

POST-FLOOD ESTABLISHMENT OF NATIVE WOODY SPECIES AND AN
EXOTIC, *ARUNDO DONAX*, IN A SOUTHERN
CALIFORNIAN RIPARIAN SYSTEM

A Thesis
Presented to the
Faculty of
San Diego State University

In Partial Fulfillment
of the Requirements for the Degree
Master of Sciences
in
Biology

by
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Fall 1996

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Fall 1996

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INTRODUCTION

Riparian ecosystems are important both as ecotones between terrestrial and aquatic systems, and as corridors across regions (Naiman et al. 1993). Riparian habitat supports a diverse array of species and is maintained by complex environmental processes. Approximately 70% of the riparian habitat in the United States has already been lost due to development, agriculture, livestock, and damming (Brinson 1981). In southern California the loss is even greater, estimated at 95% (Bell 1993). Much of the remaining riparian habitat is threatened by the invasion of exotics species. Of particular concern in southern California is the exotic *Arundo donax* (Arundineae: Poaceae), a tall cane-like grass. *A. donax* is estimated to make up 68% of the total riparian vegetation on the Santa Ana River in Orange County (Douthit 1983). Other riparian systems have less *A. donax*, but it is clear that once established it spreads at a rapid rate, and tends to exclude other species. Little is known about the invasion process or the growth of *A. donax*. If this invasive plant is to be effectively controlled, understanding its biology and its role in the riparian system is necessary.

The riparian habitat is a dynamic, flood-adapted system. Sediment builds up on the convex sides of the river channel forming depositional bars

and sediment is picked up on the concave sides, causing erosion into a cut bank (Malanson 1993). These processes result in the lateral meandering of the river.

The plant species found in riparian areas can tolerate the disturbance and depend on it for maintaining their populations. The dominant trees of riparian areas, willows (*Salix* spp.) and cottonwoods (*Populus* spp.), exemplify this dependence. Both genera produce short-lived seeds that germinate on the exposed alluvial material deposited during floods. Receding river water levels at the end of the flood season expose these wet, bare mineral substrates upon which the native seeds germinate (Hosner and Minckler 1963; Pelzman 1973). Willow and cottonwood seedling mortality is generally high due to decreased moisture through the summer season and to mechanical damage, removal, or burial during winter floods (Sigafos 1964; Noble 1979). If a seedling cohort does successfully establish, their vegetative structure traps sediment, which, over time, elevates the area from the river channel (Dietz 1952).

Floods are destructive as well as beneficial to riparian plants. Floods can mechanically damage and destroy existing vegetation (Malanson 1993). Certain characteristics allow the established woody vegetation to regain dominance relatively quickly after flood disturbance. Resprouting* from fallen or prostrate plants is an important survival strategy in this system (Atkin 1980; Barnes 1983). Deep root systems may already exist, and in some cases there are still remnants of above ground woody structures. These traits increase the

*The term resprouting will be used to refer to above ground growth from root stock with above ground vegetation removed by floods, or from stem/s on a plant that has been mechanically damaged by flood action. Vegetative establishment will be used to refer to sprouting from dispersed plant material that is no longer connected to the parent plant.

chances of a plant reaching maturity and producing seed. In addition, some species may be able to establish vegetatively* from branches or roots dispersed by the flood waters, another potential means of recovery after flood disturbance (pers. obs).

Though resprouting after mechanical damage by floods is known to play an important role in riparian dynamics, it has been given little attention in the riparian literature. This could be due partly to the chaotic nature of the post-flood disturbance scene which makes quantitative data gathering difficult. Most riparian studies have concentrated on the conditions of seedling establishment, and the distribution of riparian trees, without specifying their resprout status. Many researchers have noted the presence of resprouting by willows and cottonwood (Everitt 1968, Hupp 1983, McBride and Strahan 1984a and others) and it has been found to be an important survival strategy in these genera (Atkin 1980, Barnes 1983, Irvine and West 1979).

There have been few studies of Californian riparian systems examining resprouting and, especially, vegetative establishment. McBride and Strahan (1984a) recorded the importance of root suckers on a northern Californian stream, but did so for only one willow species. Conditions in California can be quite different from those in colder areas due to the lack of ice, which is a major factor causing flood damage in cold regions.

Since establishment is mainly a post-flood phenomena (Atkin 1980), the focus in understanding establishment dynamics in the riparian system must be on the flood-disturbed zone. The native woody riparian species are able to recover after flood induced damage, and require the flood disturbance for seedling establishment. However, the same disturbance that perpetuates the riparian system also leaves it vulnerable to invasion by exotic species. Most

exotic plant species require disturbance to successfully establish in a system, and these disturbances are usually caused by human activity (Rejmánek 1989). Few exotic species have invaded undisturbed, or naturally disturbed, systems and *A. donax* is one of these (Rejmánek 1989). Rejmánek noted that *A. donax* invades undisturbed reedswamps in South Africa. Where human disturbance has occurred *A. donax* seems to increase, but it would probably still establish if only natural disturbances were present. Once present in a drainage, however, *A. donax* can become dominant over large areas. In doing so it apparently precludes the establishment of native species, though this has not been conclusively documented. If this pre-emptive model is correct, it becomes important to understand the circumstances under which *A. donax* establishes. Of interest is when and where *A. donax* is able to invade the riparian system and how the native species are establishing at these same times and places.

The purpose of this study was to examine the establishment dynamics in the riparian habitat after disturbance by flooding on the Santa Margarita river in San Diego county. Specifically, the goals were to document how *A. donax*, *Tamarix* spp. (salt cedar, a woody exotic) and the native woody species establish after flooding, and where these events occur in terms of fluvial landforms and elevation above the river channel. A field study was carried out to document the type and location of establishment events of *A. donax*, *Tamarix* spp. and the native woody species after flooding of the winter of 1994/95. The ability of *A. donax* propagules to grow under the wide range of physical conditions imposed by unpredictable dispersal in flood waters was investigated through two experiments. A greenhouse experiment was conducted to determine the ability of stem and rhizome propagules to grow

after desiccation. A field experiment addressed the ability of dispersed rhizome pieces to sprout after being buried.

Biology of *A. donax*

A. donax is a tall, erect, perennial, cane-like grass, 2 to 8 meters high (Hoshovsky 1986). *A. donax* belongs to the Arundineae tribe, along with *Phragmites* and *Cortaderia* (Renvoize 1980). Most of this tribe, including *A. donax*, photosynthesize using the C₃ pathway (Renvoize 1980). The main stems of *A. donax* reach a diameter of 1 to 4 cm and commonly branch during the second year of growth (Fig. 1). Flowers are borne on a large plume-like terminal panicle. Seeds are wind dispersed, but it is reported that *A. donax* does not produce viable seed in most areas where it has been introduced (Perdue 1958). The root system of *A. donax* consists of fleshy, compact masses of rhizomes from which arise tough, fibrous roots that penetrate deeply into the soil. Once established, *A. donax* forms large, dense clonal rhizome masses.

A. donax was probably introduced into California in the early 1800's (Bell 1993). Although it is often reported as a native of the Mediterranean region, it may actually be an archaeophyte in this area and originally have come from eastern Asia (Fornell 1990). The main method of spread of *A. donax* is thought to be by growth of dispersed rhizome fragments (Bell 1993). Floods provide the mechanical disturbance necessary to break off rhizome sections from the parent plant, and also act as the dispersing agent by in carrying the pieces downstream. There are no records of *A. donax* seedlings in southern California, and it is generally assumed that it does not reproduce sexually, although this has not been confirmed.

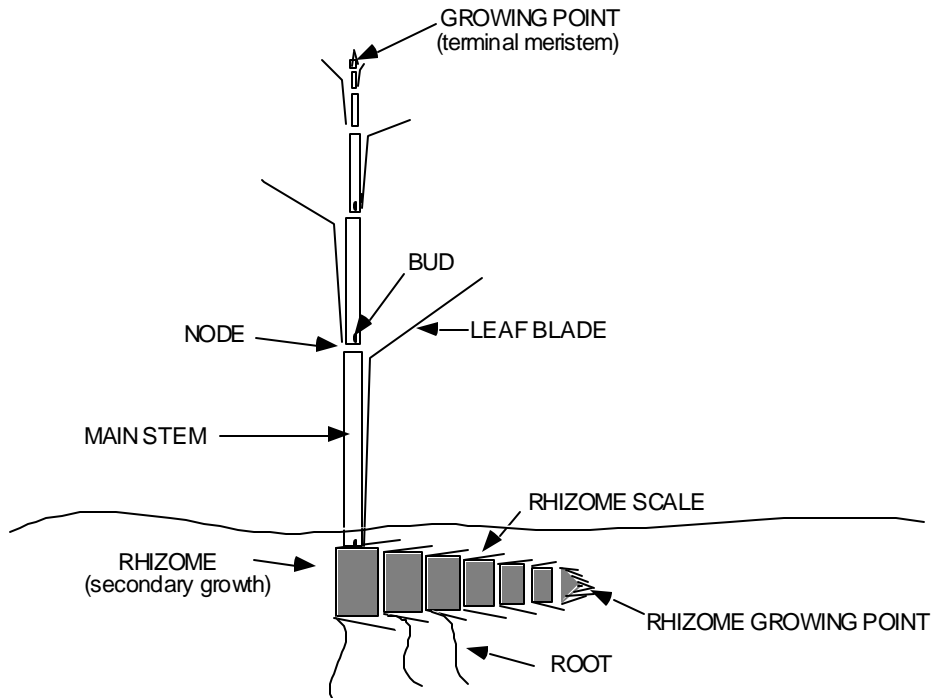


FIG. 1. Simplified diagram of the structure of an *A. donax* plant, not drawn to scale. It can be viewed as an assemblage of repeating structural elements. Secondary branches arise from the buds on the main stems.

All evidence indicates that *A. donax* does not provide either food or habitat for native species of wildlife (Bell 1993), however this has not been examined. Very little understory vegetation is found under *A. donax* due to its dense growth (per. obs.). *A. donax* does not seem provide the structure required by riparian birds for perching and nesting. Least Bell's vireo (*Vireo bellii pusillus*), an endangered species, have only rarely been found to nest in areas dominated by *A. donax* and, in those few cases, the nest was located in native vegetation surrounded by *A. donax* (B. Kus, pers. comm.) *A. donax* also appears to support little insect life (K. Williams, pers. comm.). *A. donax* is not known to have any natural predators in North America, and it is uncertain what limits its population in its native habitat (Bell 1993).

STUDY SITE

The field research was conducted along the Santa Margarita river from its source in Riverside county near Temecula to its mouth in San Diego county near Oceanside (Fig. 2). The Santa Margarita river is considered the last free-flowing river in southern California (Shapiro 1991). Presently the river has relatively low levels of human disturbances, though it has been disturbed in the past. The river can have high water levels during winter flooding, but usually dries up on parts of the lower river during the summer. The river can be divided into upper and lower sections. In general, the upper river is narrower and rockier and the lower river wider and sandier.

There are nine main native woody species in the riparian habitat. Five are willow species, of which three are trees (*Salix gooddingii*, *S. laevigata*, *S. lucida*), one is a shrub-like tree (*S. lasiolepis*), and one is a shrub (*Salix exigua*). The two cottonwood tree species, *Populus fremontii* and *P. balsamifera*, were found mostly on the upper river. Sycamore, *Platanus racemosa*, was occurred at low densities, and mulefat (*Baccharis salicifolia*) is a shrub usually found at high densities near the river channel.

A. donax is present along the entire river, but at variable densities. In places, especially along the lower river, it forms extensive stands. In other reaches, particularly on the upper river, it may occur only as isolated

FIG. 2. Location of the Santa Margarita river in San Diego and Riverside counties, California.

plants. *Tamarix* spp. occur as scattered individuals or in small groups, but rarely in extensive stands. It is most abundant along the lower river.

METHODS

Field Study

A total of forty-two transects were sampled along the Santa Margarita river in July 1995 (Fig. 3). Fourteen transects were sampled on the upper river and thirty-four on the lower section of the river. Transect locations were chosen by stratified random sampling. Some small stretches of the river were not included in the sampling because they were not accessible by roads or by foot in the time available.

The transects were two meter wide belts perpendicular to the river channel beginning in the middle of the river and extending out to the edge of the flood zone on both sides (Fig. 4). The length of the transect varied depending on the width of the river bed. The boundary of the flood zone was determined by the presence of a debris line indicating the highest flood level of the 1994-95 winter season.

Within the two meter belt, the presence and location of all individuals of *A. donax*, *Tamarix* spp., and native woody species were recorded. The status of the plant was described as: undamaged, resprout, root sprout, seedling, vegetatively established, uncertain, or dead. The term 'undamaged' described individuals that were not damaged, or only slightly damaged, by flooding. 'Resprout' described vegetative growth from a root stock with above ground vegetation removed by floods, or growth from stems on a plant mechanically damaged by flood action. 'Root sprouts' were new individuals that were produced from buds on

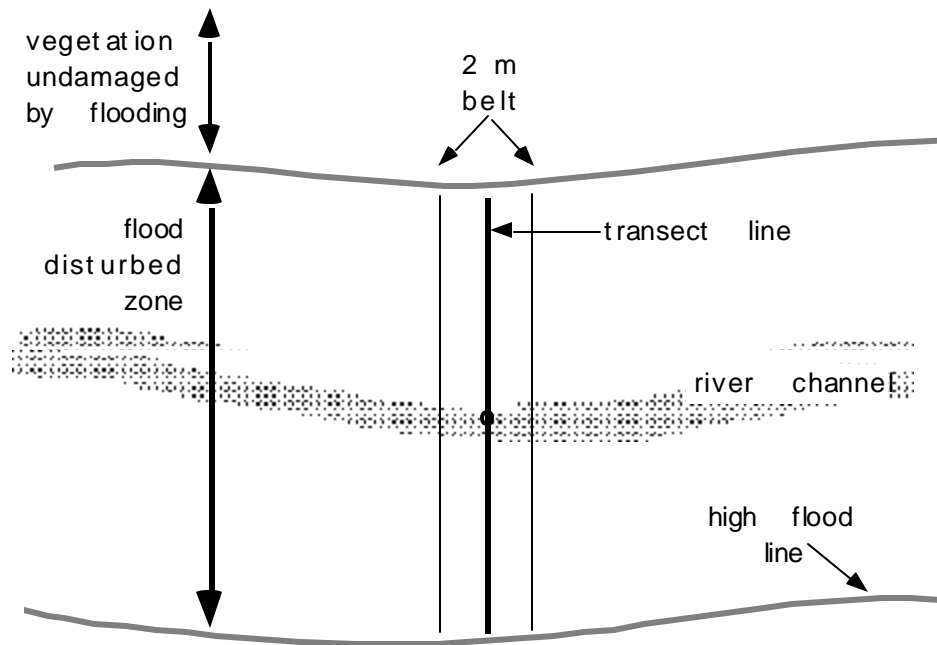


FIG. 4. Layout of transect across the flood disturbed zone. The high flood line was from the 1994-95 winter season.

shallow lateral roots usually within one inch of the surface. Seedlings were individuals less than 10 cm in height. 'Vegetative establishment' described sprouting from dispersed plant material that was no longer connected to the parent plant. If it could not be discerned whether a plant was a resprout or vegetatively established (because of deep burial) it was recorded as 'uncertain'. This category is presented in the results as 'vegetative establishment/resprout?' Dead plants were recorded only where they were rooted.

Vegetatively established plants were further classified into types based upon the plant material from which the sprout arose. *A. donax* was categorized as arising from rhizome, stem, or secondary branch. Woody

species were categorized as arising from a root fragment, a stem fragment, or an entire individual washed down river.

The elevation of the transect relative to the middle of the river channel was measured approximately every ten meters; more often if there was a sudden change greater than approximately 0.5 m. A Future Basic program was used to interpolate estimates of the elevation for every meter. The elevation and distance from the river channel of the flood debris line (high flood mark) were measured at each transect.

To document location of establishment the transects were mapped to describe the locations of four fluvial landforms following Hupp & Osterkamp (1985):

- 1) Channel bed: the surface that is wholly or partly covered by flows below mean discharge
- 2) Channel bank: horizontal to gently sloping surface extending from the edge of the channel bed to a depositional bar or floodplain shelf
- 3) Depositional bar: "sandbars" on the convex sides of the river channel composed of relatively coarse sand and gravel
- 4) Floodplain shelf: shelves above the channel bed, flat geomorphic surfaces that are irregularly inundated

Differences among species with respect to plant status and method of reproduction were evaluated by plotting the density of each species separately and of all native woody species combined. The location of establishment events in terms of fluvial landform and elevation were graphed to document patterns of distribution.

The areas sampled varied among the fluvial landforms so frequency data were presented as the number of individuals per meter². The

interpolated elevation data were divided into 0.1 m classes. As with the landform data, an unequal area was sampled within the different elevation classes. To scale the data, the number of establishment events occurring in an elevation class were divided by the area sampled of in that elevation class to give the number of individuals per meter².

A chi square test was used to determine whether the number of establishment events varied among different fluvial landforms for *A. donax* and for the native woody species as a group. The expected outcome was that the number of establishment events would be positively correlated to the area present for each fluvial landform.

