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Cattail Invasion and Persistence in a Coastal Salt Marsh: The Role of Salinity Reduction

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ABSTRACT: The hypothesis that *Typha domingensis* (cattail) can invade tidal marshes only after soil salinities are substantially reduced was tested experimentally by comparing the salt tolerance of seeds, seedlings, and plants reared from rhizomes. Germination rates for four southern California populations reached 100% in fresh water, decreasing to 2% at 20‰. The salt tolerance of seeds from three coastal populations was lower than that of the Salton Sea population. Salt tolerance of plants grown in the lab did not increase with age for seedlings up to 8 weeks old. Rhizome-bearing plants had greatly decreased growth at 10‰ and no growth at 25‰. However, rhizomes of about 5% of the plants survived 9 months at 45‰. The seeds and seedlings are salt sensitive, which explains why invasion into tidal marshes is restricted to prolonged periods of low soil salinity. The older, rhizome-bearing plants are salt tolerant, which explains how invading plants persist under hypersaline conditions.

Introduction

Species of *Typha* have invaded saline marshes in two regions where streamflow is highly seasonal. In southwestern Australia, *Typha orientalis*, an exotic to the region, is rapidly replacing the native marsh dominant, *Juncus krausii* (Pen 1983; Brock and Pen 1984). In southwestern United States, *Typha domingensis*, a native that is normally restricted to inland wetlands, became dominant in an intertidal marsh and replaced *Salicornia virginica* (Zedler and Beare 1986). In both regions, alterations in streamflow have been implicated as causing the vegetation shifts.

Above-average rainfall in winter 1980 and subsequent reservoir discharge resulted in an unusually long period of heavy streamflow in the San Diego River of Southern California. Because of this, hypersaline soils (over 40‰) in the river floodplain became oligohaline for a longer period than in previous years (Zedler and Beare 1986). Prior to 1980 the vegetation in the San Diego River salt marsh had been an almost monotypic stand of *Salicornia virginica* L. (pickleweed). In 1980, the dominant vegetation changed to *Typha domingensis* Pers. (cattail), a species commonly found farther upstream in freshwater habitats. The population persisted through vegetative regrowth through 1986. We suspected that the invasion of *Typha domingensis* was the result of artificially prolonged streamflow, rather than a natural phenomenon.

This paper presents experimental tests of four hypotheses concerning *T. domingensis* and marsh soil salinity. 1) Because *Typha* established from seed, we hypothesized that salinity must be reduced in order for germination to occur. We expected that seeds from various populations would differ in salt tolerance. 2) Because *Typha* does not normally occur in southern California coastal marshes (Zedler 1982), we hypothesized that low salinity had to persist beyond the usual period of winter flooding in order for seedlings to establish. That is, young seedlings would be sensitive to salt. 3) We expected salt tolerance to increase with seedling age. 4) Because the *Typha* population at San Diego River Marsh persisted vegetatively for several years under tidal conditions, we hypothesized that plants with rhizomes would have higher salt tolerance than seedlings.

Previous studies of *Typha domingensis* have not indicated tolerance to hypersaline conditions. Of the three species of *Typha* in California, *T. domingensis* is thought to be the most salt tolerant (Hotchkiss and Dozier 1949). It has been observed growing in desert wetlands, often in saline soils (Smith

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1961). Howard-Williams (1975) found that it could germinate up to 217 mM of Na^+ (ca. 5‰ NaCl). Von Oertzen and Finleyson (1984) saw a significant weight decrease in seedlings at salinities between 25 and 50 mM NaCl (ca. 3‰) but no leaf wilting or death. In vegetative shoots detached from parent rhizomes, Hocking (1981) found slightly reduced growth at 50 mM NaCl (ca. 3‰) and severely reduced growth at 100 mM (ca. 6‰). These studies indicate that although germination will occur at 5‰, growth is adversely affected at that concentration.

Methods

Germination Experiments

Saline conditions present during seed formation can result in seeds that produce more salt-tolerant plants (Waisel 1972; Hunt as reported in Snow 1982). Because of this, seeds for the germination experiments were collected from four different populations and tested over a range of salinities from 0 to 20‰. The four populations were 1) upstream in the San Diego River, 2) the salt marsh of the lower San Diego River, 3) San Elijo Lagoon, a coastal wetland 28 km north, where *Typha* has developed near street drains, and 4) an area where a seasonal stream empties into the hypersaline Salton Sea, 135 km to the east. The first habitat was fresh, while the other three were brackish. Seeds were collected in late fall 1982 and stored dry at room temperature until use in spring and summer 1983. A large percentage of *Typha* seeds is infertile, so only those judged viable on the basis of shape (Mason 1957) were used in the experiments.

