

THE IMPORTANCE OF LAYERING IN THE RAPID SPREAD OF *ARUNDO DONAX* (GIANT REED)

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ABSTRACT

Arundo donax L. (Poaceae) is an invasive, perennial grass that grows in many-stemmed, cane-like clumps. It does not produce viable seeds in California and is currently thought to invade habitats rapidly by rhizomes and fragments only. But, during a two-year field study in the Tijuana River Valley, California, expansion of *A. donax* clumps via rhizomes was slow, only 0.29 m 2 yr⁻¹, and new recruits from fragments were rare, only 4.7 ha⁻¹ yr⁻¹. Whereas layering, a mode of spread heretofore ignored by researchers, was common in the flood zone. Layering is the adventitious sprouting of stem tips in contact with the ground. Layering can be considered to be both expansion of a clump (while the layering stem is still alive and attached to the clump) and asexual reproduction (after the layering stem dies). When viewed as clump expansion, layering was 7.4 times faster than the annual expansion via rhizomes. When viewed as reproduction, layering produced 25 times more new recruits than fragments. Layering was therefore an important means by which *A. donax* was spreading within the flood zone.

A new general view of *A. donax* invasion is presented illustrating that fragmentation is the means by which *A. donax* invades a new site in the flood zone, expansion via rhizomes maintains an *A. donax* clump, and layering is the means by which *A. donax* spreads quickly and episodically within the flood zone. Outside the flood zone, *A. donax* expands slowly via rhizomes only and no new recruits arrive from either fragmentation or layering.

The Tijuana River Valley results challenge the current “top-down” management policy, which presumes that most new recruits come from upstream and that all clumps expand at the same rate. The results show that, on the contrary, most new recruits come from within the habitat, via layering, and that clumps in the flood zone expand faster than those outside the flood zone. I conclude that the top-down policy is counter-productive and suggest that managers shift to controlling *A. donax* “inside-out,” i.e., conduct treatments first inside and then outside the flood zone. In this way, the fastest expanding clumps – those in the flood zone – will be treated first.

Key Words: *Arundo donax*, giant reed, layering, spread, plant fragments, rhizomes, top-down, inside-out.

Arundo donax L. (Poaceae), giant reed, is a large perennial grass from the Mediterranean region that has become a serious pest in tropical and temperate parts of the world and is now on the list of the 100 World’s Worst Alien Species (Global Invasive Species Database 2005). In California it is known to severely degrade wildlands by altering vegetation structure, displacing native plant species, reducing habitat quality for native animal species, and increasing fire frequencies (Dudley 2000). *Arundo donax* is particularly damaging in California’s riparian habitats because these are already “endangered” due to losses from channelization, damming, development and agriculture (Faber et al. 1989). An enormous amount of effort and millions of dollars are currently being expended controlling *A. donax* in riparian habitats in California (e.g., Katagi et al. 2002).

In order to prioritize sites and determine the best control methods, one needs detailed knowledge of the means of spread of an invasive species (Radosevich et al. 1997; Bryson and Carter 2004). Unfortunately, as several authors have com-

plained (Hoshovsky 2003; McWilliams 2004), there are few studies of the basic biology of *A. donax*. If we divide spread into the expansion of existing plants and the establishment of new recruits, we find that neither has been well studied.

Most authors note that *A. donax* expands rapidly once established and they presume that it is via rhizomes (Else 1996; DiTomaso 1998), but there has not been a published field study that has measured the lateral expansion of clumps of *A. donax*. Instead studies have focused on the vertical growth of a single stem – under normal conditions (Perdue 1958), after a fire (Rieger and Kreager 1989) and under various lab conditions (e.g., Motamed and Wijte 1998; Boose and Holt 1999; Decruyenaere and Holt 2001).

Arundo donax reproduction studies are also rare. In California, *A. donax* does not produce viable seed (Perdue 1958; Bell 1993) and therefore does not reproduce sexually. It is currently believed that asexual reproduction through fragmentation is the primary method of establishment of new plants (e.g., Bell 1997). Else (1996)

found new recruits from fragments to be common in the lower reaches of Santa Margarita River. From that observation the current view of the reproduction and dispersal of *A. donax* has developed:

Flood events break up clumps of *A. donax* and spread the pieces downstream. Fragmented stem nodes and rhizomes can take root and establish as new plant clones. Thus invasion, spread, and therefore management, of *A. donax* is essentially an intra-basin and downstream phenomenon. (Bell 1997; see also Else 1996; DiTomaso 1998).