A non-systematic survey of flowering *A. donax* was carried out by repeated observations of *A. donax* populations from September 1995, to September 1996. When flowering *A. donax* plants were found, inflorescences were collected and examined for the presence of seeds.

Effects of Drying on Sprouting of *A. donax*

The ability of *A. donax* rhizomes and stems to sprout after drying was tested in a greenhouse experiment. Stems and rhizomes were collected on 24 February 1996, from three *A. donax* plants along the Santa Margarita river and two along the San Luis Rey river. Stems and rhizomes were soaked overnight in water, to fully hydrate, and then randomly assigned to treatments. The weight, length, maximum diameter, minimum diameter, number of nodes, and number of buds were recorded for rhizomes, and the weight, length, and diameter were recorded for stems on 25 February 1996. The term 'bud' was used to define the new growing points that produce a new rhizome or a new stem. The buds that were counted were

approximately 0.5 cm in diameter or greater. All buds were trimmed off at their base before weighing.

Rhizome pieces were dried for 0, 2, 4, 6, 8, 10, 14, 20, 26 or 31 days and stems for 0, 1, 2, 3, 4, 6, 8, 10, 15 or 20 days. For the rhizomes there were four replicates for the first nine drying periods and two replicates for the last period, giving a total of 38. For the stems there were four replicates for the first six drying periods and period 15, three replicates for periods 8 and 10, and two replicates for the last drying period, giving a total of 36. Rhizome and stem pieces from the five source plants were randomized among drying treatments. Rhizomes and stems were dried in black plastic trays on an open roof exposed to the sun. A plastic cover was placed over the drying pieces during the two incidences of rain. A cool period existed for the first four days followed by warmer temperatures for the remainder of the experiment (Fig. 5).

After drying for the assigned period, rhizomes and stems were planted in sand in plastic trays and placed on the roof. Trays were watered every two days to saturation and were fertilized with Miracle-Gro[®] (one tablespoon/gallon) twice during the experiment. The date of sprout emergence was recorded, and the height of each shoot was recorded every five to ten days until 15 May 1996. To determine the moisture loss that corresponded with the drying periods, ten rhizome and eight stems were weighted at two day intervals until day 80 of the experiment.

The effects of initial weight, length, maximum diameter, minimum diameter, number of nodes, number of buds, and parent plant source on sprouting (the bivariate response) were analyzed using a nominal logistic regression model (JMP[®] 3.1, 1989-95). The difference in the negative log

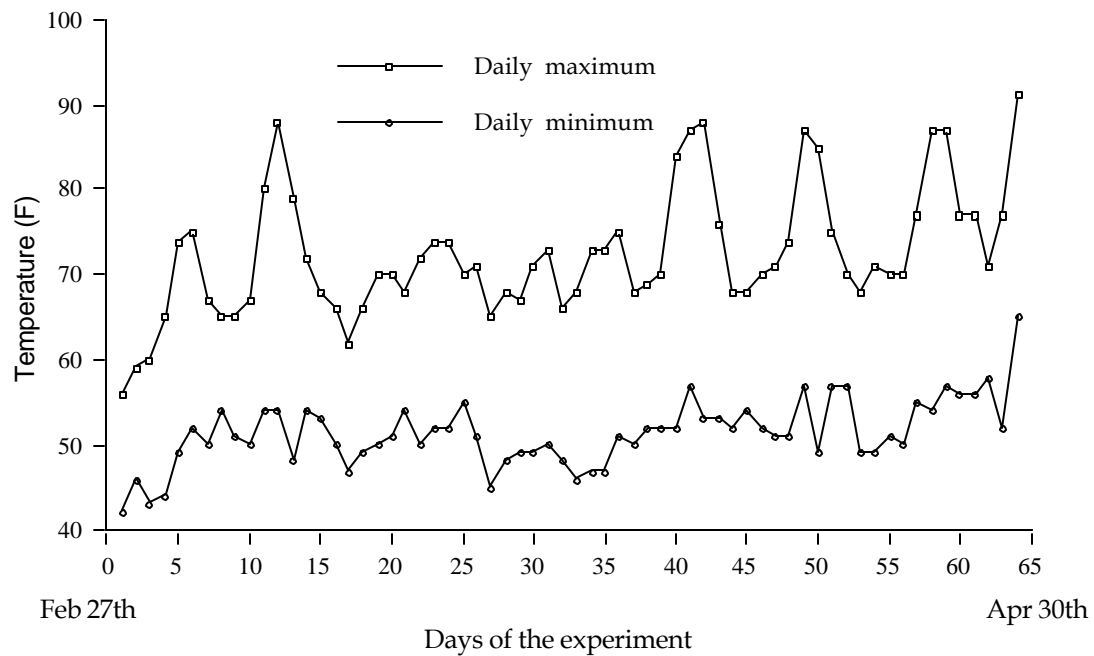


FIG. 5. Daily maximum and minimum temperatures (F) during the drying experiment. Data from the SDSU weather station.

likelihood of the model with and without an effect was tested using log likelihood ratio tests. Variables that had probabilities greater than 0.15 were removed from the model until the best fitting combination of variables was achieved. The best fitting model was achieved by low P values and high R^2 values.

Effects of Burial on Sprouting of *A. donax* Rhizomes

The effects of burial on the ability of rhizomes to sprout was tested in a field experiment. Rhizomes were collected, hydrated, and measured as described for the drying experiment. Three depths of burial were tested (10, 50 and 100 cm) with two sizes of rhizome (small and large). A completely randomized design with five replicates per treatment combination was used.

Rhizomes were planted on 26 February 1996, in a flat, 30 m x 4 m sandy area along the Santa Margarita river. There were three rows 1.5 m apart, each with 10 pieces planted at 1 m intervals. The site was visited biweekly until June 1996, and then monthly until September 1996, to record sprouting and the height and health of each shoot.

The effects of initial weight, length, maximum diameter, minimum diameter, number of nodes, and number of buds, size, depth of burial, and parent plant source on sprouting (the bivariate response) were analyzed using a nominal logistic regression model as described for the drying experiment.

RESULTS

Field Study

A total of 6974 m² were surveyed on forty two transects, 1663 m² on the upper river (n=14) and 5311 m² on the lower river (n=28). For the fluvial landform categories 6690 m² were surveyed. This is less than the total (6974 m²) because some areas had small side channels that were not included in the fluvial landform categories. Transects varied in length from 63 m to 415 m. The main native woody species recorded in the riparian flood zone were the five willow species (*Salix exigua*, *S. gooddingii*, *S. laevigata*, *S. lasiolepis*, and *S. lucida*) and *Baccharis salicifolia* (Table 1). The willow species accounted for 37% of total individuals and all were fairly evenly distributed except *S. lucida*, which was predominantly found as seedlings on the lower Santa Margarita river (Table 1). *Baccharis salicifolia* was the most abundant species, accounting for 55% of all individuals. *Populus fremontii* (cottonwood) was only recorded on the upper Santa Margarita river, and *Populus balsamifera* (black cottonwood) was found on only one transect. *Platanus racemosa* (sycamore) was generally uncommon in the flood disturbed zone, with only five individuals recorded for both the upper and lower sections of the river, although these were large trees.

There were quite distinctive differences between the upper and lower river in terms of species compositions and geomorphology. Most of the flood disturbed zone of the upper river was composed of channel bed,

TABLE 1. Number of individuals (excluding seedlings) and number of seedlings by species for transects on the upper (n=14) and the lower (n=28) Santa Margarita river.

Species	# individuals		# seedlings		Total #
	Lower	Upper	Lower	Upper	
<i>Baccharis salicifolia</i>	219	137	5032	1740	7128
<i>Salix exigua</i>	308	123	1673	25	2129
<i>Salix laevigata</i>	20	83	185	716	1004
<i>Salix gooddingii</i>	25	11	848	77	961
<i>Tamarix</i> spp.	87	4	584	5	680
<i>Salix lasiolepis</i>	156	107	84	48	395
<i>Salix lucida</i>	25	5	305	1	336
<i>Arundo donax</i>	192	0	0	0	192
<i>Nicotiana glauca</i>	0	0	47	0	47
<i>Artemisia californica</i>	1	9	0	1	11
<i>Populus fremontii</i>	0	7	0	1	8
<i>Platanus racemosa</i>	2	3	0	0	5
<i>Toxicodendron diversilobum</i>	2	0	0	0	2
<i>Baccharis pilularis</i>	0	1	0	0	1
<i>Lotus scoparius</i>	0	1	0	0	1
<i>Populus balsamifera</i>	1	0	0	0	1
<i>Quercus agrifolia</i>	0	0	0	1	1
<i>Vitis girdiana</i>	0	1	0	0	1

and no depositional bars were observed (Table 2). The upper river, which was narrower and rockier, contained more cottonwoods and fewer *A. donax* than the lower river. The low density of *A. donax* was probably due to past removal projects, and also to the smaller source of propagules and the rocky surfaces which are less favorable for colonizations. The lower river was much wider and sandier and supported more *A. donax* than the upper river. The channel bed was the dominant landform sampled in the flood disturbed zone on the lower river, but depositional bars were also quite common (Table 2). There was a larger source of propagules in the lower river than the upper river due to a greater amount of *A. donax* the river, the data were combined to illustrate patterns of establishment

TABLE 2. The area sampled (m²) by fluvial landform category for the upper and lower sections of the Santa Margarita river.

River Section	Channel bed	Channel bank	Depositional bar	Floodplain shelf	Totals
Upper	1341.6	98.8	0	146	1586.4
Lower	2950.8	248	1208	696.4	5103.2
Total	4292.4	346.8	1208	842.4	6689.6

upstream. Despite the differences between the upper and lower sections of and species distributions on the river system as a whole.

Previous and Types of New Establishment

Individuals undamaged by flooding. Overall, there were more native woody species in this category than exotics (Table 3). For all species combined there were 0.12 undamaged individuals per m². Native woody species (0.11/m²) were more abundant than in this category than the exotics, *A. donax* (0.005/m²) and *Tamarix* spp. (0.007/m²) (Fig. 6). The shrubby natives, *B. salicifolia*, *S. exigua*, and *S. lasiolepis* made up the majority of the undamaged individuals, with the tree willows (*S. gooddingii*, *S. laevigata*, and *S. lucida*) being less common.

Resprouts and root sprouting. All species were able to resprout after being damaged by flood action (Table 3). Since resprouts represent individuals that were established before the flooding, the data were scaled to give the percent of resprouting survivors. This was calculated by dividing the number of resprouts by the sum of resprouts and undamaged

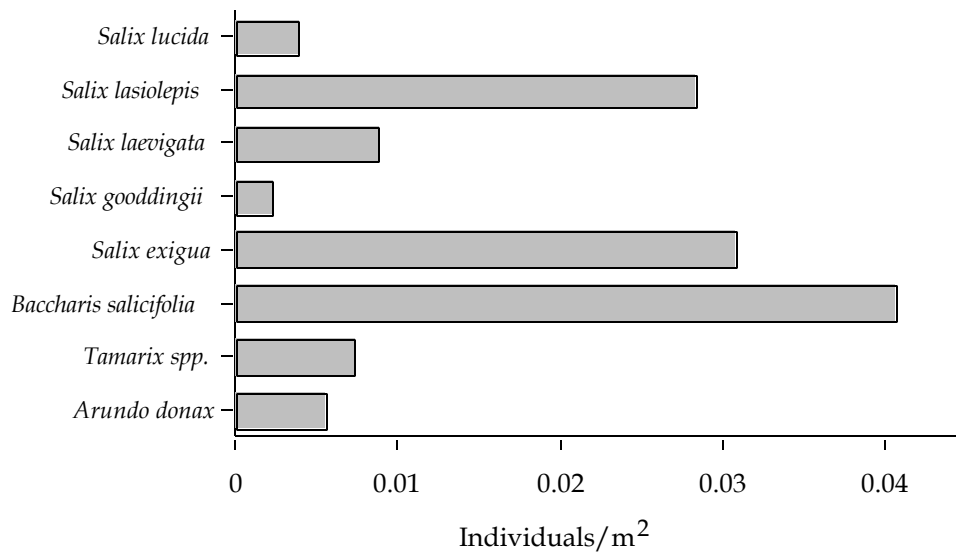


FIG. 6. Density of individuals undamaged by flooding for all species. The number of individuals observed for each species are listed in Table 3.

individuals (Fig. 7). The species that had the highest density of resprouts did not necessarily have the highest percent of survivors resprouting. Rather, *A. donax* had the highest (57%), indicating that the majority of *A. donax* plants in the flood disturbed zone were damaged by flooding and were able to recover. However, any individuals that were damaged by flooding and did not resprout may have missed due to burial.

The ability to establish by root sprouting was almost exclusively found in *S. exigua* with a density of 0.015 runners/m². Only one or two cases of runners were found for *S. gooddingii*, *S. lasiolepis*, and *Tamarix* spp. (Table 3).

Seedlings. Seedling establishment occurred at high densities for the native woody plants. As might be expected, the shrub *B. salicifolia* had the highest density (0.971/m²), and the shrubby willow *S. exigua* had the highest density of the willows (0.243/m²) (Fig. 8). Although there was

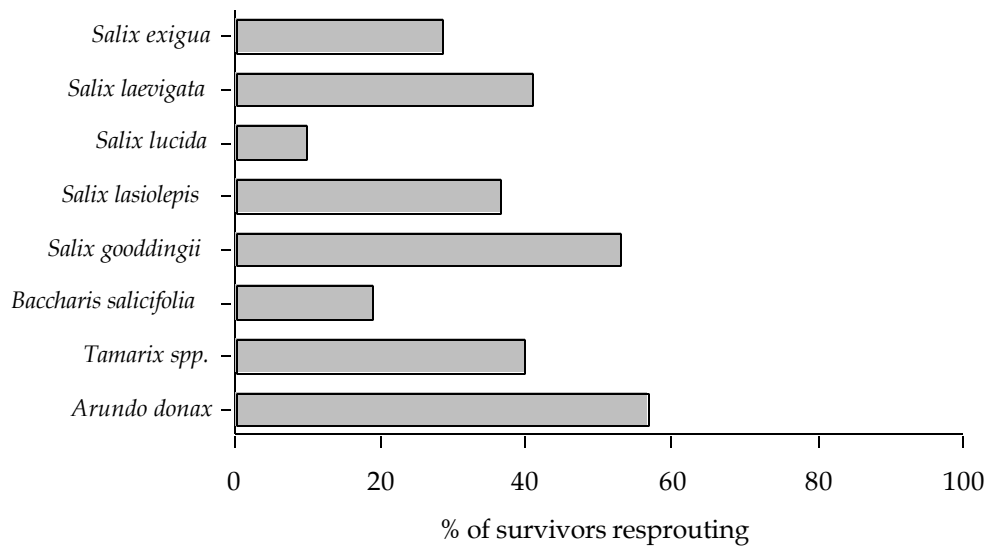


FIG. 7. Percent of survivors that resprouted for all species. The number of resprouting individuals observed for each species are listed in Table 3.

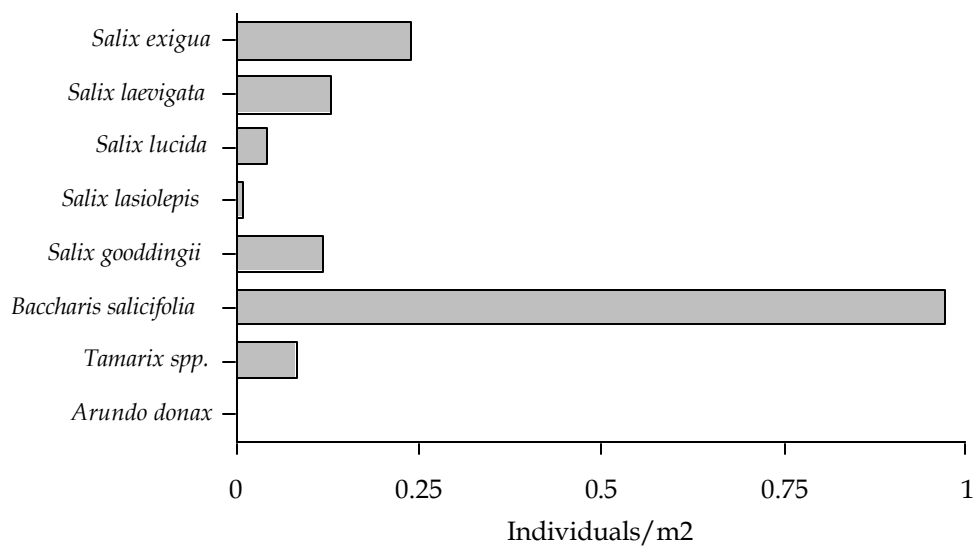


FIG. 8. Density of seedlings by species. The number of individuals observed for each species are listed in Table 3.

a higher density of undamaged individuals of *S. lasiolepis* than the three willow tree species (Fig. 6), there were few *S. lasiolepis* seedlings. Some of the differences between the willow species could be due to different flowering and seed release times.

For the exotics, seedling establishment consisted only of *Tamarix* spp. at a density of .084/m² (Fig. 8). No seedlings or flowering individuals of *A. donax* were recorded during the field study. However, after the field sampling the following cases of flowering individuals were seen: one on the San Luis Rey river near River Road in February 1996, one in a drainage off La Costa Ave in Encinitas in February 1996, three on the beach near Carlsbad in September 1996, and several along the edge of Batiquitos lagoon in September 1996. Inflorescences were examined and in all cases no seeds had formed.

