

THE IMPORTANCE OF STANDING DEAD SHOOTS OF THE NARROW LEAVED CATTAIL, *TYPHA ANGUSTIFOLIA* L.

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ABSTRACT

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Field experiments in a brackish tidal wetland dominated by *Typha angustifolia* L. demonstrated that dead shoots provide vital aeration for rhizomes of dormant *Typha*. Cutting off or bending over dead shoots at the sediment surface lowered oxygen concentrations in rhizomes and lowered above-ground production and flowering in the following growing season. The effects were more severe the earlier in the dormant season treatments were applied. Cutting had a greater effect than bending. Cutting reduced the numbers of live stems appearing in the following growing season, but bending increased their numbers while still reducing above-ground biomass. Dead shoots can be bent over by wind or snow, destroyed by fire and cut off by ice movement or by muskrats building lodges. These natural disturbances can effect the growth and reproduction of *Typha*.

INTRODUCTION

Like many aquatic plants, *Typha* species possess well-developed aerenchyma in their rhizomes and emergent shoots and leaves. Aerenchyma provides a pathway for diffusion and, in some aquatic plants, for bulk flow of oxygen to the roots (Armstrong, 1978; Dacey, 1980; Raskin and Kende, 1985). The oxygen delivered to the roots supports respiration and may also leak out into the rhizosphere, thereby locally oxidizing the soil, eliminating certain phytotoxins which form under anaerobic conditions and altering the availability of certain nutrients (Armstrong, 1978; Mendelsohn and Postek, 1982; Carpenter et al., 1983; Thursby, 1984; Dean and Biesboer, 1985).

Cutting live *Typha* shoots below the waterline results in rapid depletion of oxygen in the rhizome and anaerobic metabolism in the roots (Sale and Wetzel, 1983). Repeated cutting will eventually kill the plants and is a recommended technique for eradicating *Typha* when managing wetlands for rice cultivation or waterfowl habitat (Singh et al., 1976; Beule, 1979). Even cutting shoots of dormant *Typha* in winter can reduce growth (Weller, 1975), although root

respiration rate is probably low at that time. The effects on oxygen in rhizomes of cutting dead shoots in winter has not previously been investigated.

We have observed that dead *Typha angustifolia* L. shoots often remain standing for as long as 3 years. However, dead shoots can be bent and flattened by strong winds and heavy snowfall. Dead shoots can also be destroyed by fire (Davis and van der Valk, 1978), or cut off by ice movement (Beule, 1979) or by muskrats using the shoots for building lodges. Such natural disturbances to the dead shoots of dormant *Typha* could potentially affect productivity the following growing season. We have noticed that areas of low productivity sometimes occur where dead shoots have been matted down during the winter.

The stand of *Typha* that we studied may be particularly dependent on its dead shoots since it senesces before the onset of freezing temperatures. Usually the shoots are completely brown by mid-October, which is before the first frost and at a time when water temperatures are still 10–15 °C (unpublished data). Such high temperatures early in the dormant season probably lead to relatively high oxygen demand by the roots. In estuarine populations of *Typha*, such as ours, early senescence may be promoted by the increase in salinity that typically occurs in late summer. Moderately high salinity is stressful to *Typha* (McMillan, 1959; Hocking, 1981).

In the present study we investigate the effects of bending or cutting standing dead *Typha* shoots at various times throughout dormancy on oxygen concentrations in the rhizomes and on growth and reproduction the following growing season.

METHODS

Study site

The studies were conducted in a brackish tidal marsh on the Rhode River, a sub-estuary on the western shore of the Chesapeake Bay (38°51' N, 76°32' W). The marsh surface is 30 cm above mean low water, is flooded by 46% of high tides and is submerged on average about 7 h day⁻¹ (Jordan et al., 1986). Salinity ranges from 0 ppt in spring to as high as 18 ppt in the autumn. *Typha angustifolia* is the dominant plant in the marsh but *Scirpus olneyii* Gray and *Spartina cynosuroides* (L.) Roth are also common (nomenclature follows Radford et al., 1968). The *Typha* plants are dormant, i.e. their above-ground parts are completely brown, from mid-October to mid-April.

