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

Final Report

by

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John Boland is an ecologist who got his PhD at UCLA. He has been studying plants in the Tijuana River Valley since 2002 and has published papers on riparian community development (Boland 2014a, 2014b, 2017a), arundo (Boland 2006, 2008) and tamarisk (Whitcraft et al. 2007). He has been working on the impact of the KSHB on the riparian habitats of the Tijuana River Valley since 2015; he has documented the rapid destruction of some of the forests (Boland 2016, 2017b, 2018) and the equally rapid recovery of those forests (Boland 2017b, 2018). Recently he developed a new explanation as to why some forests are more severely impacted than others (The Enriched Tree Hypothesis; Boland and Woodward *in press*).

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1. ABSTRACT

This report presents the current status of the Kuroshio Shot Hole Borer (KSHB, *Euwallacea kuroshio*, Coleoptera: Scolytidae) in the Tijuana River Valley. It provides current rates of KSHB infestation and rates of willow mortality; documents the current state of post-KSHB recovery in the most impacted forests in the valley; compares the Tijuana River Valley infestation with other riparian sites in San Diego County; explains why the severity of the KSHB infestation in the Tijuana River Valley is likely due to the valley's high level of sewage pollution; and offers several management recommendations.

This report is the fourth in a series of annual reports about the KSHB in the valley. It adds to and further develops **four main storylines** about the KSHB in the valley:

1. **The KSHB has been destructive in some – but not all – parts of the valley.** By conducting surveys of the trees in 29 survey units in the valley, I found that the KSHB continues to spread in the valley and infest and kill more trees every year. I estimate that the KSHB has so far infested 375,558 willows and killed 122,987 willows in the valley, and I show that the highest rates of infestation and mortality were among trees growing near the river; trees farther from the river have been, and continue to be, less affected.

2. **Willow forests that were extensively damaged by the KSHB are responding with vigorous regrowth and, so far, the new growth has not been re-infested by KSHB.** By conducting surveys and following tagged individual trees, I found that post-KSHB recovery of the forest is similar to post-fire recovery of chaparral. I show that forest recovery has occurred in three ways: by the healing of mature infested trees; by the resprouting of mature KSHB-damaged trees; and by the seeding of new trees and that, remarkably, the recovering willows are not being substantially re-infested by the KSHB.

3. **The KSHB infestation in the Tijuana River Valley is in a class of its own; comparable riparian forests in San Diego County are only lightly infested or not infested.** By conducting surveys at nine riparian sites outside the influence of the Tijuana River, I found that the Tijuana River Valley stands out as an extreme case. It is the most severely KSHB-infested natural site in southern California, and the most polluted with sewage; the severe infestation seen there should not be expected to occur at other natural, unpolluted riparian sites.

4. **The Enriched Tree Hypothesis explains the surprising link between sewage pollution and KSHB impacts**. The Enriched Tree Hypothesis states that the nutrient environment and preexisting condition of trees at a site will determine the extent of KSHB infestation and impact. That is, not all trees of one species at all sites are equally susceptible to KSHB infestation. The Enriched Tree Hypothesis is a new way to think about the shot hole borer attacks in southern California.

2. INTRODUCTION

The Kuroshio Shot Hole Borer (KSHB, *Euwallacea kuroshio*; Coleoptera: Scolytidae, Gomez et al. 2018) is an ambrosia beetle native to Asia that has recently invaded southern California. Until 2015 it had been seen in avocado groves and landscape trees only (Eskalen *et al.* 2013, Umeda et al. 2016). But in 2015, it was abundant in the native riparian forests in the Tijuana River Valley and has since caused extensive damage to those forests (Boland 2016, 2017b, 2018). As the KSHB is now also being found in many other sites in southern California (Eskalen 2019) managers and other authorities are extremely concerned that their sites are also going to be as impacted by the borer.

Since 2015 I have written three annual reports on the status of the KSHB in the Tijuana River Valley (Boland 2016, 2017b, 2018). This fourth report draws on the earlier reports and presents the current status of the KSHB in the valley in three main sections:

- The impacts of the KSHB on the riparian habitats in the valley;
- The response of the vegetation in the KSHB-damaged riparian habitats; and
- KSHB infestation in other riparian habitats in San Diego County.

In addition, I discuss the errors in some of the current thinking on the spread and impact of KSHB, and present the Enriched Tree Hypothesis (Boland and Woodward *in press*) as a new way of thinking about the KSHB invasion. This is in the final section called:

- Paradigm shift.

I conclude the report with a list of research and management recommendations based on these results. This report is designed to be most useful to managers of the parks inside the Tijuana River Valley but should also be used by other scientists and land managers to make informed decisions regarding the invasive ambrosia beetles in other parts of southern California.

3. BACKGROUND

3.1. THE TIJUANA RIVER VALLEY and THE DOMINANT WILLOW SPECIES

The Tijuana River Valley in San Diego County, California, is a coastal floodplain of approximately 3,700 acres at the end of a 1,730 square mile watershed (Figure 1). The Tijuana River is an intermittent stream that typically flows strongly in winter and spring and is mostly dry in summer (Boland 2014b). Many of the forests were established in the massive flood years of 1980 and 1993 making them 38 and 25 years old respectively – young by riparian forest standards (Faber et al 1989). Because the stream has changed course many times over the years (Safran et al. 2017), the riparian forests in the valley are a mosaic of forests of different ages and at different distances from the current flows. The forests can be divided into: **Wet Forests**, which are growing in the current river beds; **Dry Forests**, which are growing in older river beds; and **Scrub Forests**, which are growing far from current river flows (Figures 2 and 3). For decades, the Tijuana River has been polluted with sewage and industrial waste as it has flowed

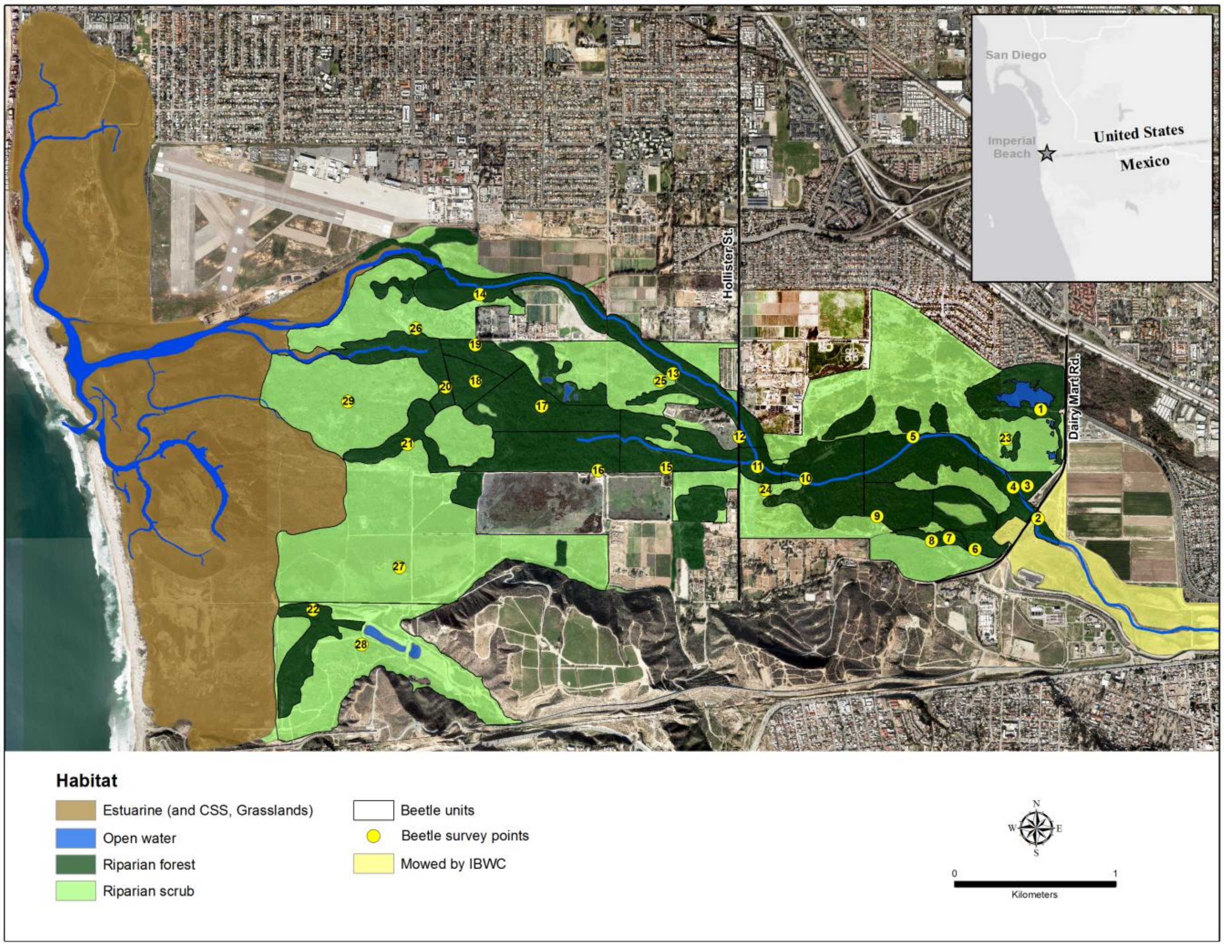


Figure 1. The location of the riparian forest and riparian scrub habitats within the Tijuana River Valley (from Boland 2016). Riparian forest units are numbered 1-22 and riparian scrub units are numbered 23-29. [Map created by John Boland and Monica Almeida, January 2016.]

through the City of Tijuana, Mexico. The trees in the Wet Forests, in particular, have therefore been frequently exposed to high nutrient levels (Boland 2018). All of these forests are dominated by just two tree species: arroyo willow (*Salix lasiolepis*, SALA) and black willow (*Salix gooddingii*, SAGO). These young forests are of low diversity and do not have some of the species seen in older forests in other parts of San Diego County; there are no oaks (*Quercus* spp.) and only a few sycamores (*Platanus racemosa*) and cottonwoods (*Populus fremontii*). The riparian scrub woodlands surrounding the forests are dominated by the perennial shrub, mule fat (*Baccharis salicifolia*).