Vegetative establishment. Most instances of vegetative establishment were of *A. donax* (0.01/m²), with only scattered cases of vegetative establishment by other species (Fig. 9). The density of vegetative establishment may actually be somewhat higher since it was sometimes difficult to distinguish resprouts from vegetatively established plants. These questionable events are presented as 'vegetative establishment/resprout?' and were recorded mostly for *A. donax* (0.006/m²), but also for *S. lasiolepis* (0.001/m²), *S. exigua* (0.002/m²) and *Tamarix* spp. (0.001/m²) (Fig. 9). Even if these uncertain events were included in the vegetative establishment category, *A. donax* still would be the only species to effectively use this form of establishment (0.016/m² versus 0.004/m² for all natives). As would be expected, the majority of

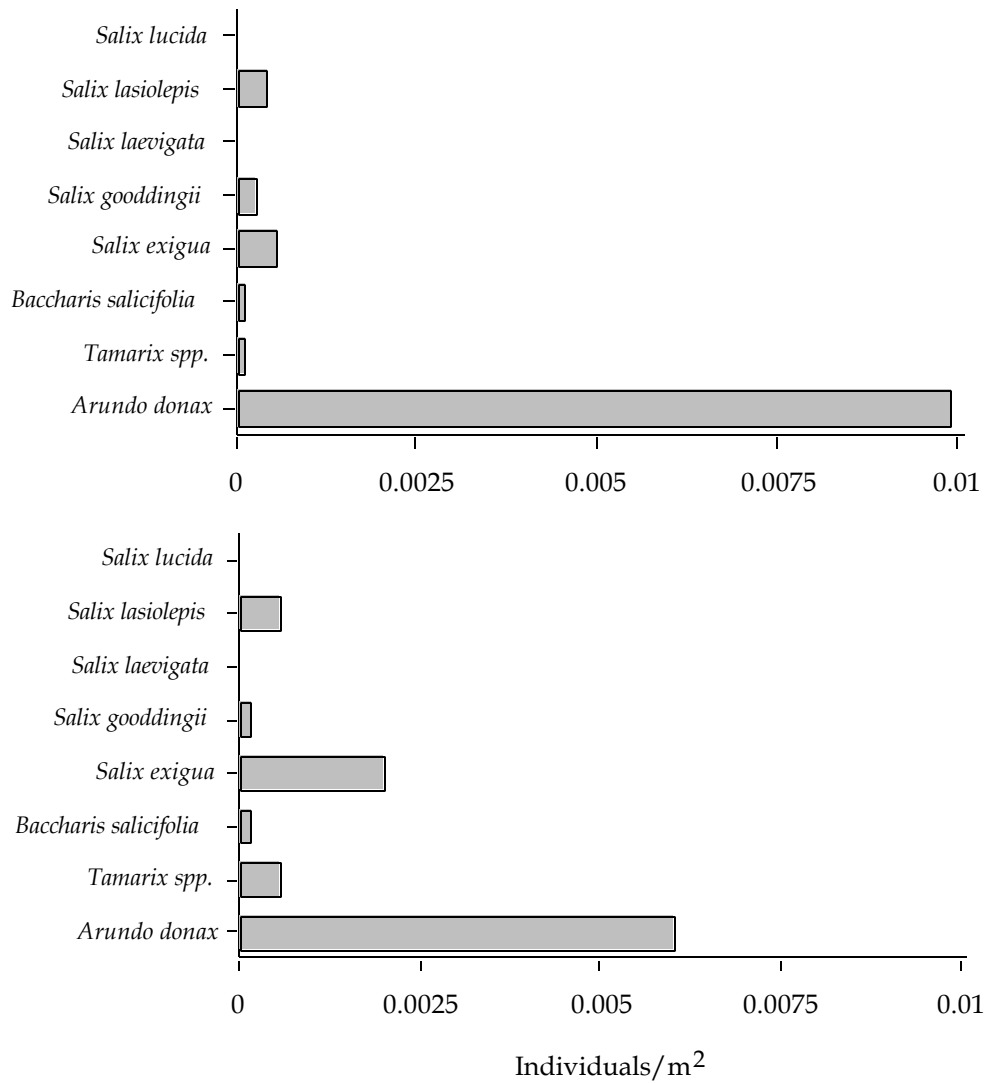


FIG. 9. Density of vegetative establishment and the uncertain category for all species. Top = Density of vegetative established plants by species. Bottom = density of individuals whose origin could not be distinguished between vegetative establishment and resprouting. The number of individuals observed for each species are listed in Table 3.

vegetative establishment events occurred on the lower section of the river, since there is a greater source of propagules upstream than is present for the upper river. Even though less area was sampled on the upper river, only two out of the total 69 *A. donax* vegetative establishment events were located on the upper river.

The plant part giving rise to each vegetatively established individual was also recorded, although this was often difficult to discern due to deep burial. Of the 69 total vegetative establishment events recorded for *A. donax*, 57% were from rhizomes, 33% were from branches, and 7% were unidentifiable.

Dead individuals. Only a few dead individuals were found for a few species (Table 3). Although *B. salicifolia* was overall the most abundant species, surprisingly, no dead individuals were found. The shrub *Salix exigua* had five dead individuals, the shrubby tree *S. lasiolepis* one, and the tree willows none. Of the exotics, only two dead *A. donax* were found. The low number of dead individuals found could be a result of dead plants washing down stream during flooding.

Previous and New Establishment by Landforms

For all plant status categories combined, native woody species had the highest density on depositional bars (2.56/m²) and the lowest on the floodplain shelf (0.64/m²) (Fig. 10). On all fluvial landforms except the floodplain shelf the majority of these individuals were seedlings. The exotic species, *A. donax* and *Tamarix* spp., occurred at much lower densities than the native species on all fluvial landforms (Fig. 11).

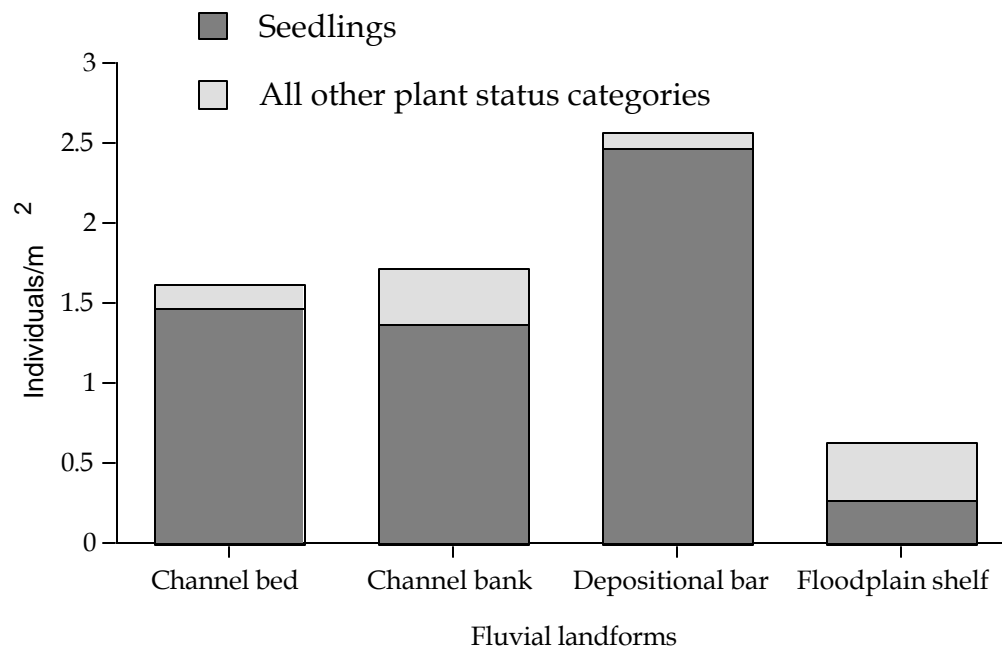


FIG. 10. Density of seedlings and all other individuals combined, for native woody species on fluvial landforms.

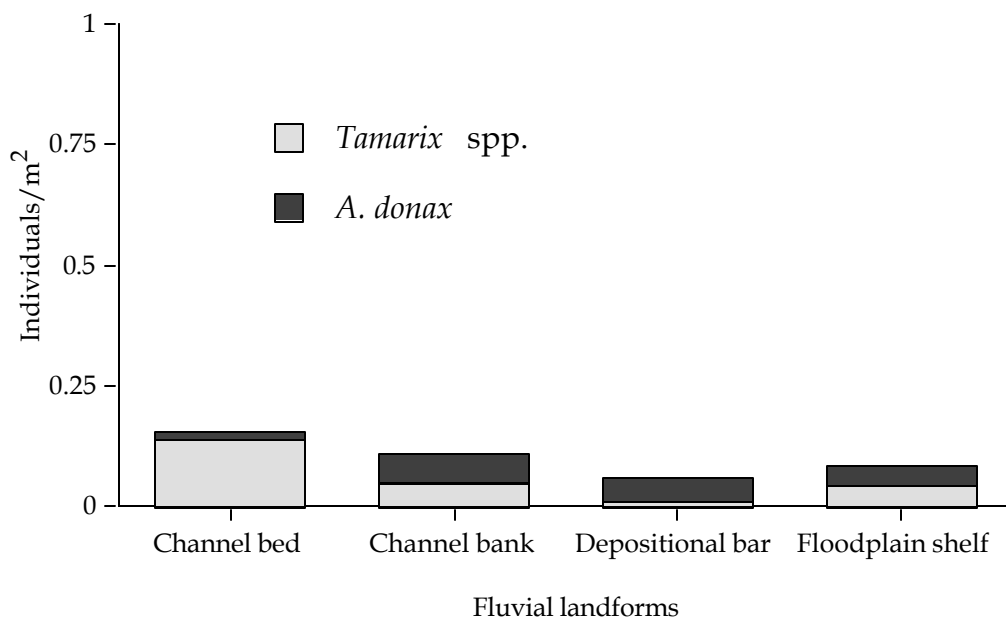


FIG. 11. Density of all individuals combined for the exotics species, *A. donax* and *Tamarix* spp., on fluvial landforms.

Tamarix spp. were more abundant on the channel bed (due to seedlings) than *A. donax*, but on all other fluvial landforms *A. donax* had higher densities.

Undamaged. The shrubby native species, *B. salicifolia*, *S. exigua* and *S. lasiolepis*, made up most of the undamaged individuals on all fluvial landforms (Table 4). There were many fewer exotics than natives

TABLE 4. Number of undamaged individuals by species in each fluvial landform.

SPECIES	FLUVIAL LANDFORMS			
	Channel bed	Channel bank	Depositional bar	Floodplain shelf
<i>Arundo donax</i>	6	7	6	14
<i>Tamarix spp.</i>	9	12	7	23
<i>Baccharis salicifolia</i>	124	26	10	112
<i>Salix exigua</i>	60	23	24	81
<i>Salix gooddingii</i>	4	2	1	4
<i>Salix laevigata</i>	41	9	1	3
<i>Salix lasiolepis</i>	97	27	23	46
<i>Salix lucida</i>	11	1	15	0
Total	352	107	87	283

on all fluvial landforms. Density of undamaged native woody species was significantly different among fluvial landforms ($X^2=373$, $df=3$, $p < 0.001$), being highest on the floodplain shelf ($0.29/m^2$) and channel bank ($0.25/m^2$). Density of undamaged *A. donax* individuals was also significantly different across fluvial landforms ($X^2=112$, $df=3$, $p < 0.001$). The density of the exotics combined was less than $0.06/m^2$ across all fluvial landforms (Fig. 12), much lower than the density of native species on all fluvial landforms.

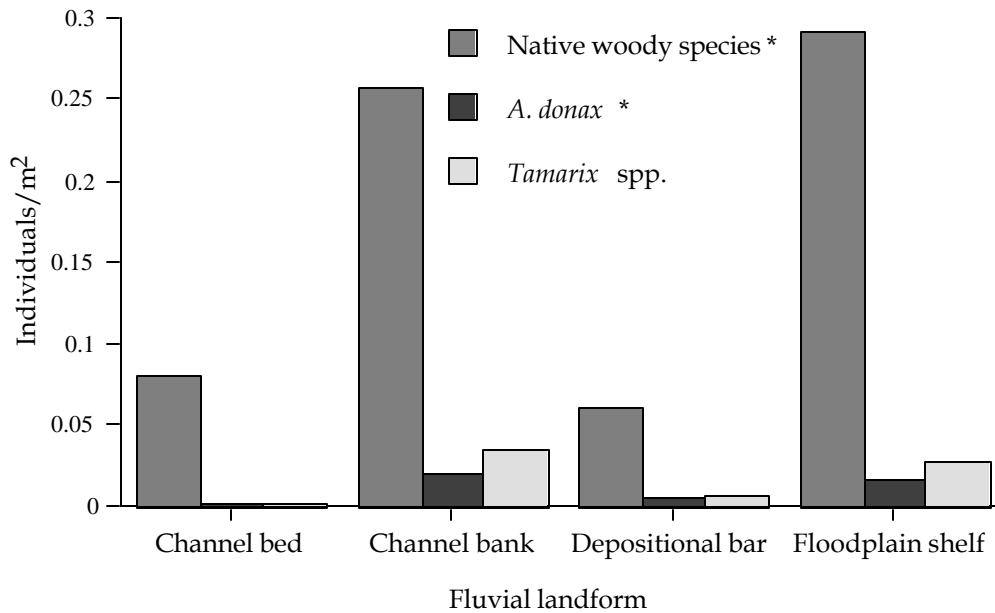


FIG. 12. Density of undamaged individuals by fluvial landform for native woody species, *A. donax*, and *Tamarix* spp. (* = $p < 0.001$, chi square test).

Resprouts and root sprouting. Overall, the majority of resprouts occurred on the channel bed where damage by flood waters was probably the greatest (Table 5). Frequency of resprouts of the native woody species varied significantly among fluvial landforms ($\chi^2=37.62$, $df=3$, $p<0.001$) being relatively constant on all the landforms except depositional bars, which had densities about five times lower (Fig. 13). The density of resprouting *A. donax* was also significantly different among fluvial landforms ($\chi^2=258.12$, $df=3$, $p<0.001$), with highest densities observed on the channel bank (Fig. 13).

Root sprouts of the native woody species occurred on all fluvial landforms and were predominantly of one species, *S. exigua* (Table 6). Root sprouts of the native woody species had the highest density on the channel bank and floodplain shelf ($\chi^2=8.47$, $df=3$, $p<0.05$; Fig. 14).

TABLE 5. Number of resprouting individuals by species in each fluvial landform.

SPECIES	FLUVIAL LANDFORMS			
	Channel bed	Channel bank	Depositional bar	Floodplain shelf
<i>Arundo donax</i>	16	7	13	13
<i>Tamarix spp.</i>	13	5	3	13
<i>Baccharis salicifolia</i>	50	7	0	7
<i>Salix exigua</i>	56	5	7	10
<i>Salix gooddingii</i>	12	1	0	4
<i>Salix laevigata</i>	39	0	0	3
<i>Salix lasiolepis</i>	38	4	2	3
<i>Salix lucida</i>	0	0	0	5
Total	224	29	25	58

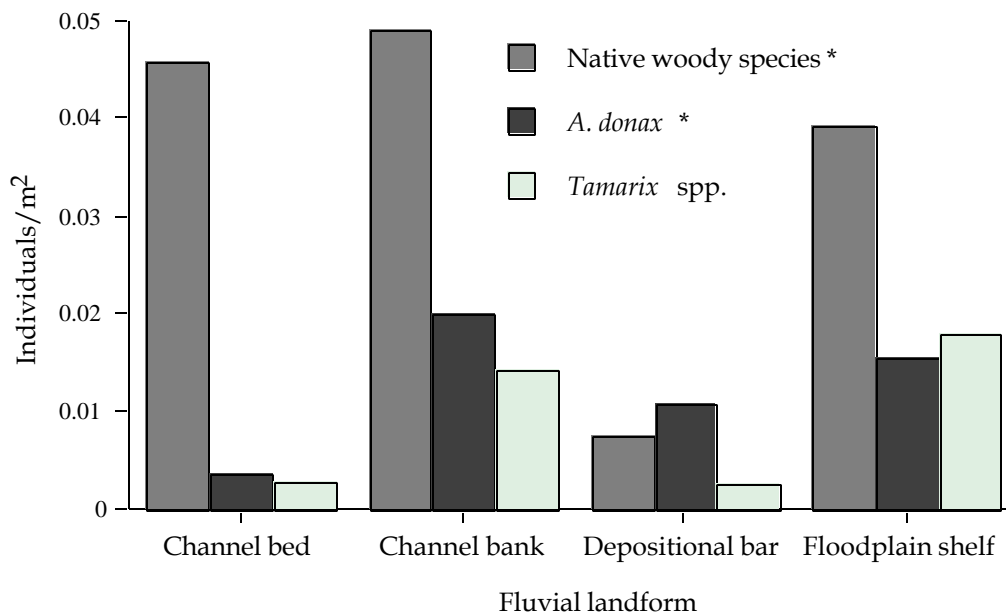


FIG. 13. Density of resprouting individuals by fluvial landform for native woody species and the exotics, *A. donax* and *Tamarix spp.* (* = $p < 0.001$, chi square test).

