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# The effect of sea-water submergence on rhizome bud viability of the introduced *Ammophila arenaria* and the native *Leymus mollis* in California

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**Abstract.** *Ammophila arenaria*, an invasive European beach grass, dominates most United States Pacific coast beaches north of San Francisco Bay, and it appears to severely reduce opportunities for regeneration of native plant species, including American beach grass, *Leymus mollis*. The knowledge of how long *Ammophila* rhizomes can survive in sea-water is important for long-tern management strategies, which must consider the probability of reinvasion of areas where *Ammophila* has been eradicated. The bud viability of both *Ammophila arenaria* and *Leymus mollis* remained high following submergence in sea-water for 7 days, and *Leymus* bud viability was still high after 13 days submergence. In fact, *Leymus* bud viability appears to be enhanced slightly by submergence for 7 days in sea-water. Since *Ammophila* rhizomes retain a mean bud viability of > 50% following submergence for 7 days, there is clearly the potential for long distance dispersal to other beaches. Even after 13 days of submergence, *Ammophila* rhizomes still had a mean bud viability of 8.5%. Assuming near-shore current speeds of 5 - 45 cm/sec, viable *Ammophila* rhizomes can be transported up to 505 km in 13 days.

**Keywords**: Invasion; Long-distance dispersal; Rhizome; Vegetative reproduction.

**Nomenclature:** Hickman (1993).

## Introduction

*Ammophila arenaria* is an invasive beach grass native to Europe, the Mediterranean, and the Black Sea (Huiskes 1979; Doing 1985; Hulten & Fries 1986). After being introduced to North America for stabilization of coastal dunes, its range now extends from San Diego, California (33¡N) to British Columbia (53¡N) (Breckon & Barbour 1974; Barbour & Johnson 1977). The species dominates most United States Pacific coast beaches north of San Francisco Bay (Barbour et al. 1976).

*Ammophila* has been planted extensively to stabilize dunes along the Pacific coast of North America (Barbour & Johnson 1977), and elsewhere (Hewett 1970; Ranwell 1972; Tsuriell 1974; Huiskes 1979; McAdam 1980; Johnson 1982; Heyligers 1985; van der Putten 1990; Lubke & Hertling 1995; Hertling 1997; van der Laan 1997). Once plants are established, they expand their territory through vigorous rhizome growth.

Over the past 15 years a number of studies have investigated manual, mechanical, and chemical methods of *Ammophila* eradication, with varying degrees of success (Pickart & Sawyer 1998; Aptekar et al. unpubl.). However, even if *Ammophila* is eliminated from a site, there is the possibility of recolonization from *Ammophila* rhizomes washed on shore by ocean currents (Ranwell 1972; WallŽn 1980; Heyligers 1985; Wiedemann 1987). Although *Ammophila* becomes only rarely or sporadically established by seeds (Gemmell et al. 1953; Greig-Smith 1961; Huiskes 1977, 1979; Pavlik 1983; Heyligers 1985), it has clearly become established in foredunes where it was not planted (Johnson 1982; Buell et al. 1995, and our observations at Goat Rock, California), and it is likely that many stands originated from rhizomes arriving by sea. The knowledge of how long *Ammophila* rhizomes can survive in sea-water is therefore important for long-term management strategies, which must consider the question of long-distance spread from existing stands and reinvasion of areas where *Ammophila* has been eradicated.

There has been speculation that *Ammophila* cannot tolerate high salinity concentrations as well as the native beach grass *Leymus mollis* (Trin.) Pilger (formerly *Elymus mollis* Trin ex Spreng) (Van Hook 1983). In California, *Leymus mollis* is one of the most salt-tolerant native dune species (Barbour 1978). Assuming that *Leymus mollis* can also spread by rhizome fragments, as can the related European beach species *Leymus arenarius* (L.) Hochst. (formerly *Elymus arenarius* L.) (Bond 1952) and *Elymus farctus* (Harris & Davy 1986a, b), the relative salinity tolerance of the two dune grass species found on the Pacific coast can affect the probability of an *Ammophila arenaria* or *Leymus mollis* colonization.