Many studies of germination use NaCl in their tests of salinity tolerance. Single salts are generally thought to be more detrimental than a mixture of salts at the same concentration. Because tolerance to ocean salts was the object of this study, a mixture of salts simulating sea water (Instant Ocean brand) was used with deionized water in all experiments.

Seeds were scattered onto filter papers floating on styrofoam disks (to keep them wet but not submerged) in treatment solutions. There were 33 seeds per dish and 3 replicates per treatment. Covered dishes were randomly assigned to a location under a bank of 35-watt fluorescent lights. An automatic timer provided 14 h per day of light at 60–70 uE m^{-2} s^{-1}. Temperatures ranged from 20 to 30 °C. The initial experiment included treatments at 0, 2.5, 5, and 10‰, with the germinating seeds counted periodically for one month. Because substantial germination occurred at 10‰, a second experiment was conducted to extend the range of salinities tested. A 10‰ treatment was used to compare with the initial experiment, and 15 and 20‰ treatments were added. Seeds were counted periodically for 6 weeks to include any delayed germination caused by high salinity. The results from both experiments were later combined for analysis, as the 10‰ treatments were not significantly different. An arcsine squareroot transformation was used to normalize the data prior to two-way analysis of variance (BMDP8V, Dixon 1981).

SALT TOLERANCE OF SEEDLINGS

Salt tolerance is generally thought to increase with age of halophytic plants. Seedlings of four ages (1, 2, 4 and 8 weeks) were used to determine if this was true for *Typha domingensis*. Seeds were planted at intervals so that all were the proper age for simultaneous salt treatment. Seedlings were grown in University of California soil mix (equal parts sand, peat moss, and redwood compost, plus nutrients and lime) in four-inch plastic pots set in standing water. They were arranged under 35-watt fluorescent lights on a 14-h light–10-h dark schedule. Temperatures ranged from 22 to 30 °C. Plants were fertilized every other week with Miracle Grow plant food (15N:30P:15K). All pots were started with 40 to 50 seeds and thinned to 25 plants prior to treatment. Salinity treatments ~~were 0~~, 10, 15, 20 and 25‰. Pots were randomly assigned to trays and to position under the lights. Water levels were maintained at the soil surface by adding deionized water.

SALT TOLERANCE OF RHIZOME-BEARING PLANTS

Salt tolerance of rhizome-bearing salts of *Typha domingensis* was investigated experimentally using plants from the San Diego River Marsh. In early April 1983, when plants were about 20 cm tall, 16 clumps of 5 to 8 ramets each were dug from the marsh, immediately planted in 5-gal plastic nursery pots and transported to an outdoor growing area at San Diego State University. Each pot was placed in a container of tap water filled to the level of the soil surface. Containers were arranged in two rows on benches with some shading from a nearby tree, but no overhead structures. Two weeks after transplantation, treatments of 0, 25, 35 and 45‰ were randomly assigned to pots, with 4 pots per treatment. For each salinity treatment, Instant Ocean was added to the standing water to increase the salinity by 5‰ per week. A gradual increase was used to simulate natural, seasonal soil salinity increase and was necessary to prevent shock. Similar experiments have used intervals of 10‰ per week (Pearcy et al. 1982) and 5‰ per 8 days (McMillan 1959). Because of the gradual increase, all salinity treatments remained the same until week 5 when the 25‰ treatment was reached. Salt additions con-