TABLE 6. Number of root sprouts by species in each fluvial landform. Numbers are not scaled to account for the different areas sampled in each fluvial landform.

SPECIES	FLUVIAL LANDFORMS			
	Channel bed	Channel bank	Depositional bar	Floodplain shelf
<i>Arundo donax</i>	0	0	0	0
<i>Tamarix spp.</i>	0	1	0	0
<i>Baccharis salicifolia</i>	0	0	0	0
<i>Salix exigua</i>	52	14	10	17
<i>Salix gooddingii</i>	1	0	0	0
<i>Salix laevigata</i>	0	0	0	0
<i>Salix lasiolepis</i>	0	0	0	2
<i>Salix lucida</i>	0	0	0	0
Total	53	15	10	19

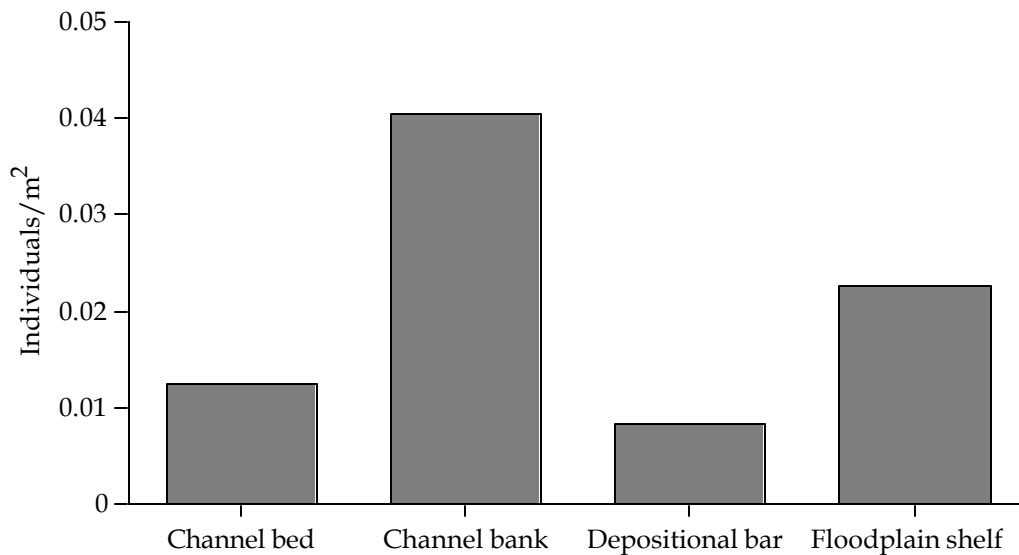


FIG. 14. Density of individuals established by root sprouting by fluvial landform for the native woody species ($p < 0.05$, chi square test).

Seedlings. Seedling establishment occurred on all fluvial landforms (Table 7). The highest densities occurred on the depositional bars, but

densities were also high on the channel bed and channel bank. The depositional bars were dominated by seedlings of the shrubby natives, *B. salicifolia* and *S. exigua*, whereas seedlings of the tree willows mainly occurred on the channel bed. *Tamarix* spp. seedlings were limited to the channel bed.

TABLE 7. Number of seedlings by species in each fluvial landform.

SPECIES	FLUVIAL LANDFORMS			
	Channel bed	Channel bank	Depositional bar	Floodplain shelf
<i>Arundo donax</i>	0	0	0	0
<i>Tamarix</i> spp.	589	0	0	0
<i>Baccharis salicifolia</i>	3854	447	2148	31
<i>Salix exigua</i>	263	6	639	1
<i>Salix gooddingii</i>	871	13	33	0
<i>Salix laevigata</i>	690	9	5	0
<i>Salix lasiolepis</i>	50	0	40	2
<i>Salix lucida</i>	204	0	98	0
Total	6521	475	2963	0

Seedling density for native woody species as a group was significantly different among fluvial landforms ($\chi^2=2053.87$, $df=3$, $p<0.001$; Fig. 15).

Seedling establishment was highest on depositional bars, the channel bed and channel bank, and lowest on the floodplain shelf (Fig. 15). *Tamarix* spp. seedlings occurred only on the channel bed (Fig. 15).

Vegetative establishment. A few cases of vegetative establishment of native woody species were found on the channel bed and depositional bars (Table 8). No statistical tests were performed due to the small sample size. *A. donax* vegetative establishment differed significantly among

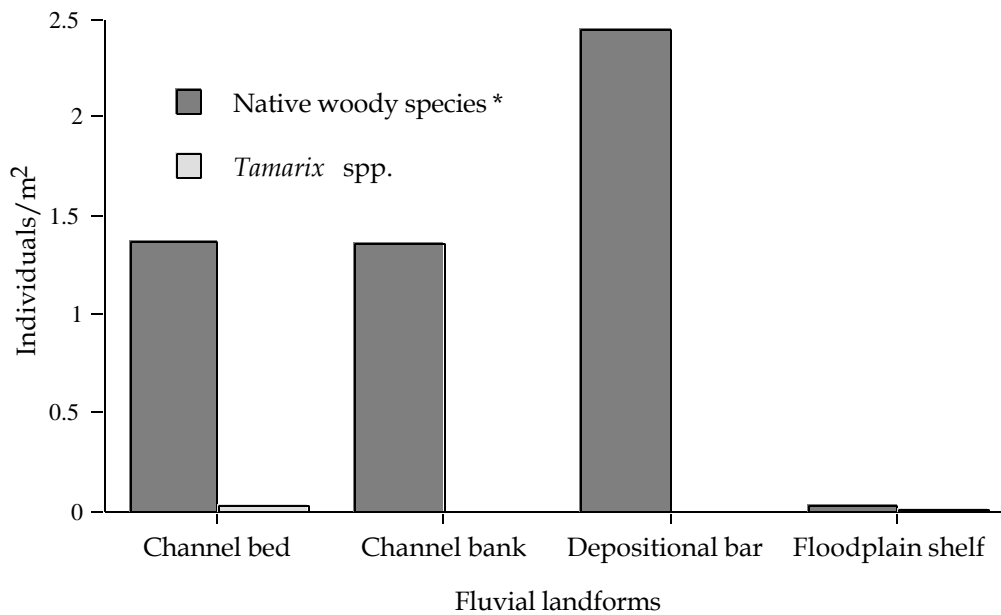


FIG. 15. Density of seedlings by fluvial landform for native woody species and *Tamarix* spp. (* = $p < 0.001$, chi square test).

TABLE 8. Number of vegetatively established individuals by species in each fluvial landform.

SPECIES	FLUVIAL LANDFORMS			
	Channel bed	Channel bank	Depositional bar	Floodplain shelf
<i>Arundo donax</i>	18	2	31	6
<i>Tamarix</i> spp.	1	0	0	0
<i>Baccharis salicifolia</i>	0	0	1	0
<i>Salix exigua</i>	1	0	2	0
<i>Salix gooddingii</i>	0	0	2	0
<i>Salix laevigata</i>	0	0	0	0
<i>Salix lasiolepis</i>	1	0	2	0
<i>Salix lucida</i>	0	0	0	0
Total	21	2	38	6

fluvial landforms ($\chi^2=51.61$, $df=3$, $p<0.001$), being highest on depositional bars and lowest on the channel bed (Fig. 16). One vegetatively established *Tamarix* spp. occurred on the channel bed.

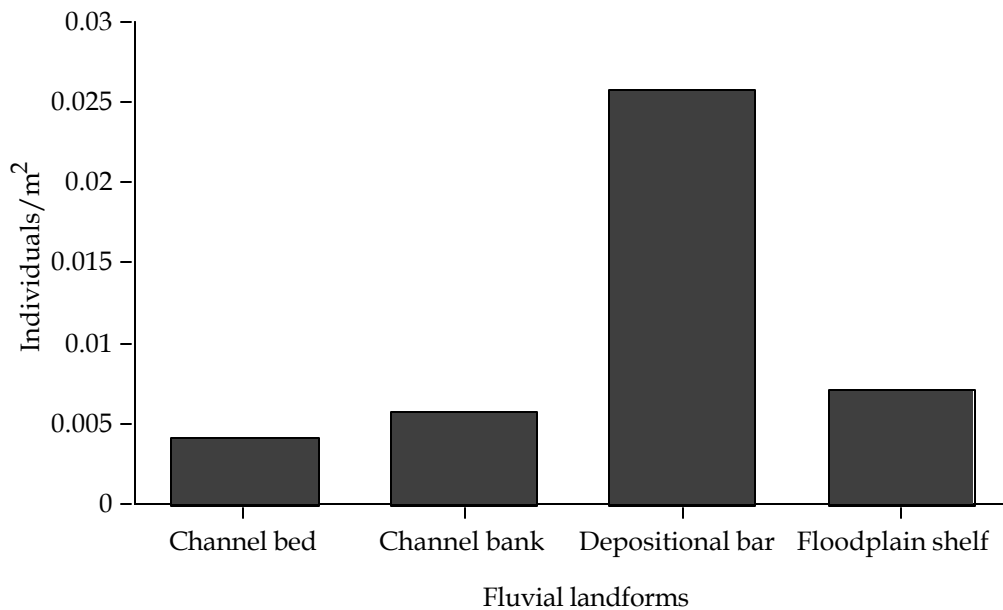


FIG. 16. Density of vegetatively established *A. donax* on different fluvial landforms ($p < 0.001$, chi square test).

Previous and New Establishment by Elevation

Establishment as a function of elevation is related to establishment by fluvial landform since the landforms tend to be concentrated within certain elevational ranges (Fig. 17). Elevations of the different fluvial landforms overlapped. The channel bed was most frequently sampled at an elevation equal to the middle of the river channel (0 m). Channel banks were at similar elevations as the channel bed, but did not extend quite as low and extended to higher elevations (Fig. 17). Depositional bars

were only found on the lower river and had a distribution similar to the channel bed, except that they extended to higher elevations. As expected, the floodplain shelf tended to occur at the higher elevations than the other fluvial landforms. The narrow, rocky geomorphology of the upper river is reflected in the shift of all records from the upper river region to slightly higher elevations compared to the lower river. On the upper river there were fewer records from -1 m to 0 m, and a few records from 3 m to 4.3 m where none occurred on the lower river.

Since elevations classes varied among transects, some elevation classes were sampled more than others (Fig. 18). Elevation classes close to 0 m, or the elevation in the middle of the river channel, were the most frequently sampled because these elevations were present on all transects. The elevation classes towards the extremes occurred on fewer transects. Thus, the estimates of establishment frequency in extreme elevation classes were probably less accurate than those estimates for frequently sampled elevation classes. The frequency data were standardized by transforming them to number of individuals per m².

New establishment of natives (by seed, root sprouts and vegetative reproduction) occurred at highest densities at elevations where there was no *A. donax* establishment (Fig. 19). In general, *A. donax* vegetative establishment was abundant where new establishment of native species was lowest. Previously established (undamaged and resprouts) natives and *A. donax* occurred over more similar elevation ranges and densities than the newly established individuals (Fig. 19). The highest density of natives occurred where *A. donax* is present, but there is still some separation in peak densities of the natives and *A. donax*.

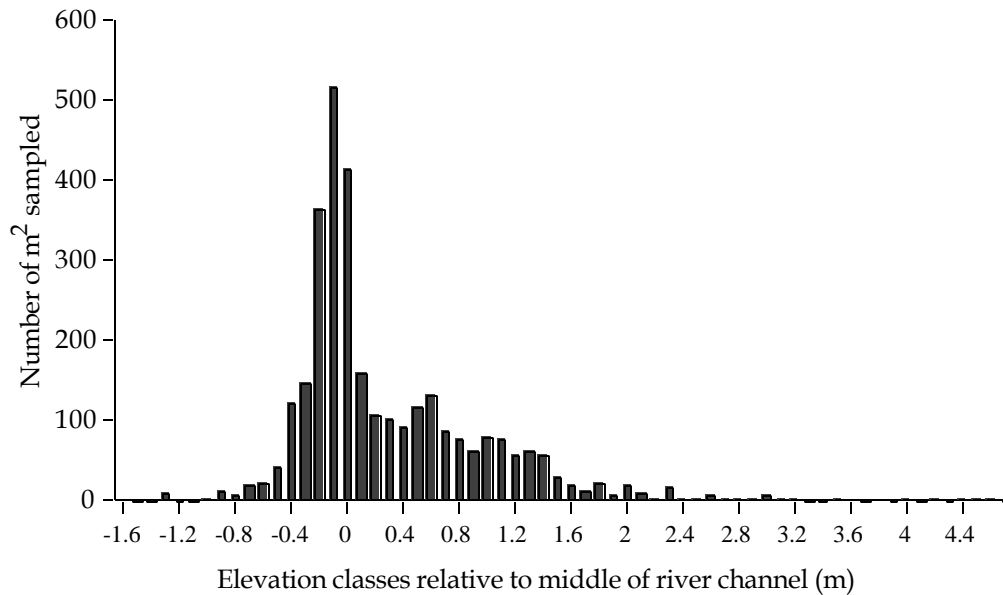


FIG. 18. Frequency distribution of the elevation classes sampled.

Undamaged individuals. The undamaged individuals of *A. donax* (Fig. 20) and *Tamarix* spp. (Fig. 21) were found between 0.1 m to 2.3 m elevation, a more restricted and higher zone than the native woody species which were found from -1.4 m to 2.2 m (Fig. 22). The distribution patterns of the individual species within the native species category varied, although most were concentrated between -0.4 m and 1.8 m (Fig. 23 to Fig. 28).

Resprouts and root sprouting. For all species resprouting, individuals were contained within -0.6 m to 1.6 m, which is presumably the band of elevation where high water flow passed during the 1994-95 flood season causing the damage that induced resprouting.

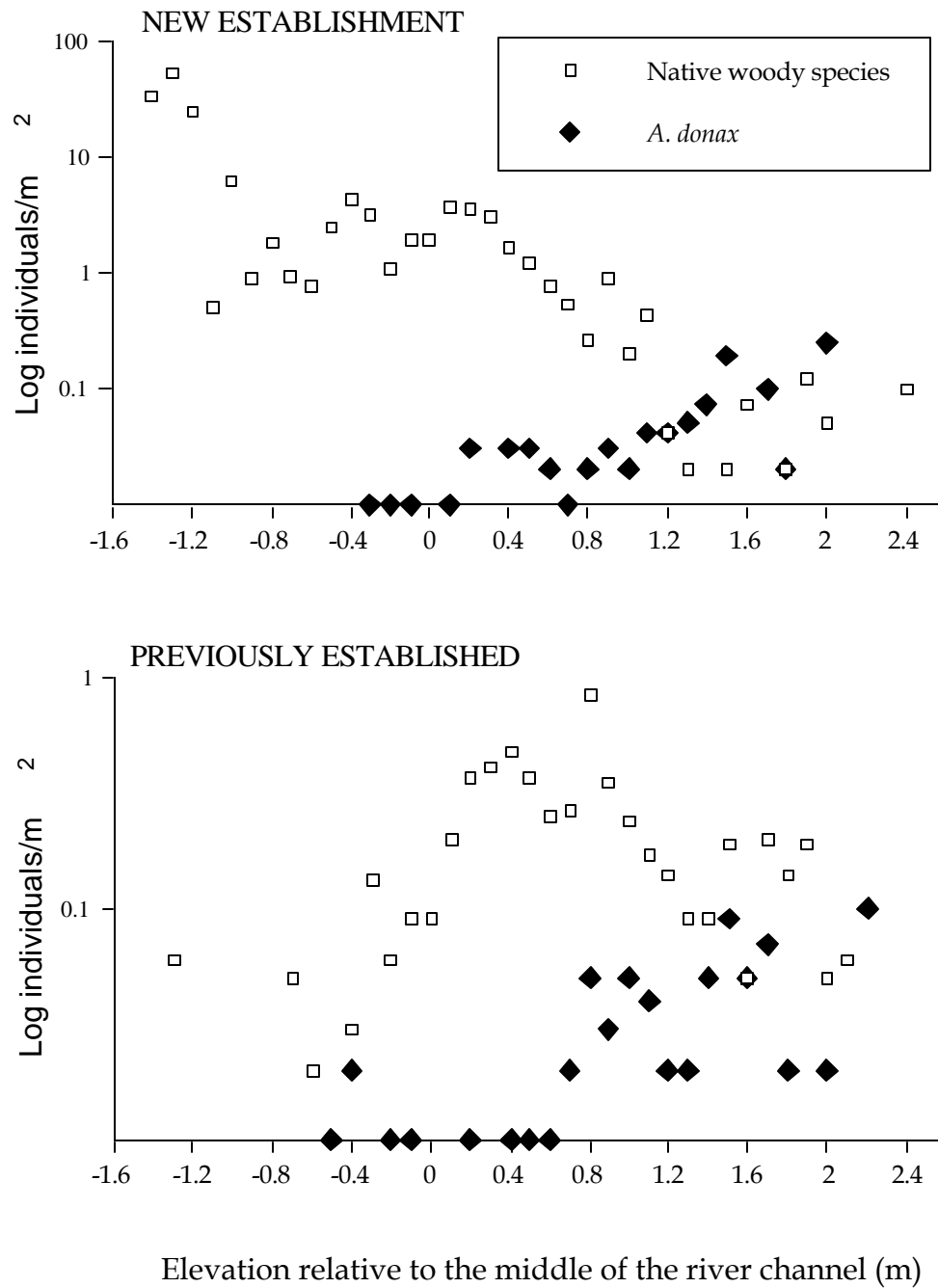


FIG. 19. Log density of previously established individuals (undamaged and resprout categories) and newly established individuals (seed and vegetative establishment categories) as a function of elevation for native woody species and *A. donax*.

