The Ecology and Management of the Kuroshio Shot Hole Borer in the Tijuana River Valley

Final Report

for

US Navy and **US Fish and Wildlife Service**

and

Southwest Wetlands Interpretive Association
Mayda Winter, Project Manager
708 Seacoast Drive, #108
Imperial Beach, California 91932

Cooperative Agreement Award F16AC01065

by

John M. Boland, Ph.D.
Boland Ecological Services
JohnBoland@sbcglobal.net

April 14, 2017

Table of Contents

1. ABSTRACT

- The tiny invasive beetle, the Kuroshio Shot Hole Borer (KSHB), first appeared in the Tijuana River Valley in 2015 and almost immediately did extensive damage. This report examines several aspects of the KSHB's attack during 2016, the KSHB's second year in the valley.

THE SPREAD OF THE KSHB

- The KSHB continued its spread within the riparian forests in the Tijuana River Valley and willow infestation rates were at 100% in many units. I estimated that a total of 355,510 willows, or 88% of the willows in the valley, were infested during the two years 2015-17.

- The KSHB invaded the dryer willow forests during 2016-17, sites that were only lightly infested during 2015-16.

- The forest canopy in the valley was severely damaged by the KSHB attack. The amount of willow canopy lost was 100% in many units and averaged 66% lost in the entire valley.

- I estimate the total number of willow deaths due to the KSHB invasion thus far to be 95,791 trees, or 24% of the willow trees in the Tijuana River Valley.

- The KSHB has not substantially impacted the riparian shrub communities, which are dominated by mule fat.

THE RESPONSE OF THE DAMAGED FORESTS

- Many willow trees that were heavily-damaged by the KSHB during 2015 resprouted in 2016. In some sites, where the previously tall tree canopy was destroyed by the KSHB, there is now an extensive short canopy of resprouting willow "shrubs" up to 4 m tall.

- I estimate the total number of willow trees with resprouts to be 71,280 trees. The average density of resprouting trees was 258 trees per acre, which is greater than the density of plants typically planted in a riparian restoration site.

- The resprouting of willows is noteworthy because it shows that the KSHB does not kill all of the willow trees that it infests, and the new low-canopy forests that these resprouts have created may provide essential breeding habitat for the endangered least Bell's vireo (*Vireo bellii pusillus*) during 2017.

- Some of the willow resprouts (9%) were attacked by the KSHB, with larger diameter resprouts being more likely attacked than smaller ones.

- Invasive plants such as arundo, castor bean and tamarisk are present and growing vigorously in the heavily-damaged forests. Treatment of these invasive plants would greatly assist the recovery of the native forests.

SHOULD MANAGERS REMOVE FALLEN DEBRIS?

- One consequence of the KSHB damage of the forests is that a tremendous amount of debris is littered on the forest floor. Some managers are considering removing this debris to reduce the threat of fire and flooding damage. But we need to know: how would the removal of the debris impact the recovery of native plants?

- I conducted a replicated experiment in the Goat Canyon sedimentation basins to determine whether the extensive debris caused by the KSHB attack impacted the number of native seedlings becoming established. The number of seedlings of willows and mule fat was negatively impacted by the presence of debris. On average there were 2.5 times more native seedlings in the open plots than in the debris plots.

- These results suggest that during the first winter after significant KSHB damage, managers should consider cleaning up the fallen debris in order to promote the natural establishment of desirable native riparian plants.

ADDITIONAL INFORMATION

- First, I examined the KSHB's preference for infesting branches of a particular size. I examined many willow trees, willow resprouts and mule fat branches and concluded that the KSHB prefers to attack willow branches with moderate to large diameters (> 4.5 cm). This is an important finding because it suggests that many young willows (<4.5 cm in diameter) will survive for a few years before they reach a size that is attacked by the KSHB.

- Second, I estimated the total number of KSHB holes in a black willow that was killed by the KSHB in 2015-16 at 26,900 holes. With a few conservative assumptions, I estimate that more than two billion (or 2×10^9) KSHB were born in the Tijuana River Valley during 2015-16. This was likely the single largest production of offspring by the KSHB in California so far.

- Third, I list eleven riparian plant species that would be appropriate to plant in KSHB-infested sites.

NEXT STEPS

- I have proposed several monitoring, research and management actions for 2017-18.

2. INTRODUCTION

The Kuroshio Shot Hole Borer (KSHB; *Euwallacea* sp.) is an ambrosia beetle native to Asia that has recently invaded southern California. It damages and kills trees through its boring activities and associated fungal pathogens (Freeman et al. 2013). Up until 2015 it had been found in avocado groves and landscape trees only (Eskalen *et al.* 2013, Umeda et al. 2016). But in 2015, it appeared in the native riparian forests in the Tijuana River Valley and within a few months it had infested more than 280,000 willow trees and caused major limb damage to more than 140,000 of the trees (Boland 2016). The extensive damage to the native forest occurred with surprising speed and is of grave concern to land managers in the valley and elsewhere in southern California.

It is difficult to predict what is going to happen during this beetle outbreak in the Tijuana River Valley because little is known about the behavior and spread of the KSHB, or any other ambrosia beetle (Hulcr and Dunn 2011). It is therefore imperative that we study this outbreak to learn about its progression and characteristics so managers within the valley and elsewhere have the data to make informed decisions.

Last year, I documented the distribution, abundance and impact of the KSHB in the Tijuana River Valley during 2015-16 (Boland 2016). This current study builds upon that work, examining the KSHB outbreak during 2016-17. I examined the KSHB outbreak from three points of view – the beetle's, the forest's and the manager's – and ask:

1. Did the beetle infestation continue to spread in the valley during 2016?
2. How did the heavily-damaged forests respond to the KSHB infestation?
3. How best can managers promote the recovery of the KSHB-damaged forests?

In this report I provide answers to these questions with the goal of updating resource managers on this emerging problem in natural habitats.

3. THE TIJUANA RIVER VALLEY

The Tijuana River Valley (32^o 33.080'N, 117^o 4.971'W) in San Diego County, California, is a coastal floodplain of approximately 1,500 ha at the end of a 448,000 ha watershed (Figure 1). The river is an intermittent stream that typically flows strongly in winter and spring and is mostly dry in summer (Boland 2014a). The river splits into two in the center of the floodplain at Hollister Bridge, and the northern arm generally carries more of the flows than the southern arm because of extensive sedimentation within the southern arm.

Riparian forests in the river bed are numerically and structurally dominated by *Salix lasiolepis* (arroyo willow) and *Salix gooddingii* (Goodding's black willow), and the surrounding riparian scrub is numerically and structurally dominated by the perennial shrub, *Baccharis salicifolia* (mule fat; Boland 2014a). Zonation of these three dominant species across the elevation gradient and the factors that produce their zonation were described in Boland (2014a).

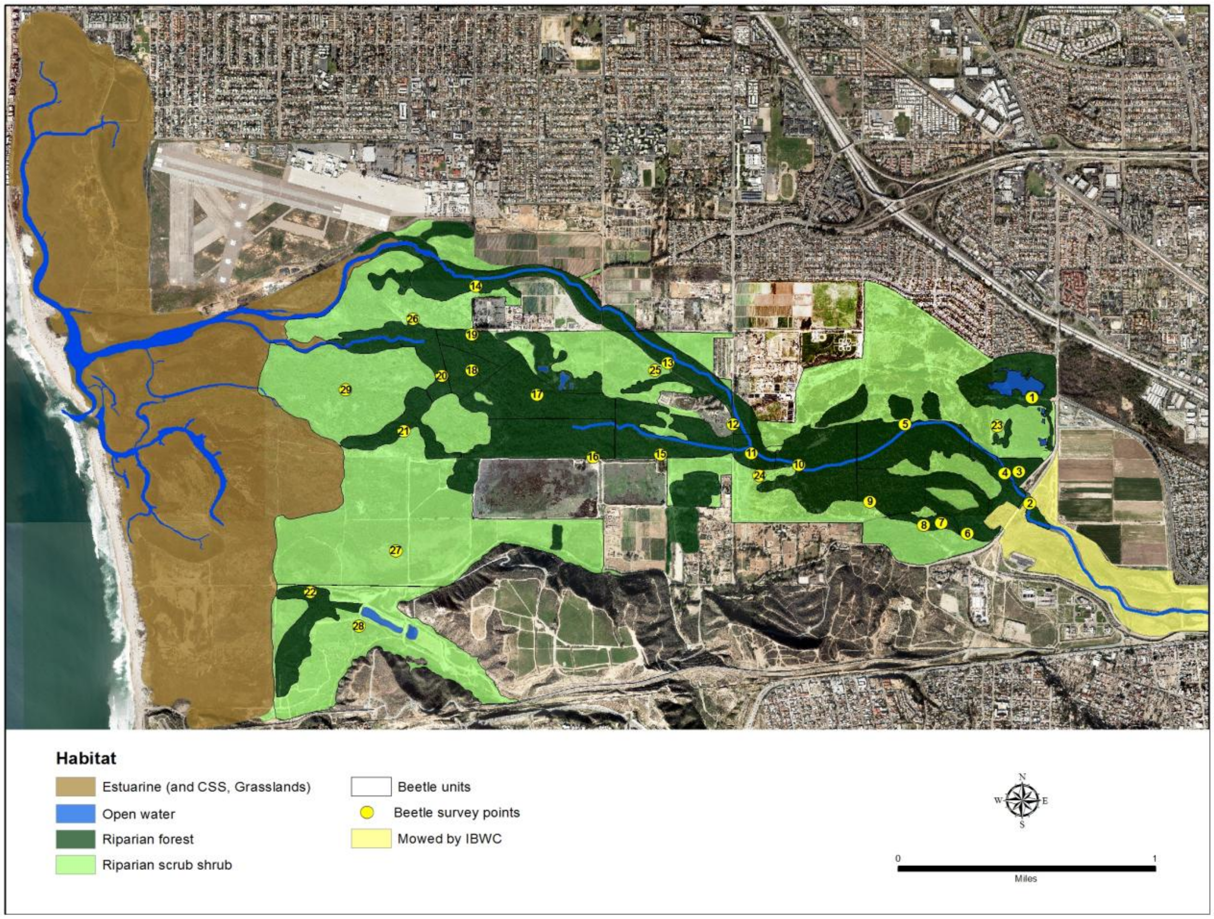


Figure 1. The location of the riparian forest and riparian scrub habitats within the Tijuana River Valley (from Boland 2016). Riparian forests units are numbered 1-22 and riparian shrub woodlands units are numbered 23-29.

The riparian forest and scrub habitats are preserved within three adjoining parks: the Tijuana River Valley Regional Park, the Border Field State Park, and the Tijuana Slough National Wildlife Refuge. The riparian habitats are relatively undisturbed and support numerous reptile, mammal and bird species, most notably the endangered *Vireo bellii pusillus* (least Bell's vireo) for which most of the riparian habitats are designated critical habitats (U.S. Fish and Wildlife Service 1994).

4. THE KUROSHIO SHOT HOLE BORER

Two ambrosia beetles are currently attacking live trees in southern California. These beetles are the Polyphagous Shot Hole Borer (PSHB; *Euwallacea* sp. near *fornicatus*) and the Kuroshio Shot Hole Borer (KSHB, *Euwallacea* sp.; Eskalen 2017). The two species are morphologically identical and are distinguished by their DNA sequences and by their associated fungi (Eskalen 2017). They are part of a species complex that also includes the Tea Shot Hole Borer (*Euwallacea fornicatus*), which has caused devastating damage to tea (*Camelia sinesis*) in at least ten different countries, including

India and Sri Lanka. The PSHB was first documented in Los Angeles County in 2003, and the KSHB was first observed in San Diego County in 2012 (Eskalen et al. 2013; Eskalen 2017; Umeda, Eskalen & Paine 2016). Both beetles are believed to be native to Southeast Asia and both attack many tree species in southern California, including native species, landscape trees, and the economically important avocado (*Persea americana*; Freeman et al. 2013; Eskalen et al. 2013). The ever-increasing list of reproductive host plants used by these species is currently at 49 species for the PSHB and 15 species for the KSHB (Eskalen 2017).

Both beetles damage or kill trees through their boring activities and their spread of fungal pathogens. Females drill into tree trunks, create networks of tunnels in the xylem, inoculate the tunnels with a fungus (e.g., *Fusarium* sp.), and live in the tunnels eating the fungus and reproducing (Biedermann et al. 2009). Within a few weeks new females emerge, fly to new trees, and perpetuate the infestation (Rudinsky 1962). The beetles are tiny (~1mm in length) and seldom seen, however their burrowing activities and impacts are easily seen (Figure 2).