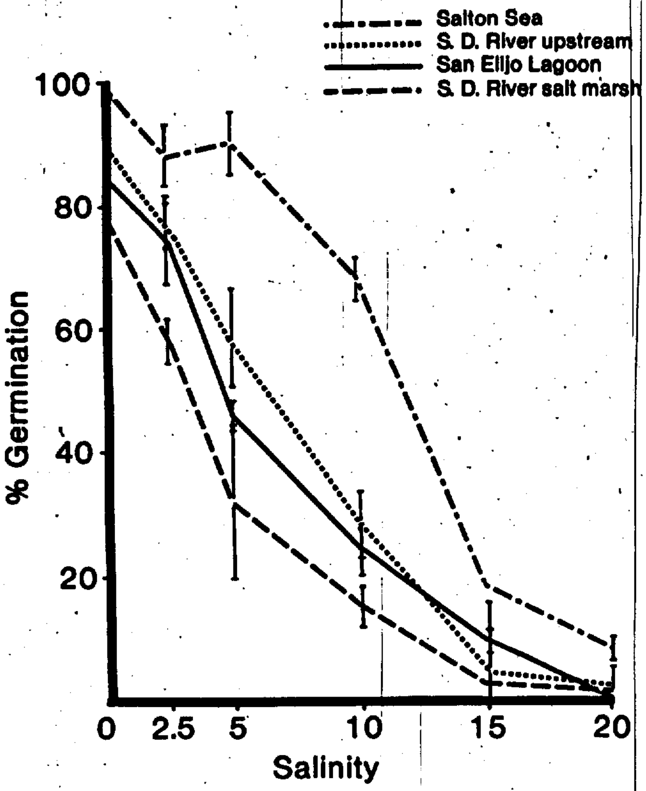

Fig. 1. Percent germination of seeds from 4 populations of *Typha domingensis* at different salinity concentrations (‰). Two-way analysis of variance results: populations F = 41, p = 0.0002; salinity F = 44, p = 0.0002; interaction n.s.

tinued for 2 more weeks to achieve the 35‰ treatment and 4 more weeks to achieve the 45‰ treatment. Water and soil salinities were checked periodically. Tap water was added once a week to maintain water levels and desired salinities through September 1983.

Height and length of necrotic tissue at the leaf tip have been found to be good indicators of salinity stress (Anderson 1977). Beginning one week after transplantation and continuing every other week until dormancy, these characteristics were measured on each leaf of 5 plants per pot. As new leaves were produced through the season, they were also measured.

To test for rhizome survival, salinity treatments were maintained through the first part of the 1984 growing season, when only the 0‰ treatment initiated growth. All pots were then transferred to fresh water and the number of live plants per pot was censused 3 months later (September 1984).

Results

GERMINATION

Germination differed both with seed source and salinity (Fig. 1). The Salton Sea population had higher germination rates at all salinities. Removal of these data from the analysis eliminated the difference among populations. The San Diego River salt marsh population does not appear to represent an extreme for local coastal areas. However, it is clear that differences can occur, and it may be that the desert environment and agricultural leachates entering the Salton Sea have contributed to that population's higher salinity tolerance.

TABLE 1. Mean percent survival (n = 4) and standard error for seedlings of four ages after one month at different salinity treatments.

Age (Week)	Salinity Treatment (‰)				
	0	10	15	20	25
1	99 (0.3)	24 (1.7)	24 (2.0)	17 (1.0)	21 (1.7)
2	99 (0.3)	14 (1.5)	10 (1.3)	13 (0.9)	16 (1.7)
4	100 (0.0)	7 (0.9)	7 (0.9)	3 (0.5)	1 (0.3)
8	98 (0.5)	9 (1.0)	9 (1.3)	0 (0.0)	0 (0.0)

The effect of increased salinity was, as expected, to decrease percent germination (Fig. 1). In addition, salts delayed germination. At 0‰, germination began one day after planting and reached almost 100% in one week. At 20‰, it took two weeks for the first seed to germinate and one month for maximum (2%) success.

SALT TOLERANCE OF SEEDLINGS

At the start of treatments, 8-week plants were about 90 mm in height, 4-week were 35 mm, 2-week were 13 mm, and 1-week were 6 mm. Percent survival was calculated after one month of treatment. Contrary to expectation, the older plants at the highest salinities showed the earliest signs of damage. Leaf tips began to dry and curl in the first few days of the experiment. After one month, these treatments had 100% mortality (Table 1). Within salinity treatments, survival of different age plants was similar, but younger plants (1–2 weeks) showed less leaf necrosis than older plants. At the highest salinity treatments, there were slightly more survivors for the younger than the older seedlings. Salinity tolerance clearly does not increase with age during the first 8 weeks.