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

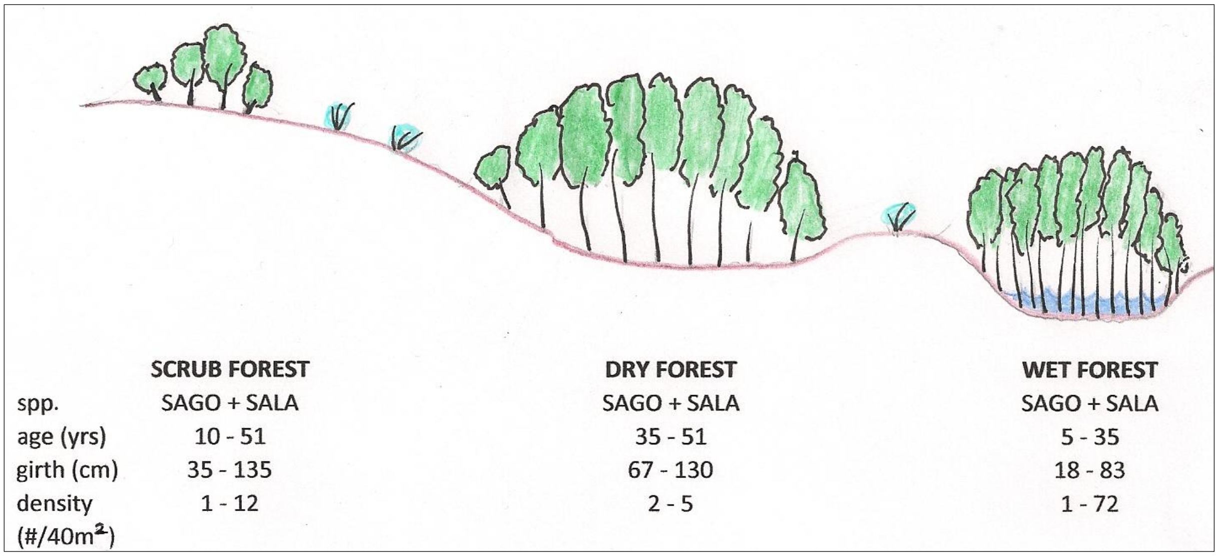


Figure 2. A diagram of a bisect through the Tijuana River Valley showing the locations of the Scrub, Dry and Wet Forests. The same willow species (black willow and arroyo willow) dominate all three forest types. The ranges of forest stand characteristics (age, girth, and density) are given for the willows (data from Boland 2016).

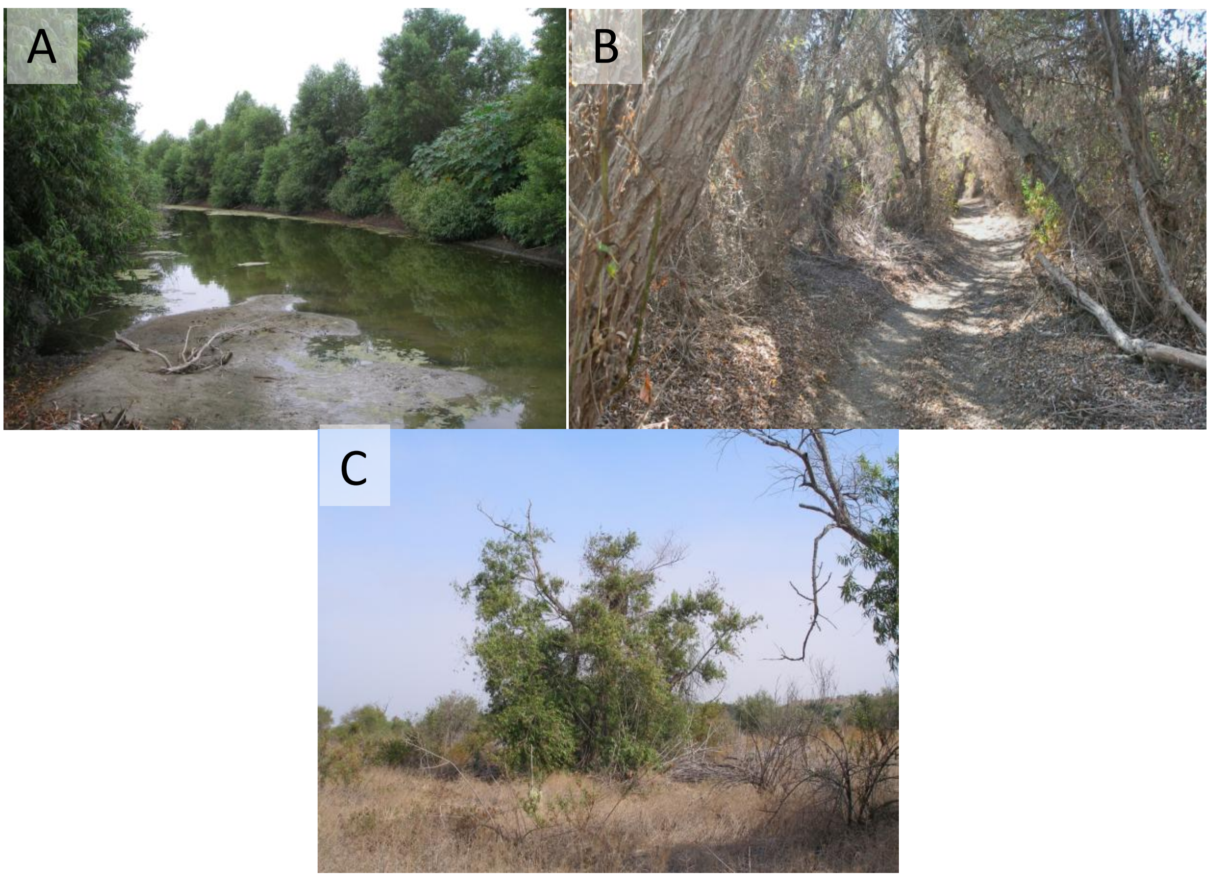


Figure 3. Typical views of the riparian forest habitats in the Tijuana River Valley. (A) Wet Forest showing the proximity of the willow trees to water, (B) Dry Forest showing a typical dry trail, and (C) Riparian Scrub showing a few dry black willows.

3.2. THE KUROSHIO SHOT HOLE BORER (KSHB)

The KSHB (*Euwallacea kuroshio*) is one of two ambrosia beetles currently attacking live trees in southern California. The other is the Polyphagous Shot Hole Borer (PSHB; *E. whitfordiodendrus*; Gomez et al. 2018). The two species are morphologically identical and are distinguished by their DNA sequences and by their associated fungi (Eskalen 2019). 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 2019; Umeda et al. 2016). Both beetles 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 two species currently stands at 64 host species (Eskalen 2019). It is sometimes convenient to refer to the two species as the Invasive Shot Hole Borers (ISHB).

When the borers attack a tree, the females drill into the trunk or branch and create galleries of tunnels in the xylem by pushing sawdust ‘tailings’ out of the entrance hole (Figure 4). They inoculate the tunnel walls 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, and start another gallery in either the natal tree or a new tree (Rudinsky 1962). The beetles are tiny (~2 mm in length) and seldom seen, however they can damage and even kill trees via their associated fungal pathogens, which may block the transport of material inside the tree (Eskalen 2019), and via their tunneling activities, which can undermine the structure of the tree trunks (Figure 4B; Boland 2016).

Figure 4. Examples of ambrosia beetle impact on willows. (A) KSHB excavate galleries within a trunk and push the sawdust tailings out of their entrance holes. (B) Trees can be undermined by many galleries and snap in high winds. [These pictures show the extremes – infested trunks do not always look like A, and infested trunks do not always break, like B.]

4. KSHB IMPACTS IN THE TIJUANA RIVER VALLEY

4.1. KSHB INFESTATION RATES OF WILLOWS IN ALL UNITS

Considering the damage that the KSHB has caused in the valley in the past few years (Boland 2016, 2017b, 2018), landowners and others need to know:

- **What is the current extent of the KSHB infestation in the valley?**

Methods

In 2015, in order to survey the large Tijuana River Valley forests consisting of a mosaic of stands of different ages, I divided the forest into survey units so that each unit was homogenous in terms of tree age and tree density (Boland 2016). A sample taken inside a unit could then be extrapolated to the entire unit. When I first started surveying the KSHB impacts in 2015, I divided the riparian habitats in the valley into 29 units, consisting of 22 forest units dominated by willows, and seven scrub units dominated by mule fat (Figure 1). I have continued to use these units for the annual surveys ever since (Boland 2017b, 2018). Furthermore, I have grouped the riparian forest units into two general categories – the Wet Forests and the Dry Forests (Figure 5). The Wet Forests are usually inundated by polluted flows each year whereas the Dry Forests are usually not inundated by those flows (Figure 6). So the willows in the valley occur in three habitats: as dense stands in the Wet and Dry Forests, and as outliers in the riparian Scrub Woodland (Figures 2 and 3).

To determine the KSHB infestation rates in 2018, I conducted the same type of surveys as in previous years, using the same survey units and survey points (Figure 1; Boland 2016, 2017b, 2018). In each unit, I started at the survey point and focused on arroyo and black willows. I examined as many live willow trees as I could in two hours and classified each as either 'currently infested' or 'not currently infested'. A tree was counted as 'currently infested' if it showed evidence of active tunneling by the KSHB, i.e., extrusion of sawdust or recent gumming out of sap from KSHB holes, or as 'not currently infested' if it had no evidence of KSHB attack or had only old, non-active KSHB holes. Surveys were conducted October-December 2018 and a total of 1,901 willows were examined. Within the Wet Forest units I further categorized each tree encountered as either a seedling (<3 years old), young tree (3-5 years old), Big Tree (relatively undamaged adult tree >5 years old), or resprouting adult tree (damaged adult tree >5 years old).

