1987

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John Michael Penko
University of Minnesota, Minneapolis

Douglas C. Pratt
University of Minnesota, St. Paul

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

JOHN MICHAEL PENKO* and DOUGLAS C. PRATT**

**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 (*Archenara oblonga* Ckt.) or a mammalian herbivore. Peak standing crop occurred at different times at the three sites and was 329 g/m² at Boot Lake, 645 g/m² at Cedar Creek, and 868 g/m² 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-Alnus*). 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 (400 m²) stand situated on an extensive mat, which fringes Boot Lake (11). The stand was located about 75 m from open water and 10 m 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 500 m² 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 1 m² 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).

*Dept. of Ecology and Behavioral Biology, University of Minnesota, Minneapolis and **Dept. of Botany and Bioenergy Coordinating Office, University of Minnesota, St. Paul*
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 Guert. (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/m². Peak standing crop underestimated net aboveground productivity by 4.9% at Boot Lake, 0.5% at Cedar Creek, and 6.3% at Lauderdale.

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 T. 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) similarly 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 1. Seasonal changes in shoot density, natality, and mortality.

<table>
<thead>
<tr>
<th>Site</th>
<th>Density (shoots m⁻²)</th>
<th>Natality</th>
<th>Mortality</th>
<th>Mortality (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Boot Lake</td>
<td>29.3 ± 4.7</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>June 20</td>
<td>41.3 ± 4.3</td>
<td>12.3 ± 6.3</td>
<td>0.3 ± 0.3</td>
<td>0.7</td>
</tr>
<tr>
<td>July 12</td>
<td>44.0 ± 4.6</td>
<td>3.0 ± 1.7</td>
<td>0.3 ± 0.3</td>
<td>1.3</td>
</tr>
<tr>
<td>July 25</td>
<td>43.3 ± 4.6</td>
<td>0.6 ± 0.6</td>
<td>1.3 ± 0.9</td>
<td>4.2</td>
</tr>
<tr>
<td>Sept. 4</td>
<td>40.6 ± 4.9</td>
<td>0.3 ± 0.3</td>
<td>3.0 ± 1.5</td>
<td>10.8</td>
</tr>
<tr>
<td>Cedar Creek</td>
<td>30.7 ± 2.2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>June 6</td>
<td>36.0 ± 3.8</td>
<td>6.0 ± 2.5</td>
<td>0.7 ± 0.3</td>
<td>1.9</td>
</tr>
<tr>
<td>June 30</td>
<td>36.7 ± 4.2</td>
<td>1.3 ± 0.7</td>
<td>0.7 ± 0.7</td>
<td>3.7</td>
</tr>
<tr>
<td>July 12</td>
<td>36.3 ± 3.8</td>
<td>0.3 ± 0.3</td>
<td>4.5</td>
<td></td>
</tr>
<tr>
<td>July 25</td>
<td>36.3 ± 3.8</td>
<td>0.3 ± 0.3</td>
<td>4.5</td>
<td></td>
</tr>
<tr>
<td>Sept. 4</td>
<td>35.7 ± 3.7</td>
<td>0.7 ± 0.3</td>
<td>6.3</td>
<td></td>
</tr>
<tr>
<td>Lauderdale</td>
<td>68.0 ± 10.1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>May 21</td>
<td>94.3 ± 11.7</td>
<td>17.0 ± 3.4</td>
<td>0.7 ± 0.5</td>
<td>1.0</td>
</tr>
<tr>
<td>June 2</td>
<td>93.5 ± 7.9</td>
<td>12.1 ± 4.8</td>
<td>3.1 ± 0.9</td>
<td>3.6</td>
</tr>
<tr>
<td>June 10</td>
<td>93.3 ± 8.5</td>
<td>2.0 ± 1.4</td>
<td>2.3 ± 1.1</td>
<td>6.1</td>
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<tr>
<td>July 1</td>
<td>89.8 ± 7.9</td>
<td>0.3 ± 0.3</td>
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<td>July 31</td>
<td>75.3 ± 5.1</td>
<td>14.5 ± 2.5</td>
<td>24.4</td>
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<tr>
<td>Sept. 6</td>
<td>47.3 ± 1.4</td>
<td>28.0 ± 3.3</td>
<td>53.0</td>
<td></td>
</tr>
</tbody>
</table>

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

a ± one standard error.
Midsummer standing crop at the Lauderdale site was somewhat less than the average for nonfloating Minnesota *T. glauca* stands (1036 m²; 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 perimeter 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.

**Acknowledgements**

Fieldwork was supported by grants to John Michael Penko from the Dayton Natural History and the Cedar Creek Natural History Area research funds. Computer access was provided by a grant from the University of Minnesota Computer Center. We thank J. Jensen of the Minnesota DNR Scientific and Natural Areas Program for permission to work at Boot Lake. We also thank Eville Gorham, Ellen Garver, and two *Minnesota Academy of Science* journal reviewers for their comments.

**References**


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