SALT TOLERANCE OF RHIZOME-BEARING PLANTS

Prior to salinity treatment, the maximum length of leaf tip necrosis on field-collected plants was 2 mm, and leaf elongation averaged 18 cm wk^{-1}. This growth rate increased in control pots until flowering occurred in late June. Thereafter, growth continued under 0‰ conditions, but at gradually slower rates (Fig. 2). Once salinity treatment began in the remaining pots, there was a rapid decline in growth rate and an increase in leaf tip necrosis. Thus, even 5‰ was sufficient to slow leaf elonga-

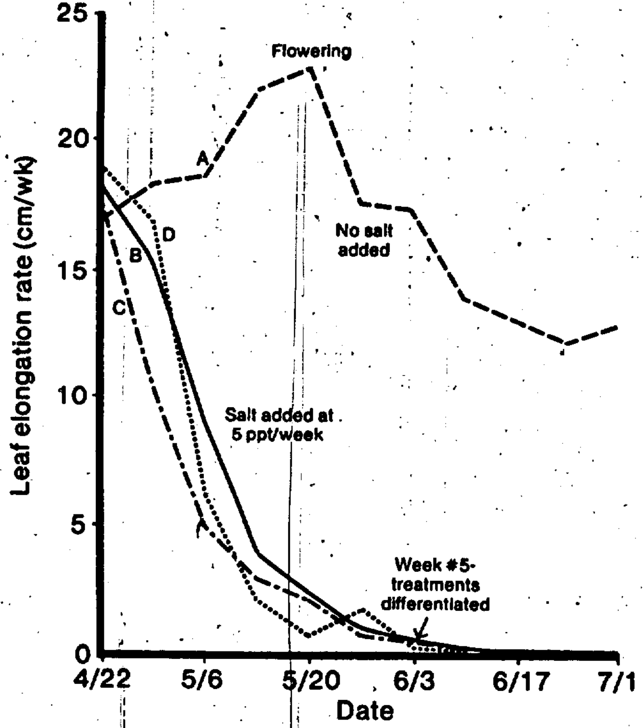

Fig. 2. Leaf elongation for mature plants grown in 1983 without salt (A) and with soil salinities increased by 5‰ per week (B, C, D). The 25‰ treatment (B) was reached on June 3; the 35‰ treatment (C) was reached June 17; and the 45‰ treatment (D) was reached July 1.

tion. By week 4, plants had been exposed to 20‰ and growth rates averaged only 3 cm wk^{-1}. Very little plant growth occurred after week 5 when the 25‰ salinity treatment was reached. Because of this, comparison among the treatments for differences in growth rates was not possible. However, the plants were still green at this time, so salinity effects were measured as leaf tip necrosis until dormancy. No plants in the treatment pots flowered. At the end of 10 weeks, the amount of necrotic tissue at the leaf tips was approximately twice as great at the highest treatment (45‰) than at the lowest (25‰) (Table 2). By the end of August, all aboveground structures in all salinity treatments were completely brown, while those in fresh water retained some green parts throughout the year.

It is clear that rhizome-bearing plants are stressed by salinity, because growth rates slowed with soil salinities as low as 5‰, and all aboveground structures had died by September 1983. While the plants in fresh water began growing again in February 1984, those at all salinity treatments were still dormant in June 1984. Growth initiation was prevented by soil salinities of 25‰ and higher.

Percent survival of plants transferred to fresh water in June 1984 was calculated by dividing the number of plants per pot in September 1984 by the number planted in April 1983. Shoots initiated in the 1985 growing season were not counted. All plants survived when maintained in fresh water; there were 1.2 × as many individuals as were planted. Percent survival after 9 months of salinity followed by 3 months of fresh water was 99% at 25‰, 10% at 35‰, and 5% at 45‰. Average heights of plants at all salinity treatments and 0‰ were not significantly different (Table 2).

Discussion

The experiments demonstrate that the salinity tolerance of *Typha domingensis* varies with life history stage, as hypothesized. Seeds and seedlings are more sensitive than older, rhizome-bearing plants. Invasion into salt marshes is restricted by the plant's least tolerant stages, namely seed germination and seedling establishment. Salinity must drop and remain low until plants develop salt-tolerance. The duration of that low-salinity condition must be determined to understand what normally prevents *T. domingensis* from becoming established in coastal salt marshes. The following arguments support the conclusion that low-salinity periods of 2 to 3 months allow *T. domingensis* invasion and establishment.

Typha sp. produce between 60,000 and 125,000 fertile seeds per pistillate spike (Linde et al. 1976). The San Diego River salt marsh is less than 1 km downstream from several large stands of *Typha domingensis*. Considering such a substantial seed

TABLE 2. Mean (n = 4) and standard error for the characteristics of *Typha domingensis* when grown a) at different salinities and b) after their return to fresh water.