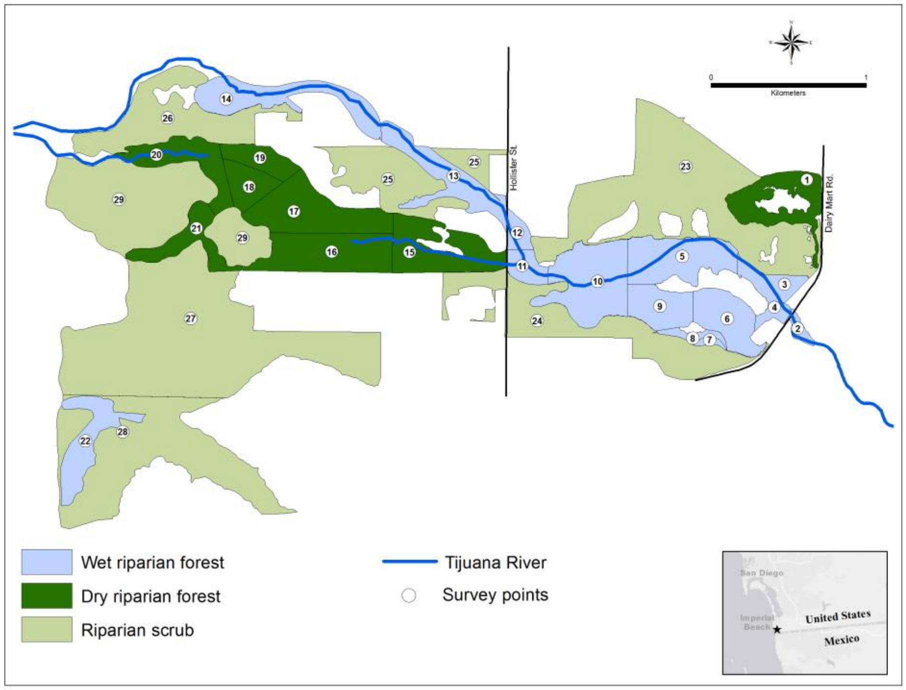


*Figure **5**. The identification of the Wet and Dry Forest units within the Tijuana River Valley. [Map created by John Boland and Monica Almeida, February 2019.]*

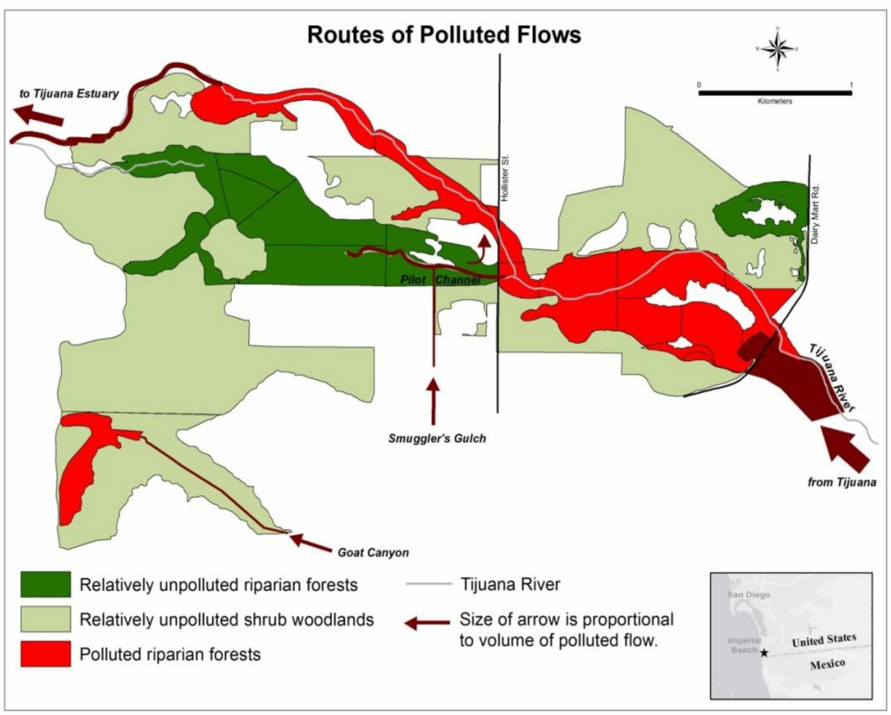


Figure 6. The main routes taken by the polluted flows through the Tijuana River Valley. The sizes of the arrows are proportional to the volume of polluted flows. [Map created by John Boland and Monica Almeida, February 2018.]

Results

Overview

- An estimated total of 375,558 willows or 91% of all the willows in the valley have been infested by the KSHB (Table 1).
- The infestation started in the Wet Forest units in 2015 (Table 1A); at that time the willows in the Wet units had a mean infestation rate of 95%.
- The infestation then moved into the Dry Forest units (Table 1B); by 2016 the willows in the Dry units had a mean infestation rate of 73%.
- The only willows that have not so far been substantially infested are those growing in the Riparian Scrub (Table 1C); in 2018 the willows in the Scrub units had a mean infestation rate of 2%.
- The course of the KSHB infestations, or their trajectories, were different in the Wet, Dry and Scrub units (Figure 7). In the Wet Forests infestation rates started very high and then declined substantially, in the Dry Forests infestation rates started low and then became moderate, whereas in the Scrub units infestation rates have been very low for the entire period.

Details within the Wet Forest, Dry Forest and Scrub units

- During 2018, most of the willows in the Wet Forests were seedlings, young trees or resprouting trees, and the KSHB infestation rates in these size/age classes was low, <5% (Table 2A). Only the scattered Big Trees showed a moderate rate of current infestation; the mean infestation rate for Big Trees was 14% (Table 2A). The KSHB is not heavily infesting the recovering trees in the Wet Forest units.
- During 2018, most of the willows in the Dry Forest units were old big trees, and the mean infestation rate for these trees in the Dry units was 53% (Table 2B).
- During 2018, most of the willows in the Scrub units also were old trees, and mean infestation rate for these trees was 2% (Table 2C).

Discussion

The surveys show that during the past four years most of the willow trees in the Wet and Dry Forests have been infested by the KSHB. Only the scattered willows in the Scrub habitats remain largely uninfested. The course or trajectory of the KSHB infestation has been different in the different habitats. When the KSHB first arrived in 2015 it was most abundant in the willows growing in the Wet Forest units. Later it turned to infesting the trees in the Dry Forests. So far the KSHB has been present in, but only minimally attacked the willows in the scrub units, which are growing in marginal willow habitat that could be called “Very Dry Forests.” Therefore it appears that the KSHB ranked the willows in the following way: #1 willows in the Wet Forests, #2 willows in the Dry Forests, and #3 willows in the Scrub Forests. These are important observations because they show that the KSHB does not consider all willows equal – in the Tijuana River Valley it has preferred the fast-growing willows in the wetter sites to the slow-growing willows, of the same species, in the drier sites.

*Table 1. Willow infestation rates in the Tijuana River Valley survey units during the four survey years. * = no adult trees available, called 0% infestation; ** = no data collected during survey period, infestation rate estimated later; and nd = no data.*

SITES			INFESTATION RATES					
UNIT	AREA	WILLOWS	2015	2016	2017	2018	MAX	
#	acres	est total #	%	%	%	%	%	TOTAL #
A. Wet riparian forests								
2	4.4	16,026	94%	100%	1%	4%	100%	16,026
3	7.5	5,517	100%	100%	0%	0%	100%	5,517
4	12.7	1,282	91%	100%	7%	3%	100%	1,282
5	44.7	13,561	96%	100%	19%	0%	100%	13,561
6	30.3	9,194	95%	100%	5%	0%	100%	9,194
7	2.0	4,407	100%	0%*	0%	1%	100%	4,407
8	5.2	37,953	87%	76%	7%	14%	87%	33,063
9	25.2	10,211	100%	0%*	7%	0%	100%	10,211
10	56.9	17,280	98%	100%	15%	1%	100%	17,280
11	11.6	9,365	100%	100%	0%	0%	100%	9,365
12	7.8	9,421	100%	0%*	1%	0%	100%	9,421
13	37.1	37,526	97%	100%	21%	6%	100%	37,526
14	44.1	84,717	75%	95%	45%	14%	95%	80,866
22	31.7	48,124	95%	100%	92%	11%	100%	48,124
mean			95%	77%	16%	4%	99%	
total	321.1	304,583						295,843
B. Dry riparian forests								
1	36.2	7,319	74%	74%	6%	2%	74%	5,442
15	45.8	16,204	8%	52%	17%	10%	52%	8,386
16	51.3	25,936	6%	79%	77%	88%	88%	22,694
17	52.9	16,069	0%	73%	93%	88%**	93%	14,997
18	17.5	7,062	2%	52%**	68%	91%	91%	6,410
19	16.9	8,524	61%	91%	83%	73%	91%	7,783
20	31.8	9,643	10%	52%**	80%	38%	80%	7,714
21	23.6	7,172	6%	66%	86%	72%	86%	6,134
mean			21%	67%	64%	58%	82%	
total	275.8	97,929						79,562
C. Riparian shrub								
23	189.3	6,184	nd	nd	0%	0%	0%	0
24	94.0	1,436	nd	nd	0%	9%	9%	131
25	97.9	253	nd	nd	0%	0%	0%	0
26	78.3	70	nd	nd	10%	0%	10%	7
27	262.7	1,360	nd	nd	0%	0%	0%	0
28	169.6	384	nd	nd	0%	4%	4%	16
29	142.9	850	nd	nd	0%**	0%**	0%	0
mean			nd	nd	1%	2%	3%	
total	1,034.8	10,537						154
Grand Total	1,631.7	413,050						375,558
% total infested								91%

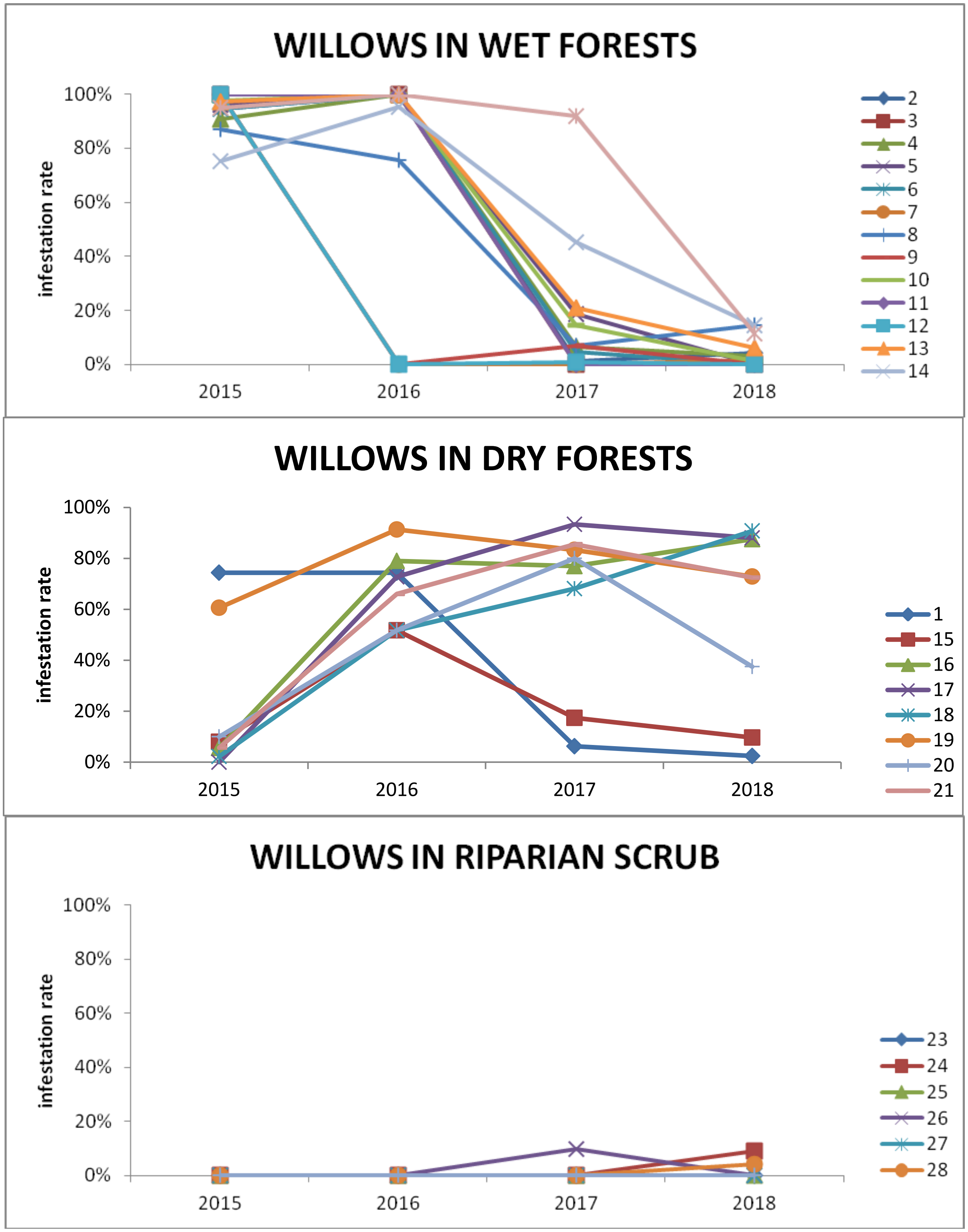


Figure 7. Infestation rates of willows within the Tijuana River Valley riparian survey units from 2015 to 2018. This is a graphic representation of the data in Table 1.