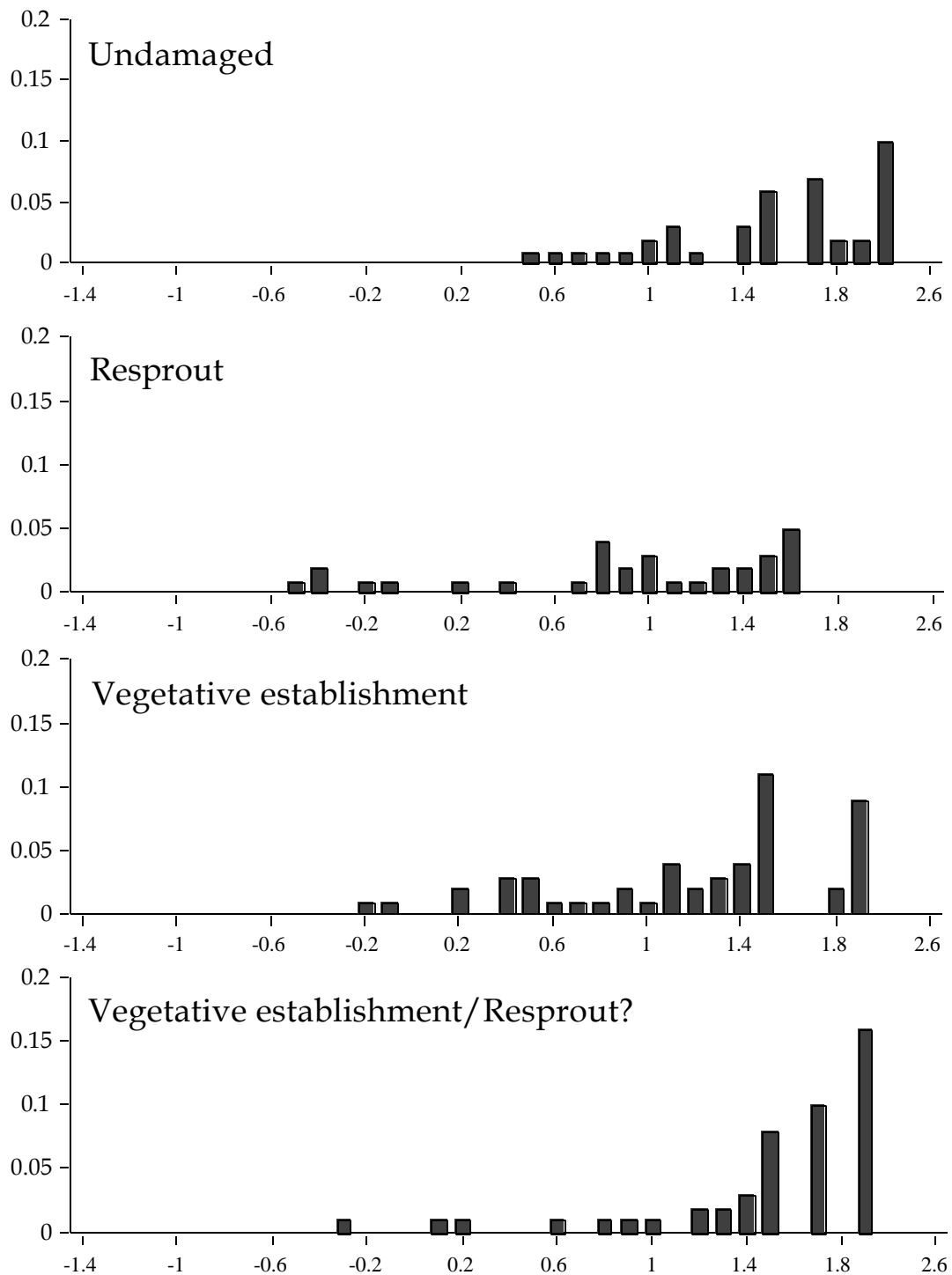


FIG. 20. Density per m^2 (y axis) of *A. donax* for different plant status categories as a function of elevation (m) relative to the middle of the river channel (x axis).

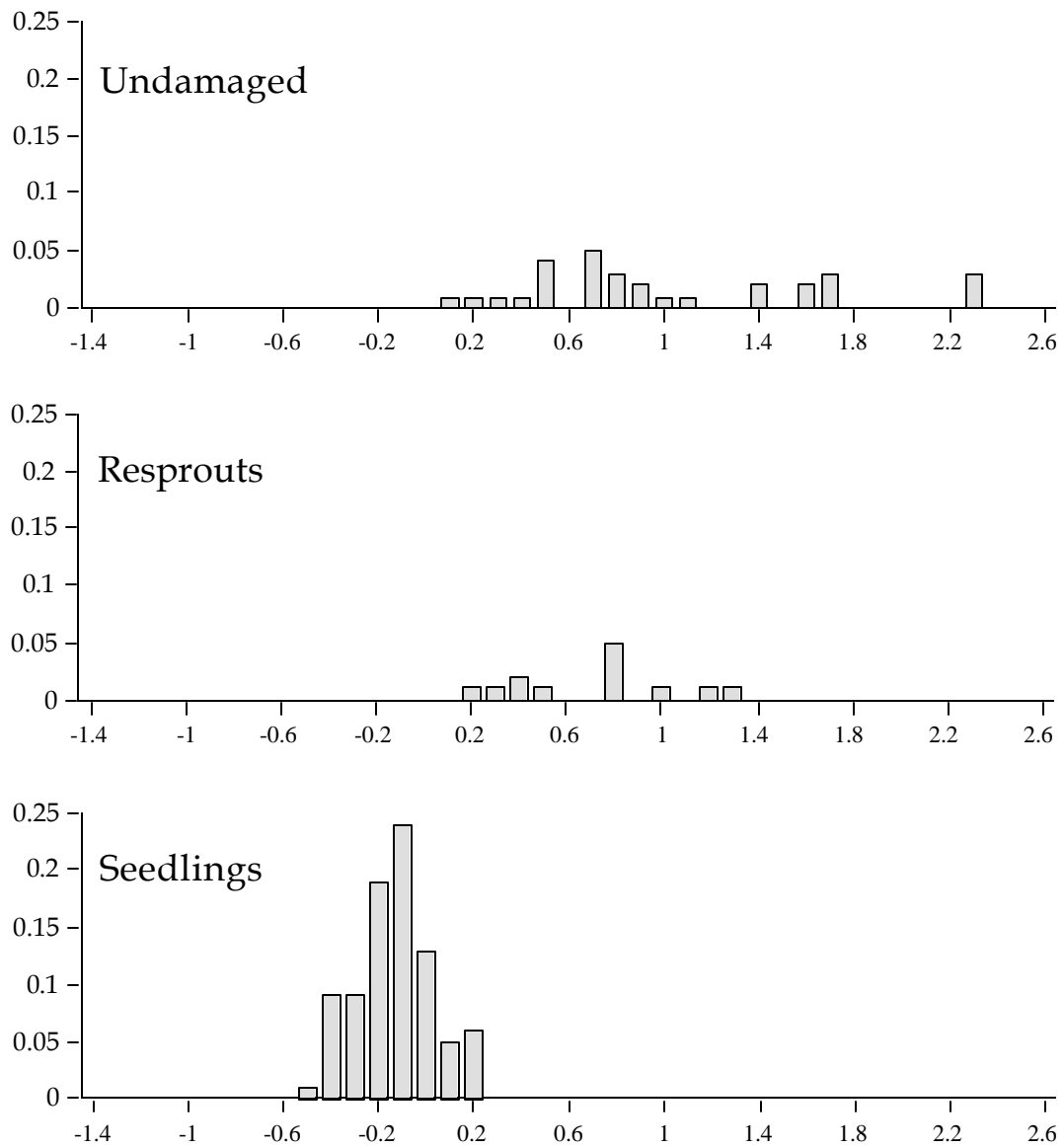


FIG. 21. Density per m^2 (y axis) of *Tamarix* spp. for different plant status categories as a function of elevation (m) relative to the middle of the river channel (x axis).

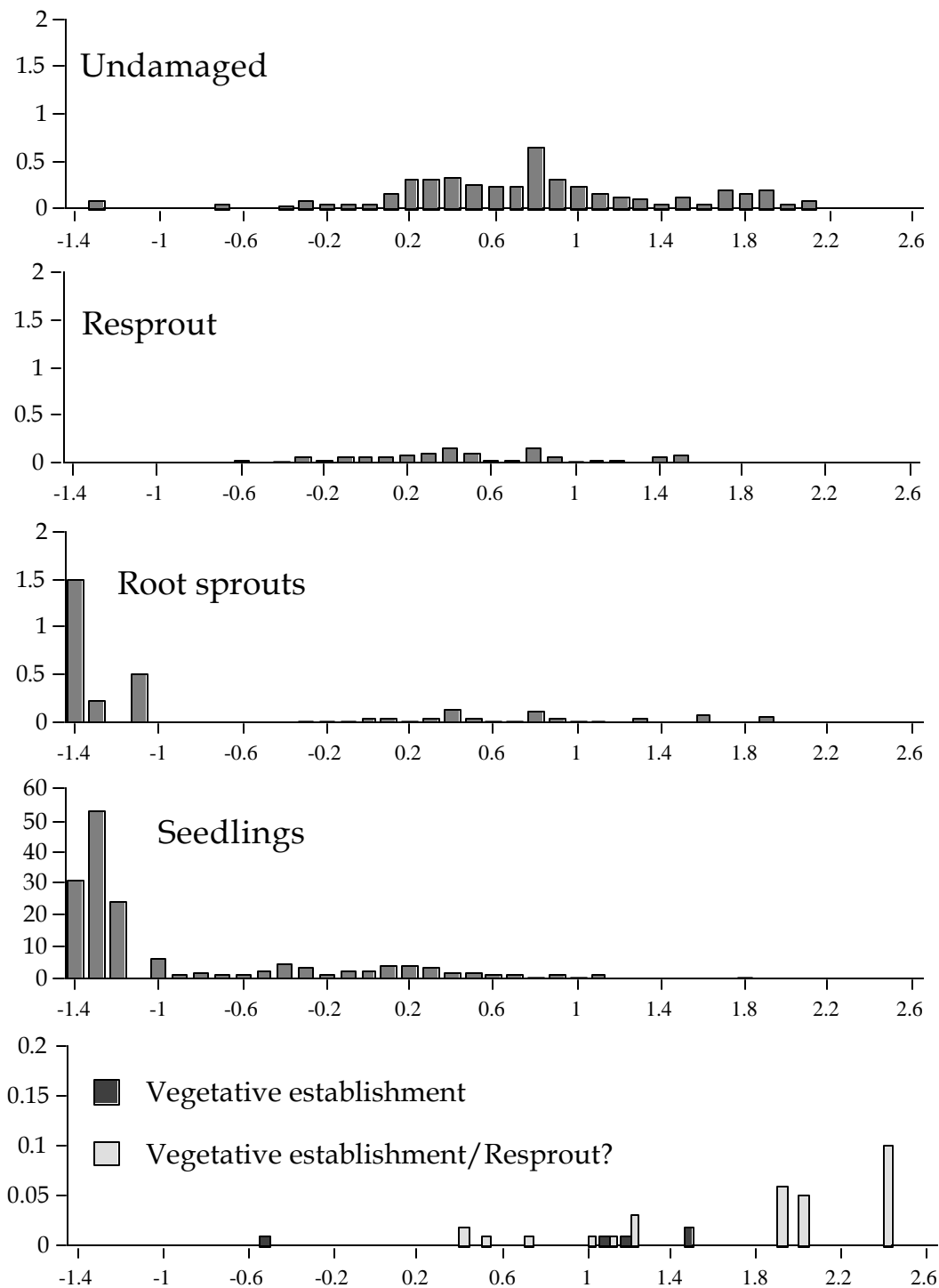


FIG. 22. Density per m^2 (y axis) of native woody species for different plant status categories as a function of elevation (m) relative to the middle of the river channel (x axis).

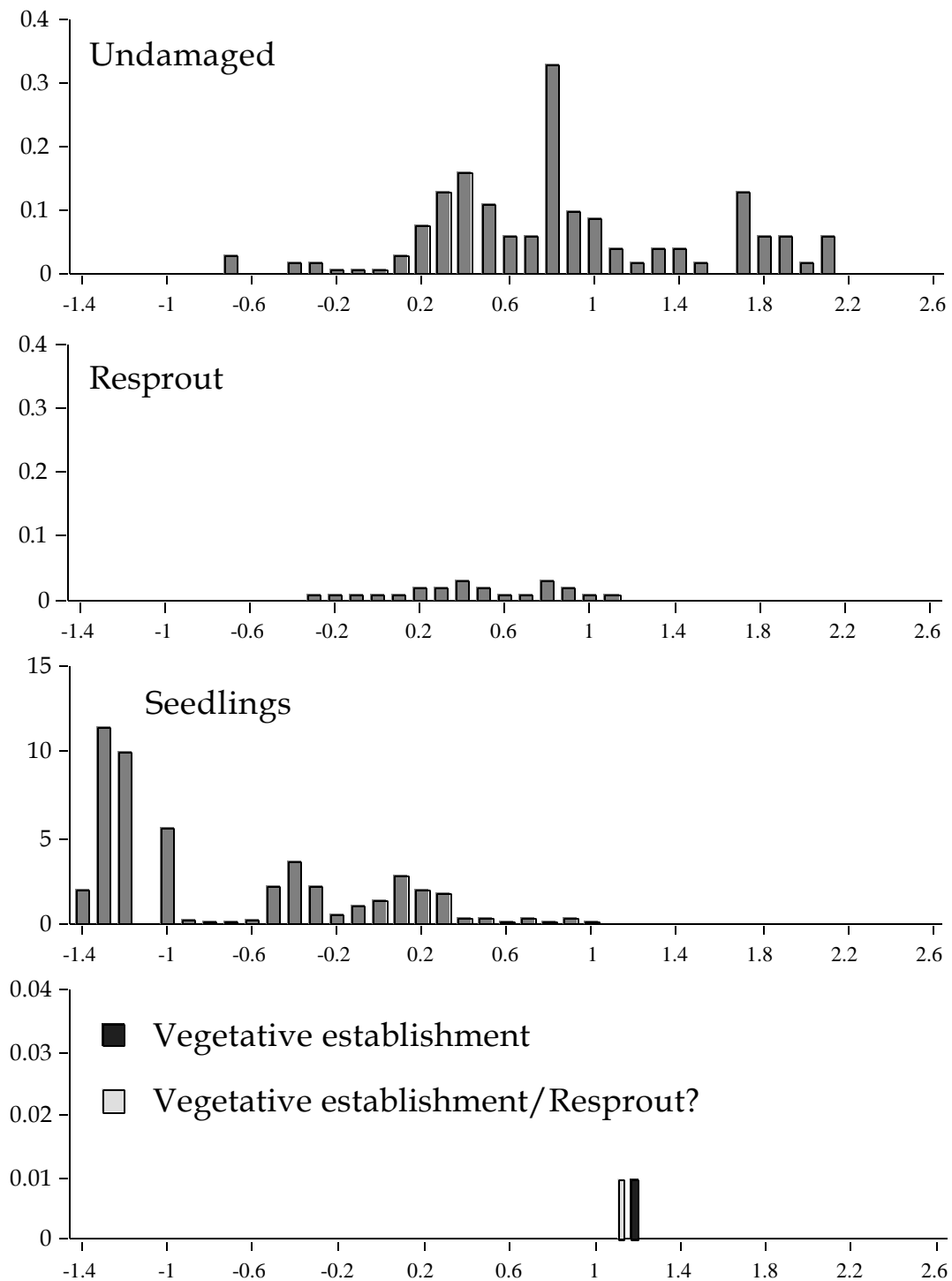


FIG. 23. Density per m^2 (y axis) of *Baccharis salicifolia* for different plant status categories as a function of elevation (m) relative to the middle of the river channel (x axis).