This view that plant fragments drive the reproduction and dispersal of *A. donax* plays an important role in determining management policies. In particular, the emphasis on invasion from upstream has led to the policy of conducting control activities from the “top-down” in a watershed (e.g., Else 1996; Vartanian 1998). This policy has, in turn, driven management activities and funding decisions. Yet the top-down policy is based on very few data — mainly anecdotal evidence and the surveys by Else (1996), which were conducted during only one month at only one watershed. The extensive control effort being waged against this plant calls for more studies of its spread so that the empirical basis of management policies can be strengthened.

The main goals of this paper are to: (1) describe the lateral expansion of established *A. donax* clumps in the wildlands of the Tijuana River Valley; (2) examine the mechanisms and frequency of establishment of new clumps within the valley; (3) compare the observed spread with that predicted by the current literature; and (4) suggest changes to the current management policies.

STUDY SITE

The Tijuana River Valley is a valuable wildland within urban Greater San Diego (Fig. 1). The valley is a coastal flood plain at the downstream terminus of the 448,000 ha Tijuana River watershed (Concur 2000). The valley stretches from the international border crossing at San Ysidro to the ocean at Imperial Beach and spans 1,457 ha at approximately sea-level (Southwest Wetlands Interpretive Association 2002). It consists of riparian, coastal sage scrub, freshwater, tidal estuarine channels, and coastal salt marsh habitats. The valley is mostly public land and includes a county regional park, a state park, a national wildlife refuge, and an estuary that is a designated National Estuarine Research Reserve and Ramsar Wetland of International Importance.

Several invasive, non-native plants are present in the valley, including *A. donax*, salt cedar (*Tamarix* spp.), and castor bean (*Ricinus communis* L.). Managers of the public lands considered these invasive species a major threat to the sensitive ecosystems within the valley (Concur 2000) and an invasive plant control program was begun in 2002 (Southwest Wetlands Interpretive Association 2002; Boland 2004). A study of the invasive species found that *A. donax* was particularly abundant on the edges of the dense willow forest and occupied approximately 17 of the total 1,457 ha (Southwest Wetlands Interpretive Association 2002). In addition, *A. donax* was common upstream in Mexico (Woch 2005).

This study was started in May 2003, ran for two years, and was influenced by three rainfall seasons. The 2002–2003 season had an average amount of rainfall (27.0 cm in San Diego), the 2003–2004 season was relatively dry (13.2 cm), and the 2004–2005 rainfall season was the third wettest in San Diego history with a total of 57.2 cm of rain (Western Regional Climate Center 2005). The unusually heavy rainfall in San Diego produced only moderately heavy flows in the Tijuana River Valley because the upstream dams were refilling after several dry years. Flow rates in the valley have been collected since 1962, and the 2004–2005 flood season was a 1-in-5-year event for flood duration (number of days when flows were >10 m³ sec⁻¹), and a 1-in-9-year event for maximum flow (International Boundary & Water Commission 2006).

In this paper, I use the term “flood plain” to mean the relatively flat area that borders the river and is subject to flooding, and the term “flood zone” to mean the part of the flood plain that was actually flooded the previous winter. The flood zone may also be called the “active floodplain.” The size of the flood zone varies from year-to-year and was widest, during this study, in the winter of 2004–2005.

ARUNDO DONAX

A. donax is a reed-like perennial grass that grows in large clumps, or patches, many meters across and several meters tall (Fig. 2). The clump is composed of: mature branched stems, or culms, (A); younger, unbranched stems (B); rhizomes or root-stock (D); and roots (E). It also includes many standing dead stems, both branched and unbranched (C).

The clump does not produce viable seeds in California and spreads via rhizomes (D), fragments (F) and layers (G). Fragmentation occurs when a piece of a plant, either rhizome, stem or branch, breaks off the original clump and grows into a new plant elsewhere (Else 1996; DiTomaso 1998; Cronk and Fennessy 2001; Decruyenaere and Holt 2001). Layering, also called tip-layering