This study investigated the length of time *Ammophila arenaria* and *Leymus mollis* rhizomes can remain submerged in sea-water and still maintain viable buds capable of producing new plants when washed on shore. Vegetative reproduction can be a key factor in the long-distance dispersal of many exotic species in aquatic habitats and floodplains (Rejm‡nek 1999). This study indicates that it could also be an important factor in coastal environments.

## Methods

Rhizomes of *Leymus mollis* and *Ammophila arenaria* were collected at Kehoe Beach, Point Reyes National Seashore, California (38¡09' N, 122¡57' W) in February 1994, and cut to lengths of 20 cm, 40 cm, and 80 cm. Rhizomes were bathed in tanks with flow-through sea-water (33.4 to 34.3 ppt) at the University of California Bodega Marine Station for 18 hr (1 day), 67 hr (3 days), 168 hr (7 days), or 312 hrs (13 days). Control rhizomes were not placed in sea-water, but planted in washed and sterilized sand in greenhouse flats in Davis, California. Submerged rhizomes were planted in washed and sterilized sand after sea-water treatment. None of the rhizomes were washed prior to planting. Flats were watered every third day. Rhizomes were allowed to grow for one month before harvesting. Fourteen to 21 rhizomes replicates were used for each submergence duration/rhizome length treatment. Bud viability was measured as the percent of rhizome nodes that produced vegetative shoots and roots following treatment. Both species have dormant buds at all nodes (Greig-Smith et al. 1947; Hobbs et al. 1983; Pavlik 1983). Maximum bud viability for each treatment was measured as the bud viability of the rhizome replicate with the highest bud viability for that treatment.

Statistical analysis was done using 3-way ANOVA on angular-transformed data with the intention to test for effects of species, duration of submergence, and rhizome length. One-way ANOVA and two-sided DunnettÕs test (Hsu 1996) were used for testing of treatment effects in comparison to controls.

## Results

*Leymus mollis* had significantly more nodes per rhizome interval than *Ammophila* (3.9 per 20 cm of rhizome vs. 2.5; *t*-test, $n_1 = n_2 = 250$, $p<0.001$). This is consistent with PavlikÕs (1983) data on horizontal rhizomes of laboratory-grown plants. Unfortunately, absolute numbers are not comparable because PavlikÕs measurements were on a per plant basis, and did not include measurements of rhizome length.

Bud viability following sea-water submergence was significantly lower for *Ammophila arenaria* than for *Leymus mollis* ($p<0.001$, Tables 1 and 2). Bud viability significantly decreased for *Ammophila* and initially increased for *Leymus* as the duration of sea-water submergence increased (Table 2). There was also a significant interaction between species and submergence duration ($p<0.001$, Table 1). Rhizome length did not significantly affect rhizome bud viability (Tables 1 and 3), so in additional analyses we grouped all three rhizome lengths for each submergence duration treatment. This is in contrast to *Elymus farctus*, in which longer rhizome segments produce disproportionally more shoots than shorter segments (Harris & Davy 1986a, b).

Mean bud viability of *Ammophila* rhizomes in the control was 63.8%, maximum was 100%. The decline in bud viability was significant following 7 days of sea-water submergence, when it dropped to a mean of 51.2% ($p<0.05$), and it was highly significant at 13 days of submergence when it dropped to 8.5% ($p<0.01$) (Table 2). Up until 13 days of submergence, 17% - 28% of the rhizome segments for each treatment had 100% bud viability. At 13 days the maximum bud viability for a rhizome segment fell to 75%. In the control and in treatments of  7 days, 83% - 94% of rhizomes had at least one viable bud, whereas after 13 days of submergence only 25% of rhizomes had a viable bud.