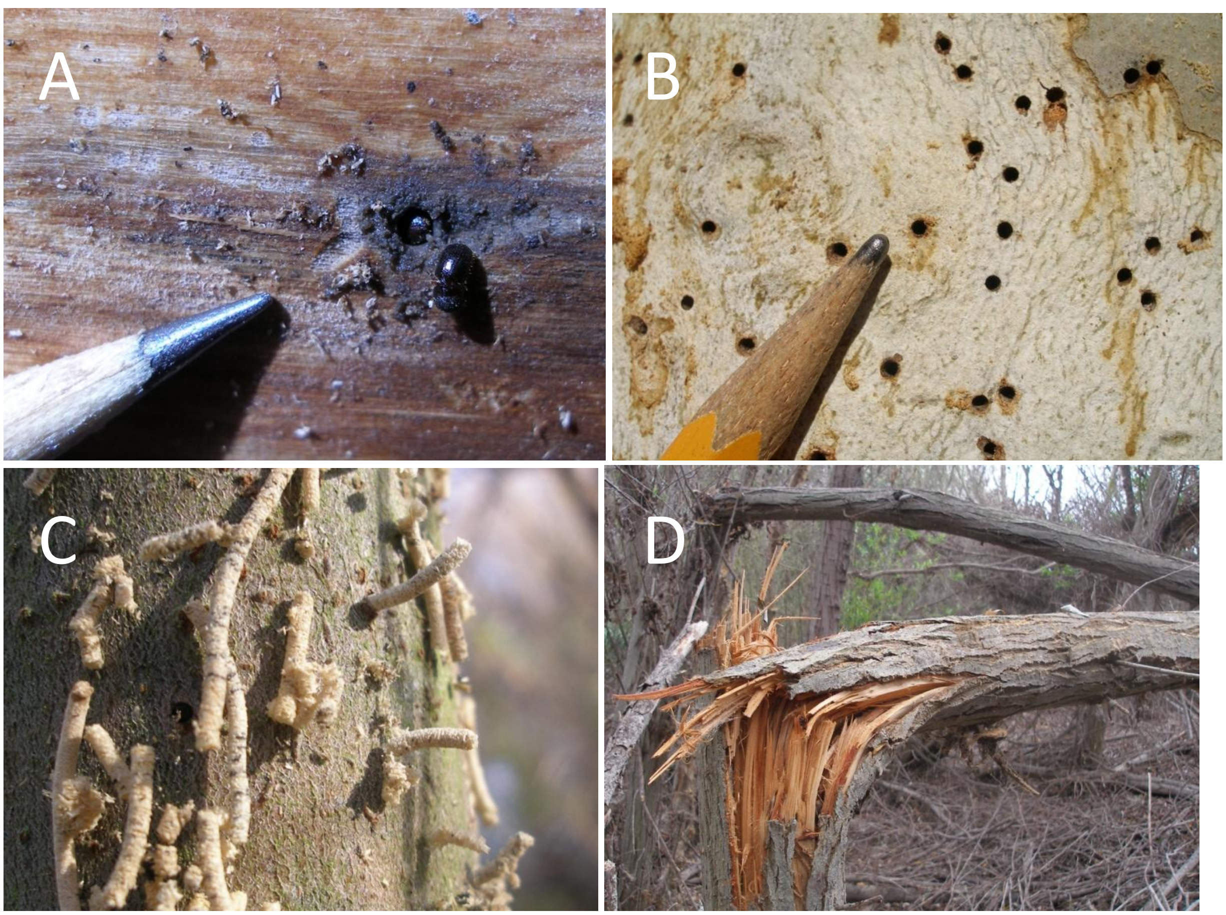


Figure 2. Photos of the KSHB in the Tijuana River Valley (from Boland 2016). (A) Two beetles at the entrance to a tunnel. (B) Holes in the bark of a sycamore. (C) Extrusion of sawdust plugs indicating active burrowing within an arroyo willow. (D) Beetle-infested trunks of arroyo willows snapped by the wind.

5. SUMMARY OF 2015-16 STUDY

These are the main results from my 2015-16 study of the KSHB's impact in the Tijuana River Valley (Boland 2016):

- I divided the riparian habitats of the valley into 29 survey units so that the vegetation within each unit was relatively homogenous in terms of plant species composition, age and density. This resulted in 22 forest units, which were dominated by two willow species, *Salix lasiolepis* (arroyo willow) and *Salix gooddingii* (Goodding's black willow), and seven shrub units dominated by *Baccharis salicifolia* (mule fat). I surveyed the dominant plant species for evidence of KSHB infestation and evidence of major damage such as limb breakage.

- Evidence of KSHB infestation was found in 25 of the 29 units. In the forest units, infestation rates ranged from 0 to 100% and were high (>60%) in 16 of the units. In the scrub units, infestation rates were lower and ranged from 0 to 33%. Overall, I estimated that more than 280,000 (70%) of the willows in the valley were infested with the KSHB

- Infestation rates were significantly correlated with the wetness of a unit; wetter units had higher infestation rates.

- Evidence of major physical damage due to the KSHB was found in 24 units, and dense stands of willows were reduced to broken trunks in several areas. I estimated that more than 140,000 willows had suffered major limb damage.

- Before-and-after photos show the kind of damage seen in the more heavily infested and damaged forest units (Figure 3). The native riparian forest in this unit went from a dense stand of tall willows to a jumble of broken limbs in just a few months.

- Of the 23 common plant species examined, 14 showed evidence of beetle attack. The four species with the highest rates of infestation were all native riparian trees in the Salicaceae (willow) family. The three species considered to be the worst invasive plants in the valley, *Ricinus communis, Tamarix ramosissima* and *Arundo donax* had low rates of infestation.

Several findings from this study had significance for resource managers:

- The KSHB attack caused extensive damage to trees soon after being first discovered so, if managers are to control the spread of the beetle, they will need to develop an effective early detection and rapid response program;

- Infestation rates were highest in units that were wettest, so resource managers trying to detect the beetle in other areas should thoroughly search trees near water, particularly nutrient-enriched water; and

- The infestation altered the structure of the forest canopy, and this was likely to promote the growth of invasive plant species that will now need more attention.

Figure 3. The willow forest in Unit 2 during May 2015 and February 2016 showing the KSHB-induced damage to the dominant willow trees (from Boland 2016).

6. TASK 1 – THE SPREAD OF THE KSHB

The seasonal behavior of the KSHB sets in motion a series of events that determine when one should do certain surveys. The KSHB is mostly dormant early in the year and actively reproducing and spreading during summer and fall (Figure 4). I have therefore measured willow infestation rates near the end of this period, during Dec-Feb. The willows, having been undermined by KSHB activity, are mostly damaged and snapped by winds that occur during winter storms. I have therefore measured willow damage rates near the end of this period, during Jan-Feb. Finally, willows leaf out during spring – first arroyo willows and then black willows. It is at this time when you can determine whether a tree has been killed or not and I have therefore estimated willow mortality rates during June-July.

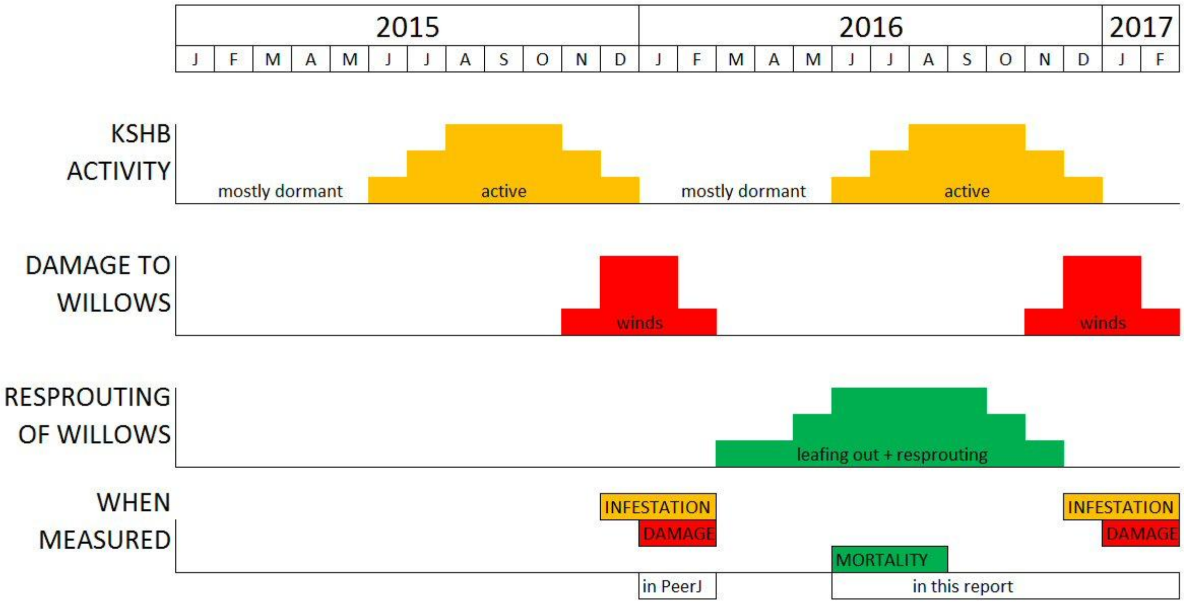


Figure 4. The seasonality of KSHB activity, destructive winds and willow growth dictate the best times to survey willow infestation rates, damage rates and mortality rates. The 2015-16 infestation and damage rates are in the PeerJ paper (Boland 2016), whereas the 2015-16 mortality rates and the 2016-17 infestation and damage rates are in this report.

6.1. KSHB-INDUCED WILLOW MORTALITY 2015-16

My paper on the impact of the KSHB on the Tijuana River Valley (Boland 2016) gave infestation and damage rates but, because it was completed and published in the spring, could not give mortality rates. In order to provide a more complete the picture of the impact of the KSHB during 2015-16 I measured mortality rates in summer 2016.

Methods. To determine the magnitude of willow tree mortality (and resprouting), I resurveyed my 22 forest units in the valley (Boland 2016) during July and August 2016. These are the units numbered 1 to 22 in Figure 1. I examined approximately 74 willow trees (arroyo willows and black willows) within each unit and determined whether each was alive (i.e., leafing out) or recently dead (i.e., not leafing out). A mortality rate was calculated and the number of trees killed was extrapolated for each forest unit.

Results. As of summer 2016, willow mortality rates due to KSHB were as follows.

- The willow mortality rates in the units ranged from 0% (in Units 15, 17 18 and 21) to 97% (in Unit 3).
- The higher willow mortality rates were mainly between Dairy Mart bridge and Hollister; the lower mortality rates occurred mainly west of Hollister (Figure 5).
- I estimated the total number of willow deaths due to the KSHB to be **95,761 trees**, or 24% of the willow trees in the Tijuana River Valley. This means that the average number of willow tree deaths over the entire valley was 160 per acre.
- Mortality rates were positively correlated with 2015-16 infestation rates and damage rates, and negatively correlated with tree age and the unit's distance from water (Table 1).

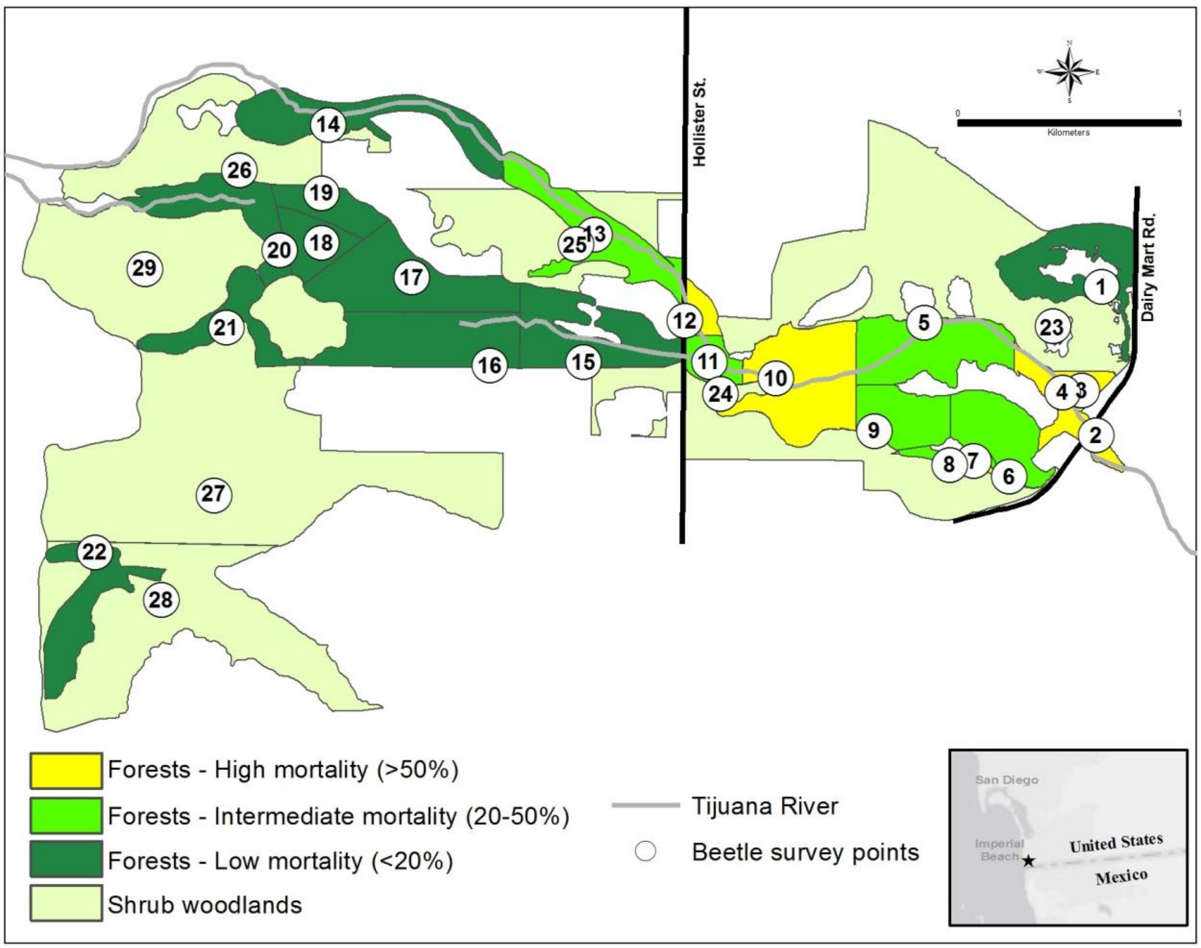


Figure 5. Willow mortality rates in the riparian forests of the Tijuana River Valley as of summer 2016. In this figure, and in all the remaining figures, unit numbers follow those in Figure 1 and Boland (2016).