Table 2. Details of willow infestation rates in (A) the Wet Forest, (B) Dry Forest, and (C) Scrub units during 2018. nd = no data because flooding prevented access to units.

A. INFESTATION RATES IN WET UNITS

UNIT	SEEDLINGS			YOUNG TREES			BIG TREES			RESPROUT. TREES			TOTAL		
	# INF	TOT	% INF	# INF	TOT	% INF	# INF	TOT	% INF	# INF	TOT	% INF	# INF	TOT	% INF
2	0	103	0%	9	168	5%	0	4	0%	4	47	9%	13	322	4%
3	0	52	0%							0	17	0%	0	69	0%
4	0	6	0%	0	16	0%	2	20	10%	0	25	0%	2	67	3%
5							0	4	0%	0	41	0%	0	45	0%
6							0	5	0%	0	22	0%	0	27	0%
7				1	22	5%				0	47	0%	1	69	1%
8				4	38	11%	4	6	67%	2	26	8%	10	70	14%
9										0	45	0%	0	45	0%
10	0	10	0%				0	6	0%	1	71	1%	1	87	1%
11	0	47	0%	0	17	0%	0	1	0%	0	45	0%	0	110	0%
12	0	2	0%	0	162	0%				0	7	0%	0	171	0%
13				0	7	0%	4	10	40%	0	48	0%	4	65	6%
14							16	111	14%						14%
22							6	53	11%						11%
Total	0	220		14	430		32	220		7	441		53	1,311	
mean			0%			3%			14%			1%			4%

B. INFESTATION RATES IN DRY UNITS

UNIT	BIG TREES		
	# INF.	TOTAL	% INF.
1	2	82	2%
15	9	93	10%
16	56	64	88%
17	nd	nd	nd
18	59	65	91%
19	51	70	73%
20	9	24	38%
21	42	58	72%
Total	228	456	
mean			53%

C. INFESTATION RATES IN SCRUB UNITS

UNIT	BIG TREES		
	# INF.	TOTAL	% INF.
23	0	16	0%
24	2	22	9%
25	0	33	0%
26	0	24	0%
27	0	15	0%
28	1	24	4%
29	nd	nd	nd
Total	3	134	
mean			2%

4.2. KSHB-INDUCED MORTALITY RATES OF WILLOWS IN ALL UNITS

Although the infestation rate of willows has been very high – 100% of the willows were infested in some of the units – not every infested tree dies (Boland 2018). Therefore an important question to ask is:

- **How many trees have been killed by the KSHB attack?**

Methods

A way to determine mortality rates within a unit is to inspect each tree at a survey point and count the number of living and the recently dead trees; this is the method used in previous years (Boland 2017b, 2018). This is the kind of survey I did in the Dry Forest and Scrub units in 2018; in these units, I examined as many willows as I could in two hours and classified each as either 'alive', 'recently dead from KSHB attack', or 'dead from some other cause'. An average of 45 ± 27.3 trees (n = 13 units) was surveyed in each of these units. From these data, the mortality rate and the estimated total number of trees killed were then calculated. This kind of survey could not be done in most of the Wet Forest units this year because most of the recently dead trees had been swept away by flows during the winters of 2016-17 and 2017-18; in these units, my earlier surveys are used as the best mortality estimates (Boland 2017b, 2018). As each survey is an estimate of the mortality since the KSHB invasion in 2015, when two or more surveys have been conducted in a unit the highest rate (the maximum) is used to estimate the total number of willows killed by the KSHB in that unit.

Results

- An estimated total of 122,987 willows or 30% of all the willows in the valley have been killed by the KSHB (Table 3).
- Mortality rates have been considerably higher in the Wet Forest units than the Dry Forest units. Mean max mortality rates in the Wet units were 49%, whereas in the Dry units they were only 9% (Table 3, Figure 8).
- The remarkable differences in mortality rates between the Wet and Dry Forest units can be seen in the photos taken in Wet Unit 3 and Dry Unit 15 (Figure 9). The KSHB was destructive in the Wet and hardly noticeable in the Dry, even though the sites were composed of the same willow species.
- The only willows that have not so far been extensively infested by the KSHB are those growing in the Riparian Scrub habitats; these willows in the Scrub units also had the lowest average mortality rate of 2%.

Discussion

The total number of willows in the valley estimated to have been killed by the KSHB continues to grow each year and is now at 122,987 trees. This is the highest mortality figure for any site in southern California. Even so this number is likely to be an underestimate because any KSHB-killed trees that were snapped at ground level would not get counted and the extensively-damaged Wet Forest units could not be accurately surveyed this year.

As with the infestation rates, the mortality rates were not equal everywhere; the KSHB has mainly infested and killed willow trees in the Wet Forests. This within-Tijuana River Valley pattern in KSHB impact is discussed further in Section 8.2.

Table 3. Willow mortality rates in the Tijuana River Valley survey units during the three survey years. nd = no data.

UNIT	AREA	WILLOWS	WILLOW MORTALITY RATES				
#	acres	est total #	2016	2017	2018	MAX %	MAX # trees
source	Boland 2016		Boland 2017	Boland 2018	this report	3 years	
A. Wet Rip. Forests (2 willow spp.)							
2	4.4	16,026	67%	nd	nd	67%	10,738
3	7.5	5,517	97%	nd	nd	97%	5,352
4	12.7	1,282	57%	nd	nd	57%	731
5	44.7	13,561	29%	nd	nd	29%	3,933
6	30.3	9,194	44%	nd	nd	44%	4,045
7	2.0	4,407	55%	nd	nd	55%	2,424
8	5.2	37,953	29%	nd	nd	29%	11,006
9	25.2	10,211	42%	nd	nd	42%	4,288
10	56.9	17,280	51%	nd	nd	51%	8,813
11	11.6	9,365	26%	nd	nd	26%	2,435
12	7.8	9,421	78%	nd	nd	78%	7,349
13	37.1	37,526	41%	nd	nd	41%	15,386
14	44.1	84,717	13%	22%	15%	22%	18,826
22	31.7	48,124	10%	41%	29%	41%	19,970
mean			46%	32%	22%	49%	
total	321	304,583					115,294
B. Dry Rip. Forests (2 willow spp.)							
1	36.2	7,319	6%	8%	1%	8%	563
15	45.8	16,204	0%	0%	0%	0%	0
16	51.3	25,936	6%	1%	0%	6%	1,556
17	52.9	16,069	0%	3%	nd	3%	434
18	17.5	7,062	0%	3%	0%	3%	228
19	16.9	8,524	15%	12%	13%	15%	1,279
20	31.8	9,643	2%	33%	11%	33%	3,214
21	23.6	7,172	0%	4%	0%	4%	272
mean			4%	8%	4%	9%	
total	276	97,929					7,547
C. Riparian scrub (2 willow spp.)							
23	189.3	6,184	nd	0%	0%	0%	0
24	94.0	1,436	nd	0%	9%	9%	131
25	97.9	253	nd	0%	0%	0%	0
26	78.3	70	nd	0%	0%	0%	0
27	262.7	1,360	nd	0%	0%	0%	0
28	169.6	384	nd	0%	4%	4%	16
29	142.9	850	nd	0%	nd	0%	0
mean			nd	0%	2%	2%	
total	1,035	10,537					147
Grand Tot.	1,632	413,050					122,987
% total mortality							30%

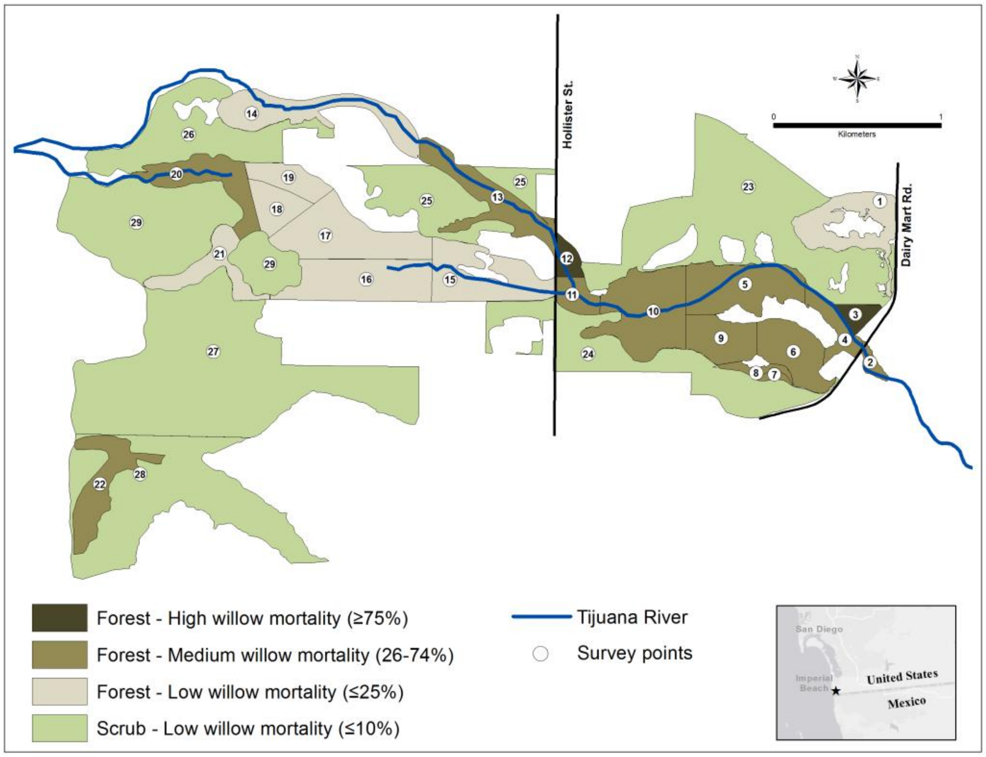


Figure 8. The distribution of willow mortality within the Tijuana River Valley. [Map created by John Boland and Monica Almeida, February 2019.]