Experimental design

We conducted field experiments for 2 years. In the first year we set up several 3 × 3-m plots when the plants were dormant. In these plots, standing dead shoots were either bent over, cut off at the sediment surface, or left undis-

turbed. The plots were arranged in sets of three adjacent plots with one plot in each set representing each treatment. This helped control for the effects of spatial variation. Replicate sets of plots were established at three times during the dormant period: early November, mid-December and late March. Three replicate sets of plots were established at each time period to study effects on growth in the following growing season and three additional replicate sets were established in November and March to study effects on oxygen concentrations in rhizome aerenchyma. The replicate sets were interspersed to avoid 'pseudoreplication' (Hurlburt, 1984). In late October of the second year we established six additional sets of replicate plots consisting of pairs of adjacent 3×3-m plots with one plot of each pair having dead shoots bent and the other having dead shoots left undisturbed.

Effects were tested by analysis of variance (ANOVA). Treatment (cut, bent, undisturbed) and date of treatment (November, December, March) were considered fixed factors, while set (i.e. group of adjacent plots) was considered a random factor nested in date of treatment. Replicate measurements of oxygen concentration in rhizomes within each plot were averaged before analysis to produce one measurement per plot, since plots were nested within sets (Underwood, 1981). We had to assume that there were no treatment×set interactions, since there was only one plot per treatment per set of adjacent plots. When treatment×date of treatment interactions were significant we calculated Tukey's honestly significant difference ranges for unconfounded pairwise comparisons (i.e. within treatment or within date), using the technique of Cicchetti (1972). Data expressed as percentages were arcsine, square-root transformed before analysis (Sokal and Rohlf, 1981).

In late summer of the 2 years following treatments (when above-ground biomass had peaked) the heights of the 12 tallest plants, and the total number of shoots and the number with inflorescences per square meter were determined for the inner 2×2-m sections of the 3×3-m plots. We confined our measurements to the inner 2×2 m to avoid possible edge effects. The inner 2×2-m sections were divided into four 1×1-m quarters and the height of the tallest three plants in each quarter was measured. We estimated biomass using a regression relating biomass in 1×1-m plots to numbers of shoots per square meter and average height of the three tallest plants ($\ln(\text{g dry weight m}^{-2}) = -8.90479 + 2.334997(\ln(\text{cm height})) + 0.7022776(\ln(\text{shoots m}^{-2}))$, $r^2=0.847$, $n=22$).

Measurements of oxygen in rhizomes

Oxygen concentrations in rhizome aerenchyma were measured in the first year of the experiment. Rhizomes in three replicate sets of plots that were treated in November and March were sampled 3 weeks after treatment while the plants were still dormant. The plots treated in November were also sam-

pled in April after green shoots had emerged. Seven randomly chosen rhizomes were sampled per plot. The rhizomes were carefully exposed by hand excavation of the substrate. Then, after interstitial water had submerged the exposed rhizomes, gas samples were drawn with 1-cm³ tuberculin syringes. Prior to sampling, the syringes were filled with sodium citrate solution (425 g sodium citrate plus 15 g citric acid per liter) to exclude air. The concentrated citrate solution was used because of its low capacity to dissolve gases (Scholander et al., 1955). After drawing gas into a syringe we withdrew the needle and drew in some interstitial water to form a barrier between the sample and the air. This interstitial water was immediately expelled into a beaker of citrate solution and replaced by citrate solution, leaving a bubble of sampled gas isolated from air by citrate solution. The needle was then inserted into a rubber stopper for transport to the laboratory.