Table 1. Patterns in the distribution of mortality across units – correlations with six unit attributes.

MORTALITY RATES ACROSS UNITS -- CORRELATIONS				
Attribute	**n**	r^2	**significance**	**p**
Infestation rate of willows (2015-16)	22	0.538	significant	<0.01
Major limb damage to willows (2015-16)	22	0.684	significant	<0.01
Age of willows in units	22	0.313	significant	<0.01
Girths of willows in units	20	0.121	not	
Density of willows in units	22	0.031	not	
Distance of unit from water ('wetness')	22	0.323	significant	<0.01

Discussion. The KSHB swept through the forests during summer and fall 2015, and caused a huge number of deaths to willow trees. My estimate of 95,761 trees killed means that 24% of the willow trees in the Tijuana River Valley were killed.

The impacts of the KSHB were not equal everywhere; the beetle mainly infested, damaged and killed willow trees in the wetter forests. This wetness pattern suggested that the KSHB had a preference for trees in or near the water in the valley.

In 2016, I suggested that this pattern could be because the trees in these wetter areas were growing more vigorously, due to the water and soils being nutrient-enriched by frequent cross-border sewage flows (Boland 2016). This idea needs to be pursued further because, if the KSHB is showing a preference for fast-growing willows within the Tijuana River Valley, then it is likely that it will show a preference for similarly fast-growing trees outside the valley (see Section 11). This will guide authorities to the plants most at risk, i.e., willows growing in or near nutrient-enriched water.

6.2. KSHB INFESTATION WITHIN UNITS – 2016-17 vs. 2015-16

Important questions for the 2016-17 surveys to answer were: Is the beetle continuing to invade all parts of the valley, including the dryer sites? Or is the beetle remaining in the wetter sites, where the first year's infestation was greatest? These questions arose because, in 2015-16, the beetle's impacts in the valley were not equal everywhere – the highest infestation rates were in the wetter forests and the lowest infestation rates were in the dryer forests (Boland 2016), so it appeared possible that for some reason the dryer forests were acting as vital refuges for the willows from the beetle.

Methods. In order to determine the KSHB infestation rates during 2016-17, I resurveyed my 29 units in the valley (Boland 2016) during December 2016 and January 2017. I examined as many willow trees (arroyo willows and black willows) as I could within each forest unit and ~57 mule fat within each shrub unit. A plant was counted as infested if it had beetle holes, extrusion of sawdust plugs or frass, or gumming out of sap. In addition, the severity of the KSHB attack was measured by counting the number of holes within a quadrat (15 x 15 cm = 225 cm^2) placed at breast height on the trunk.

The severity is the average number of holes in the infested trees; zeros of the non-infested trees are not included. The surveys could not be completed within six units – in three of the forest units there were no original trees left standing, i.e., the KSHB had already infested them all (!), and in another three units flooding prevented access. The flooded units had been visited prior to the flooding and an infestation estimate is given here; they will be completely surveyed when the flood waters subside.

Results.

- As of January 2017, the willows in the valley were extensively and severely infested by the KSHB. Willow infestation rates were 100% in many units (Table 2).
- I estimate that the KSHB infested an additional 67,890 willows during 2016-17. When added to the 287,620 willows infested during 2015-16, a total of 355,510 willows, or 88% of the willows in the valley, were infested during the two years.

Table 2. Infestation rates for the Tijuana River Valley, as surveyed in winter 2016-17.

UNIT	AREA	# PLANTS	% INFESTED	SEVERITY
	ha			holes/225cm^2
A. Riparian forests (willows)				
1	14.64	39	74%	9.7
2	1.78	40	100%	8.0
3	3.02	1	100%	15.0
4	5.13	4	100%	8.3
5	18.08	24	100%	15.0
6	12.26	2	100%	7.5
7	0.80	no trees	no trees	no trees
8	2.11	41	76%	17.7
9	10.21	no trees	no trees	no trees
10	23.04	2	100%	2.0
11	4.68	4	100%	3.0
12	3.14	no trees	no trees	no trees
13	15.01	6	100%	15.3
14	17.84	66	95%	21.2
15	18.52	114	52%	1.6
16	20.75	77	79%	7.1
17	21.42	33	73%	7.3
18	7.06	flooded	high	ND
19	6.82	46	91%	12.5
20	12.86	flooded	high	ND
21	9.56	32	66%	10.1
22	12.83	53	100%	17.9
B. Riparian shrub (mule fat)				
23	76.6	52	12%	ND
24	38.0	55	2%	ND
25	39.6	58	10%	ND
26	31.7	52	8%	ND
27	106.3	65	0%	ND
28	68.7	61	0%	ND
29	57.8	flooded	low	ND

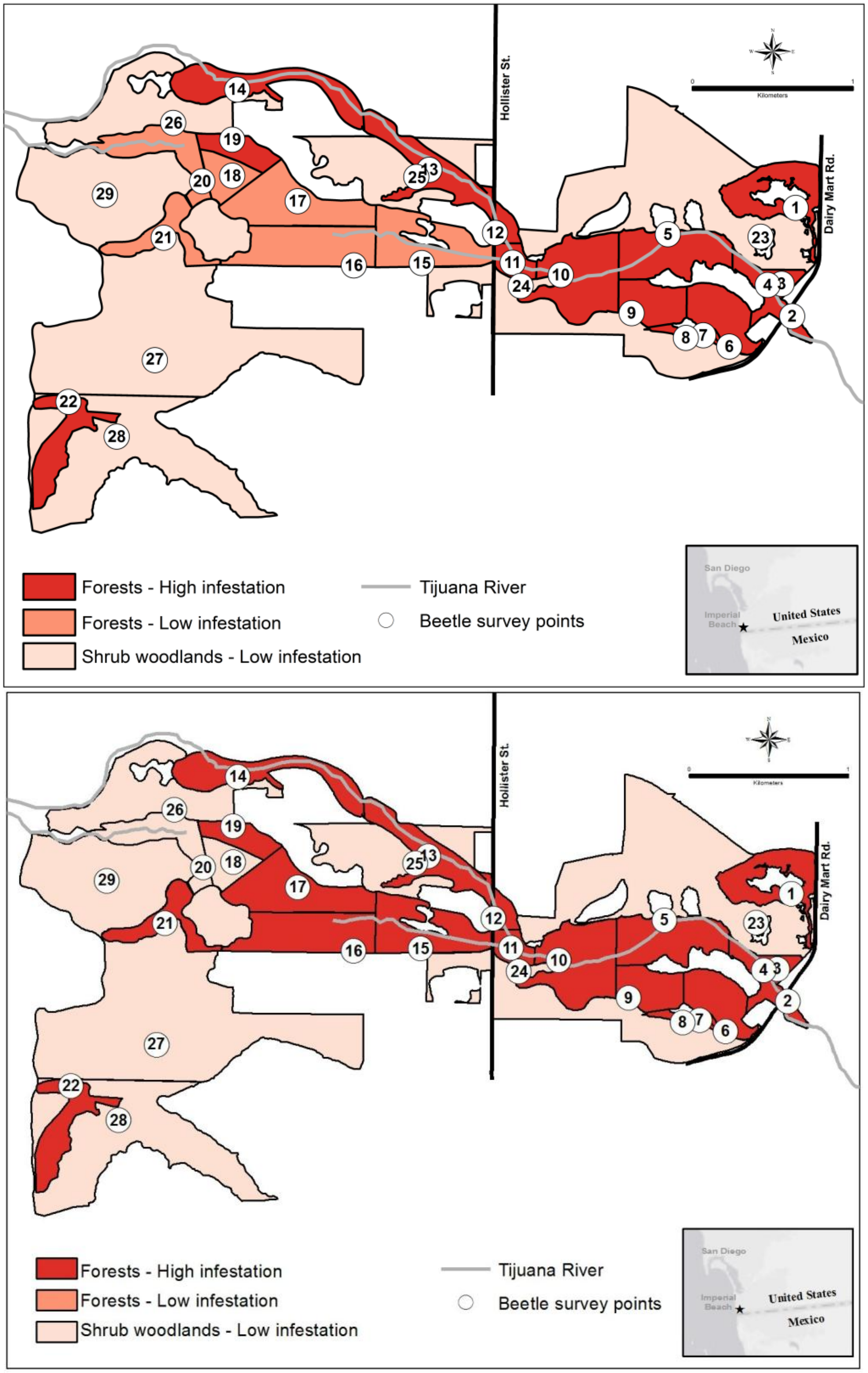


Figure 6. KSHB infestation levels in the riparian survey units for 2015–16 (above) and 2016-17 (below). The wetter forest units are #1-14 and #22, and the dryer forest units are #15-21. The 2016-17 map illustrates the data in Table 2.

- Comparison of the infestation rate maps for 2015-16 and 2016-17 show how the KSHB infestation has spread, and show that now all of the riparian forests have high infestation rates (Figure 6).
- The KSHB invaded even the dryer willow forests. Infestation rates increased in all of the dryer sites (Figure 7).
- Mule fat infestation rates in the shrub units were low, all were <15%. Some of the larger mule fat branches had been attacked (see data below) but these mule fat plants have so far been able to survive KSHB attacks.

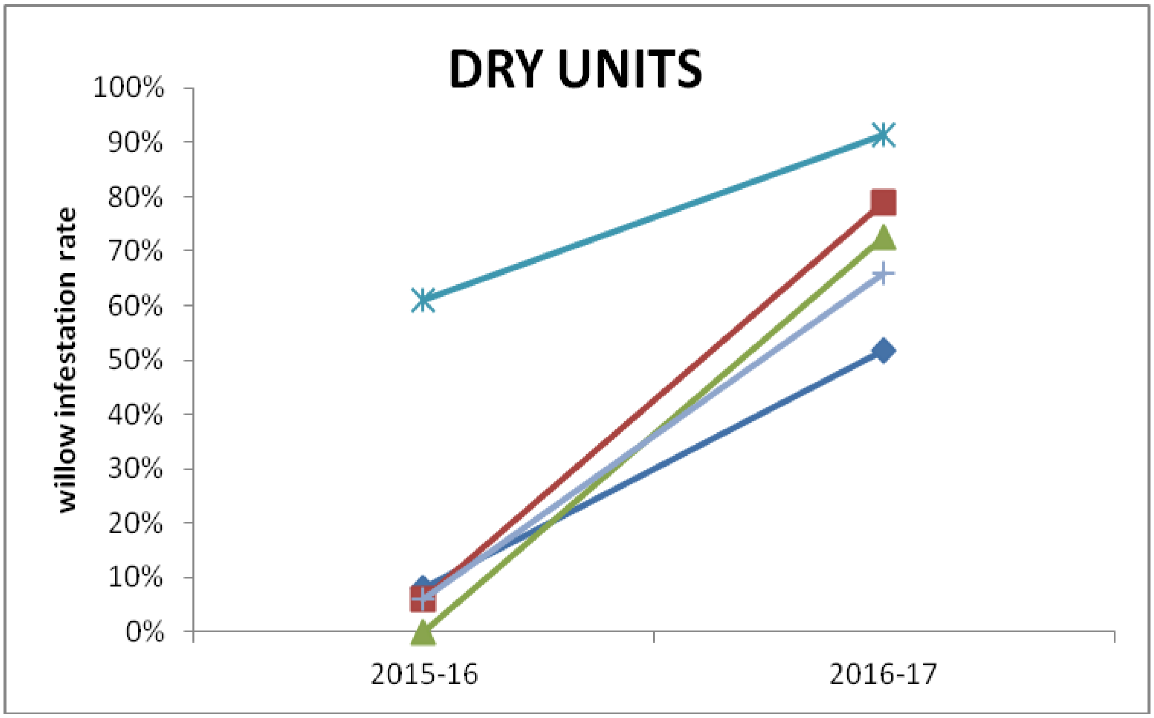


Figure 7. Changes in willow infestation rates in the dryer sites from 2015-16 to 2016-17. The dryer units are Units 15 – 21.

Discussion. An important reason for surveying the infestation rates was to determine whether the KSHB was continuing to spread within the valley and, in particular, whether it was attacking the willows living in the dryer sites. I conclude that the KSHB is continuing to spread within the wetter sites and is attacking the willows living in the dryer sites. Therefore, there appears to be no refuge from the KSHB infestation for the willows in the valley.

There is a subtle difference between the KSHB's influence in the wet and dry units, however. The willow trees in the wet sites were quickly attacked by a large number of beetles and most of these trees have died and have been broken by the winds. In contrast, the willow trees in the dry sites were attacked more slowly by fewer beetles, and most of these trees are still alive and standing tall. So, at the moment, the dry forests – from Hollister down the southern arm of the river – look generally sound. It remains to be seen whether these subtle differences persist.

The major good news is that the KSHB has not substantially invaded or damaged the riparian shrub lands that border the forests. These large areas are dominated by mule fat and support many native riparian species, including the least Bell's vireo (*Vireo bellii pusillus*).

6.3. KSHB INFESTATION OF INDIVIDUAL WILLOW TREES 2016-17

An interesting question to ask of these trees in the path of the KSHB is: What is the course and timing of the KSHB infestation in a typical tree? In particular, how long does it take for a tree to go from 'not infested' to 'infested' to 'dead'?