Figure 9. The large differences in KSHB impact within the valley. (A) Wet Forest Unit 3 where the mortality rate was highest. (B) Dry Forest Unit 15 where the mortality rate was lowest. In both units the black willow was the most abundant tree.

4.3. SURVIVORSHIP OF TAGGED WILLOWS

In order to determine how quickly a tree could be killed by the KSHB, I followed the speed of deterioration in many individual trees. I asked:

- **How long does it take a typical Dry Forest tree to go from being 'not infested' to 'infested' to 'dead'?**

Methods

I tagged more than 200 willows during February 2016 and revisited them in December 2018 to see how the infestation was progressing. The tagged trees were scattered in Units 13 – 21, i.e., mainly Dry Forest units. When revisiting the trees I classified each as either: 'not infested–alive'; 'not infested–dead'; 'infested–alive'; or 'infested–dead'. Infested–alive included trees that had been heavily damaged by the KSHB and were resprouting as well as undamaged live trees that had signs of active KSHB infestation. [Two sites, containing 60 tagged trees, could not be reached because of early flooding; those trees will be assessed when flood waters subside and their results will be included later.]

Results

- Of the 119 tagged willows that were not infested at the start in February 2016, most (91 trees, or 76%) were 'infested–alive' in December 2018 (left side of Figure 10). This means they became infested during the nearly three year period but did not die. Only a few of these 119 trees became infested and died (12 individuals, 10%).

- Of the 64 tagged willow trees that were infested at the start in February 2016, most (54 trees, or 84%) were still 'infested–alive' in December 2018 (right side of Figure 10). This means they continued to live, even though infested, throughout the nearly three year period. Only a few of these trees died (10 individuals, 16%).

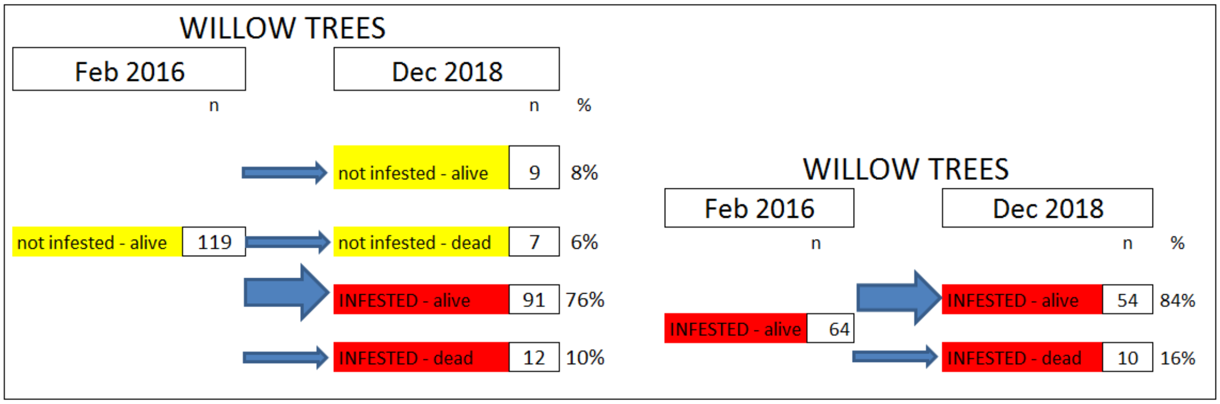


Figure 10. The change in condition of tagged trees from February 2016 to December 2018. One set of trees started as 'not infested' (n = 119; on the left), another set started out 'infested' (n = 64; on the right). These trees were mainly in the Dry Forests.

- Putting the timelines together to approximate a hypothetical six year period, the results suggest that an uninfested tree at the beginning of Year 1 had a 76% chance of becoming infested by the end of Year 3, and that an infested tree at the start of Year 3 had an 84% chance of surviving until the end of Year 6.

Discussion

The results from the tagged trees showed that, although Dry Forest trees were being infested, only a small percent have been killed by the infestation. Most of the trees that were infested when they were first tagged have survived for three years. The low mortality rates mean that, at the moment, the Dry Forests continue to look generally sound (Figure 9B). Whether the mortality rates stay low will need to be determined by future monitoring.

4.4. CONCLUSIONS

The first of the three main storylines coming out of the KSHB's invasion of the Tijuana River Valley is that the KSHB can be **very destructive but its impact is not equal everywhere in the valley**. The new surveys show most of the willow trees in the Wet and Dry Forests have been infested by the KSHB and that the KSHB is estimated to have killed 122,987 willows, or 30% of the willows in the valley. This is the largest number of trees reported killed by the KSHB anywhere in southern California.

But the trajectories of the infestation and the willow mortality rates were different in the Wet Forest, Dry Forest and Scrub units. The pattern of KSHB infestation shows that the KSHB had a **preference for willows in the Wet Forest units**. It is in the Wet units where the infestation rates were immediately high in 2015-16 (Boland 2016) and it is in the Wet units where mortality rates have been the greatest (Boland 2017, 2018). As the willow species in all of the units (Wet, Dry and Scrub) are the same two species, the KSHB is likely responding to the condition of the trees in the different sites. In the Wet units the trees are frequently inundated by the river, and are healthy and fast-growing, but as one moves away from the river into the Dry Forest and Scrub units the sites are drier and the trees appear less-healthy and slower-growing. **The notion that all individuals of a given tree species are equally susceptible to infestation at all locations (e.g., McPherson et al. 2017) is incorrect.** The pattern of KSHB impact within the Tijuana River Valley is explained by a hypothesis in Boland (2018) and Boland and Woodward (*in press*), and is discussed further in Section 8.2 below.

5. RESPONSE OF VEGETATION IN THE KSHB-DAMAGED RIPARIAN HABITATS

The initial KSHB infestation in the Tijuana River Valley in 2015 was alarming because it caused the quick, dramatic collapse of the tall willow canopy in many of the Wet Forest units. In 2016 I published before-and-after photos of the forest at Dairy Mart bridge to illustrate the damage the KSHB had caused in just a few months (reprinted here as Figure 11A and B; Boland 2016). Now I have added a third and fourth photo to the series to illustrate the remarkable forest recovery at the same site (Figure 11C and D). In this section I will describe how the most heavily-damaged forests in the Tijuana River Valley, the Wet Forests, have responded to the KSHB infestation.

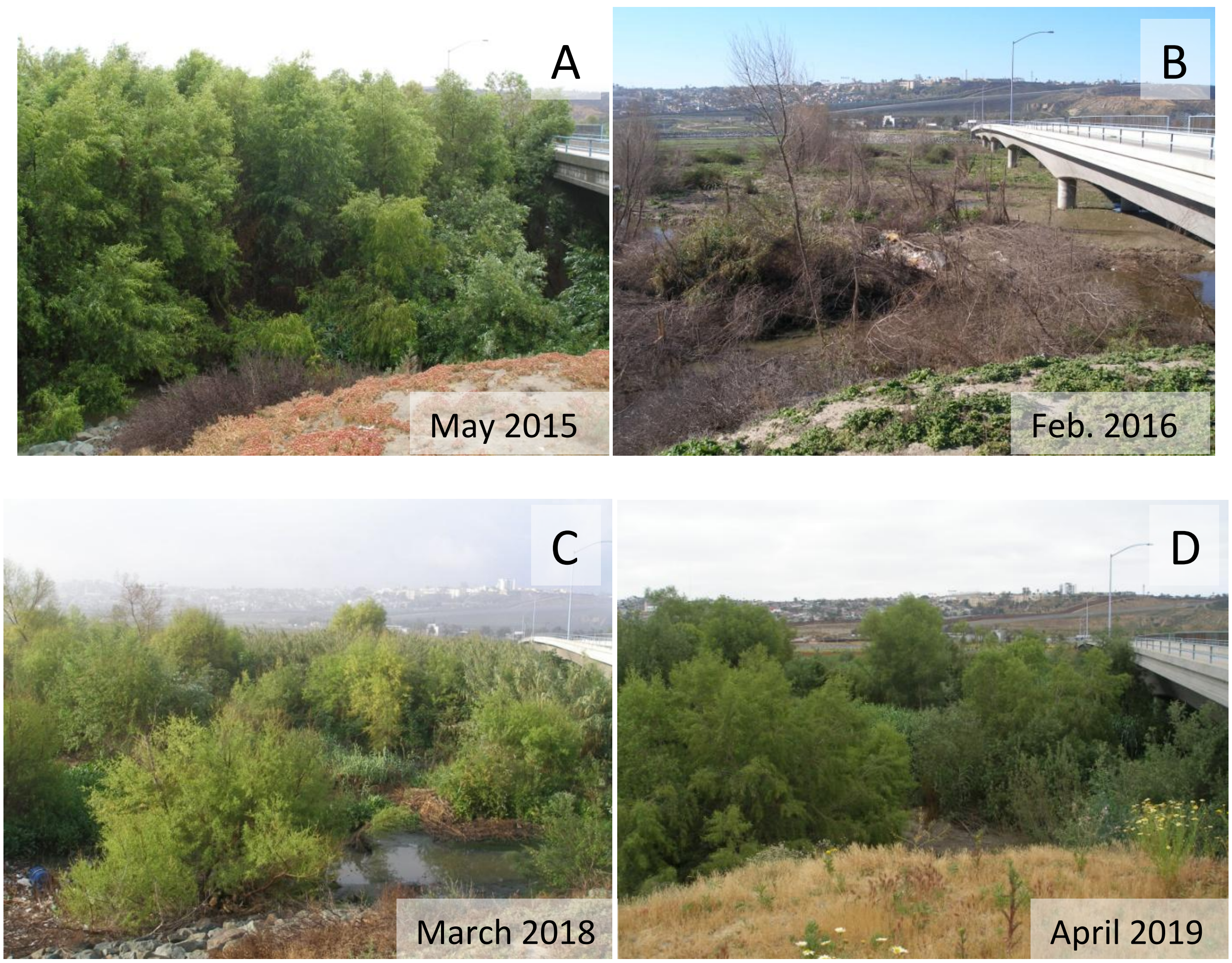


Figure 11. The Wet Forest at Dairy Mart bridge from 2015 to 2019 showing the initial impact of the KSHB on the willow canopy followed by the substantial forest recovery. (A) Before the KSHB infestation (May 2015). (B) After the KSHB infestation (February 2016). (C and D) During forest recovery (March 2018 and April 2019).