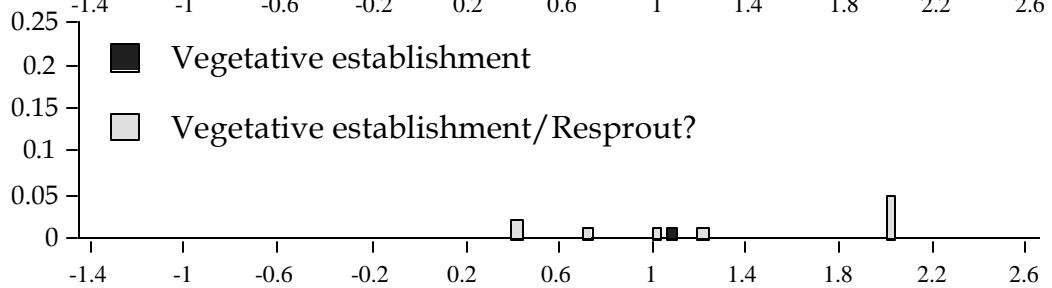
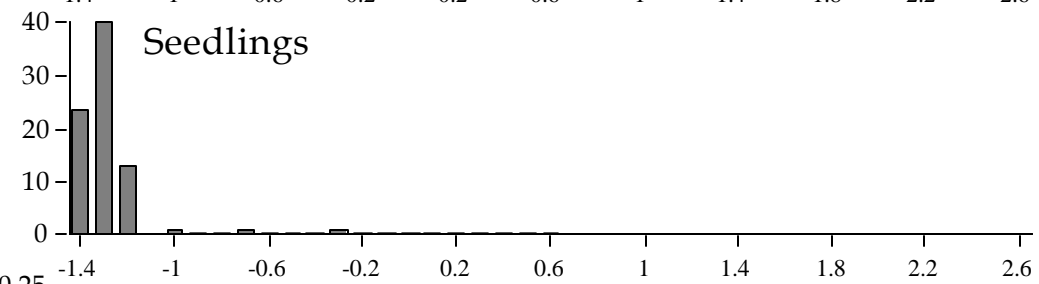
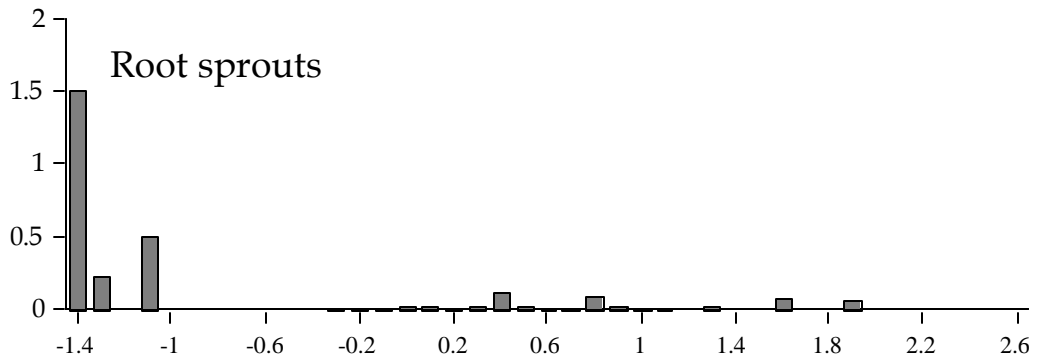
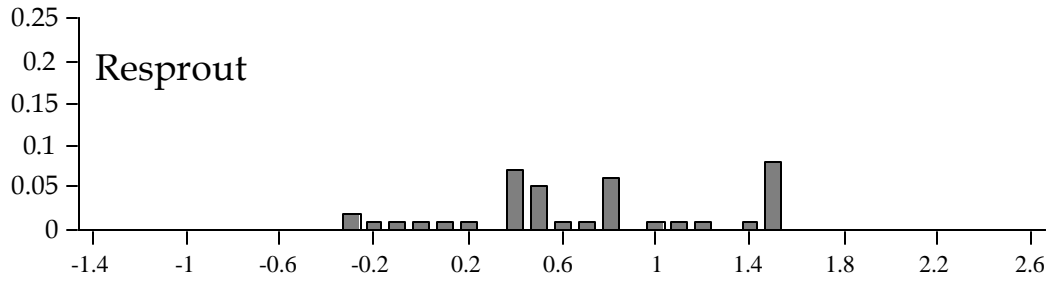
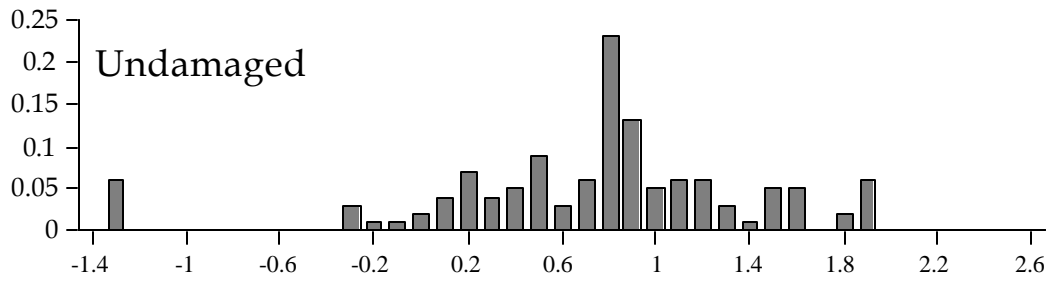


FIG. 24. Density per m^2 (y axis) of *Salix exigua* for different plant status categories as a function of elevation (m) relative to the middle of the river channel (x axis).

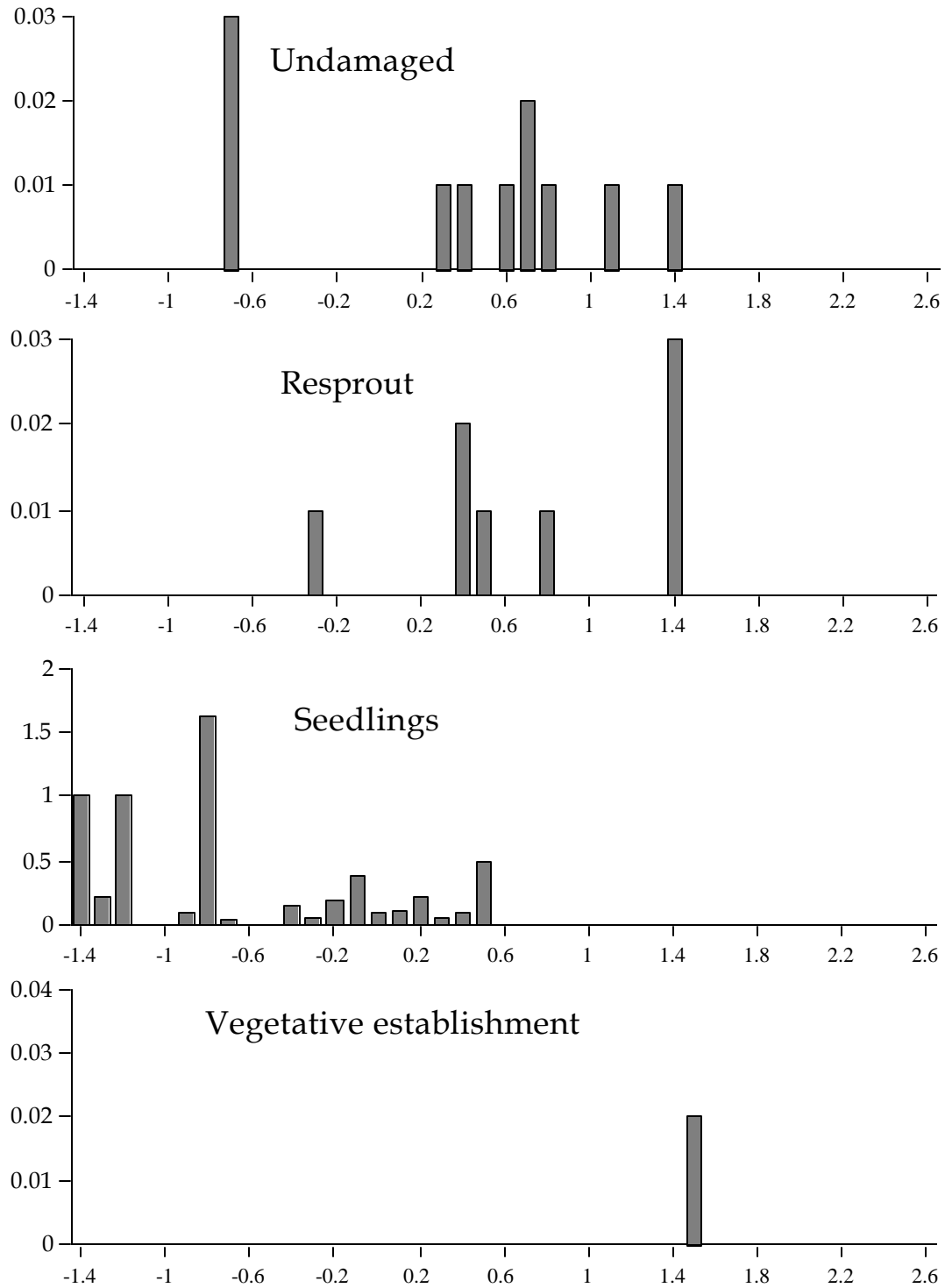


FIG. 25. Density per m^2 (y axis) of *Salix gooddingii* for different plant status categories as a function of elevation (m) relative to the middle of the river channel (x axis).

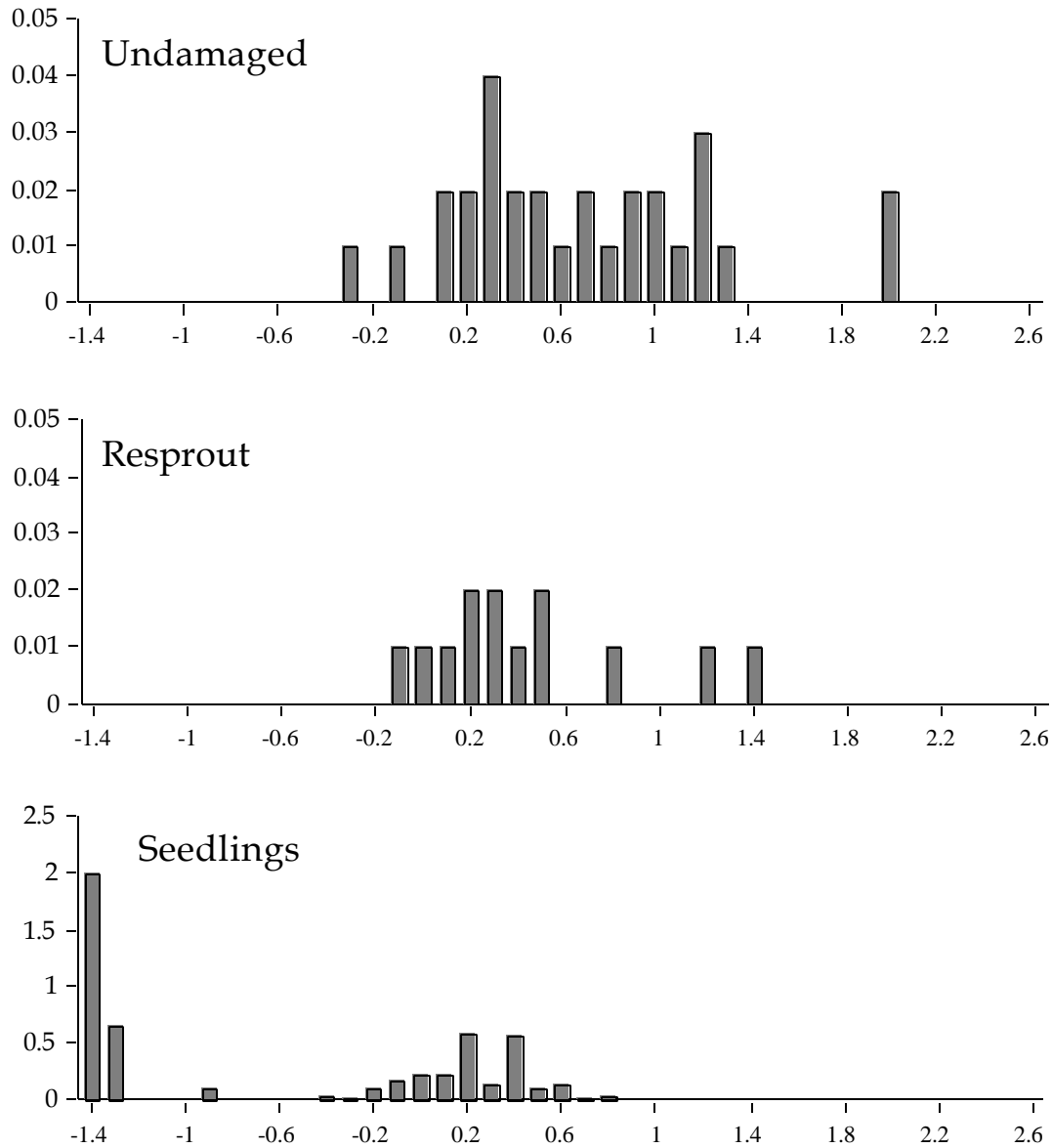


FIG. 26. Density per m^2 (y axis) of *Salix laevigata* for different plant status categories as a function of elevation (m) relative to the middle of the river channel (x axis).

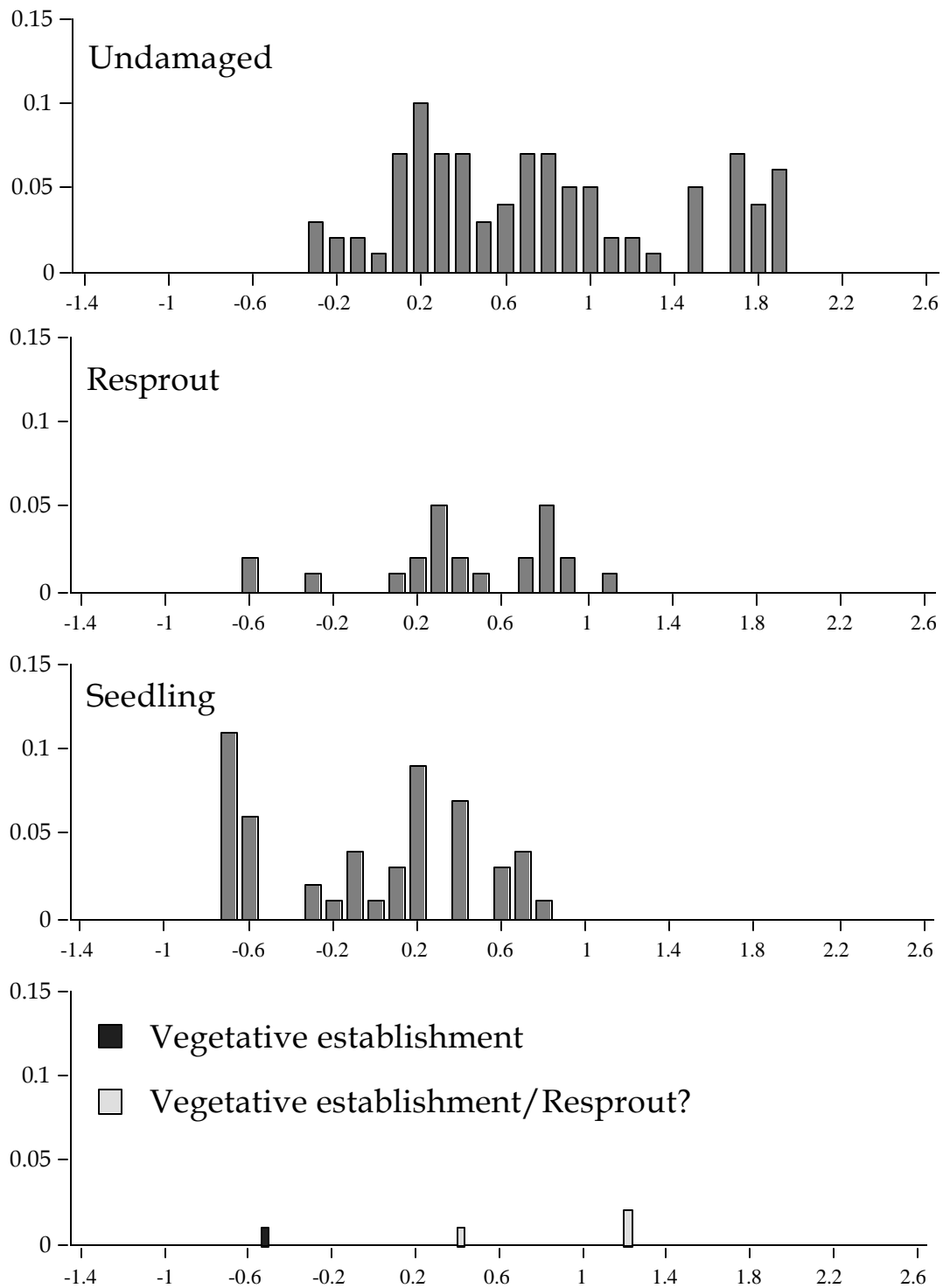


FIG. 27. Density per m^2 (y axis) of *Salix lasiolepis* for different plant status categories as a function of elevation (m) relative to the middle of the river channel (x axis).