Methods. In order to follow the course of the KSHB infestation in specific trees, I labeled 390 trees during February - March 2016 and then revisited the trees to see how they were doing in September 2016 and during winter 2016-17 (December to February). The trees were initially labeled with either a yellow dot ('not infested, alive') or a red dot ('infested, alive') and then when revisited were classified as one of the following: 'not infested, alive'; 'not infested, dead'; 'infested, alive'; or 'infested, dead'. [A more complicated division of the infested trees, using severity of beetle colonization, was also used but those results do not significantly add to the goal of understanding the speed of deterioration within a tree, and so are not presented here.] Most of the labeled trees were in the dryer, less-infested forests in Units 15-21. A total of 299 trees were accessible during winter 2016-17, so I am able to report what happened to these trees in the course of approximately 1 year.

Results. Of the 194 labeled willow trees that were 'not infested, alive' at the start of the year, 95 trees, or 49%, were 'infested, alive' at the end of the year (Figure 8). So they became infested during 2016 but were not killed by the infestation. An example of one of these trees is shown in Figure 9. This arroyo willow, growing in dry Unit # 21, was not infested in February 2016 (when the yellow dot was applied), was mildly infested in September 2016 (when the additional red dot was applied) and then showed severe infestation in October 2016 (when the picture was taken). Notice the many sawdust tubes coming out of the KSHB holes along the entire trunk.

Of the 105 labeled willow trees that were 'infested, alive' at the start of the year 90 trees, or 86%, were still 'infested, alive' at the end of the year (Figure 8). So they continued to live, even though infested, throughout the year. Only a few individuals died during the course of the year. Together the results suggest that a typical willow tree which was not infested at the beginning of Year 1 and then became infested during Year 1 had an 86% chance of surviving until the end of Year 2.

Discussion. The results showed that the KSHB infestation continued to spread into the dryer forests but that few trees in these dryer forests died immediately from the infestation. The trees in these dryer forests are deteriorating slower than was seen in the wetter forests last year, when trees became infested and died within a year (as seen in Figure 3).

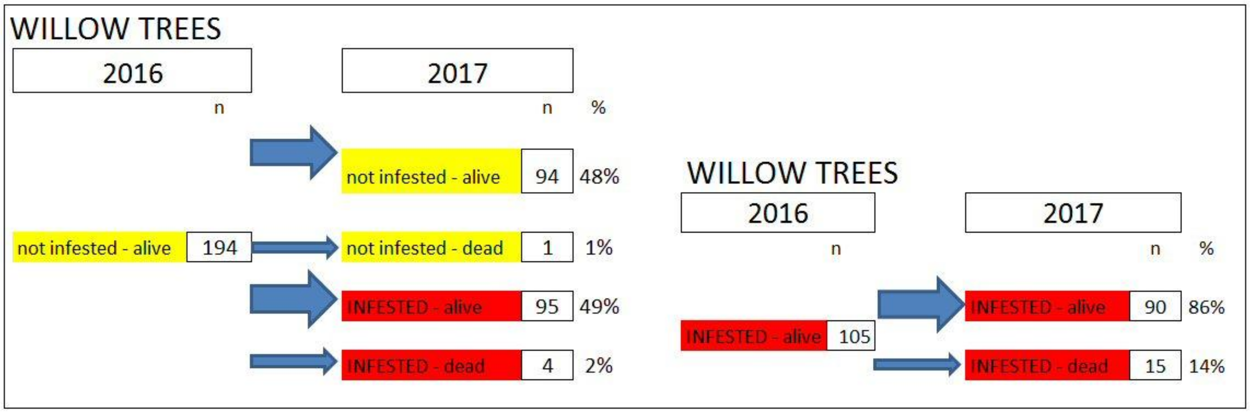


Figure 8. The fate of labeled trees from early 2016 to early 2017. One set of trees started as 'not infested' (n = 194), another set started out 'infested' (n = 105).

Figure 9. Progress of the KSHB attack during 2016. This arroyo willow, growing in dry Unit # 21, was not infested in February 2016 (when the yellow dot was applied), was mildly infested in September 2016 (when the additional red dot was applied), and was severely infested in October 2016 (when the photo was taken). Notice the many sawdust tubes coming out of the KSHB holes along the entire trunk. This shows that some trees in the dry sites went from being not infested to being severely infested in just a few months.

6.4. KSHB IMPACTS TO THE WILLOW FORESTS 2015-17

It is clear that the KSHB has damaged and killed many trees in the Tijuana River Valley forests. To show the amount of structural impact to the forests and where the damage was greatest, I conducted a valley-wide survey of the amount of willow canopy lost.

Methods. I observed each forest unit from as many places as possible and estimated the amount of canopy lost since the start of the KSHB-attack. I drew on my 15 years of working in these sites, some of my 'before' photos, some of my 'before' data and 'reconstructions' from recently-broken willow trunks.

Results. In the last two years, 100% of the willow canopy was lost in many units, and an average of 66% of the canopy was lost in the entire valley. Higher losses were seen in the wetter units between Dairy Mart and Hollister (Units 2-12), and lower losses were seen in the dryer units west of Hollister (Units 15-21; Figure 10).

Discussion. Most of the forests in the valley have been completely altered by the KSHB attack. Extensive areas that once supported tall willow forests are now supporting shrubs. The highest losses of canopy were seen in the wetter units and I think that is because these units contained the trees that were most preferred by the KSHB – they were attacked first and most severely. The lower losses of canopy were seen in the dryer units and I think that is because they contained trees that were less preferred by the KSHB – they were mostly attacked during 2016 but were still standing at the time of the census.

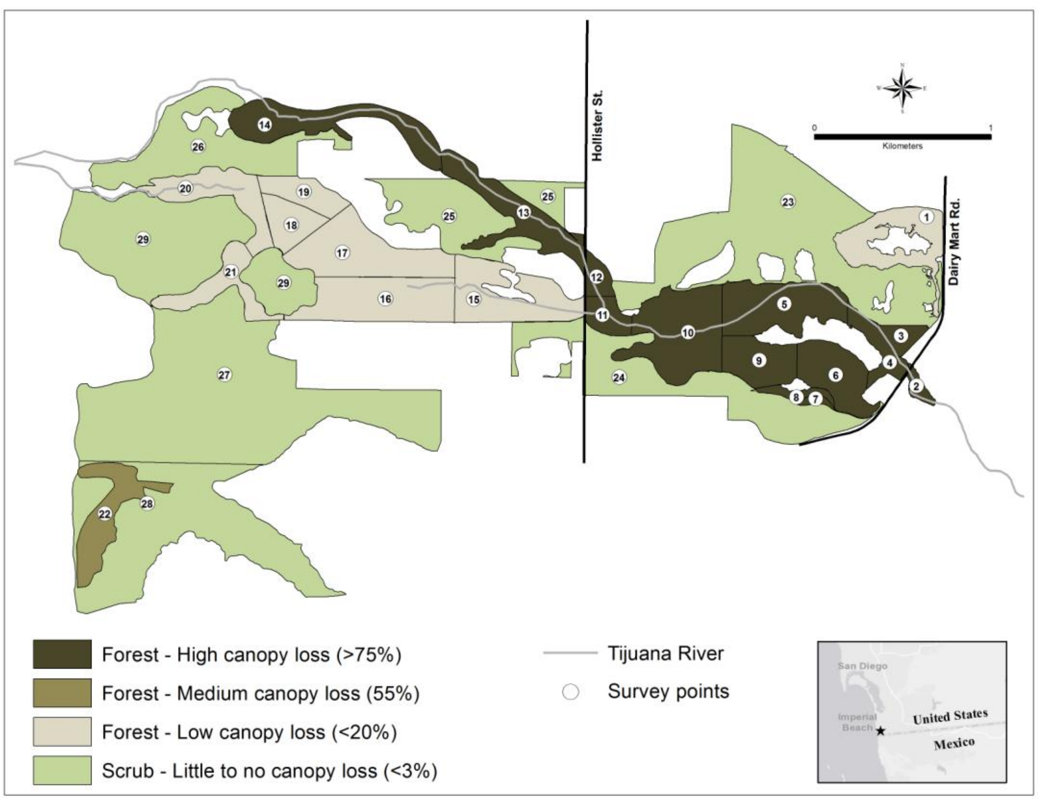


Figure 10. Rates of canopy loss in the riparian survey units, as of winter 2016-17.

7. TASK 2 – THE RESPONSE OF THE DAMAGED FORESTS

This KSHB attack has devastated the wetter forests in a unique way – damaging or killing most of the trees making up the structure of the forest canopy, leaving understory shrubs untouched, and covering the ground with woody debris. More common disturbances, like fires and floods, would have also influenced the understory and removed the debris. A crucial question regarding the KSHB attack was therefore: What was the response of the damaged forests to this novel disturbance?

A pair of photos shows in general how the riparian forests have responded (Figure 11). First, many of the willows resprouted from their broken stumps showing, importantly, that not all infested trees were killed even when severely damaged. Second, new willow seedlings were rare. And third, invasive plants like castor bean (*Ricinus communis*) and arundo (*Arundo donax*) became more abundant and/or more obvious.

I address each of these aspects of the response of the forests below.

7.1. RESPROUTING OF HEAVILY-DAMAGED WILLOW TREES

Methods. To quantify the magnitude of willow tree resprouting, I resurveyed the 22 forest units in the valley during July and August 2016. I examined approximately 74 willow trees (arroyo willow and black willow) within each unit and determined whether each was a) dead (no leafing out), b) alive and not seriously damaged by the KSHB, or c) alive but seriously damaged by the KSHB and resprouting. I then estimated the total number of trees in each category within each unit. In Section 6.1 I focused on the category 'a' results and here I focus on the category 'c' results – the resprouts.

Results. Resprouting of snapped willow trees was common, and growth of these resprouts during early 2016 was vigorous (Figure 12). In some sites, where the previously tall tree canopy had been destroyed by the KSHB there was now an extensive low canopy of willow resprouts (Figure 13). The resprouting rates of the willows in the heavily-damaged units ranged from 3% to 74%, and the total number of **trees with resprouts was estimated to be 71,280 trees** (Table 3). If one considers only the heavily-damaged sites (Units 2-13), the average number of willows resprouting was 258 trees per acre.

Discussion. There are three important points about this vigorous and widespread production of resprouts. First, it shows that the KSHB (and its associated fungi) does not kill all of the trees that it infests. Most of the resprouting trees had been heavily infested with the KSHB during 2015, their trunks had been snapped during winter 2015-16, and they were still alive and had sufficient reserves to resprout in 2016. This suggests that the degree of virulence, or pathogenicity, of the KSHB fungal symbionts is moderate rather than severe.

Figure 11. A pair of photos taken of the forest at Hollister Bridge (Unit 11) immediately after the 2015 KSHB attack (March 2016; top) and after the forest had responded (December 2016; bottom).

Figure 12. Growth of resprouts on an infested, snapped arroyo willow in Unit 13. The first photo (left) was taken in March 2016 and the second of the same tree in Sept. 2016.

Figure 13. Resprouting willows form a shrub canopy within part of this heavily-damaged site at Hollister Bridge (Unit 12). This photo was taken in October 2016.

Table 3. Results of the summer 2016 surveys showing the estimated number of dead, alive, and resprouting willow trees in the Tijuana River Valley following the KSHB attack during 2015-6. Data are for the 22 riparian forest units (following Boland 2016 and Figure 1).

UNIT	AGE	AREA	GIRTH	DENSITY	SURVEY	DEAD		ALIVE - NOT SNAPPED		ALIVE - SNAPPED + RESPROUTING	
#	yr	acres	cm	TOTAL	n	RATE	TOTAL	RATE	TOTAL	RATE	TOTAL
1	35	36.2	130.8	7,319	71	6%	439	90%	6,587	4%	293
2	5	4.4	25.9	16,026	187	67%	10,738	6%	962	27%	4,327
3	15	7.5	52.7	5,517	65	97%	5,352	0%	0	3%	166
4	35	12.7	73.7	1,282	37	57%	731	8%	103	35%	449
5	35	44.7	ND	13,561	59	29%	3,933	25%	3,390	46%	6,238
6	22	30.3	83.8	9,194	63	44%	4,045	19%	1,747	37%	3,402
7	10	2.0	39.0	4,407	55	55%	2,424	0%	0	45%	1,983
8	5	5.2	18.3	37,953	132	29%	11,006	54%	20,494	17%	6,452
9	22	25.2	ND	10,211	57	42%	4,288	0%	0	58%	5,922
10	22	56.9	66.0	17,280	37	51%	8,813	3%	518	46%	7,949
11	35	11.6	81.3	9,365	39	26%	2,435	0%	0	74%	6,930
12	22	7.8	73.7	9,421	36	78%	7,349	0%	0	22%	2,073
13	22	37.1	54.6	37,526	49	41%	15,386	12%	4,503	47%	17,637
14	22	44.1	34.3	84,717	83	13%	11,013	83%	70,315	4%	3,389
15	35	45.8	71.1	16,204	130	0%	0	82%	13,287	18%	2,917
16	35	51.3	79.5	25,936	54	6%	1,556	94%	24,380	0%	0
17	35	52.9	83.8	16,069	65	0%	0	100%	16,069	0%	0
18	35	17.5	67.3	7,062	54	0%	0	100%	7,062	0%	0
19	35	16.9	79.8	8,524	59	15%	1,279	85%	7,245	0%	0
20	35	31.8	82.6	9,643	46	2%	193	96%	9,257	2%	193
21	35	23.6	77.0	7,172	53	0%	0	100%	7,172	0%	0
22	10	31.7	43.9	48,124	195	10%	4,812	88%	42,349	2%	962
TOTAL		596.9		402,513	1,626		95,791		235,441		71,280
							24%		58%		18%

Second, the average density of resprouting trees (258 plants per acre) was greater than the number of plants typically planted in a riparian restoration site (usually ~200 plants per acre; River Partners 2007) showing that the forest is, to some extent, restoring itself.