*Leymus mollis* rhizome bud viability did not decline significantly from the control mean bud viability of 59.6% at any submergence duration. In fact, there

**Table 1.** Three-way analysis of variance of angular transformed bud viability of *Ammophila arenaria* and *Leymus mollis* rhizomes following submergence in sea-water for 0, 1, 3, 7, and 13 days. Rhizome lengths of 20, 40, and 80 cm were used.

| | df | Sum of squares | Mean squares | *F* | *p* |
|---|---|---|---|---|---|
| Species (A) | 1 | 4.849 | 4.849 | 30.638 | 0.0001 |
| Time (B) | 4 | 18.783 | 4.696 | 29.669 | 0.0001 |
| Rhizome length (C) | 2 | 0.393 | 0.197 | 1.242 | ns |
| AB | 4 | 7.707 | 1.927 | 12.175 | 0.0001 |
| AC | 2 | 0.266 | 0.133 | 0.839 | ns |
| BC | 8 | 1.314 | 0.164 | 1.037 | ns |
| ABC | 8 | 1.804 | 0.226 | 1.425 | ns |
| Error | 513 | 81.191 | 0.158 | | |

**Table 2.** Rhizome bud viability following submergence in sea-water. Means significantly different from control (DunnettÕs test): * $p$ <0.05, ** $p$ <0.01.

| Submergence duration [hours (days)] | Mean bud viability % (SE) | Maximum bud viability % | Rhizomes with max. bud viability % | Rhizomes with >1 viable buds % |
|---|---|---|---|---|
| *Ammophila arenaria* | | | | |
| 0 (control) | 63.8 (4.2) | 100 | 28.3 | 90.0 |
| 18 (1) | 54.3 (4.7) | 100 | 18.5 | 83.3 |
| 67 (3) | 64.8 (3.9) | 100 | 27.7 | 94.4 |
| 168 (7) | 51.2 (8.5)* | 100 | 17.3 | 86.5 |
| 312 (13) | 8.5 (2.4)** | 75 | 0 | 24.1 |
| *Leymus mollis* | | | | |
| 0 (control) | 59.6 (3.0) | 100 | 6.7 | 98.3 |
| 18 (1) | 64.7 (3.8) | 100 | 19.6 | 96.1 |
| 67 (3) | 65.4 (3.6) | 100 | 23.5 | 98.0 |
| 168 (7) | 70.5 (3.4)* | 100 | 25.5 | 100.0 |
| 312 (13) | 48.6 (3.5) | 100 | 5.9 | 94.1 |

was a slightly significant increase in mean bud viability to 70.5% at 7 days submergence ($p < 0.05$). At 13 days submergence, mean bud viability was 48.6%. Each submergence period had a maximum rhizome bud viability of 100%. Even at 13 days submergence, 94.1% of rhizomes still had at least one viable bud and 5.9% of rhizomes had 100% bud viability (Table 2).

**Table 3.** Rhizome bud viability of different length rhizomes following submergence in sea-water. Rhizome length had no significant effect on bud viability (see Table 1).

| Submergence [hours (days)] | Mean % bud viability of different length rhizomes (SE) 20 cm | 40 cm | 80 cm |
|---|---|---|---|
| *Ammophila arenaria* | | | |
| 0 (control) | 70.2 (9.5) | 65.3 (6.7) | 56.2 (4.8) |
| 18 (1) | 59.2 (9.3) | 56.7 (7.3) | 53.3 (6.6) |
| 67 (3) | 75.4 (7.0) | 62.5 (5.5) | 52.9 (7.0) |
| 168 (7) | 50.4 (10.2) | 54.4 (5.8) | 47.6 (5.3) |
| 312 (13) | 8.3 (4.2) | 3.6 (2.8) | 16.4 (5.4) |
| *Leymus mollis* | | | |
| 0 (control) | 58.9 (5.7) | 60.2 (5.2) | 59.8 (4.9) |
| 18 (1) | 65.1 (7.2) | 69.4 (6.6) | 58.3 (5.0) |
| 67 (3) | 63.3 (6.9) | 62.6 (6.1) | 71.8 (5.2) |
| 168 (7) | 72.2 (6.1) | 75.6 (4.3) | 61.9 (6.9) |
| 312 (13) | 39.6 (5.8) | 59.2 (5.6) | 48.4 (5.7) |

## Discussion

Bud viability of both *Ammophila arenaria* and *Leymus mollis* remained high (> 50%) following submergence in sea-water for 7 days, and *Leymus* bud viability was still fairly high after 13 days submergence. *Leymus* bud viability appears to be enhanced slightly by submergence for 7 days in sea-water. Since *Ammophila* rhizomes retain a mean bud viability of over 50% following submergence duration of up to one week, there is clearly the potential for long distance dispersal to other beaches, supporting what others have suspected. Even after 13 days of submergence, *Ammophila* rhizomes still had a mean bud viability of 8.5%.