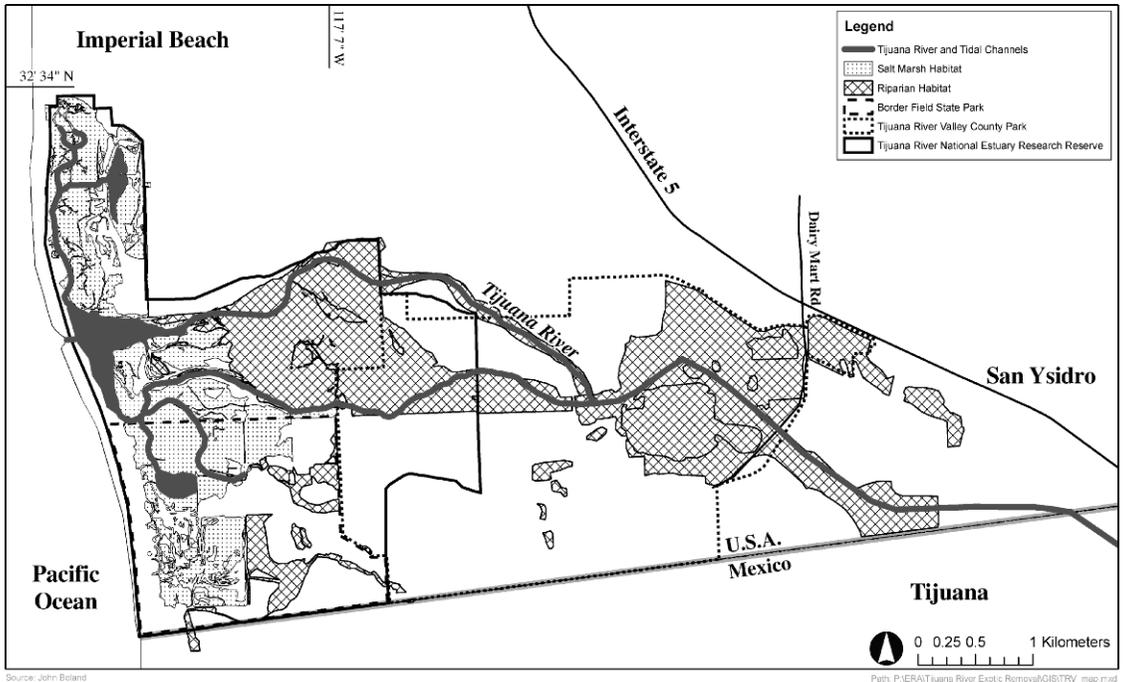


FIG. 1. Map of Tijuana River Valley showing the main habitat types and the boundaries of the parks and research reserve.

or ground-layering, occurs when a normal stem forms roots and shoots adventitiously where it contacts the soil (Grace 1993). Because the layering stem is frequently embedded in mud it usually dies within a few months leaving a fully independent young plant several meters from the original clump (personal observation).

The three means by which *A. donax* invades space – rhizomes, fragments, and layers – are a mix of asexual reproduction and growth. Asexual reproduction is defined as the “numerical increase in physiologically independent plant units by clonal means” (Grace 1993). Fragmentation is therefore clearly asexual reproduction

because an independent plant is formed. The expansion of an *A. donax* clump via rhizomes is clearly vegetative growth because rhizomes are long-lived and the stems growing from the rhizomes remain interconnected. On the other hand, layering can be considered both expansion of a clump and asexual reproduction; it is expansion when the layering stem is still alive because the layer is still attached to the clump, and it is asexual reproduction when the layering stem dies, because the new shoots have become an independent plant. Because of the dual nature of layering, I examined it as both expansion of a clump (along with rhizomes) and as asexual reproduction (along with fragments).

METHODS

Expansion of Clumps via Rhizomes

The lateral expansion of *A. donax* via rhizomes was monitored for two years at 19 clumps in the Tijuana River Valley. The clumps were randomly chosen using a cluster sampling design; 9 occurred inside and 10 outside the flood zone of 2005. The clumps were roughly circular and the basal circumference of each clump was measured using measuring tape and converted to basal diameter; the average starting basal diameter was 5.5 m (std. dev. = 2.4; range = 2.1–11.8 m; n = 19). In order to monitor horizontal expansion of each clump, two stakes were driven into the soil

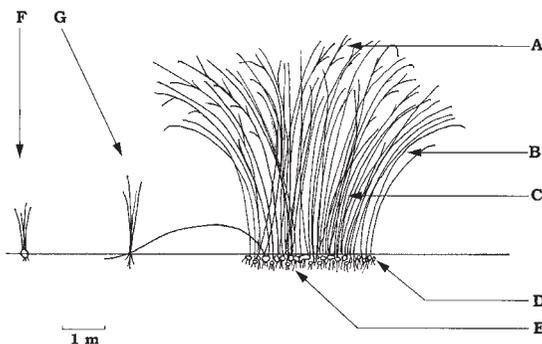


FIG. 2. Diagram of a clump of *A. donax* showing its various structures including the creation of new clumps via layering and fragmentation. See text for explanation of the letters.