Third, the new low-canopy forests that these resprouts have created may provide essential breeding habitat for the endangered least Bell's vireo during the next breeding season. The vireo is known to require dense, young forests; "*early to mid-successional riparian habitat is typically used for nesting by the Least Bell's Vireo because it supports the dense shrub cover required for nest concealment as well as a structurally diverse canopy for foraging*" (Kus 2002). The abundant, vigorous resprouts gives hope that the forests will continue to provide valuable habitat even though they have been severely impacted by the KSHB.

7.2. KSHB INFESTATION OF WILLOW RESPROUTS

An obvious question about the willow resprouts growing on trees that were heavily infested with KSHBs is: Are the resprouts also being infested with the KSHB? To answer that question I conducted a survey of resprouts and examined them for KSHB infestation.

Methods. Within six of the heavily-damaged units, I chose 5 – 6 resprouting willow trees for close examination. All the resprouts on each tree were examined for signs of KSHB infestation and the diameter of each resprout was measured. A total of 302 resprouts on 34 trees were examined in November 2016.

Results. The resprouting willows had an average of nine resprouts per tree. These resprouts were all less than a year old. Many of the resprouts were greater than 3 m in length, creating a dense shrub that was about the size of a large mule fat shrub (as in Figure 12). The resprouts ranged in diameter from less than 0.5 cm to greater than 5.5 cm. Only 27 of the 302 resprouts (**9%**) had been attacked by the KSHB, and the larger resprouts were more likely to be attacked than the smaller resprouts (Figure 14). All resprouts, even the attacked ones, looked in good health – none had been killed by the KSHB.

Discussion. In November 2016, the KSHB was having no obvious impact on the willow resprouts. The resprouts were growing and creating a new, low canopy in the most heavily-damaged willow forests. However, these conditions may change during 2017

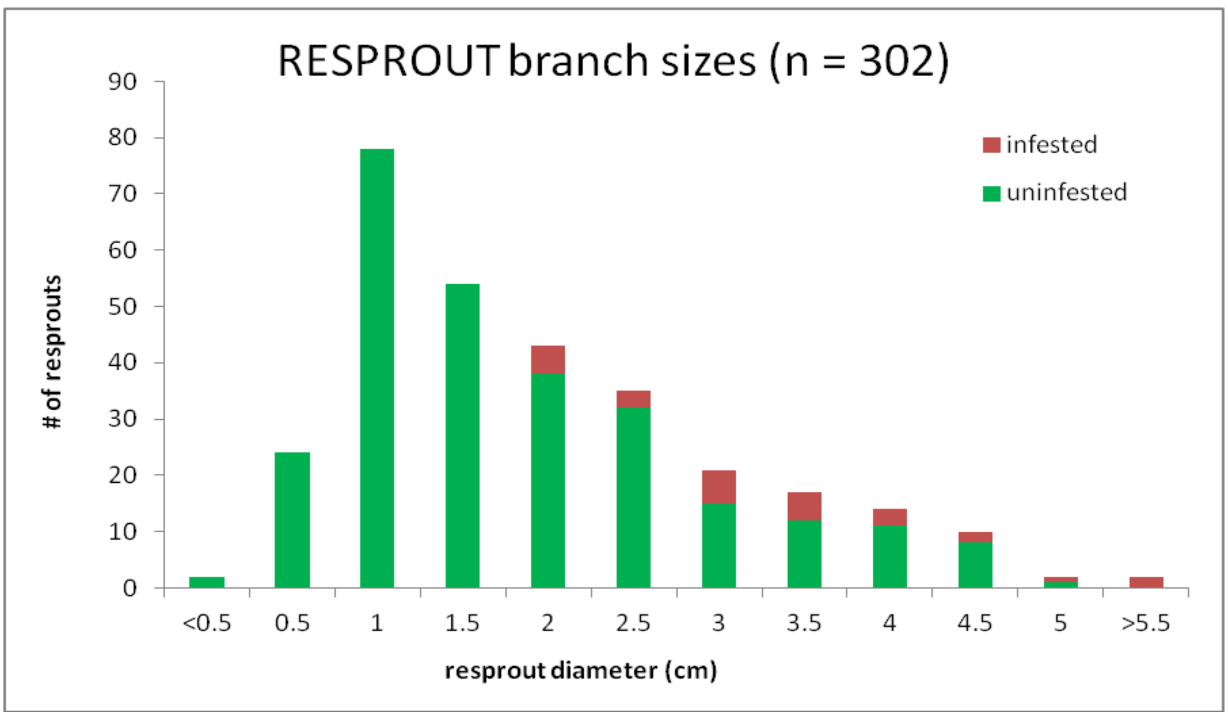


Figure 14. The size frequency of willow resprouts in the Tijuana River Valley in November 2016, including the frequency of KSHB beetle infestation.

because, as the resprouts grow, their diameter will increase and they may become more attractive to the KSHB, which is showing a size preference for larger resprouts. The KSHB is like many ambrosia beetles in that it shows a preference for host branches of a certain size (Wood 1982).

We will have to wait and see whether the resprouts are attacked by the KSHB and whether the resprouts can provide suitable habitat for least Bell's vireos in spring and summer 2017.

7.3. RECRUITMENT OF WILLOW SEEDLINGS AND DENSITIES OF INVASIVE SPECIES

In addition to willow resprouts, I examined two other responses of the forests to the KSHB infestation – the production of willow seedlings and the growth of invasive plants.

Methods. During October 2016 I resurveyed the fixed belt transects (20m x 2m = 40 m^2) within the 11 most-heavily-damaged forest units. I counted all of the live willow trees, willow seedlings and invasive plants within the transects, and I compared these surveys to those I had done in 2015.

Results. The belt transects showed that willow tree numbers in heavily-damaged forests were substantially lower in 2016 than 2015 (Figure 15). The original tall canopy had been almost completely lost and the willows remaining alive were mostly resprouting snapped trunks. Some willow seedlings were present in the units but they were in only a few sites (4 of 11) and at low densities (4 seedlings per transect; Figure 15). Under more suitable conditions the seedling density would be much greater (>1,800 seedlings per transect; Boland *in press*). Also many invasive plants were present in these heavily-damaged sites and most were growing vigorously (Figure 15). Arundo and tamarisk were present at numbers similar to last year's whereas many new castor bean plants had become established.

Discussion. The key change from 2015 to 2016 was the loss of the high willow canopy in heavily-damaged sites. That loss of canopy has allowed invasive species to flourish and, in particular, has allowed castor bean, a fast invader of light gaps, to become very abundant.

Because invasive plants are competing with the native plants (both native resprouts and native seedlings), managers should try to spray the invasives with herbicides in these heavily damaged forests to improve the habitat value and to stimulate native plant recovery.

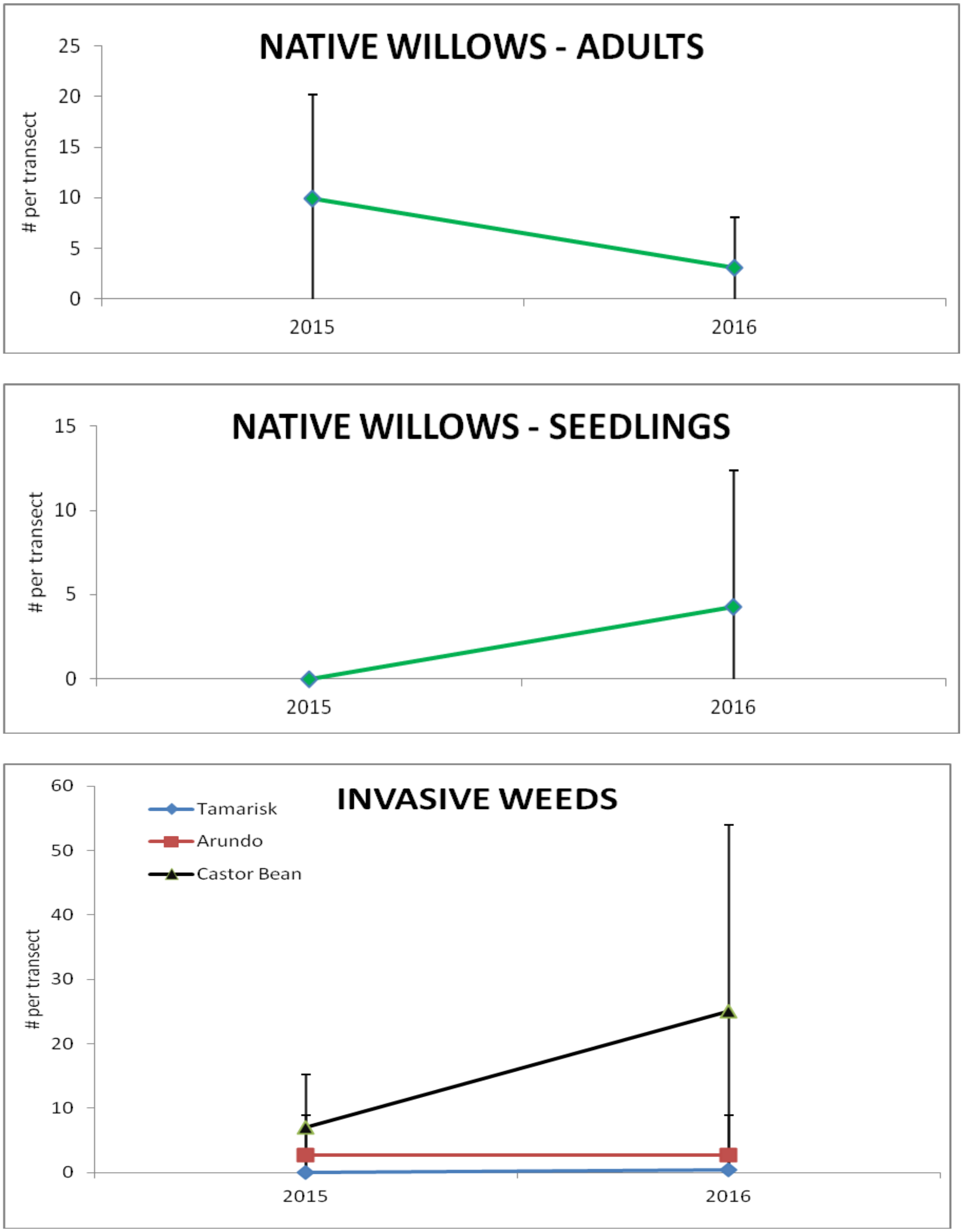


Figure 15. The changing densities of plants along the belt transects in the 11 most heavily-damaged forest units. Values are averages $\pm$ *1 std deviation (n = 11). The belt transects were 40* m^2 *in area.*

7.4. OVERALL ABUNDANCES OF TWO INVASIVE SPECIES

The three species considered to be the worst invasive plants in the valley, castor bean (*Ricinus communis),* tamarisk *(Tamarix ramosissima)* and arundo (*Arundo donax;* SWIA 2002*),* are not substantially attacked by the KSHB (Boland 2016) and now are benefiting from the deaths of willows – their major competitor. These three species have been the focus of an invasive species treatment program in the valley (SWIA 2002) and of several ecological studies in the valley (Boland 2006, 2008; Whitcraft et al. 2007).

To estimate the current distribution and abundance of two of these species, castor bean and arundo, I conducted a winter 2016-17 survey of the valley. [Tamarisk loses its leaves in winter and becomes difficult to quantify in this kind of overview survey. I will redo these surveys in summer when it has leafed-out and include tamarisk then.]

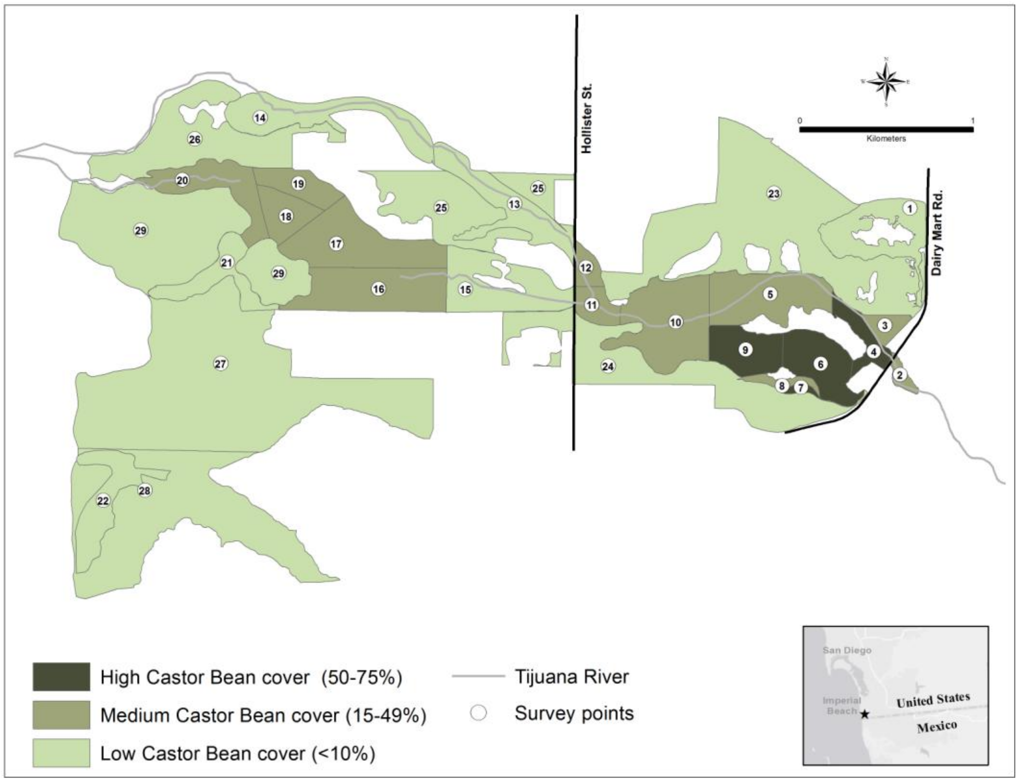
Methods. Each unit was observed from as many places as possible during winter 2016-17 and the percent cover of the two invasives was estimated. In addition, arundo could be clearly seen and identified on the latest Google Earth aerial photos of the valley and the percent cover of arundo within units was estimated from the photos. The percent cover of arundo was averaged from the two sources (the field surveys and the Google Earth surveys).