5.1. RECOVERY OF WILLOWS BY GROWING OVER KSHB GALLERIES

A few willows, living in the Tijuana River Valley Wet Forests, have survived the 2015-16 KSHB attack relatively undamaged; I call them 'Big Trees' (Boland 2018). Their bark is usually peppered with many KSHB holes, but the holes appear old, i.e., they do not look like they are currently being used by KSHB because there is no frass coming out of them. Here I answer the question:

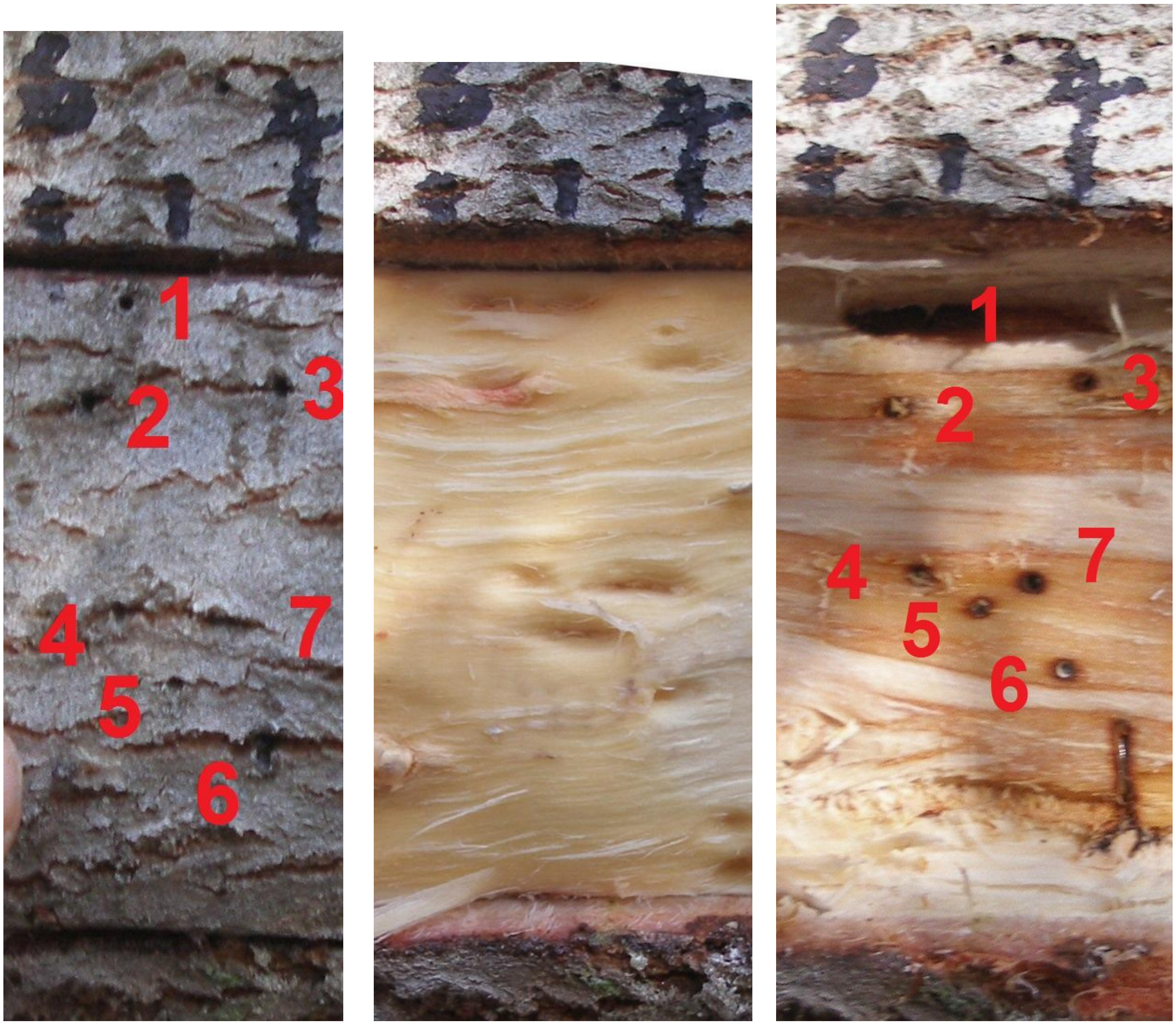
- **What is going on underneath these old KSHB holes?**

Methods

I found a living arroyo willow in Unit 12 that had many 'old' KSHB holes and I drew a 9 x 6 cm quadrat on the bark that included 12 holes. I then drew a cm scale along the upper edge of the quadrat and conducted a dissection. I first cut the bark off the trunk, which exposed the new wood underneath, and took several photos. I then chiseled approximately 1 cm of new wood out, which exposed the old wood underneath and took several more photos. These cuts revealed what was going on underneath the old KSHB holes.

Results

- The KSHB holes were easily seen in the bark and numbered 1 – 7, as in Figure 12A.
- There were no KSHB holes or tunnels immediately under the bark in the new wood (Figure 12B).
- There were KSHB tunnels in the old wood deep in the trunk and these deep tunnels matched perfectly with the holes in the bark (Figure 12C). These deep tunnels were no longer in use by KSHB.
- I conclude that this tree had survived a heavy KSHB attack and the wood had grown over the old KSHB tunnels as illustrated in Figure 13.



A. THE BARK SURFACE B. BARK REMOVED C. BARK AND NEW WOOD REMOVED

Figure 12. Dissection of old KSHB holes in an arroyo willow. (A) Bark in place. (B) Bark removed revealing new wood. (C) Bark and 1 cm of new wood removed revealing old wood with KSHB tunnels. The scale drawn on the bark above the cut is in cm and the numbers on the bark are ‘6’ and ‘4’. The KSHB holes in the bark are numbered 1-7 in A and are matched in the deep old wood in C.

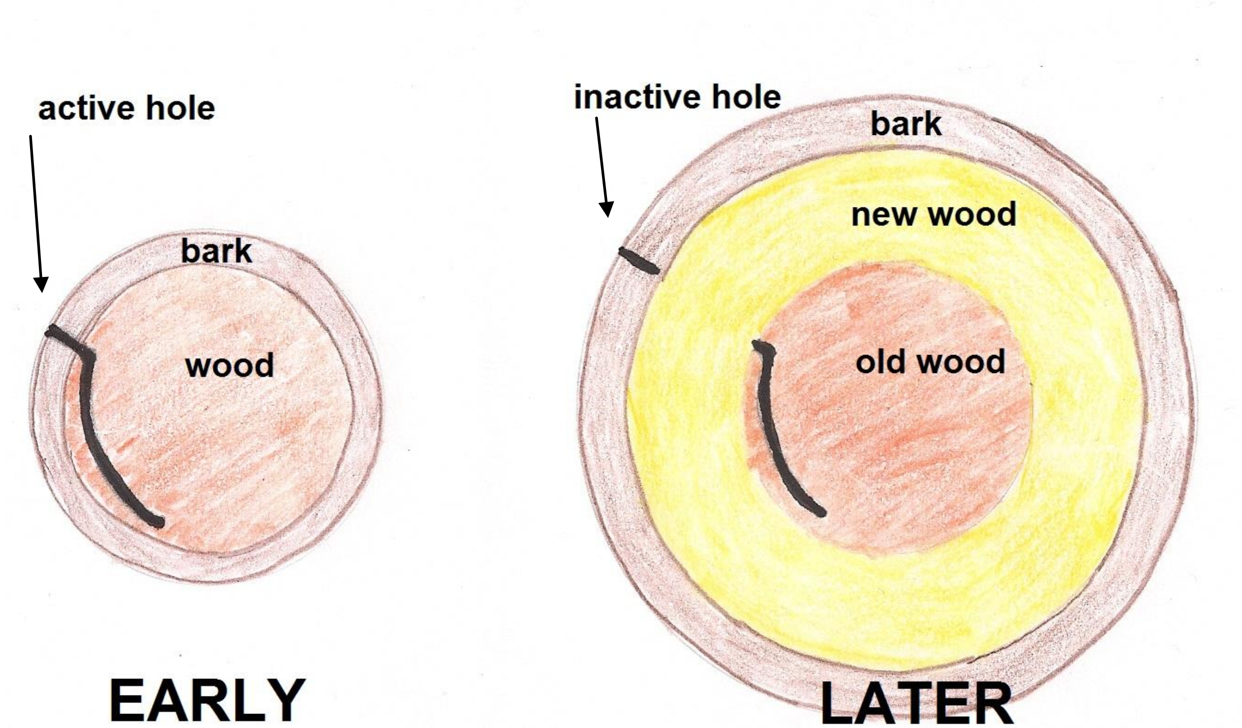


Figure 13. An illustration showing the growth of new wood over a KSHB gallery. EARLY: An active KSHB hole connected to the gallery in the wood below. LATER: The same KSHB hole now inactive and no longer connected to the gallery below because of the addition of new wood. The "Later" diagram illustrates what was seen in the dissection in Figure 12, i.e., the inactive holes in the bark were separated from the tunnels in the old wood by new wood with no tunnels.

Discussion

This observation shows that some willows have survived the KSHB attack by growing over the problem; they have laid down new wood over the KSHB-infested old wood and continued to grow. This observation is important for several reasons. **First**, this is the first time, to my knowledge, that this type of 'healing' after a KSHB attack has been demonstrated. **Second**, it makes one realize that there can be old KSHB holes on a living tree. This means that when surveying trees for KSHB infestation one must keep in mind that some KSHB holes may be old and no longer in use. **And third**, it shows that not all KSHB-attacked trees die; trees can heal themselves after a KSHB attack. This is an important finding because managers are currently being advised that all infested trees will die, which is certainly not the case.