at the leading edge of the upright stems. The stakes were placed on either side of the clump on a randomly chosen diameter – either in a north-south or east-west direction. The stakes were placed, numbered, and photographed in May 2003, and revisited in May 2004 and May 2005. During revisits, the expansion outwards from the stake (i.e., the distance between the stake and furthest new stem) was measured with a meter stick. The expansion of each clump over two years is reported as the average of the May 2005 measurements made at that clump's stakes (± 1 SE). Three stakes at three different clumps were lost through vandalism; therefore three clumps are represented by a single May 2005 measurement. The expansion rates of the clumps inside and outside the flood zone were compared using a t-test (F-test indicated homogeneity of variances; $p = 0.01$).

Expansion of Clumps via Layering

Expansion via layering was measured at the 19 monitored clumps for two years (May 2003–May 2005). During each visit, the entire periphery of the clump was searched for newly established plants from layers. Each new recruit was excavated and determined to be a layer if it was clearly growing from a stem that was still attached to the parent plant. When a layer was found, the most distant shoot on the layer was labeled with flagging tape, and its distance from the clump was measured. The average distance of expansion via layers was calculated for the clumps that produced layers ($n = 6$) and this was compared to the average distance of expansion via rhizomes at the same clumps using the Wilcoxon two-sample test (data are presented as means ± 1 std. err.). The non-parametric test was used because the F-test indicated that the variances were not homogeneous ($p > 0.05$).

Frequency of Layering Clumps in the Valley

A survey was also conducted to determine the frequency of layering clumps in the valley as a whole. The proportion of clumps expanding via layers during 2005 was estimated by sampling at ten sites throughout the valley during August 2005. The sites, five inside and five outside the flood zone of 2005, were chosen in a stratified-random manner. At each site, a westward transect was walked and every *A. donax* clump within 15 m was examined until a total of 20 clumps had been reached. At each clump the entire periphery was searched for newly established plants from layers. A new recruit was considered to be a layer only if it was clearly growing from a stem that was still attached to the parent plant. [Old layers, which have many, tall stems and thick rhizomes, were not included in the counts.] Each clump was

tallied as either having: 0, 1–4, or >4 layers. A total of 100 flood zone and 100 outside-flood zone clumps were examined in this way.

Density of New Recruits from Fragments and Layers

The valley was surveyed for new recruits during June 2005 using the same procedures as Else (1996). Eight transects across the river valley were chosen in a stratified-random manner. The transects were 2 m-wide belts which ran perpendicular to the river channel and extended from the southern edge to the northern edge of the 2005 flood zone. The boundary of the flood zone was determined by the presence of debris indicating the highest flood level of the 2004–2005 flood season. The lengths of the transects varied depending on the width of the flood zone (range = 97–865 m; $n = 8$). The total area surveyed was 0.84 ha. Within the transect, the length of each established *A. donax* adult was measured and the numbers of new *A. donax* recruits from fragments and layers were counted. Each new recruit was excavated and determined to be a layer if it was clearly growing from a stem that was still attached to the parent plant, or a fragment if it was growing from a plant part that was not attached to the parent plant. Non-parametric tests were used on these data. The Wilcoxon's signed-rank test was used to test for differences between the numbers of new recruits from fragments and those from layers within the transects ($n = 8$ transects), and the Chi-square Test with Yates' correction was used to test for differences between the total numbers of recruits from fragments in these transects (0.84 ha) and in the transects conducted at Santa Margarita River by Else (1996; 0.70 ha). The average density of new recruits from fragments and layers in the valley was estimated from these surveys and is reported as the number per hectare.

When only a few new recruits from fragments were found in the whole-valley surveys a second set of surveys was conducted during June 2005 in the eastern part of the valley around the Dairy Mart Road Bridge. The Tijuana River enters the valley in the east and the first obstacles to its flow are the bridge and the willow forest nearby. The site had many debris piles and if fragments were abundant anywhere in the valley they were expected to be common there. Five survey areas, each $100\text{ m} \times 50\text{ m}$, were placed around the bridge and in the forest. Within each survey area, six randomly-chosen belt transects ($2\text{ m wide} \times 50\text{ m long}$) were surveyed using the same procedures as described above, i.e., along the transects, the length of established *A. donax* adults was measured and new *A. donax* recruits were excavated, determined to be fragments or



FIG. 3. Photograph of a layering stem. The stem (coming in from the left) has become buried and has formed new shoots, rhizomes and roots adventitiously at a buried node. This layer was produced in open space 6 m from the parent clump and was 0.6 m tall. (A blackboard has been placed in the background.)

layers, and counted. A total area of 0.3 ha was surveyed in this eastern site.