The percent oxygen by volume in the samples was determined as soon as possible by measuring the volume of the sample bubble before and after absorbing the oxygen with pyrogallol solution. The pyrogallol solution was prepared by adding 15 g pyrogallol (1,2,3-trihydroxybenzene) to 100 ml of 20% sodium hydroxide solution, covering with a layer of paraffin oil and then stirring to dissolve the pyrogallol (Scholander et al., 1955). The analysis proceeded as follows: The needle was removed from the syringe while keeping citrate solution in the tip of the syringe between the bubble and the air. The volume of the bubble was measured using the graduations on the syringe. The tip of the syringe was submerged in the pyrogallol solution under mineral oil. Most of the citrate was then expelled and replaced with pyrogallol. Then the pyrogallol was repeatedly drawn and expelled from the syringe, taking care not to expel any of the sample bubble. The volume of the bubble was measured repeatedly until it no longer changed, indicating that all the oxygen had been absorbed by the pyrogallol. The technique was checked by analyzing bubbles of air and finding 21% oxygen by volume.

RESULTS

Cutting or bending the standing dead shoots reduced maximum above-ground biomass and plant height, with cutting having the greatest effect (Fig. 1). The treatments had greater effects the earlier in the dormant season they were applied (Fig. 1). Since there were significant ($P < 0.05$) interactions of treatment and date of treatment, unconfounded pairwise comparisons of interactive cell means were tested with Cicchetti's (1972) modification of the Tukey test for post hoc comparisons (Fig. 1). The second year data were tested by a separate ANOVA. The effects of bending on biomass and height were only significant in the second year (Fig. 1).

Cutting dead shoots reduced the numbers of live shoots per square meter in the following growing season, with the effect being greater with earlier cutting

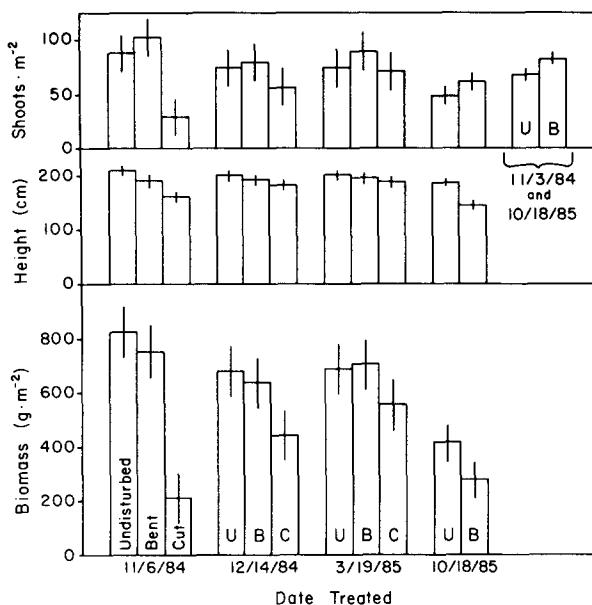


Fig. 1. Average numbers of shoots per square meter, average height of the 12 tallest shoots and average above-ground biomass. First and second year data were analyzed by separate ANOVAs. Vertical lines show 95% confidence limits for pairwise comparisons within years. The limits for the first year were calculated by Cicchetti's (1972) modification of the Tukey method. Data on shoots per square meter from plots treated in the autumns of 1984 and 1985 were also analyzed together in one ANOVA.

(Fig. 1). In contrast, bending dead shoots increased the numbers of live shoots per square meter, but the effect was statistically significant ($P=0.027$) only if data from plots treated on 3 November 1984 and 18 October 1985 were combined in one ANOVA. The increase in shoots per square meter in bent plots was offset by the decrease in plant height, resulting in lower biomass in bent plots than in undisturbed plots.

In the first year, cutting or bending dead shoots also reduced flowering (Fig. 2), with cutting having the greatest effect. Plants in cut plots often produced no inflorescences, therefore cut plots were omitted from the ANOVA since the data would not be normally distributed. The ANOVA including bent and undisturbed plots indicated that the effect of bending was significant ($P=0.02$), while the effect of date of treatment was not ($P=0.09$). A nonparametric test pooling sites and dates (STP, Sokal and Rohlf, 1981) indicated that plants in cut plots produced significantly ($P<0.05$) less inflorescences than those in either undisturbed or bent plots. In the second year, inflorescence production in all the plots was too low to test for treatment effects.