Results. Both castor bean and arundo were abundant in the riparian forests and less abundant in the riparian shrub habitats (Figure 16). Both species were most abundant in the heavily-damaged eastern forests, particularly in Units 4 – 9, where castor bean reached up to 75% cover and arundo reached up to 43% cover. In some units these two species together dominated the vegetation (Figure 17).

Discussion. Last year I predicted that castor bean and arundo were "*likely to grow tall and thrive in the absence of a willow canopy*" (Boland 2016). Indeed, this has been the case this year – both species are abundant, particularly in the willow forests that have been heavily-damaged by the KSHB.

The KSHB attack has therefore had an ecosystem-wide impact. The KSHB has preferentially attacked the arroyo and black willows that are the dominant trees in the Tijuana River Valley (Boland 2014a), and those foundation species are being substantially replaced by invasive species. A riparian community dominated by invasives is unlikely to provide the same habitat quality and food-chain support for animal species in the valley, including the endangered *Vireo bellii pusillus*. Therefore the KSHB's impact is wide-spread; as I said last year: "*the KSHB is affecting not only its preferred host species but also the structure and function of the entire ecosystem*" (Boland 2016).

These data reemphasize the idea that managers should try to spray the invasives with herbicides to improve habitat value and to stimulate native plant recovery.



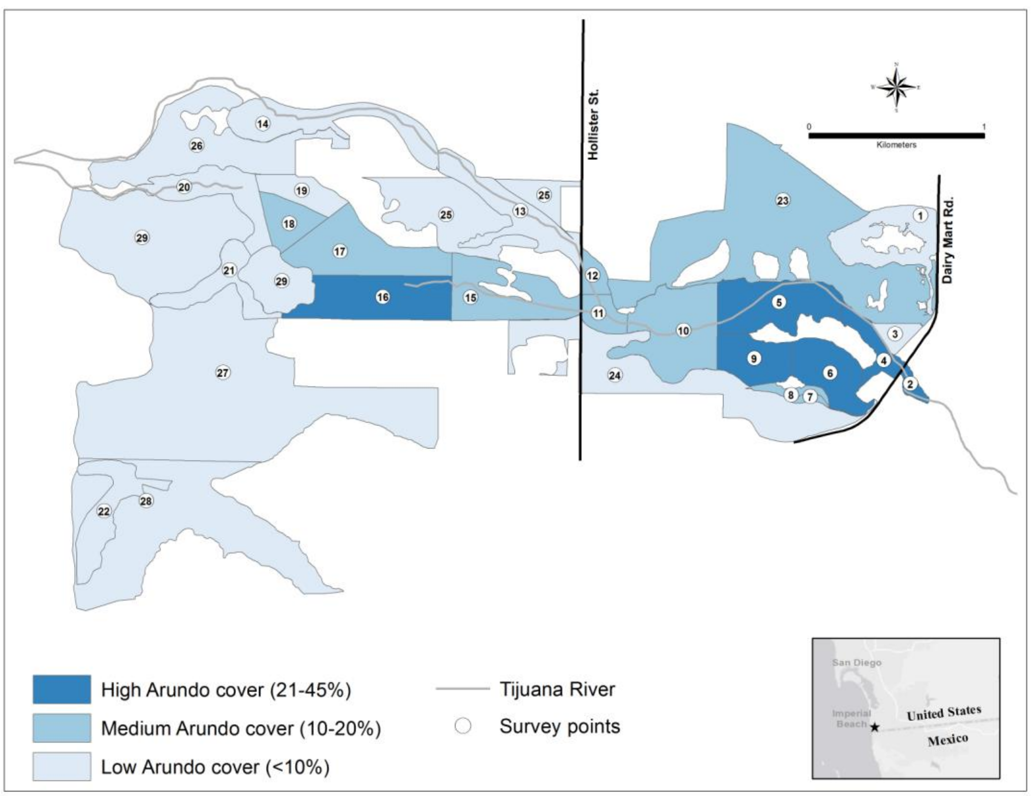


Figure 16. Percent cover values of two invasive species, castor bean and arundo, in the riparian survey units, as of winter 2016-17.

Figure 17. Units 5 and 6 showing the dominance of castor bean and arundo.

7.5. PREDICTIONS

The KSHB infestation has followed a particular sequence in the willow trees: the trees have become **infested**, then **damaged,** and then they've either died or **resprouted**. This sequence took just one year in the Eastern Wet Units (2-12; Boland 2016), but is taking more than two years in the Western Wet Units (13,14 and 22), and is likely to take more than three years in the Dry Units (1 and 15-21). So different parts of the valley are at different stages along this infested-damaged-resprouting sequence (Figure 18).

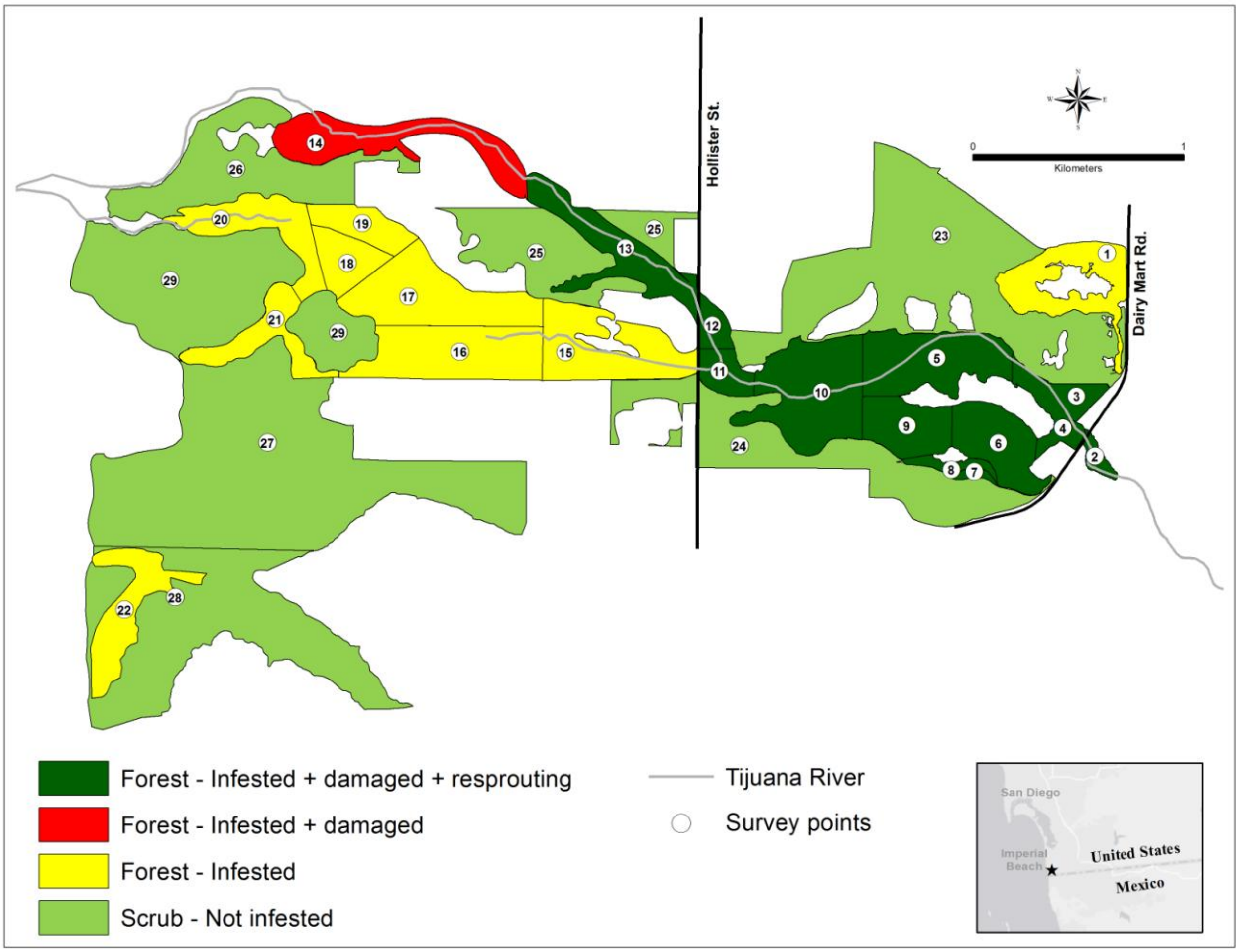


Figure 18. The general status of the vegetation within the riparian survey units, as of winter 2016-17.

Why there are these differences between these groups of units has still to be determined, but we can use this sequence and their timing to make some predictions about what is going to happen next to the riparian sites in the valley. First, I predict that the Western Wet Units (13, 14 and 22), which were heavily damaged during December 2016, will see extensive resprouting during April 2017 (Figure 19).

Second, I predict that the Dry Units (15-21) will be fully infested during 2017, heavily damaged during December 2017, and will experience extensive resprouting during April 2018 (Figure 19). Together these two predictions mean that all the forests in the valley will have been infested and heavily-damaged by December 2017.

Third, I predict that the shrub habitats, which are dominated by mule fat, will continue to be **not** heavily infested by the KSHB.

Finally, it appears that the KSHB has had the fastest and greatest impact on willows growing in the Wet Sites, i.e., growing in nutrient-enriched water, and so I predict that the next site, outside the Tijuana River Valley, to be infested and heavily damaged by the KSHB will be a site where the trees are fertilized or are growing in nutrient-enriched water.

	SEQUENCE OF EVENTS IN THE RIPARIAN FORESTS INFESTED BY THE KSHB				
SITE	**NOT INFESTED** →	**INFESTED** →	**DAMAGED** →	**RESPROUTING** (some)	TOTAL TIME
EASTERN WET UNITS (Units 2-12)	April 2015	August 2015	December 2015	April 2016	1 year
WESTERN WET UNITS (Units 13,14 and 22)	April 2015	August 2015	December 2016	April 2017?	~2 years?
DRY UNITS (Units 15-21)	April 2015	December 2016	December 2017?	April 2018?	~3 years?

Figure 19. The sequence of events in a forest before, during and after being infested by the KSHB. The timing of these events are given for the Wet and Dry Units. The shaded dates are predictions.

7.6. CONCLUSIONS

The most surprising and important finding described here was the presence of abundant resprouts on some of the KSHB-infested and heavily-damaged willows. These resprouts grew vigorously and densely on an estimated 71,280 tree stumps and, in less than a year, had created shrubs about the size of large mule fat shrubs and a dense, low vegetation layer. The resprouts show that not all infested willows were killed by the KSHB and its associated fungi as some experts had predicted in 2015. The resprouting willows are now a welcome and crucial component of the recovering riparian community.

It is possible that for the next couple of years the main riparian forest will be composed mainly of these resprouting willow 'shrubs' (and mule fat shrubs). This is because the KSHB is likely to attack all large willow trees, and only resprouts that are smaller than the beetles preferred branch size will grow and survive.

Something similar has happened in other parts of the US leading to the replacement of forest trees by resprouting shrubs. I cite two examples. **The first is the American Chestnut.** The chestnut blight is a fungal infection that had a devastating impact on the American Chestnut in the eastern United States. "*Within 50 years, more than 99% of mature trees perished. Today you will typically encounter this species as a small tree or as stump sprouts that look more like tall shrubs than the massive trees that once grew. Mature specimens are rare since the fungus typically kills young trees before they can reproduce*" (Wojtech 2011).

The second example is the beech tree. Beech bark disease is a fungal disease that causes mortality in beech trees in the eastern United States. This disease is the result of a beech scale insect attack, creating a wound that is subsequently invaded by the fungi. "*The weakened trunks of most infected trees eventually snap, leaving a bare trunk less than half its former height. Root sprouts, which often emerge before the trunk breaks off, are typically reinfected before they can grow into mature trees*" (Wojtech 2011).

In both examples the disease attacked adult trees but not young trees, and this resulted in the survival of many resprouting tree stumps which look like shrubs. It is possible that the Tijuana River Valley's tall willow forests could also be reduced to a short, willow-shrub forests, composed mainly of resprouting willows and mule fat. Figure 13 suggests what that new forest would look like. It is possible that many native species, even least Bell's vireos, could fare well in this kind of forest.

In order to promote the development of this new shrub forest managers should spray the competing invasives (particularly castor bean, arundo and tamarisk) to ensure the development of the best possible shrub forest.

8. TASK 3 – SHOULD MANAGERS REMOVE FALLEN DEBRIS?

A consequence of the KSHB attack during 2015 was that many forest trees were knocked down and the remains of their canopies lay on the ground in the heavily-damaged forests (Figure 20). The woody debris was extensive and dense – a couple meters deep in some areas. There was some discussion about trying to remove the debris to reduce the threat of fire and flooding damage. But there is also an important ecological question: should the debris of fallen trunks and branches caused by the KSHB infestation be removed to improve the recovery of the native plants? I conducted an experiment to address this question and to provide recommendations.