RESULTS

Expansion of Clumps via Rhizomes

Of the 19 *A. donax* clumps monitored in 2003, all were alive when re-examined in 2004 and 2005. Nine of the clumps had been inundated by flooding that occurred during the record rains of 2004–2005 but none was damaged; the only obvious changes were that some of the standing dead stems had been removed and sedimentation (up to 15 cm at the stakes) had occurred. There were no obvious changes to the ten clumps that had not been inundated.

The *A. donax* clumps expanded slowly via rhizomes. Over the two years of monitoring the mean expansion of the basal edge of a clump was only 0.29 ± 0.04 m 2 yr^{-1} (range = 0–0.63 m; $n = 19$). The two-year expansion rates were significantly faster at clumps that were growing inside the flood zone (mean = 0.41 ± 0.05 m 2 yr^{-1} ; $n = 9$) than those growing outside the

flood zone (mean = 0.18 ± 0.04 m 2 yr^{-1} ; $n = 10$; t-test $p < 0.01$).

Expansion of Clumps via Layering

No layers were formed at monitored clumps during the relatively dry winters of 2002–2003 and 2003–2004, when the clumps were not inundated by floodwaters. But, during the wet winter of 2004–2005, 80 layers were formed at the inundated monitored clumps. Layers were typically formed when an attached stem bent over or fell over and flooding caused its tip to become embedded in wet mud; within a few weeks the embedded nodes sprouted stems and roots, and then grew into new, multi-stemmed plants (Fig. 3). The layers tended to be produced at the edge of the canopy and the average distance of the layers from the base of the monitored clump was 3.31 ± 0.40 m ($n = 6$) for the clumps that produced layers. This expansion distance was significantly greater than the average distance of expansion via rhizomes at the same clumps over the two years (0.45 ± 0.06 m 2 yr^{-1} ; $n = 6$; Wilcoxon two-sample test; $p < .005$).

TABLE 1. THE DENSITY OF *A. DONAX* RECRUITS FROM FRAGMENTS AND LAYERS IN SURVEYS CONDUCTED IN THE SANTA MARGARITA RIVER (ELSE 1996) AND THE TIJUANA RIVER VALLEY. ELSE (1996) DID NOT COUNT LAYERS.

Site	Santa Margarita River	Tijuana River Valley – entire valley	Tijuana River Valley – eastern river
Source	Else (1996)	this study	this study
Survey area (ha)	0.697	0.837	0.300
Established <i>A. donax</i> % cover	—	10%	1%
<i>A. donax</i> recruitment from fragments			
Fragments (#)	69	4	1
Fragments per ha	98.9	4.7	3.3
<i>A. donax</i> recruitment from layers			
Layers (#)	—	99	6
Layers per ha	—	118.2	20.0

These data show that some clumps within the flood zone expanded rapidly by producing many distant layers.

Frequency of Layering Clumps in the Valley

The valley-wide surveys of clumps provided a broad measure of the frequency of layering in the valley and in particular a measure of the proportion of clumps undergoing rapid expansion. Inside the flood zone, layering was common: 88% of the randomly chosen clumps had layers (79% had >4 layers; 9% had 1–4 layers; 12% had 0 layers; n = 100 clumps). Outside the flood zone, all clumps had 0 layers (n = 100 clumps). These results show that layering only occurred within the flood zone and that most clumps inside the flood zone spread quickly by producing many layers.

Density of New Recruits from Fragments and Layers

The belt surveys showed that new *A. donax* recruits growing from fragments were rare in the Tijuana River Valley. Only four were present in the transect surveys of the entire valley (Table 1). This was significantly fewer than the 69 recruits from fragments counted by Else (1996) over a smaller area in the Santa Margarita River (Table 1; Chi-square Test with Yates’ correction; $p < .005$). Even at the eastern river site within the Tijuana River Valley, where I expected fragments to be abundant, only one was present.

