand at Peltier Lake (7). This site also had a heavy litter cover and relatively short growing season. Peak aboveground standing crop at Boot Lake is lower than nearly all other reported values for *T. glauca* or other *Typha* spp (7).

The Double Sampling Method

Double sampling by regression has been used to estimate the standing crop or growth rate of *Typha* (9, 10, 13) and other emergent macrophytes (e.g., 1, 3, 24). Double sampling has several advantages over conventional "clip plot" harvest techniques. If used in conjunction with permanent plots, it can provide unambiguous information concerning shoot emergence and mortality. Double sampling is well suited for use in sensitive areas such as Boot Lake where the damage caused by harvesting plots would be unacceptable. The technique may also be particularly useful in situations where logistic problems make the harvest technique impractical (25) or in tropical wetlands where continuous shoot turnover (26) may make standing crop a very poor estimate of productivity.

Using regressions to determine shoot biomass added little variance to estimates of standing crop in this study. Lieffers (9) also found that between plot variance was the most important source of error in his study of *T. latifolia*.

The double sampling method used in this study does, however, have a number of drawbacks, which should be recognized. Repeated trampling around the periphery of permanent plots may have an adverse affect on shoot growth within plots (5, 27). Unless coupled with difficult and time consuming belowground excavations, the method fails to account for mortality prior to shoot emergence. In situations where litter cover is very thick, or in deep water habitats, care must be taken not to overlook shoots. Finally, this method alone does not take into account leaf mortality. In *T. glauca* such losses seem relatively minor and are generally confined to leaf tips and small outer sheath leaves. In other macrophytes, however, losses due to leaf mortality can be substantial (28) and must be accounted for.

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