Figure 20. Examples of willow debris on the ground in the heavily-damaged forest sites. Photo A is from Unit 2 and Photo B is from Unit 8.

Methods. To test the hypothesis that fallen, woody debris influenced the number of riparian seedlings becoming established, I conducted a replicated experiment in the Goat Canyon sedimentation basins. The eastern basin had been cleared during fall 2015 and sediment was suitable for riparian plant recruitment during spring and summer 2016. During early May 2016, I laid out 16 pairs of plots in a randomized block design, and each pair consisted of a 'woody debris' plot and 'no debris-control' plot. Each plot was 3m x 3m in size and either contained a firmly-anchored pile of woody debris (like that found in the heavily-damaged riparian forests) or no debris (Figure 21). Three months later I counted the number of arroyo willow, black willow, and mule fat seedlings (here referred to as the Big 3) within three 50 x 50 cm quadrats placed side-by-side within each plot. The difference in the number of seedlings in the pairs was tested using Wilcoxin's signed-ranks test (Sokal and Rohlf 1995).

Results. Seedlings of the Big 3 were common in the Goat Canyon sedimentation basins during July 2016. In the experimental plots, Big 3 seedlings were more dense in the control plots than under the piles of debris in 14 out of 16 pairs (Figures 21 and 22). The presence of debris significantly and negatively impacted the number of seedlings ($p < 0.01$, $n = 16$). On average there were 2.5 times more seedlings in the control than in the debris piles. The top five most-dense sites were all control sites with the highest being 23 seedlings per quadrat, or 92 seedlings per m^2. These results were confirmed by observations elsewhere in the valley, where willow seedlings were often seen growing in openings but not under fallen canopy debris (Figure 23).

Figure 21. Seedlings growing in a pair of 'woody debris' (left) and 'no debris – control' (right) plots.

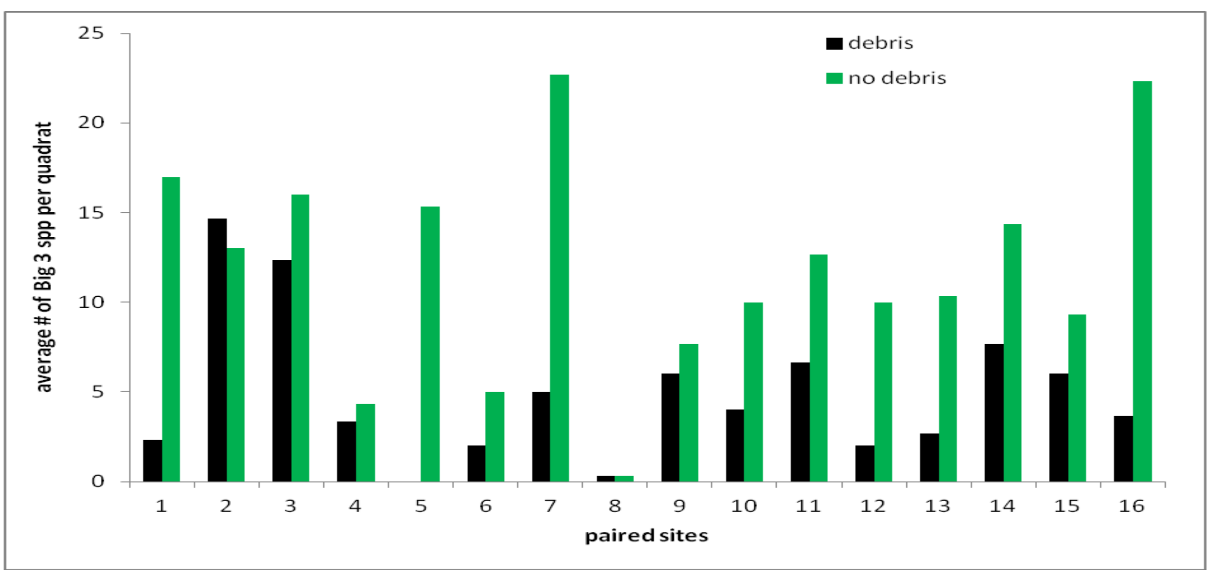


Figure 22. The impact of debris on the number of seedlings of native riparian species (The Big 3) that recruit into a site.

Figure 23. Black willow seedlings (behind the meter stick) growing in Unit 10. Notice that they have recruited outside the debris pile and that none are growing within the debris pile. It is likely that more seedlings would have recruited had this trunk and debris been removed in early 2016.

Discussion. Debris lying on the sediment did significantly reduce the number of seedlings of native species that became established. This was probably because the debris both prevented some seeds from settling on the sediment – seeds of all Big 3 species are wind-dispersed and need to land on moist sediment in order to germinate – and it reduced the amount of light reaching the sediment – seedlings of all Big 3 species also require full sun for growth and development (Boland 2014b).

These results and other observations in the valley show that more seedlings of the desired native riparian species will become established in a site if the fallen debris is removed. However, removal of debris does have two considerations – it will work in only some places and it needs to be timed correctly. Removal of debris to allow the establishment of the Big 3 seedlings will only work in sites that have moist, sunny sediment in spring, i.e., sites that are suitable for the germination of their wind-dispersed seeds and the growth of their seedlings. Also the removal must be done only during winter, i.e., before 15 March, because the site needs to be left undisturbed during the critical seedling establishment phase of March to June (Boland *in press*).

Removing fallen trees will also be expensive and I think this will mean that the removal will not be done in many places. But I can envision at least two situations in which a land manager would decide to remove debris. **Situation #1** – is a heavily-damaged site that has easy access, several volunteers who are willing and able, and is likely to be moist or wet during spring. Under these circumstances the broken, branches and trunks could be removed during winter by the volunteers to allow natural recovery during spring and summer. The easy access and volunteers would mean the work would be relatively inexpensive. **Situation #2** – is where a land manager examines the amount and location of the debris and she has serious flood- or fire-concerns. Under these circumstances the debris should again be removed during winter to allow natural recovery during spring and summer. The manager can say that she was doing the removal for flood, fire and ecological reasons.

In most sites the removal is unlikely to be done because of high costs. In these sites fewer seedlings of the Big 3 will become established but eventually the fallen trees and branches will decompose. Within the valley the branches that are on the ground and wet are decomposing and breaking down the fastest. Also, long branches are breaking up into shorter branches and these smaller branches are being swept downstream. So there is a natural clearing of debris. It is unknown which plant species will become established in these slow-clearing sites.

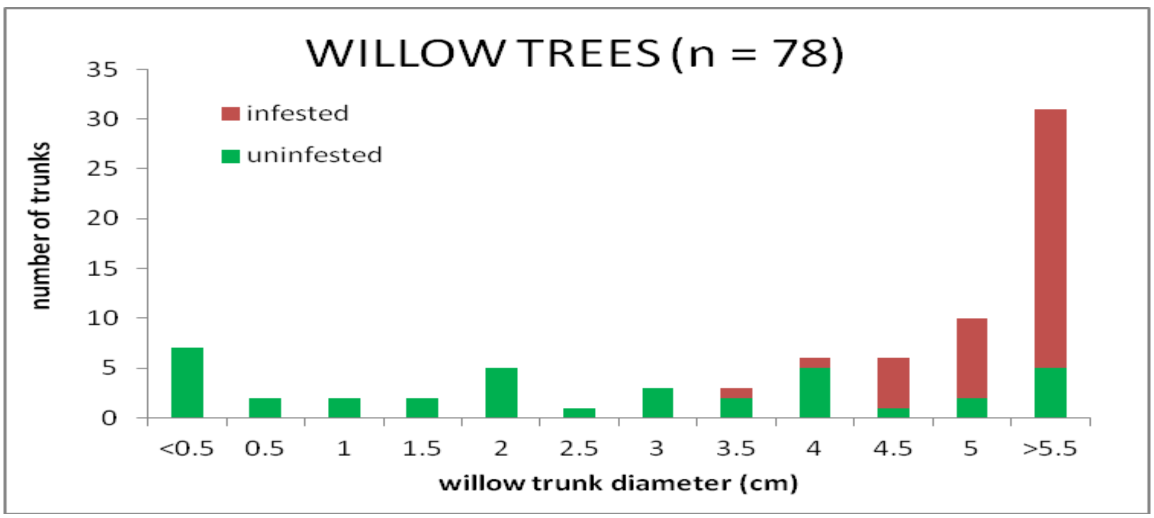
Finally, there weren't enough **arundo, castor bean and tamarisk** recruiting into the Goat Canyon experiment to test whether these invasive species were also influenced by the debris. But, from my past work on these species, I would say that arundo and castor bean are not influenced by debris, because they can establish in the shade, whereas tamarisk is influenced by debris, because it recruits in the same way as willows and mule fat – on moist sediment, in the sun.

9. ADDITIONAL INFORMATION

9.1. BRANCH SIZE PREFERENCES OF THE KSHB

Many ambrosia beetles show a preference for host branches of certain sizes (Wood 1982). Here I examine willows and mule fat to determine the KSHB's size preferences.

Methods. I examined every living willow along a 50 m transect at the New Road site (Unit 8), measured its diameter at breast height, and noted whether it was infested with the KSHB or not (n =78 trees). I also randomly chose 15 mule fat shrubs (five each from Units 2, 10, and 13), measured the diameter of each upright branch at approximately shin height, and noted whether the branch was infested with the KSHB or not (n = 208 branches). The willow surveys were conducted in October 2016 and the mule fat surveys in November and December 2016.



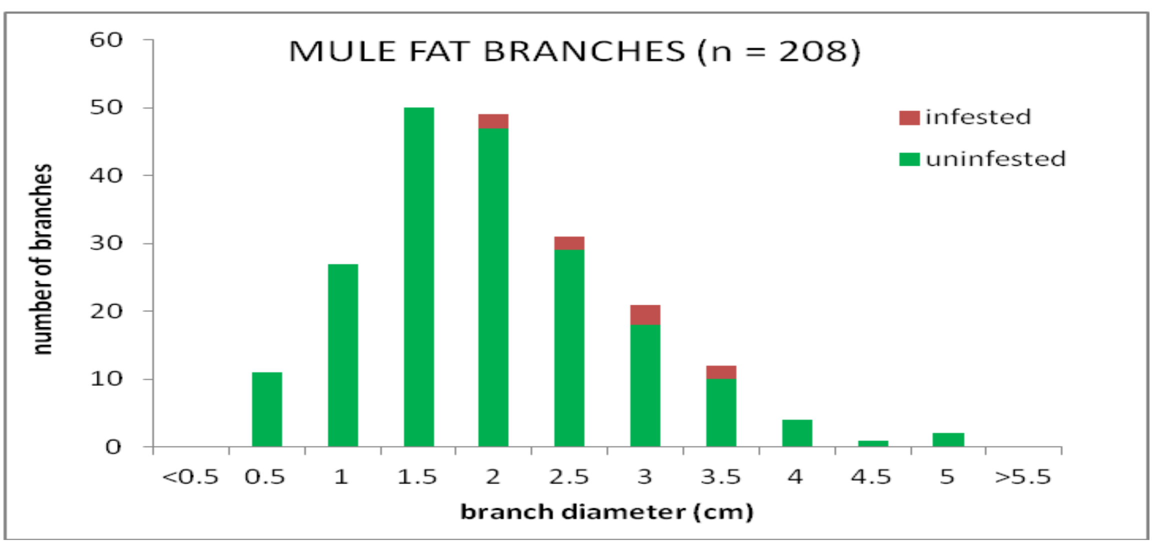


Figure 24. Branch size preferences of the KSHB on willows and mule fat.

Results. Many willow trees in the New Road site were infested (53%), and KSHB holes were found in trees with a diameter of 3.5 cm or greater (Figure 24). The mule fat branches were less heavily infested (4%), and KSHB holes were found in branches with a diameter of 2 cm or greater (Figure 24).

Discussion. It appears from these surveys and from the earlier survey of infested willow resprouts (Figure 14) that the KSHB can attack small diameter willow and small mule fat branches, but that it prefers to attack willow trees with moderate to large diameters (> 4.5 cm). This is an important finding because it suggests that many young willows (<4.5 cm in diameter) will survive for a few years before they reach a size that is attacked by the KSHB.

9.2. KSHB HOLES ALONG A TREE and KSHB-PRODUCTION IN THE VALLEY DURING 2015-16

Here I address the questions: “How many KSHB holes are in a KSHB-infested willow tree?” and “How many KSHB were likely produced in the Tijuana River Valley in 2015-16?”

Methods. I present data collected on Tree #1, a 13m-tall black willow that had been growing east of Dairy Mart Bridge and was pictured in Figure 3. The tree had been attacked by the KSHB during 2015 and snapped by winds during winter 2015-16. In October 2016 it was lying on the ground and there was access to its entire length (Figure 25a). I counted the number of KSHB holes within a 2 x 20 cm quadrat (Figure 25b) placed at 1m intervals along the trunk and extrapolated the quadrat counts to the entire tree.

Results. The number of KSHB holes per quadrat peaked between 3 and 5 m along the trunk and declined up the tree (Figure 26). I calculated that the tree had a total of approximately 26,900 holes. Each hole leads to a KSHB tunnel system in the trunk within which the KSHB breeds. If we conservatively presume that just one KSHB was born behind each hole then an estimated 26,900 KSHB were born within this tree in 2015-16. As the KSHB killed 95,761 willow trees in the valley in 2015-16 (Section 6.1), we can estimate that: 95,761 x 26,900 = 2,575,970,900 beetles were born in the Tijuana River Valley during 2015-16.