On the other hand, the belt surveys confirmed that new *A. donax* recruits growing from layers were common in the Tijuana River Valley. Ninety-nine layers were present along transects across the entire valley (i.e., within 0.84 ha) making layers 25 times more common than recruits from fragments (Table 1). This difference was statistically significant (Wilcoxon’s signed-rank test; n = 8 transects; $p < .01$). Because layers are produced by established adults, it might be presumed that where adults are rare

layering would be relatively unimportant. But in the eastern river, where established *A. donax* clumps were rare (only 1% cover), there were more new recruits from layers than from fragments (Table 1).

DISCUSSION

Spread of *A. donax* by Rhizomes, Fragmentation and Layering

The current view of *A. donax* spread is that it is fast and accomplished by rhizomes and fragments only (e.g., Dudley 2000). As pointed out by Hoshovsky (2003) and McWilliams (2004) this view is based on mainly anecdotal evidence and little published field data (cf. Else 1996). In this two-year study within the Tijuana River Valley I found that *A. donax* expanded slowly via rhizomes, and new recruits from fragments were rare; but layering was common and layering resulted in clumps expanding quickly and adding many new recruits. These findings show that there needs to be a re-evaluation of spread by *A. donax* and the roles played by its different plant parts – rhizomes, fragments and layers.

The thick, short-noded, many-branched rhizomes of *A. donax* consolidate space rather than quickly invade new space. The fastest expansion via rhizomes was in the flood zone and averaged only 0.41 m² yr⁻¹. Although not expanding quickly, rhizomes are constantly reinvading space within their own clumps and sending up more stems within the clump which results in clumps becoming more dense and there being no “dead center” (personal observations). *Arundo donax* rhizomes appear to fit the description of “pachymorphic” rhizomes, which are designed for carbohydrate storage, and protection from fire, frost, grazers, and desiccation, rather than for fast expansion (Cronk and Fennessy 2001).

Fragments did produce new recruits within the flood zone of the Tijuana River Valley but they were rare in comparison to the number found along the Santa Margarita River by Else (1996).

Considering that conditions were ideal for the production of many new fragment recruits – 2004–2005 had a long and wet rainy season – this may be close to the maximum invasion density for the valley. Fragments are likely to be important in the long-distance dispersal of *A. donax* but, at these densities, they cannot account for the fast spread of *A. donax* within a site.

Layering was common in the flood zone of the Tijuana River Valley during 2005; most of the randomly-chosen clumps in the flood zone had five or more layers. By Grace's (1993) definition of asexual reproduction, layering is first expansion of a clump (like rhizome growth) and then asexual reproduction (like fragmentation). When viewed as expansion, layering was 7.4 times faster than the annual expansion via rhizomes, and when viewed as reproduction, layering produced 25 times more new recruits than fragments. It is clear that layering was an important means by which *A. donax* spread in the flood zone.

How frequently *A. donax* clumps expand at this rate is unknown. It is possible that abundant layering occurs only when rainfall is sufficient to bend stems and flooding is sufficient to produce enough sedimentation to bury stem tips. The 2004–2005 flooding was a 1-in-5 to 1-in-9-year event (International Boundary & Water Commission 2006) and abundant layering may therefore be as episodic as once every 5 to 9 yrs. Even at this frequency, layering would result in faster expansion of clumps than rhizomes, and more new recruits than fragments.

Layering is a common trait of many invasive plants (Reichard 1996), and is important in the spread of several invasive species including, *Rosa multiflora* Englm. (Gleason and Cronquist 1991), *Cotoneaster* spp. (Sigg 2000), *Rubus discolor* Weihe & Nees (Hoshovsky 2000), and *Lonicera japonica* Thunb. (Florida Exotic Pest Plant Council 2003). But layering has been largely ignored in the *A. donax* literature; it is not mentioned at all in papers that have focused on spread, e.g., Bell 1993; Else 1996; Bell 1997; DiTomaso 1998; and Hoshovsky 2003. Dudley (2000) in his excellent review of the literature on *A. donax* did describe layering, i.e., “root formation does occur where an attached culm has fallen over and is in contact with the substrate,” but went on to say that *A. donax* “spreads vegetatively either by rhizomes or fragments” leaving out layering entirely.