a) Plants Grown in Salinity Treatments (Data at End of 1983 Growth)	Treatment (‰)			
	0	25	35	45
Total leaf elongation (cm)	128 (9.2)	43 (4.0)	30 (3.3)	37 (2.9)
Leaf number per plant	5 (0.3)	3 (0.2)	3 (0.1)	3 (0.1)
Leaf tip necrosis (cm)	5 (1.0)	10 (5.1)	16 (5.5)	20 (3.6)

b) Same Plants, Moved to Fresh Water (Data at End of 1984 Growth)	Former Treatment (‰)			
	0	25	35	45
Percent survival	121 (17.7)	99 (22.1)	20 (9.5)	5 (4.5)
Mean height of plants (cm)	210 (7.0)	175 (17.8)	148 (0.0)	183 (0.0)

source, the low (2%) germination rate seen at 20‰ may not be a deterrent to invasion. The ability to germinate, however, does not insure establishment. From observations made during both the germination and seedling experiments, it is clear that salinity not only affects germination and seedling survival, but also seedling growth. A decrease in growth is evident at salinities as low as 5‰, and it becomes pronounced at 10‰.

Although it is generally suggested that salt tolerance increases with age, plants up to 8 weeks old did not tolerate an increase in soil salinity. Instead, the older plants (8 weeks) showed the greatest salt damage. The explanation for this is suggested in work by Bernstein and Hayward (1958), who pointed out that plants grown without water stress tend to produce more aboveground growth. Then, when an increase in salinity causes moisture to become limiting, there is severe injury. For this reason they suggest that younger plants, because they generally have less aboveground mass (a higher root : shoot ratio), are able to adjust better to increases in salinity than older plants. This is supported by the results of Sharma and Pradhan (1983), who found that plants grown in saline areas have a higher root : shoot ratio. This suggests that salt tolerance may not develop until well after 8 weeks of growth. Even the rhizome-bearing plants showed salinity stress, as indicated by decreased growth at 5‰, no growth at 25‰, and leaf death above 25‰.

Rhizomes of *Typha domingensis* have previously been shown to be the most salt-tolerant plant part (Hocking 1981). Because rhizomes resprouted after salinity caused leaf death, they appear to be critical in developing salinity tolerance. However, it is not clear when the rhizomes are formed. Seedlings 20 to 33 cm tall (probably about 2 months old) have rhizomes that are only 3 to 4 mm in diameter (Linde et al. 1976). Linde et al. (1976) point out that because of their small size there would no appreciable food storage at this time, and they would be expected to be quite vulnerable to injury. By the end of the first growing season *Typha domingensis* plants grown from seed had dense mats of rhizomes that were already producing new vegetative shoots (Smith 1961). So, sometime between 2 months of age and the end of the first growing season, rhizomes are formed.

We believe that continued survival requires occasional periods of good growing conditions. This *Typha* population survived the high salinity years of 1981–82 with little growth and flourished in 1983 (Zedler and Beare 1986). McNaughton (1966) pointed out that even the more salt-tolerant coastal stands of *Typha* included in his study must grow primarily during periods when the bays where they grow are flushed by freshwater runoff. Field observations in 1984 in the San Diego River salt marsh show that spring growth is not initiated at salinities above 10 to 15‰. Our experiments with plants reared from rhizomes showed that a 3-month period is sufficient for *Typha domingensis* to grow and flower under favorable conditions, even if this occurs four months later than normal. Plants in freshwater areas in San Diego have been observed to begin growth in late February or early March and enter dormancy in late fall. The climate appears to be favorable for growth for about 8 months of the year. Thus, soil salinities of 0–5‰ for any 3-month period between February and August should allow normal leaf growth and maintenance of a vigorous population.

Under natural conditions, streamflow would decline in April after winter rainfall ends, and *Typha* would not be able to establish in intertidal marshes. Only the release of water from upstream reservoirs would produce high streamflows through the growing season and allow invasion. Streamflow management is thus important to the maintenance of the native halophytes.

In Southern California, salt marshes have been reduced to less than 25% of their original area (Speth 1969), and all of the region's 26 coastal wetlands have been disturbed in various ways. The remaining marshes provide critical habitat for several endangered species. One of these, the Belding's Savannah sparrow, depends entirely on salt marshes (with a preference for *Salicornia virginica*) for cover, nesting habitat, and feeding (Massey 1979). Thus, conservation of natural vegetation is important.

This work suggests several management recommendations for preventing *Typha* invasions elsewhere in the region. Major reservoir releases should be confined to brief periods, so that the entire flood period (including natural runoff) does not exceed 2 to 3 months. Major discharges of treated wastewater should be restricted to the normal wet season. Dry season discharges should be limited in volume. In areas where *Typha* prevents reestablishment of salt marsh species, control measures should be considered.

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