Discussion. These data are interesting in two ways. **First**, they provide a rough estimate of the magnitude of a ‘mass attack’ by the KSHB on a single willow. In this case it was approximately 26,900 holes. When tens of thousands of beetles attack a single tree it becomes so undermined by the tunnels that it is easily snapped by high winds. In this case the tree was also killed by the KSHB and its associated fungi. **Second**, these data show the enormous reproductive powers of the KSHB in that it can produce an estimated two billion offspring in just one year. Surely this 2015-16 reproduction in the valley was the single largest production of offspring by the KSHB in California so far.

Figure 25. (a) Tree #1, a 13m-tall black willow that had been killed by the KSHB during 2015-16. Its snapped trunk is on the right (standing 1.7m tall) and the remainder of the tree is laying down on the left. (b) The 2 x 20 cm quadrat used in the study.

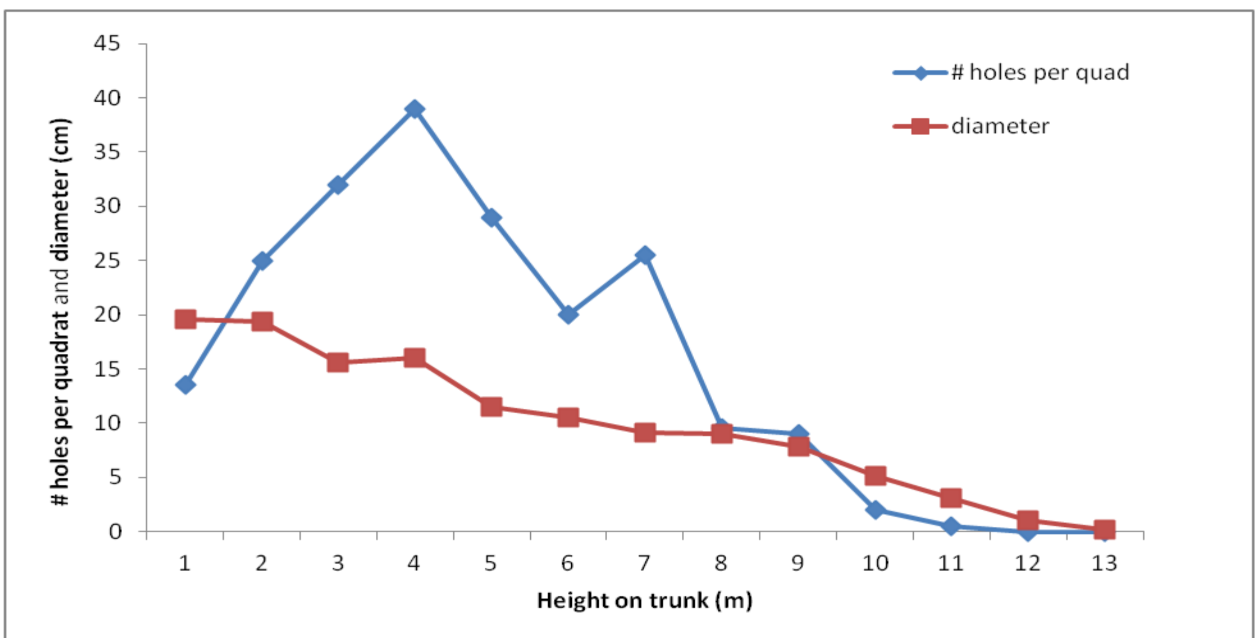


Figure 26. The density of KSHB holes along the length of Tree #1. Quadrat = 40 cm^2.

9.3. WHICH SPECIES COULD BE PLANTED IN AN KSHB-INFESTED SITE?

Land managers in the valley have been asking me: "Which native, riparian plant species should I plant in a site that has been infested with the KSHB?" Here I provide a list of plant species that occur in the Tijuana River Valley but have not been severely impacted by the KSHB and are therefore likely to do well in a KSHB-infested riparian site (Table 4). This list comes from my recent observations and my initial surveys in the valley (Boland 2016). Notice that the native species that have not been severely impacted are mainly shrub species. These shrubs are not substantially attacked by the KSHB probably because their branches have small diameters (smaller than the KSHB's preferred branch sizes). In addition, if a branch on a shrub is attacked by the KSHB the shrub is able to 'grow around the problem,' by sending up new branches.

Table 4. Species that have been not severely impacted and impacted by the KSHB.

Species	Common name
NATIVE SPECIES - NOT SEVERELY IMPACTED	
Baccharis salicifolia	Mule fat
Baccharis pilularis	Coyote brush
Ambrosia monogyra	Singlewhorl burrobrush
Salix exigua	Narrow-leaf willow
Malosma laurina	Laurel sumac
Peritoma arborea	Bladderpod
Sambucus nigra	Blue elderberry
Scirpus spp.	Tule
Artemisia dracunculus	Tarragon
Chloracantha spinosa	Spiny aster
Isocoma vernonioides	Coastal goldenbush
NATIVE SPECIES - SEVERELY IMPACTED	
Salix lasiolepis	Arroyo willow
Salix gooddingii	Black willow
Salix laevigata	Red willow
Populus fremontii	Western cottonwood
NON-NATIVE SPECIES - NOT IMPACTED	
Arundo donax	Giant reed
Ricinus communis	Castor bean
Tamarix ramosissima	Salt cedar
Tropaeolum majus	Garden nasturtium
Araujia sericifera	Cruel vine
Phytolacca icosandra	Tropical pokeweed
Schinus molle	Peruvian pepper
Myoporum laetum	Myoporum
Acacia cyclops	Cyclops wattle
Eucalyptus spp.	Gum tree
Schinus terebinthifolius	Brazilian pepper
Nicotiana glauca	Tree tobacco

10. OVERALL CONCLUSIONS

The riparian forests in the Tijuana River Valley are the first native forests to be substantially infested by the KSHB in southern California. Because little is known about the behavior and spread of the KSHB, or any other ambrosia beetle, in natural habitats (Hulcr and Dunn 2011) these forests are an important source of information about this emerging pest, its impact on natural riparian forests and the forest's response.

In this study I have examined the KSHB outbreak from three points of view – the beetle's, the forest's and the manager's – and have therefore approached the problem from several angles to give as clear a picture of what is occurring as possible.

I have documented some important and surprising discoveries and want to highlight three of them. **First, the destructive power of the beetle is astounding** – some forests went from tall dense stands of willows to mere tree stumps in less than a year and I have estimated that the KSHB has killed 95,761 willows, or 24% of all of the willows in the valley. The beetle continues to spread and its trail of destruction in the valley is not yet complete.

Second, the resprouting of many of the heavily-infested and damaged willows is wonderfully unexpected. Several experts had predicted that the KSHB-attacked forests were 'dead'. But the KSHB (and its associated fungi) did not kill all of the trees that it infested, instead many of the willows resprouted and are now producing a new low-canopy forest that may provide essential habitat for native species, including the endangered least Bell's vireo. In addition, the willows and mule fat have produced many seedlings that are also assisting in the forest recovery.

Third, managers can improve the quality of the forest that develops after a KSHB attack. Managers can clean-up the fallen debris in areas suitable for native riparian seedling development, and they can treat – with herbicide – the invasive plants that start to develop in the site. Within the Tijuana River Valley these invasives are arundo, castor bean and tamarisk. Through these actions a manager can greatly enhance the growth of native seedlings and resprouts and enhance the developing shrub forest.

11. NEXT STEPS – MONITORING, RESEARCH and MANAGEMENT

Further study of the KSHB in the Tijuana River Valley is essential. It is important to learn as much as we can about the KSHB in the Tijuana River Valley because the Tijuana River Valley is, so far, the only natural habitat significantly impacted by the KSHB and because so little is known about the ecology, behavior and spread of the KSHB, or any other ambrosia beetle, in natural habitats.

I therefore want to continue:

- to follow the **invasion of the KSHB** in the riparian habitats;
- to follow the **response of the riparian habitats** to the KSHB, including the growth and survivorship of the willow resprouts and seedlings; and
- to be an **on-site expert** looking for any more unexpected developments.

In addition, I now think that it is possible that:

- the **Tijuana River Valley is a 'special case.'** By this I mean that the Tijuana River Valley has characteristics that are especially attractive to the KSHB and that is why it is the only natural site being substantially invaded and damaged. I would like to research this idea because, if it is true, then it follows that not all riparian habitats are under threat – only those that are contaminated with sewage and other fertilizers. This would be a huge relief! It would also change our way of thinking about the whole invasion of California by the shot hole borers and likely change where we direct our future efforts and funds.

Furthermore, I would like:

- to spearhead the **control of the worst invasive species** in the KSHB-damaged forests, i.e., the herbicide treatments of arundo, castor bean and tamarisk. SWIA already has the people, program and permits in place to conduct these treatments, and they could start as soon as 15 September 2017. I think the northern arm of the river would be a great place to start, i.e., treat the invasives in these valuable forests from Hollister bridge to the Navy's airfield (Units 13 and 14).

12. ACKNOWLEDGEMENTS

I thank the US Navy and US Fish and Wildlife Service for funding this project and SWIA, particularly Mayda Winter, for administering it. I thank Chris Peregrin and Cara Stafford for allowing me to use the Goat Canyon sedimentation basins for the debris experiment, and the US Navy, US Fish & Wildlife Service, IBWC, California State Parks, and the County of San Diego Department of Parks and Recreation for allowing me access to their properties.

I also thank Elizabeth Onan and Monica Alfaro for field assistance, Monica Almeida at TRNERR for producing the maps, Tiffany Shepherd and Brian Collins for useful suggestions on an early draft of this report, and Deborah Woodward for field assistance and for editing this report.

13. LITERATURE CITED

Biedermann P.H.W., K.D. Klepzig and M. Taborsky. 2009. Fungus cultivation by ambrosia beetles: behavior and laboratory breeding success in three Xyleborine species. *Environmental Entomology* 38: 1096-1105.

Boland, J.M. *in press.* Linking seedling spatial patterns to seed dispersal processes in an intermittent stream. *Madroño* 64.

Boland, J.M. 2016. The impact of an invasive ambrosia beetle on the riparian habitats of the Tijuana River Valley, California. *PeerJ* 4:e2141; DOI 10.7717/peerj.2141. Available online at: https://peerj.com/articles/2141.pdf

Boland, J.M. 2014a. Factors determining the establishment of plant zonation in a southern Californian riparian woodland. *Madroño* 61: 48–63.

Boland, J.M. 2014b. Secondary dispersal of willow seeds: sailing on water into safe sites. *Madrono* 61: 388-398.

Boland, J.M. 2008. The roles of floods and bulldozers in the break-up and dispersal of *Arundo donax* (giant reed). *Madroño* 55 (3): 216-222.

Boland, J.M. 2006. The importance of layering in the rapid spread of *Arundo donax* (giant reed). *Madroño* 53 (4): 303-312.

Eskalen A. 2017. Shot hole borers/fusarium dieback. Available at http://eskalenlab.ucr.edu/shotholeborerhosts.html (accessed 7 March 2017).

Eskalen, A., R. Stouthamer, S.C. Lynch, M. Twizeyimana, A. Gonzalez and T. Thibault. 2013. Host range of *Fusarium* dieback and its ambrosia beetle (Coleoptera: Scolytinae) vector in southern California. *Plant Disease* 97: 938-951.

Freeman S., M. Sharon, M. Maymon, Z. Mendel, A. Protasov, T. Aoki, A. Eskalen and K. O'Donnell. 2013. *Fusarium euwallaceae* sp. nov – a symbiotic fungus of *Euwallacea* sp., an invasive ambrosia beetle in Israel and California. *Mycologia* 105: 1595-1606.

Hulcr, J., and R. Dunn. 2011. The sudden emergence of pathogenicity in insect-fungus symbioses threatens naive forest ecosystems. *Proceedings of the Royal Society B* 278: 2866-2873.

Kus, B. 2002. Least Bell's Vireo (*Vireo bellii pusillus*). *In* The Riparian Bird Conservation Plan: a strategy for reversing the decline of riparian-associated birds in

California. California Partners in Flight. Available online at: http://www.prbo.org/calpif/htmldocs/species/riparian/least_bell_vireo.htm

River Partners. 2007. Riparian restoration plan for the Drumheller Slough Unit, Sacramento River National Wildlife Refuge, Glenn County, California. Prepared for U.S. Fish and Wildlife Service, Bureau of Reclamation, and Wildlife Conservation Board.

Rudinsky, J.A. 1962. Ecology of Scolytidae. *Annual Review Entomology* 7: 327-348.

Sokal, R., and J. Rohlf. 1995. Biometry. W. H. Freeman and Company, New York, NY.

SWIA 2002. Tijuana River Valley invasive plant control program. 26 pages plus 41 maps in Appendix. Plan used to support CEQA and NEPA documents. Prepared by Tierra Environmental Services.

Umeda, C., A. Eskalen and T.D. Paine. 2016. Polyphagous Shot Hole Borer and *Fusarium* Dieback in California. Pages 757-767. In: T.D. Paine and F. Lieutier (eds.). Insects and diseases of Mediterranean forest systems. Springer International Publishing, Cham, Switzerland.

U.S. Fish and Wildlife Service. 1994. Endangered and threatened wildlife and plants: Designation of critical habitat for the least Bell's vireo. Final Rule. *Federal Register* 59: 4845-4867.

Whitcraft, C.R., D.M. Talley, J.A. Crooks, J.M. Boland, and J. Gaskin. 2007. Invasion of tamarisk (*Tamarix* spp.) in a southern California salt marsh. *Biological Invasions* 9: 875–879.

Wojtech, M. 2011. Bark. University Press of New England, Hanover.

Wood, S.L. 1982. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. *Great Basin Naturalist Memoirs* 6: 1-1356.