I suggest the following general history of *A. donax* invasion into a section of flood zone at a site like the Tijuana River Valley (Fig. 4). It is based on the results of this paper and describes the invasion over approximately 10 yrs showing when the different plant structures (fragments, rhizomes, and layers) are important. The starting point is an idealized section of flood zone with a permanent pool (left), a stand of dense willows

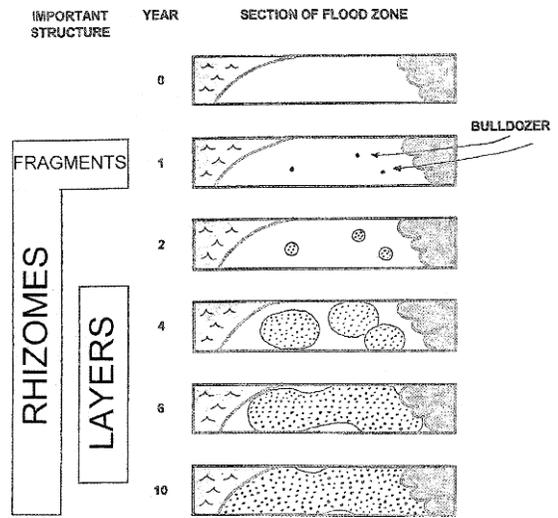


FIG. 4. General history of *A. donax* invasion into an idealized portion of flood zone over 10 yrs showing when the different plant structures (fragments, rhizomes, and layers) are important.

(right) and some open ground with low-growing annuals (center). A bulldozer disturbs an *A. donax* stand upstream and during Year 1 three rhizome fragments are washed into the site. [Bulldozers appear to be the most common cause of clump break-up and rhizomes are the most viable plant fragments (Boland unpublished data).] Fragments, although rare, are important in the initial invasion of a large area of bare space. The fragments become established and slowly expand via growth of their rhizomes to become small clumps.

By Year 4 the clumps' stems are long enough to bend over and touch the ground and they start producing layers. Many layers are produced during favorable years and the clumps expand rapidly and episodically via layering during the next few years. Layering is important as a means of rapidly invading open space near the clump. But there are barriers to the spread via layering – layers do not form in permanent pools of water and stems cannot lay down in dense willows or dense *A. donax*. Therefore *A. donax* does not enter the pool or the dense willows.

Finally, the entire open space is taken over by *A. donax*, which is being maintained by the continuous expansion of rhizomes only. Each plant structure plays a different role in the invasion: fragments provide the initial long-distance dispersal; rhizomes maintain the clump; and layers carry out the fast spread into open space.

In dry sites, outside the flood zone, the history is less dynamic; *A. donax* clumps expand slowly outwards via rhizomes only. There are no new recruits from layers or from fragments. These areas remain strikingly similar from year to year.

The history described in Fig. 4 comprises a new vision of the dynamics of *A. donax* at a flood zone site in southern California. There are three important points in this new vision (compare with Else 1996; Bell 1997; Dudley 2000). First, recruitment via fragments is less common than previously reported, and fast spread is not due to frequent new invasions via fragments. Second, layering is more common than recognized and clumps use layering to quickly invade open space. And third, because layering is the production of new recruits by the existing clumps, the majority of new recruits come from within the site rather than from outside the site, i.e., most recruits come from layers, not from fragments.

Recruits from Fragments: Tijuana River Valley v. Santa Margarita River

Fragments have been considered the primary mechanism of *A. donax* invasion because Else (1996) found them to be abundant in the Santa Margarita River (Bell 1997; DiTomaso 1998; Dudley 2000). But fragments were not abundant in the Tijuana River Valley, not even in the eastern river site where one would have expected them to be common among the debris trapped at the bridge and in the forest. This was not because conditions were poor for the production of fragments – the significant rainfall of 2004–5 should have produced ideal conditions for recruitment via fragments.

I propose two hypotheses to account for the significant difference in density of recruitment from fragments in the two rivers. First, I suggest that the invasion rates Else (1996) obtained were unusually high because intensive *A. donax* control activities were being conducted on the Santa Margarita River at the time. These control activities included the mechanical removal of whole *A. donax* clumps (roots, rhizomes and stems), the grinding of the material in a tubgrinder, and the return of the ground material to the site without herbicide application (Slader Buck personal communication). The chances that living pieces of *A. donax*, particularly rhizomes, accidentally escaped these activities were high. I suggest that these fragments were washed downstream by the winter floods of 1994–1995 and that when Else (1996) did her surveys in July 1995 she counted unnaturally high densities of recruits from fragments. Support for this hypothesis comes from descriptions of later mechanical removal operations in the same watershed; Giessow and Giessow (1999) found high densities of recruits from fragments in an area where mechanical removal had been used and wrote that “most of the *Arundo* resprouts that occurred resulted from small pieces of rhizome that broke off during the mechanical removal process.” In addition, the rainfall during the season before

Else’s surveys was 71% above average (Western Regional Climate Center 2005). There was therefore more than sufficient rainfall to disperse the fragments and to provide moist conditions for their successful recruitment. I suggest that these circumstances combined to produce an unnaturally high number of new recruits from fragments in the areas that Else surveyed in Santa Margarita River in July 1995.