5.2. RECOVERY OF WILLOWS BY PRODUCTION OF RESPROUTS

A damaged willow tree produces resprouts, i.e., new upright branches that grow out of the surviving trunk. Reprouts are an important means by which the willows in the Tijuana River Valley have recovered after the KSHB attack (Boland 2017b, 2018). Here I give details on the monitoring of individual resprouts and answer the question:

- **What are the rates of survivorship and growth of willow resprouts in areas that were previously heavily infested by KSHB?**

Methods

In October–November 2016, I tagged 34 resprouting willow trees for monitoring over time. These tree stumps were scattered throughout the heavily-damaged Wet Forest, in Units 2, 8, 10, 11, 12 and 13. At that time, I measured characteristics of the tree stump, e.g., height, circumference and KSHB holes per 45 cm^2 (Table 4). In addition, I examined all the resprouts on each tagged tree for signs of KSHB infestation, and I measured the diameter of each resprout. I also measured the length of the largest resprout on each tree, tagged it and named it the focal resprout. I examined and remeasured these reprouts during October–November 2017 and October–November 2018. During these revisits, I looked for signs of KSHB infestation, measured the diameter of all of the live resprouts, and measured the length of the focal resprouts. In addition, I measured the total height and width of the ‘new’ tree created by the resprouting stump and calculated its volume (as a cone). These surveys therefore address the growth and survivorship of the resprouting willow trees.

Results

- Of the 34 resprouting willows tagged in 2016, 33 were alive and growing in 2018 (Table 4). One tree died; it was growing on an embankment high above the water line and appeared to die from lack of water rather than due to KSHB infestation.
- The resprouts on the surviving willows exhibited vigorous growth. For example, one arroyo willow stump was1 m tall in March 2016, 3.6 m tall in October 2016, 5.5 m tall a year later and 6.2 m tall in September 2018 (Figure 14).
- Although the total number of resprouts on the trees declined, the remaining resprouts increased in length and diameter (Table 4 and Figure 15).
- The average diameter of the resprouts during 2018 was 5.1 cm and 1% were infested (Figure 15); of the 264 resprouts, 189 resprouts (72%) had diameters greater than one inch.
- By November 2018, the resprouting willows were large and shrub-like (Figure 14D). The average ‘new’ tree had 8.3 resprouts, was 5 m tall and 5.9 m wide, and occupied a total volume of approximately 38.6 m^3 (Table 4).
- Only two of the resprouts showed signs of KSHB infestation in November 2018 (Table 4 and Figure 15).
- The resprouts that were infested in 2016 were growing strongly in 2018. No resprouts have been killed by the KSHB.
- The resprouts are old enough and vigorous enough to flower; I observed flowers on all of the living resprouting trees (33/33) during spring 2018.

Figure 14. The rapid growth of a resprouting arroyo willow (R1) between 2016 and 2018. (A) The resprouting tree was 1m tall on March 8, 2016. (B) 3.6m tall on October 7, 2016. (C) 5.5m tall on November 7, 2017. (D) 6.2m tall on September 21, 2018. For scale, a person (arrowed) is standing in the same place in each photo.

Table 4. Survivorship and growth of tagged willow tree stumps with resprouts.

Characteristic	2016	2017	2018	% change 2017-18	
source	Boland 2017	Boland 2018	this report		
ORIGINAL TREES					
Number of labeled resprouting trees		34			
Labeled trees location -- Units		2, 8, 10, 11 and 13			
Stump height in m -- mean (std dev)		4.1 (2.1)			
Stump circumference in cm – mean (std dev)		92.3 (43.0)			
Number of KSHB holes per 45 cm^2 – mean (std dev)		27.4 (12.0)			
FOCAL RESPROUTS					
Number of labeled focal resprouts	34	34	33	-3%	decreased
Resprout length in m -- mean (std dev)	3.0 (0.7)	4.4 (1.3)	5.1 (1.2)	16%	increased
Resprout diameter in cm -- mean (std dev)	3.1 (1.0)	5.9 (1.9)	7.7 (2.9)	31%	increased
ALL RESPROUTS - SIZE					
Total number of resprouts	302	316	264	-16%	decreased
Resprout diameter in cm -- mean (std dev)	2.2 (1.2)	3.4 (2.2)	5.1 (3.3)		increased
ALL RESPROUTS - INFESTATION BY KSHB					
Number of resprouts infested with KSHB	27	0	2		increased
Percent of resprouts infested with KSHB	9%	0%	1%		increased
Number of resprouts killed by KSHB	0	0	0		same
NEW TREE - SIZE					
Number of resprouts per tree -- mean	8.9	9.3	8.3	-11%	decreased
Width of new tree in m -- mean	nd	4.0	5.0	25%	increased
Height of new tree in m -- mean	nd	5.2	5.9	13%	increased
Volume of new tree in m^3 -- mean	nd	21.8	38.6	77%	increased

Discussion

Documenting the continued survival and rapid growth of old KSHB-infested willows in the Wet Forests is informative for several reasons. **First,** it underscores the fact that a KSHB-infested tree can survive and regrow. A heavily-infested, heavily-damaged tree may at first appear to be dead, but given a little time it may be able to recover via resprouting from its stump. **Second,** the rapid growth of resprouts shows how quickly the heavily-damaged willow trees in the Wet Forests of the Tijuana River Valley are recovering. They went from dead-looking stumps riddled with many KSHB holes to voluminous, 6 meter tall shrubs in less than three years. It therefore appears that the KSHB-damaged forests have the ability to rapidly restore themselves. **Third,** surprisingly and fortunately these resprouting trees are not being reinfested by KSHB. It is not known if or when the KSHB will return to these areas, attack the resprouts, and interrupt the forest recovery. But, at present, the willows are growing and flowering vigorously and providing essential habitat for the animals in the valley.

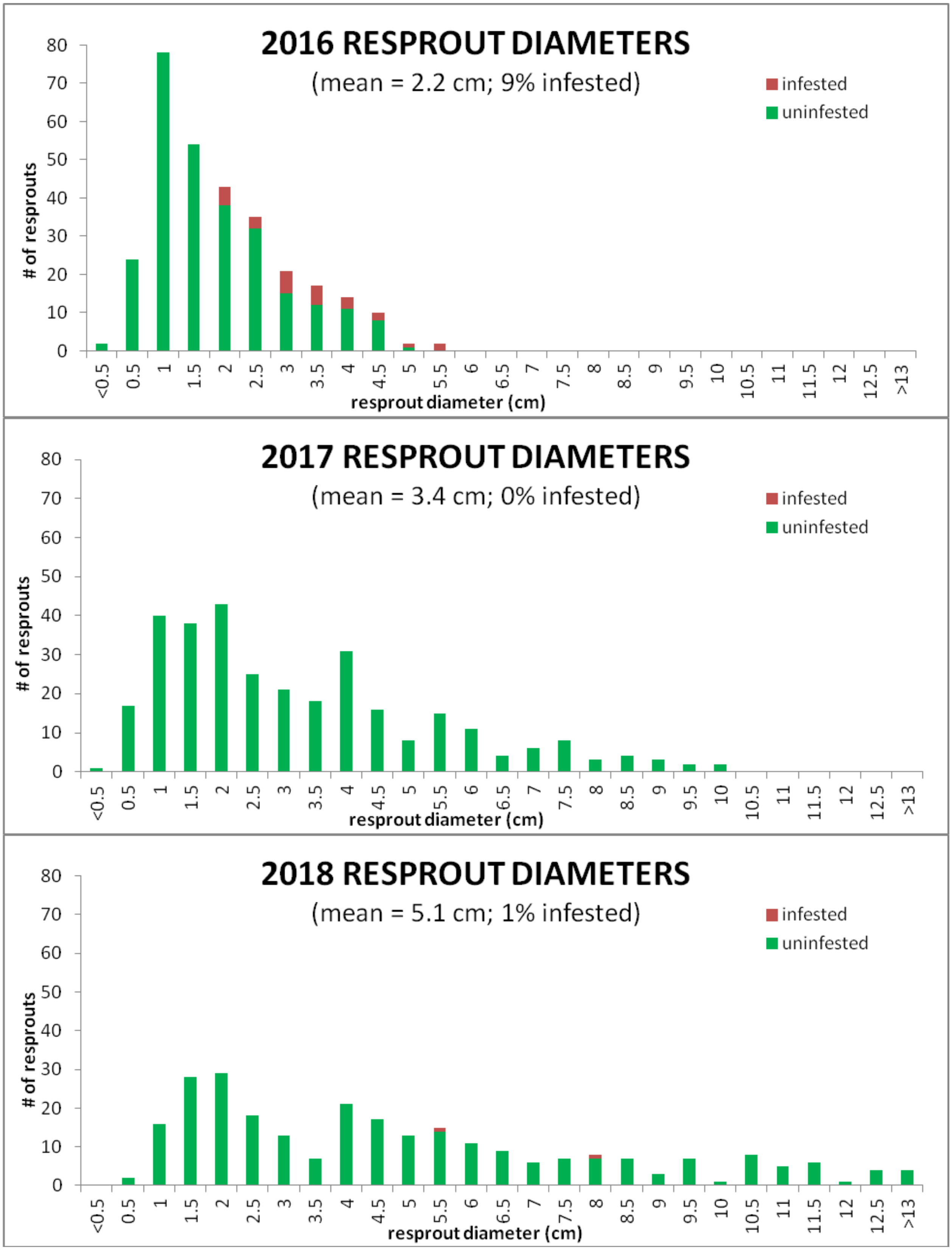


Figure 15. The size frequency of willow resprouts growing on old KSHB-infested trees.

5.3. RECOVERY OF WILLOWS BY PRODUCTION OF SEEDLINGS

Three large stands of willow seedlings were present in the Wet Forests in 2017-18 (Boland 2018). The purpose here is to answer the question:

- **Are the large stands of willow seedlings described in Boland (2018) surviving and growing?**

Methods

The stands of seedlings (now saplings) were revisited during October 2018, rephotographed and their areas measured.

Results

- The stands of seedlings were surviving and growing. They had grown substantially taller (Figure 16).
- The sizes of the stands in October 2018 were as follows Unit 2 (143 m^2), Unit 3 (390 m^2), and Unit 12 (613 m^2).
- The plants in these stands were not being attacked by KSHB.

Discussion

These three large stands of willow seedlings were all doing well – they were growing taller and not being attacked by the KSHB.

These stands illustrate how willows typically establish via seeds: winter flows remove the existing vegetation and debris in an area thereby exposing bare sediment; during spring many thousands of willow seeds land on the moist sediment and they germinate immediately (Boland 2014b); the seedlings grow very quickly and within a year the once bare area is covered by a dense stand of tall, young trees (Figure 16A, C, E). As the stand develops it is thinned, with the shortest trees not surviving, and within a few years the stand looks like a typical stand in the Tijuana River Valley – tall and dense and consisting of same-aged trees (Figure 11A).

The ease with which native willows became densely established in these sites over the past two years illustrates the effectiveness of natural restoration projects (Briggs 1996, Boland 2014a). In projects of this type, riparian revegetation is allowed to occur with little or no human intervention. Natural restoration is superior to the more-commonly conducted horticultural restoration because it produces a forest community with a high density of trees, in which the species are in the appropriate down-slope zonation, and the trees are of the appropriate sex ratios and genetic diversity. This is the most suitable method for riparian sites that are inundated by floods during winter and have natural seed sources nearby (Boland 2014a). Natural restoration is therefore the best method for restoring the Wet Forests when the arundo is treated.