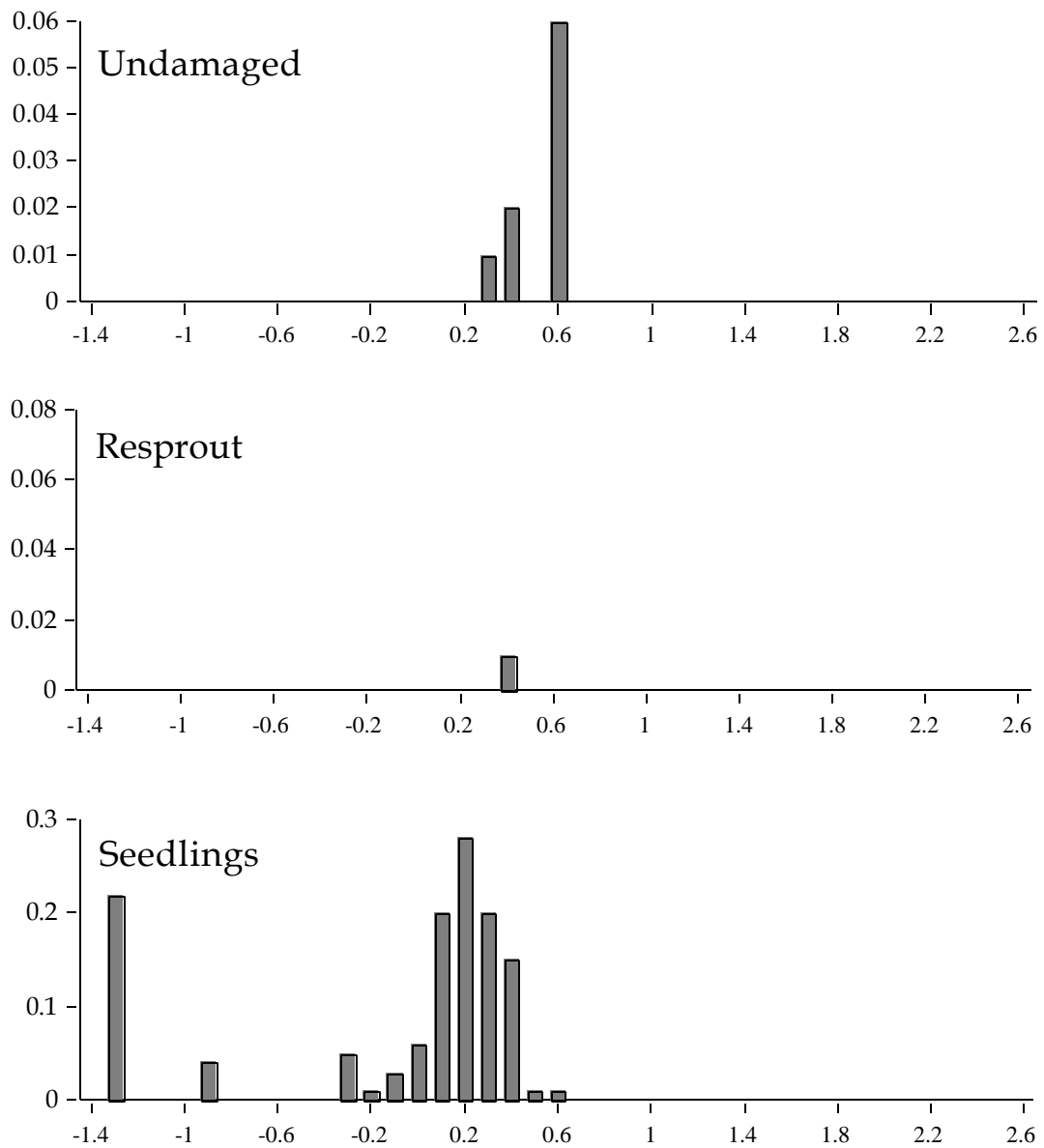


FIG. 28. Density per m^2 (y axis) of *Salix lucida* for different plant status categories as a function of elevation (m) relative to the middle of the river channel (x axis).

The main native that sprouted from roots, *S. exigua*, had most root sprouts at the lower elevations between -1.4 m and -1.2 m, and a few cases from 0.4 m to 1.9 m (Fig. 24).

Seedlings. Seedlings of the native woody species were found from -1.4 m to 1.1 m (Fig. 22), but most occurred in the lowest elevation classes of -1.4 m to -1.2 m. These seedlings were composed mostly of the native shrubs, *B. salicifolia* (Fig. 23) and *S. exigua* (Fig. 24). The tree willows *S. gooddingii* (Fig. 25), *S. laevigata* (Fig. 26) and *S. lucida* (Fig. 28) also had peak seedling densities low elevations, but at lower densities than the shrubs. *S. lasiolepis* differed from the other willow species in having seedlings in the -0.8 m to 0.8 m classes and none in the lowest classes (Fig. 27). *Tamarix* spp. seedlings were found only over a narrow range of lower elevations, -0.5 to 0.2 m (Fig. 21), but were absent in the lowest elevation classes where native woody species were at the highest density.

The two shrub species had similar patterns of seedling establishment as each other, except that *B. salicifolia* had higher densities than *S. exigua* at the higher elevations, suggesting it is able to tolerate higher and drier conditions (Fig. 29). However, at the lower elevations closer to the river channel where it was moister, *S. exigua* had the highest densities. The tree willows had similar patterns to each other, though with different density peaks (Fig. 29).

Vegetative establishment. *A. donax* established vegetatively from -0.2 m to 1.9 m, but the majority of plants occurred between 1.5 m and 1.9 m (Fig. 20). There were also some possible vegetative establishment events that were indistinguishable in the field from resprouting plants.

These uncertain events were also within the same elevation range as the positively identified vegetative establishment events, suggesting that these may indeed be vegetative establishment events rather than resprouts.

Vegetative establishment was infrequent for all other species. There were only two cases of vegetative establishment for *Tamarix* spp. at 1.2 m and 1.4 m, elevation classes where individuals of *Tamarix* spp. already existed. Vegetative establishment was rare for the native species and consisted of scattered events from -0.6 m to 2.4 m (Fig. 22).

Effect of Drying on Sprouting of *A. donax*

To approximate the moisture loss of the stems and rhizomes being dried and planted, additional pieces were monitored for moisture loss by weighing at two day intervals. Moisture loss was measured from day 0 to day 80 of the experiment, thus going beyond the maximum drying periods tested in the study. Data from these monitored stems and rhizomes were averaged to give an estimate of moisture loss over time. Moisture loss (opposite of percent of initial weight) over time was rapid for both stems and rhizomes for approximately the first 20 days, and then began to level off somewhat (Figs. 30 & 31).

A total of 36 stems were dried from 0 to 20 days and only one, dried for 15 days, did not sprout. Of the 35 stems that grew, all but one sprouted from both nodes, with one sprout dominating and the other drying up and dying. At the maximum drying period (20 days) stems were approximately $73 \pm 1.6\%$ of initial weight (or 27% moisture loss).

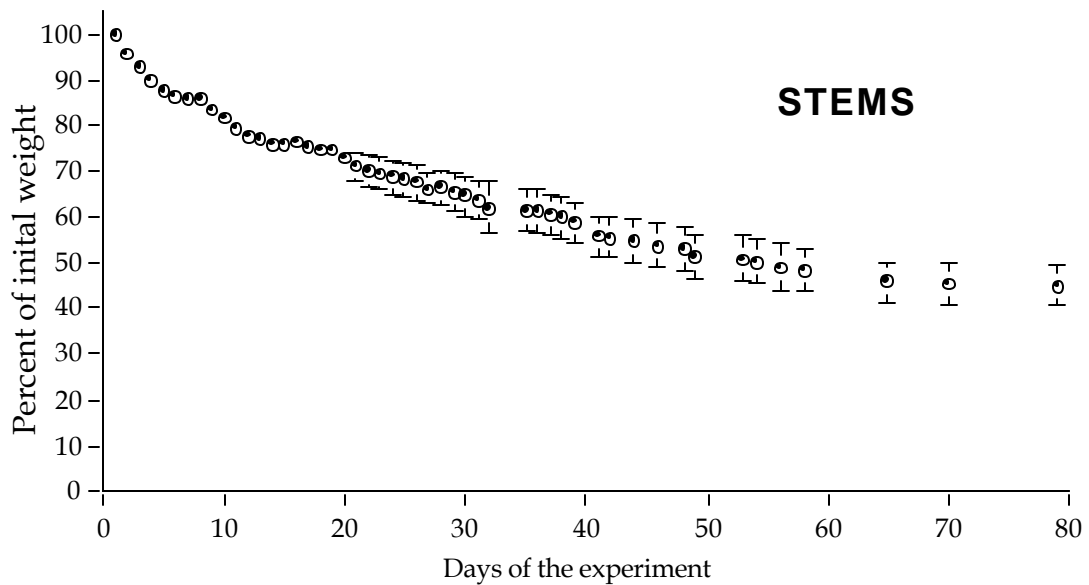


FIG. 30. Percent of initial weight for the stems that were monitored to determine water loss (\pm SE). $N=8$ for days 0-15, $n=4$ for days 16-20, and $n=2$ for days 21-79. The longest drying period in the experiment was 20 days.

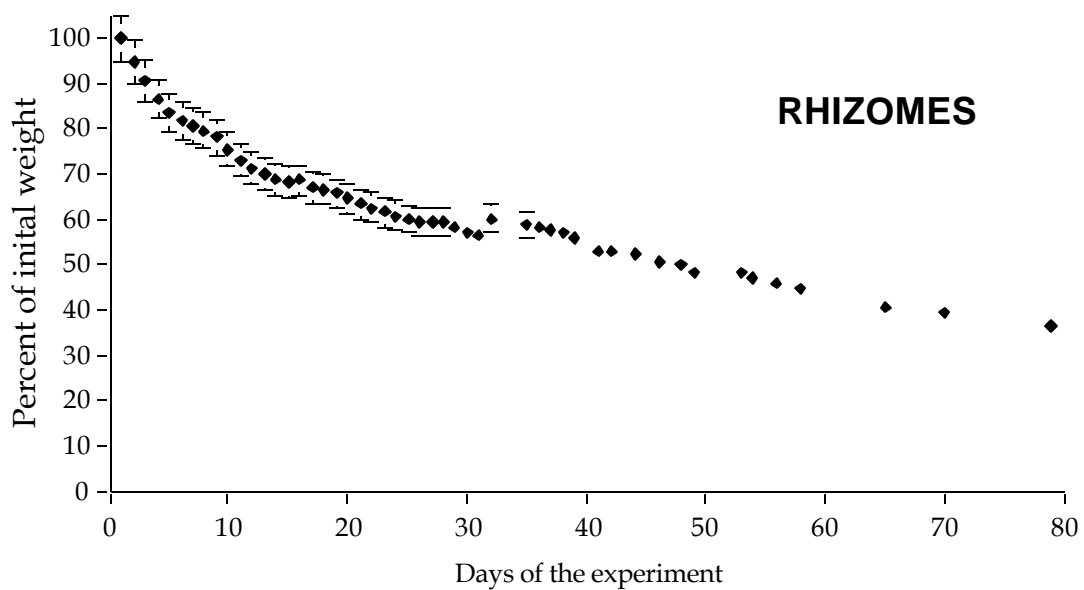


FIG. 31. Percent of initial weight for the rhizomes monitored to determine water loss (\pm SE). $N=10$ for days 0-26, $n=6$ for days 27-31, and $n=4$ for days 32-79. The longest drying period in the experiment was 31 days.

Rhizomes did not sprout as frequently as the stems, with only 25 sprouting out of a total of 38 rhizomes dried from 0 to 31 days (Table 9). Contrary to what might be expected, sprouting was not directly related to drying. Although no rhizomes sprouted from the longest drying period (31 days), there were only two replicates for this period versus four for all other drying periods (Table 9). At the maximum drying period (31 days) the average percent of initial weight of the monitored rhizomes was $56.5 \pm 3.7\%$ (Fig. 31). However, rhizomes only sprouted up to the 26 day treatment, so rhizomes were able to sprout after losing approximately $59.5 \pm 2.6\%$ of initial weight (or 40.5% moisture loss).

TABLE 9. The number of sprouting and non-sprouting rhizomes in each drying period.

Days dried	Sprouted?		Total
	Yes	No	
0	2	2	4
2	4	0	4
4	3	1	4
6	3	1	4
8	3	1	4
10	2	2	4
15	4	0	4
20	3	1	4
26	1	3	4
31	0	2	2

The best fit logistic regression model ($P < 0.004$, $df = 2$, $R^2 = 0.21$) to explain rhizome sprouting included the number of buds present on the rhizome at the time of planting and the drying period (Table 10). There was no significant interaction between these two factors. The only pattern

apparent was that all the rhizomes that lacked buds did not sprout, indicating that bud presence was necessary for growth to occur.

TABLE 10. Logistic regression analysis relating independent variables to sprouting of rhizomes (yes or no) for the drying experiment.

Step	Model	-Log likelihood	DF	R ²	P
1	# buds	2.762	1	0.11	0.019
2	# buds + days dried	4.382	2	0.18	0.013

Effects of Burial on Sprouting of *A. donax* Rhizomes

A total of 30 rhizomes were buried in the field experiment, with ten each at the 10 cm, 50 cm and 100 cm depths. Six rhizomes sprouted at both the 10 cm and 50 cm depths, and five sprouted at the 100 cm depth (Table 11). Contrary to what was expected, depth of burial did not significantly effect the sprouting of buried rhizomes (Table 12). Ability to sprout was also not significantly explained by the initial weight, size, maximum diameter, minimum diameter, or parent plant source (Table 12). The best fit logistic regression model ($P < 0.001$, $df = 2$, $R^2 = 0.34$) included the number of buds at the time of planting and the number of nodes present at the time of planting. Rhizomes that sprouted had one to four buds, and none of the rhizomes lacking buds grew (Fig. 32).

TABLE 11. Summary of results of the burial experiment. Height measurements are the averages at day 120. There were ten replicates for each depth of burial.

Depth of burial (cm)	# Sprouted	# of days to emergence	Ave ht (cm) \pm SE	Ave # of shoots	# died
10	5	24	69 \pm 4.6	1.3	2
50	5	45	74.3 \pm 10.6	1	2

100	6	66	86.6 ± 7.8	4	0
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TABLE 12. Results of logistic regression analysis relating independent variables to sprouting (yes or no).

Step	Model	-Log likelihood	DF	R ²	P
1	# buds	4.454	1	0.22	0.003
2	# buds + # nodes	7.031	2	0.34	0.001

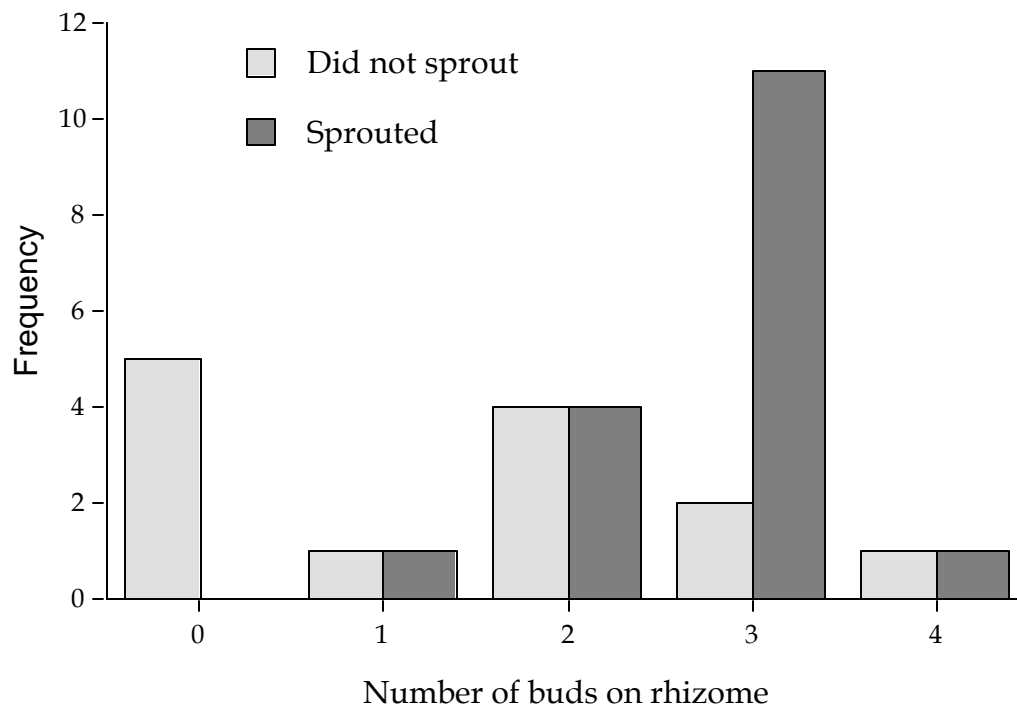


FIG. 32. Number of buds present on rhizomes at the time of planting and sprouting status.

As expected, the rhizomes buried closer to the surface emerged more quickly. Sprouts of rhizomes buried at 10 cm first emerged between days 20 and 24, rhizomes buried at 50 cm first emerged between days 32 and 45, and

rhizomes buried at 100 cm first emerged between days 52 and 66 (Fig. 33). Since the field site was checked approximately every two weeks, the emergence of sprouts may have occurred between visits.