Second, it is also possible that the invasion rate at Santa Margarita River was high because there are no dams on the river to block the downstream flow of water-borne propagules, whereas most of the other major watersheds in southern California, including Tijuana River, are dammed. It is possible that dams are important barriers to the dispersal of the water-borne propagules of *A. donax*.

These hypotheses are not mutually exclusive, both may be correct, and both may explain some of the observed difference in the recruitment rates at Tijuana River and Santa Margarita River. It is clear that more research needs to be done on recruitment rates at these and other sites, and on the influence of dams and mechanical treatment techniques on fragment recruitment downstream. But, it appears that the general importance of fragments in the spread of *A. donax* may have been exaggerated because of where and when Else (1996) did her study.

Strategy for the Control of *A. donax*

New information about the spread of an invasive species inevitably leads to a re-evaluation of the strategies being used to control that species. The current management strategy for the control of *A. donax* is to use mainly chemical treatments and to begin in the upper watershed and progressively work downstream (i.e., “top-down;” e.g., Else 1996; Vartanian 1998). This strategy is based on the assumption that *A. donax* clumps are constantly producing abundant fragments that invade downstream sites; thus, one should eliminate the upstream source of recruits before treating plants downstream. This assumption, however, is only partly correct; in the Tijuana River Valley, new recruits from fragments did occur but they were relatively rare. Instead, layering by existing clumps created the vast majority of the new recruits in the flood zone. A space in the Tijuana River flood plain was 25 times more likely to be invaded by a layer from within than by a fragment from without (Table 1). Even at sites where *A. donax* was rare (i.e., only 1% cover), recruitment from layers was more common than recruitment from fragments. Therefore, the spread of *A. donax*, contrary to the current view (e.g., Bell 1997 quoted in the Introduction), was mostly a within-site phenomenon rather than a downstream phenomenon.

The top-down policy is also based on a second, but unstated, assumption that all clumps of *A. donax* are expanding at an equal rate. The Tijuana River Valley results show that this assumption is not correct; *A. donax* clumps inside the flood zone expanded more quickly, via both rhizomes and layers, than clumps outside the flood zone.

The two assumptions that are the basis for the top-down policy are therefore not valid and the top-down approach is actually counter-productive. The control of *A. donax* is expensive and slow, and one finds that under the top-down approach, while controlling some slow-expanding *A. donax* in the upper reaches, other clumps are rapidly expanding into open space in the lower reaches. By the time a top-down project makes it to the coastal flood plain, it is likely that the area has been choked with *A. donax*, is badly degraded and the costs of control have greatly increased.

A more productive management strategy would be to work "inside-out." Under this strategy, treatments would be conducted within the flood zone first and then later in sites outside the flood zone. This would allow control activities to be concentrated in areas where *A. donax* is expanding quickly, and sites with fast-expanding plants should always be given the highest priority (Moody and Mack 1988). A second aspect of the "inside-out" strategy is that treatments should be started wherever *A. donax* is expanding quickly and this could be along any reach regardless of its position within a watershed, i.e., whether at the top, middle or bottom of the watershed. Biologists need to examine their watersheds and identify sites that look like Years 2 and 4 illustrated in Fig. 4 because these are sites where rapid spread is occurring or is imminent (cf. "nascent foci" of Moody and Mack 1988). Treating these sites first will prevent the rapid expansion of *A. donax* and reduce overall costs. The restoration sites can be anywhere in the watershed because the threat of reinvasion by fragments is relatively low. It is also worth noting that when *A. donax* recruits into a site – whether via fragments (Quinn and Holt 2003) or layers (personal observation; Fig. 4) – it does so mainly into open areas and does not easily invade closed canopies. Controlling *A. donax* and restoring native vegetation in the flood zone will tend to close the canopy and reduce the likelihood of future establishment of *A. donax* in that site.

Unfortunately, managers have been prioritizing sites on incomplete information about the way *A. donax* spreads and valuable resources have been wasted treating slowly expanding clumps in the upper reaches of watersheds. With an "inside-out" strategy managers can focus their resources in places where they will be most effective in reducing the spread of *A. donax*.

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