The deleterious effects of bending and cutting dead shoots may result from deprivation of oxygen in the roots. Bent and cut plots had lower oxygen con-

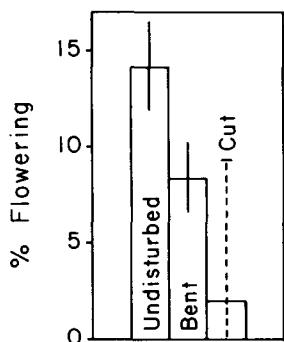


Fig. 2. Average percent of shoots flowering in the first year experiment. All treatment dates were combined since date had no significant effect. For the cut treatment, the data were omitted from the ANOVA and the range is shown. For the other treatments, the least significant difference ($P=0.05$) ranges are shown.

centrations in rhizomes than did undisturbed plots (Fig. 3). The lowest oxygen concentrations resulted from cutting, the treatment which also had the greatest effects on growth and reproduction. Plots treated in November had the same pattern of oxygen concentrations 3 weeks after treatment as did plots treated in March. However, the plots treated in November showed no effects on oxygen concentrations when resampled in late April when green shoots had emerged. This suggests that the growing shoots provided oxygen for the rhizomes.

DISCUSSION

The oxygen concentrations we measured in rhizomes of undisturbed *Typha* plants in November were around 15% (Fig. 3) which is about the same as Sale and Wetzel (1983) measured in summer. The slightly higher concentrations we measured in April, around 18% (Fig. 3), may reflect lower root respiration at that time. However, the difference between the November and April levels in undisturbed plants is not statistically significant.

Sale and Wetzel (1983) found that when *Typha* shoots were cut off below the water level in summer the oxygen concentrations in the rhizomes dropped to zero in 8 h. We did not expect such rapid depletion in our study because the plants were dormant and root respiration was probably lower than in the summer. Also, the plants we studied were immersed only at high tide, and we sampled at low tide. Nevertheless, there was a depletion of oxygen in rhizomes of cut plants; although oxygen concentrations were much greater than zero 3 weeks after cutting (Fig. 3). It is possible that the cut shoots became permanently waterlogged or clogged with silt after repeated tidal immersions and thereby became less effective pathways for oxygen transport even when uncovered at low tide. Oxygen concentrations in rhizomes may fluctuate with the tide, as in *Spartina* spp. (Gleason and Zieman, 1981), but we did not investigate that

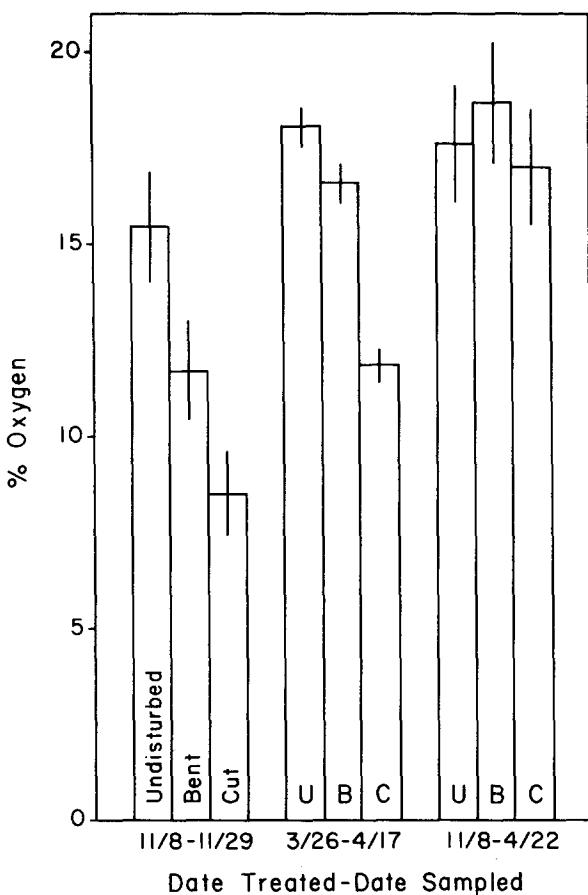


Fig. 3. Percent oxygen by volume in rhizomes. Different samplings were analyzed by different ANOVAs. Tukey's honestly significant difference ranges ($P=0.05$) are shown for comparisons within samplings.

possibility. The oxygen depletion we observed in *Typha* rhizomes with bent shoots suggests that bending the shoots collapses the air spaces at the location of the bend, thus reducing, but not eliminating, oxygen diffusion.