The size and extent of the region open to invasion of *Ammophila* from any particular site depends on direction and speed of ocean currents. Pacific coast near-surface ocean currents closely follow the regional winds (Anon. 1981; Lentz & Chapman 1989; Maser & Sedell 1994). Near-surface currents flow predominantly to the south from April to July, and predominately to the north from August to March, with the storm season lasting from December to March (Largier et al. 1993). Nearshore currents vary in speed from 5 to 45 cm/sec (Wiedemann 1987; Maser & Sedell 1994). At these rates, ocean borne rhizomes can potentially be transported 4.3 to 38.9 km/day, thus traveling up to 505.4 km within 13 days, when *Ammophila* rhizome bud viability is still ca. 10%.

*Leymus mollis* bud viability does exhibit higher salt-tolerance than *Ammophila*. *Leymus* mean bud viability remained > 48% even after 13 days of sea-water submergence. This is in agreement with previous studies on *Ammophila*, *Leymus* spp., and *Elymus* spp. Soil salinity higher than 1.5% to 2% is lethal to *Ammophila* (Beneck 1930; Salisbury 1952; Chapman 1976; Sykes & Wilson 1989). The European dune species *Leymus arenarius* can tolerate salinity concentrations of up to 12% (Beneck 1930; Salisbury 1952; Wallen 1980). *Ammophila* is also considerably less salt-tolerant than *Elymus farctus*, the most salt-tolerant species on New Zealand dunes (Sykes & Wilson 1989). *Leymus* rhizomes therefore have the potential to spread to and colonize sites even further away from a source population than can *Ammophila*. However, since there is currently considerably less *Leymus* growing along the coast of the Pacific United States, and since *Leymus* rhizomes are less brittle and do not break into fragments as easily as *Ammophila* rhizomes (pers. obs.), it is more likely that any one particular beach would receive *Ammophila* rhizomes, rather than *Leymus* rhizomes.

*Ammophila* is now considered a pest in natural areas for many of the same reasons it was once desirable

(Johnson 1982; Heyligers 1985; Wiedemann & Pickart 1996). It is extremely successful in coastal dunes and rapidly traps moving sand in its tall, densely packed shoots (Salisbury 1952; Ranwell 1972; Huiskes 1979). The result is the formation of large, dynamic dunes that eventually stabilize. This has changed the topography of the Northern California coast, creating prominent steep foredunes where none existed prior to its introduction (Cooper 1958, 1967; Wiedemann et al. 1974; Wiedemann & Pickart 1996). Dunes at Bodega Head, for example, grew in height 4 cm/yr during the past 50 yr, whereas non-vegetated areas were deflated at the same rate (Danin et al. 1999). Californian dunes dominated by *Ammophila* have lower plant species diversity (Breckon & Barbour 1974; Barbour et al. 1976; Pitts & Barbour 1979; Boyd 1992; Aptekar unpubl.) and arthropod species diversity (Slobodchikoff & Doyden 1977) than those dominated by native taxa. *Ammophila* therefore directly or indirectly threatens native plant communities, including *Leymus mollis*-dominated foredunes and Ôdune matÕ communities (Van Hook 1983; Pickart 1988; Anon. 1988; Buell et al. 1995; Wiedemann & Pickart 1996), as well as the state- and federally-listed endangered plant *Erysimum menziesii* (Van Hook 1983). The reduction in the amount of open sand areas in dunes resulting from *Ammophila* spread has severely reduced nesting habitat for the federally-listed threatened snowy plover (Pickart & Sawyer 1998).

The high potential for viable *Ammophila* rhizomes to wash onto beaches indicates that care must be taken to properly dispose of *Ammophila* rhizomes following excavation projects. Intact rhizomes should not be left on the beach or foredune where they could get washed to sea by high tides or storms and colonize other areas. Appropriate disposal of *Ammophila* rhizomes could include bagging and removing them from the site, burning, or allowing them to dehydrate in an area well removed from the reach of tidal waters or drainage routes to the ocean.

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