At the outset it was not expected that rhizomes buried at 100 cm would be able to grow, let alone achieve higher shoot heights than the other burial classes. Although the 100 cm depth rhizomes emerged at approximately 32 days after the 10 cm depth rhizomes, by day 120 the 100 cm depth shoots had a greater average height than the 50 cm and 10 cm shoots (Fig. 33). Total length of the stems produced is actually the above ground height plus the burial depth. The average growth rate (including the height grown underground) was significantly higher for the 100 cm depth rhizomes than for the 50 cm depth rhizomes (Student's $t = 4.8$, $P < 0.001$) and the 10 cm depth rhizomes ($t = 8.8$, $P < 0.001$), but the 50 cm and 10 cm depth growth rates were only marginally significant ($t = 2$, $P = 0.08$; Fig. 34). Rather than reducing sprouting, deeper burial in fact seemed to provide better conditions for growth as the 100 cm class had the highest survival by the end of the experiment. Two of the 10 cm depth sprouts and two of the 50 cm depth sprouts died while none of the 100 cm depth rhizome sprouts died (Table 11). The 100 cm sprouts also had more shoots per plant than the other depth classes.

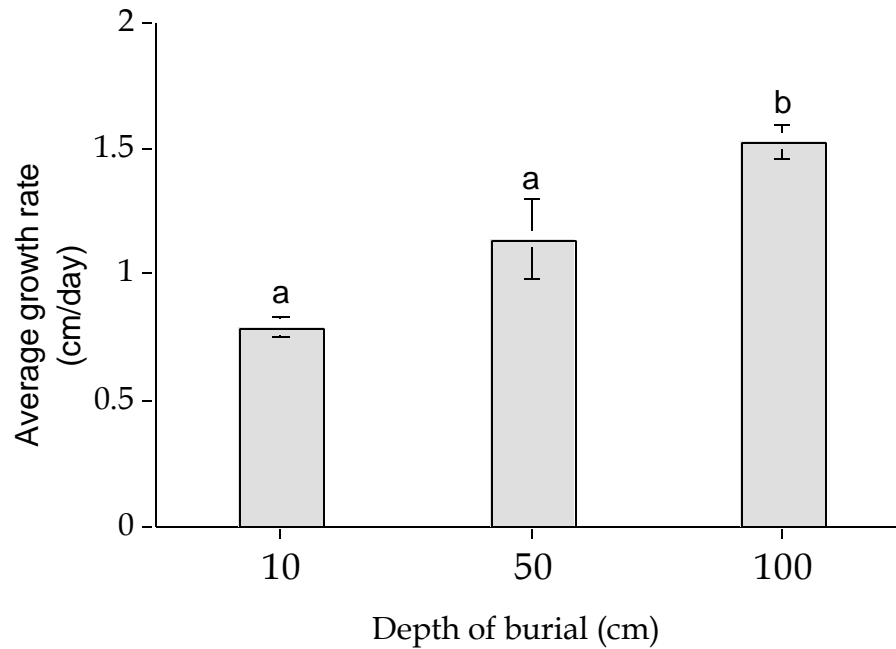


FIG. 34. Average growth rate (cm/day) for rhizomes at the 10, 50 and 100 cm depths of burial. The height grown underground is included. For the 10 cm and 50 cm depths $n = 5$, and for the 100 cm depth $n = 6$. Depths with different letters are significantly different with a Student's t test at $\alpha = 0.01$.

DISCUSSION

The results of this study show that the native woody species and *A. donax* establish by different mechanisms after flood disturbance. Though many of the native woody species are known to be capable of establishing vegetatively, they rely on sexual reproduction, and were rarely found to reproduce by vegetative establishment. *A. donax* spreads solely by vegetative establishment of stems and rhizomes. The absence of *A. donax* seedlings and the non-viable seed of the few flowering individuals found supports previous reports of *A. donax* having non-viable seed. It is uncertain why the seed is not viable, although Bhanwra (1988) found that seed set was poor in India due to the failure of meiosis in the majority of ovules.

It is not clear which mode of establishment, seedling establishment by native woody species or vegetative establishment by *A. donax*, is more effective. Both rely on the disturbance caused by flooding. Native seedling establishment is prolific and widely broadcast by the wind, both up and down river. The dependence of *A. donax* on vegetative establishment limits it to downstream spread unless aided by humans. This may be a severe limitation on its rate of spread within a riparian system that has only a few *A. donax* individuals as sources of propagules. Although native seeds can spread over a large area due to wind dispersal, successful establishment is limited to unvegetated areas left by receding flood waters and mortality is high due to desiccation during the summer and scouring and burial during winter floods. Mortality of vegetatively established *A. donax* is unknown.

Results of the experiments in this study show that stems and rhizomes are tolerant of desiccation, and that rhizomes can be buried to at least 100 cm and still emerge and grow. This evidence suggests that success of vegetatively established plants is probably fairly high. Growth from plant parts, especially rhizomes, is rapid and *A. donax* achieves greater size in shorter periods of time than native woody seedlings. Rhizomes and stems both contain more energy than any of the native woody seeds, which are all wind dispersed and very small, therefore initial growth of *A. donax* will be greater.

Although *A. donax* is generally referred to as 'displacing' or 'crowding out' natives (Bell 1993), no competition studies have been carried out to test this, in the lab or field. However, due to the presence of large monoculture stands of *A. donax* in riparian forests, it is clear that native species must have been displaced to some extent. Of interest is how and when this 'displacement' occurred. Is *A. donax* colonizing alongside new native woody species after flooding, is it establishing in relatively open areas, is it invading into relatively mature riparian shrubs and trees, or is it able to do all of these?

Establishment of native woody seedlings and *A. donax* occurred on the same fluvial landforms. Establishment was not random with respect to landforms, indicating that physical characteristics of dispersal and/or growth requirements partly determined the settlement locations of new individuals. The presence of high densities of native woody seedlings on depositional bars, the channel bed, and the channel bank can be attributed to the requirements of these seedlings for bare, moist surfaces. Establishment patterns of seedlings are shaped by the suitability of the location where the seed lands. Vegetative establishment of *A. donax* occurred at the highest

density on depositional bars. This suggests that floating pieces of rhizome and stem are more likely to be deposited on the convex side of the river channel where most deposition occurs. Since *A. donax* pieces are probably removed from the parent plant by the force of flood waters, pieces are rarely deposited in the channel bed since it is full of water during this time. The peak discharge during the flood season prior to sampling (9150 cubic feet/sec) was above average for 1974-1995 (6074 cubic feet/sec), but not drastically so, and there were no very large flood events such as occurred in the 1992/1993 '100 year' flood (peak discharge = 31,000 cubic feet/sec). The low density of vegetatively established *A. donax* found on the floodplain shelf and at elevations higher than two meters is to be expected. Most of the *A. donax* that is currently on the floodplain shelf is probably from deposition in the '100 year' flood of 1993/1994 and from other large flood events.

The co-occurrence of high densities of native woody seedlings and *A. donax* propagules on depositional bars suggests that this may be a potential site of competition between *A. donax* and natives, where *A. donax* could be 'displacing' natives. If the fluvial landform categories are further investigated in terms of elevation above the river channel, some separation of native seedling establishment and *A. donax* establishment is apparent. Native seedling establishment occurred at lower elevations than establishment of *A. donax*. Although these two types of establishment occur at the highest densities on the same landform, potentially little overlap may occur due to this elevational separation. These data support the idea that establishment of native seedlings occurs when flood waters are low and subsiding, after *A. donax* has already been dispersed at higher elevations, when flood waters are

at or near their maximum. This separation would be more or less depending on the level of the floods in a particular year.

Vegetative establishment of *A. donax* occurred in the elevational classes where most of the native woody species that were not damaged by flooding (i.e. already established individuals) were growing. It is possible then, that *A. donax* might, over time, 'displace' these individuals. Rather than competing with the first colonizing stage after a flood disturbance (seedlings), *A. donax* may be competing with what could be termed the 'second successional' stage of larger individuals that have survived through at least one season of flooding and are farther up the elevation gradient from the river channel. This suggests that a willow species that can spread by means other than sexual reproduction would have a potential advantage. *S. exigua* was the most common native species that reproduced asexually, by means of root sprouting. Although all willows are able to root sprout, *S. exigua* produced root sprouts more frequently than the other willows examined in this study, possibly because *S. exigua* is generally the closest to the river channel. In these locations *S. exigua* is exposed to flood disturbance that may trigger root sprouting from shallow roots. The production of root sprouts may enable *S. exigua* to spread more rapidly than the other willow species and better compete with *A. donax*. Root sprouts are produced from established individuals, therefore generally occur in different areas from seedling establishment. Root sprouts of *S. exigua* occurred over the entire range of *A. donax* establishment, suggesting competition may occur between them, although the peak of new *A. donax* establishment was at higher elevations than peak densities of root sprouting.

Previous research on plant invasions indicates that only very few exotic species can invade successional advanced plant communities (Rejmánek 1989). However, in a year of large floods, *A. donax* pieces may be deposited into mature riparian forests by the highest flood waters. In most cases *A. donax* would probably survive due to its tenacious growth. The ability of *A. donax* rhizomes to grow in the dark (as shown in the 100 cm burial treatment) indicates that they could also grow under thick vegetation or when buried under flood debris. In this scenario, *A. donax* would be invading a mature successional community through a natural disturbance. Once established, *A. donax* can maintain itself and spread through its extensive rhizome system. It is clear that *A. donax* is dependent on flood waters for dispersal, but it is the magnitude of the flood that determines the 'successional stage' of the community into which it invades. In low intensity flooding, *A. donax* establishment would predominantly occur at lower elevations. In high intensity floods, *A. donax* propagules would predominantly be deposited in the higher elevation zones of mature riparian vegetation, where no native species recruitment would be occurring. The rate of spread and effect of *A. donax* interspersed among mature riparian trees once it has grown into a dense understory is uncertain, and warrants study. Observations in the field suggest that native trees amongst an understory of *A. donax* are generally weaker and are prone to rotting and loss of large branches (pers. obs.).

Although vegetative establishment was the only form of recruitment for *A. donax*, the number of vegetatively established plants encountered was quite small, especially in comparison to the density of native woody seedlings. However, the results of the experiments in this study indicated

that these few vegetative establishment events probably have a high survival rate. The apparent success of *A. donax* vegetative establishment is partially explained by its ability to withstand drying. During a flood event *A. donax* pieces can be deposited on the top of a surface that dries out rapidly when the flood water recedes. In this study, rhizomes and stems were able to sprout after up to 40.5% and 32% moisture loss, respectively. This ability may allow stems and rhizomes deposited in less than ideal conditions the flexibility to survive until conditions change, for example, with a new rainstorm. Since the maximum drying period tested in this study did not significantly reduce sprouting for stems, further tests should be conducted to determine the limits on growth following desiccation. It was apparent, however, that *A. donax* vegetative fragments were quite resistant to drying, at least when grown in wet conditions.

This study also showed that the ability to sprout after being buried can aid *A. donax* vegetative establishment. During flooding, a deposited piece of rhizome or stem may be buried by depositional material and debris with successive floods. The field experiment showed that *A. donax* buried up to one meter was still able to sprout and survive. If buds are present on the rhizome, sprouting can occur when the rhizome is buried up to at least 100 cm. Burial may in fact be advantageous, if deeper soil provides the rhizome with more moisture. Since this experiment was carried out in the field, moisture levels could not be controlled and the 100 cm depth was moister than the 50 or 10 cm depths (pers. obs.).

The presence of *A. donax* on beaches and estuaries in San Diego county has interesting implications. When walking on the beach, the amount of *A. donax* rhizome and stem that is washed up on shore is striking. A possible

mode of spread is through tidal action (pers. obs.). Pieces of *A. donax* from a river system may be carried to the ocean and spread through tidal action into estuaries and other riparian systems that previously had no source of *A. donax*. This potential mode of spread is supported by the presence of *A. donax* in most of the estuaries in San Diego county, although a survey of other sources of *A. donax* infection (i.e. due to human activity) has not been investigated. Further study on the relationship between the location of *A. donax* in estuaries and the maximum tidal influx height would be of interest.

This study was conducted over one growing season, and by nature of the riparian system, there can be a lot of variation from year to year due to different flood regimes and levels. The annual disturbance in the riparian system creates a situation in which one year's establishment is often destroyed by the next year's flooding. Survival in many cases may be very low and, if flooding following establishment is low, survival may be patchy. This study has not specifically addressed survival and no data exist from other studies to provide an indication of general mortality rates for *A. donax* establishment events. Information was not collected on the quantity or quality of propagules of natives and exotics that entered into the system. Furthermore, this study was conducted in one drainage, and is thus limited in being an analysis of the events occurring in one year in one riparian system.

Management Implications

Several recommendations to improve the management of *A. donax* result from this study. The absence of *A. donax* seedling establishment indicates that removal should be carried out from top to bottom of a

watershed. This often requires cooperation between many different agencies and landowners, but is necessary to prevent continued infection of treated areas from upstream sources. The availability of *A. donax* from nurseries and garden magazines (pers. obs.) must be eliminated to prevent new sources of *A. donax* from arising. If *A. donax* is spreading by tidal action into estuaries, annual surveys of estuaries could be conducted to remove any newly established *A. donax* plants while they are still small and manageable.

The concentration of *A. donax* establishment events on certain fluvial landforms and within certain elevational ranges has potential implications for its removal. In areas where *A. donax* infestation is particularly severe, and where removal is not scheduled for the immediate future or will take an extensive period to complete, selective removal is a potential tool. This removal would be an interim strategy to target new establishment events on the landforms where establishment most commonly occurs. This selective removal could help limit the spread of *A. donax*. Since survival studies have not been carried out, it is unknown what percentage of *A. donax* vegetative establishment events actually survive. If survival is low, removal targeting these areas may not be worth the effort. In addition, since the riparian system is so dynamic and unpredictable, establishment events of one year may be completely destroyed by high flooding the next year, possibly making the removal unnecessary. However, the tenacious nature of *A. donax* rhizomes, and stems, and the ability of damaged plants to resprout, as demonstrated in this study, indicate that newly established plants could survive burial and flood damage.

The ability of stems and rhizomes to sprout after desiccation has important implications for *A. donax* removal projects. One of the most

commonly used methods for *A. donax* removal is cutting the stems and spraying the stumps with glyphosate herbicide. The presence of cut stems on the ground is of concern if they are able to sprout and produce new individuals, but the removal of stems is costly. Though this study showed a remarkable ability of stems to sprout after drying, growing conditions in the experiment were continually moist. My observations from an *A. donax* removal project currently being carried out on the Santa Margarita river by the Navy is that very few cut stems sprout and only do so if they are exposed to continuously moist conditions. My recommendation is that the cut stems do not need to be removed, except under specific conditions. Removal of the cut stems would be warranted if they are in wet conditions or are cut immediately before an imminent flood that may disperse them downstream.

ACKNOWLEDGMENTS

I would like to thank the California Native Plant Society and the San Diego Chapter of Achievement Rewards for College Scientists (ARCS) for supporting this study. Thanks to Marine Corps Base Camp Pendleton for access to their portion of the Santa Margarita river.

I would like to thank my advisor, Dr. Paul Zedler, for taking me on as one of his students and letting me do this project. Leslie Seiger was a great help in her review.

And lastly, my gratitude to Jason Giessow for his help in every aspect of this study and my life.

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ABSTRACT

ABSTRACT

Post-flood establishment of native woody species and *Arundo donax*, a bamboo-like exotic grass, was studied on the Santa Margarita river in southern California. Type (seed and vegetative), distribution, and density of establishment events were compared.

Native woody species and *A. donax* share the ability to resprout readily after being damaged by floods. Establishment of new individuals by *A. donax* was primarily vegetatively, whereas native woody species established mostly by seed. Only a few cases of vegetatively established native woody species were observed, and no *A. donax* seedlings were observed.

The distribution of establishment events was examined on fluvial landforms (channel bed, channel bank, depositional bar, and floodplain shelf). Vegetative establishment by *A. donax* and native seedling establishment occurred at the highest density on the same fluvial landform, depositional bars. There was also a high density of native seedlings on the channel bank and channel bed where there was little *A. donax* establishment. When establishment was examined in terms of elevation relative to the middle of the river channel, separation existed between *A. donax* vegetative establishment and native seedling establishment. Native seedlings occurred at the lowest elevation classes and *A. donax* at higher elevation classes, with little overlap occurring. This separation supports that native seedlings are

establishing when the flood waters are receding, and that *A. donax* is establishing when floods are at or near their maximum levels.

Although vegetative establishment was the only method of spread for *A. donax*, the densities recorded were very low, especially in comparison to native seedling densities. However, experiments performed to examine the ability of *A. donax* propagules to grow under a wide range of physical conditions that might be imposed upon them in unpredictable flood dispersal suggests that survival of *A. donax* vegetative establishment is probably quite high. A greenhouse experiment examined the effect of desiccation on the ability of rhizomes and stems to sprout. Stems were able to lose approximately 23% moisture and still sprout, and rhizomes 40% moisture and still sprout. A field experiment showed that the ability of rhizomes to sprout was not affected by depth of burial (10, 50 and 100 cm), and that deeper burial produced larger shoots with lower mortality rates. The ability of rhizomes to grow in the dark indicates that they could survive burial by alluvial deposits and flood debris, and that they could grow when deposited under the canopy of other vegetation.

Although the native woody species are prolific producers of seed, the seedlings have a high mortality rate and grow slowly compared to vegetatively established *A. donax*. The ability of rhizomes and branches to withstand drying and the ability of the rhizomes to sprout at a variety of depths may partly explain *A. donax*'s success at establishing after flood events and its rapid spread and dominance in some riparian systems. The results of this study provide information applicable to the *A. donax* removal efforts in southern California riparian systems.