It is possible that bulk flow of gas as well as diffusion may occur in *Typha*. In rice, *Oryza sativa* L., gas is drawn into the roots by a partial vacuum created by consumption of oxygen and dissolution of respiratory carbon dioxide (Raskin and Kende, 1985). In *Spartina alterniflora* Loisel., changes in water demand may alternately expand and contract root parenchyma, thereby changing the volume of aerenchyma and pumping gases out and in (Dacey and Howes, 1984). In water lilies, *Nuphar luteum* (L.) Sibthorp and Smith, pressurization of gases in young leaves induces flow from young leaves through rhizomes and out of old leaves (Dacey, 1980). Analogous gas flow may occur in *Typha* during

the growing season when both live and standing dead shoots are connected to the rhizome. However, gas flow may be somewhat restricted at the meristem where the shoots and rhizomes join. Air spaces in the shoots do not fully develop in *Typha* until after growing away from the meristem (Kaul, 1974). Similarly, basal meristems in *Cladium mariscoides* Crantz lack air spaces and block gas flow between growing leaves and rhizomes, although flow through dead and live, non-growing leaves can occur (Conway, 1936). Our results suggest that the meristems of *Typha* do not completely block gas flow since plants with emergent growing shoots had high oxygen concentrations in rhizomes whether or not their dead shoots had been cut (Fig. 3). However, more research is needed to elucidate the mechanisms of gas transport in *Typha*.

The effects of cutting and, less clearly, the effects of bending dead shoots on productivity in the following growing season were more severe the earlier in the growing season they were applied. This may reflect a more severe effect on oxygen depletion while the substrate was still warm or the cumulative effect of long periods of oxygen deprivation. The treatments appear to have greater effects on oxygen levels in November than in March (Fig. 3). However, the differences may reflect short-term variations in oxygen concentrations possibly linked to tidal inundation. Also, when the plots treated in March were sampled, growing shoots were just beginning to emerge and may have supplied some oxygen to the rhizomes.

Deprivation of oxygen to overwintering *Typha* may reduce production in the following growing season partly by killing below-ground tissues. Some mortality of below-ground tissues is evident when dead shoots are cut since fewer live shoots appear than when plants are undisturbed (Fig. 1). In a preliminary experiment, complete mortality of plants occurred in some plots where dead stems had been cut during the autumn. We do not know why cutting was more destructive in those plots than in others, but the cut stubble in those plots may have been submerged longer due to poorer drainage. Plugging of the aerenchyma probably resulted in anoxic conditions in the rhizomes leading to anaerobic metabolism and death of tissues due to build-up of toxins (Sale and Wetzel, 1983).

Depletion of carbohydrate reserves may have played an important role in reducing productivity and flowering in plots where dead shoots had been bent. The fact that greater numbers of shoots grew in plots where dead shoots had been bent (Fig. 1) suggests that there was little or no mortality of meristems and that bud development may have been stimulated as occurs when growing *Typha* shoots are injured (Linde et al., 1976; Ogden, 1981). Bending dead stems also lowers oxygen concentrations in rhizomes (Fig. 3), although apparently not enough to cause tissue death. Low oxygen in the rhizomes may induce anaerobic metabolism in parts of the roots that are distant from the aerenchyma. Anaerobic metabolism in *Typha* roots leads to production of ethanol (Sale and Wetzel, 1983) which is toxic and may be excreted as in *Spartina*

alterniflora (Mendelsohn et al., 1981). Excretion of ethanol would waste stored energy reserves and could account for the lower biomass and inflorescence production in the growing season after bending the dead shoots.

Our experiments demonstrate the importance of standing dead shoots to *Typha* during winter dormancy. Even bending the dead shoots, which often occurs naturally in our marsh, has measurable effects. Natural disturbance of dead *Typha* shoots during the non-growing season is one of the many factors which may influence growth and reproduction in unmanaged populations of *Typha*.

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