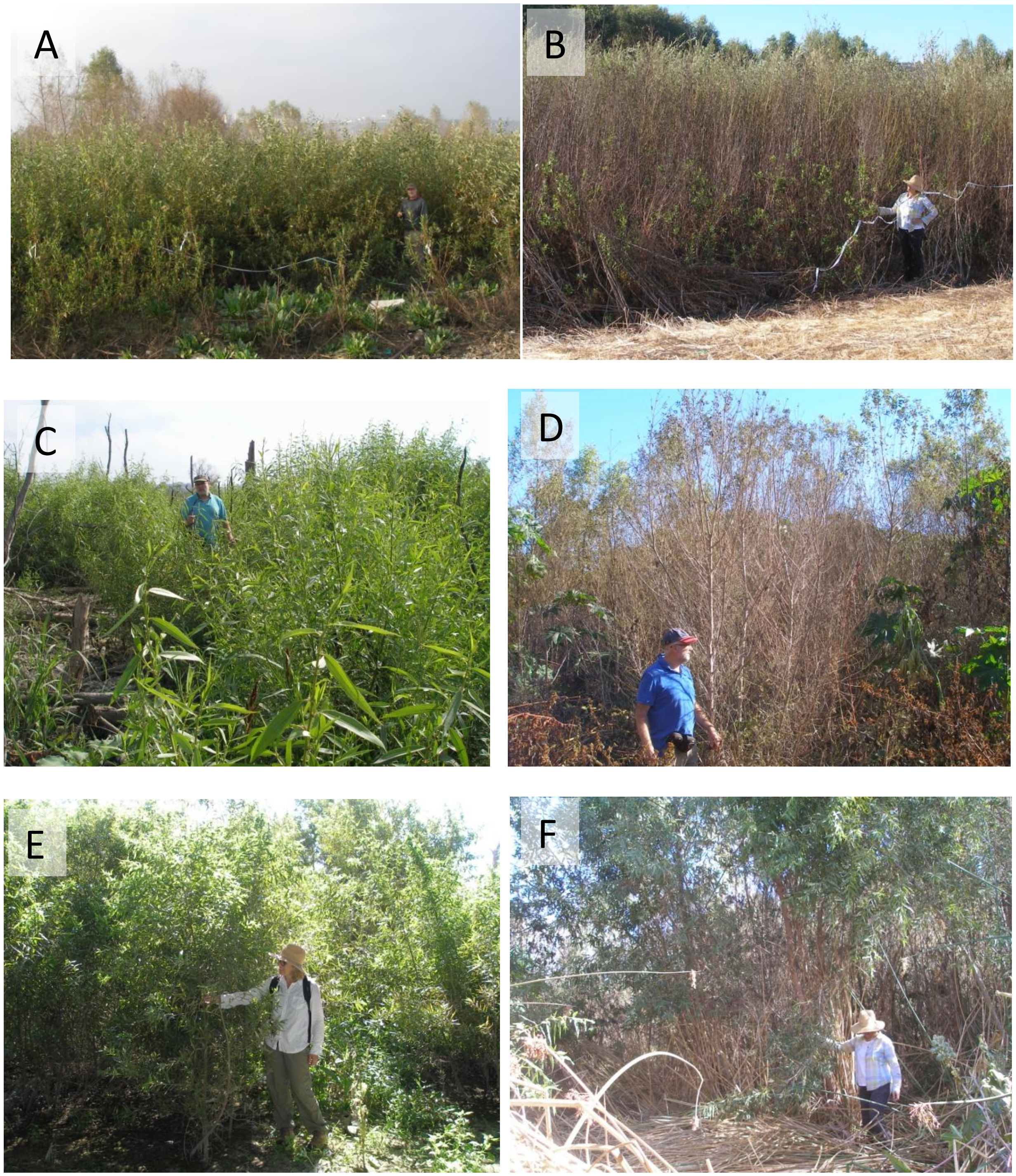


Figure 16. The continued survivorship and vertical growth of three stands of willow seedlings in the Wet Forests. Photos on left were taken during 2017 and those on right were taken in October 2018. TOP PAIR: Arroyo willows in Unit 2. MIDDLE PAIR: Black willows in Unit 3. BOTTOM PAIR: Black willows in Unit 12. There is a person in each photo to show scale. These seedlings were not being attacked by KSHB.

5.4. VEGETATION IN THE RECOVERING RIPARIAN FORESTS

The Wet Forests are green and densely vegetated and are obviously rebounding after their destruction by the KSHB in 2015-16 (Figure 11). But:

- **What plant species are growing in these heavily-damaged sites?**
- **Are they mostly native or non-native species?**

Methods

During September-October 2018, I conducted vegetation surveys to determine plant species composition in each of the Wet Forest units using the same methods as in my earlier annual surveys, i.e., percent cover measurement of species inside belt transects (20 m x 2 m = 40 m^2; Boland 2016, 2017b, 2018). I then assigned each species present to one of the following categories: willow seedlings, willow Big Trees, willow resprouting trees, native annuals, or non-native plants. I also walked through the accessible parts of each unit to record the presence of unrecorded species outside the belt transects.

Results

- Fifteen native species and 12 non-native species were present in the belt transects (Table 5).
- Native species were more abundant than non-native species; the mean percent cover of natives was 73% and of non-natives was 29% (Table 6).
- Resprouting willow trees were the most abundant native plants, with mean percent cover of 45% (Table 6).
- The three native species that were found for the first time in the Tijuana River Valley in 2017 – sticktight (*Bidens frondosa*), false daisy (*Eclipta prostrata*) and dotted smartweed (*Persicaria punctata*) – were still abundant in several sites during 2018 (Table 5). Each formed a dense ground cover in places where sunlight reached the ground.
- Native bulrushes, *Schoenoplectus americanus* and *S. californicus*, were common outside of the belts where there was plenty of light and perennial water.
- Castor bean was the most abundant non-native species in the belts, with a mean percent cover of 17% (Table 6).
- *Arundo donax*, giant reed, had a mean percent cover of only 4% in the belt transects, but was more abundant outside the belts.

Discussion

In 2018, native plants were abundant in most of the belt transects inside the KSHB-damaged Wet Forest units. The native species that were doing particularly well were those that flourish in light gaps; this included willows resprouting from damaged stumps, willow seedlings, bulrushes, and the three ‘new’ ground-cover species. The non-natives however were quite abundant and they were surveyed more thoroughly in Section 5.6 below.

*Table 5. Plant species that occurred in the belt transects in fall 2018. An *** indicates a species that has not been recorded in the Tijuana River Valley before.*

NATIVE SPECIES	
Willows	
Salix gooddingii	Goodding's black willow
Salix lasiolepis	Arroyo willow
Native annuals	
*Bidens frondosa****	Sticktight
*Eclipta prostrata****	False daisy
Helianthus annuus	Western sunflower
Persicaria lapathifolia	Willow weed
*Persicaria punctata****	Dotted smartweed
Pluchea odorata	Salt marsh fleabane
Solanum americanum	White nightshade
Stephanomeria sp.	Wreath-plant
Xanthium strumarium	Cocklebur
Other natives	
Baccharis salicifolia	Mule fat
Datura wrightii	Jimson weed
Schoenoplectus americanus	American tule
Schoenoplectus californicus	Southern bulrush
NON-NATIVE SPECIES	
Araujia sericifera	Cruel vine
Arundo donax	Giant reed
Atriplex prostrata	Spearscale
Chenopodium sp. (album?)	Lamb's quarters
Ficus carica	Edible fig
grasses, e.g, *Pennisetum clandestinum*	Kikuyu grass
Phytolacca icosandra	Tropical pokeweed
Ricinus communis	Castor bean
Rumex conglomeratus	Whorled dock
Schinus terebinthifolius	Brazilian pepper tree
Tamarix ramosissima	Tamarisk
Urtica urens	Dwarf nettle

Table 6. The percent cover of plants along the belt transects within the Wet Forest units in 2018.

UNIT	NATIVE PLANTS						NON-NATIVE PLANTS				
	willow seedlings	willow Big Trees	willow resprouting trees	native annuals	other natives	TOTAL NATIVES	Tamarisk	Castor Bean	Arundo	other non-natives	TOTAL NON-NATIVES
2	0%	0%	26%	65%	0%	91%	0%	5%	0%	0%	5%
3	72%	0%	0%	11%	0%	83%	1%	31%	0%	6%	38%
4	0%	0%	8%	1%	0%	9%	0%	70%	20%	0%	90%
5	0%	0%	75%	0%	13%	88%	0%	8%	25%	0%	33%
6	0%	20%	4%	29%	0%	53%	0%	15%	15%	0%	30%
7	0%	0%	90%	0%	1%	91%	0%	11%	0%	0%	11%
8	0%	0%	98%	0%	0%	98%	0%	0%	0%	0%	0%
9	0%	0%	54%	5%	2%	61%	0%	26%	0%	21%	47%
10	1%	10%	14%	59%	0%	84%	0%	11%	0%	31%	42%
11	0%	0%	35%	0%	35%	70%	0%	23%	0%	17%	40%
12	0%	0%	50%	0%	3%	53%	0%	26%	0%	30%	56%
13	0%	0%	79%	29%	29%	137%	0%	2%	0%	10%	12%
14	0%	0%	68%	0%	0%	68%	0%	0%	0%	0%	0%
22	0%	0%	24%	0%	15%	39%	0%	3%	0%	0%	3%
mean	**5%**	**2%**	**45%**	**14%**	**7%**	**73%**	**0%**	**17%**	**4%**	**8%**	**29%**

5.5. WILLOW CANOPY COVER IN THE RECOVERING RIPARIAN FORESTS

The most obvious damage by the KSHB to the riparian forests in the Tijuana River Valley was to the willow canopy in the Wet Forests. Before 2015 this canopy was high and dense but the KSHB attack in the Wet Forests caused the willow canopy to collapse (Figure 11A and 11B; Boland 2016). Here I ask the question:

- **What is current willow canopy cover in the Wet Forests in the valley?**

Methods

In winter 2018-19, I estimated the percent cover of willow canopy in each of the Wet Forest units, by making observations from as many accessible places within each unit as possible.

Results

- The willow canopy declined rapidly from 2015 to 2017 in most of the Wet Forest units (Figure 17).
- Since 2017 the canopy in most units has shown a general increase (Figure 17); the mean canopy cover rose from 5% in 2017 to 26% in 2018.

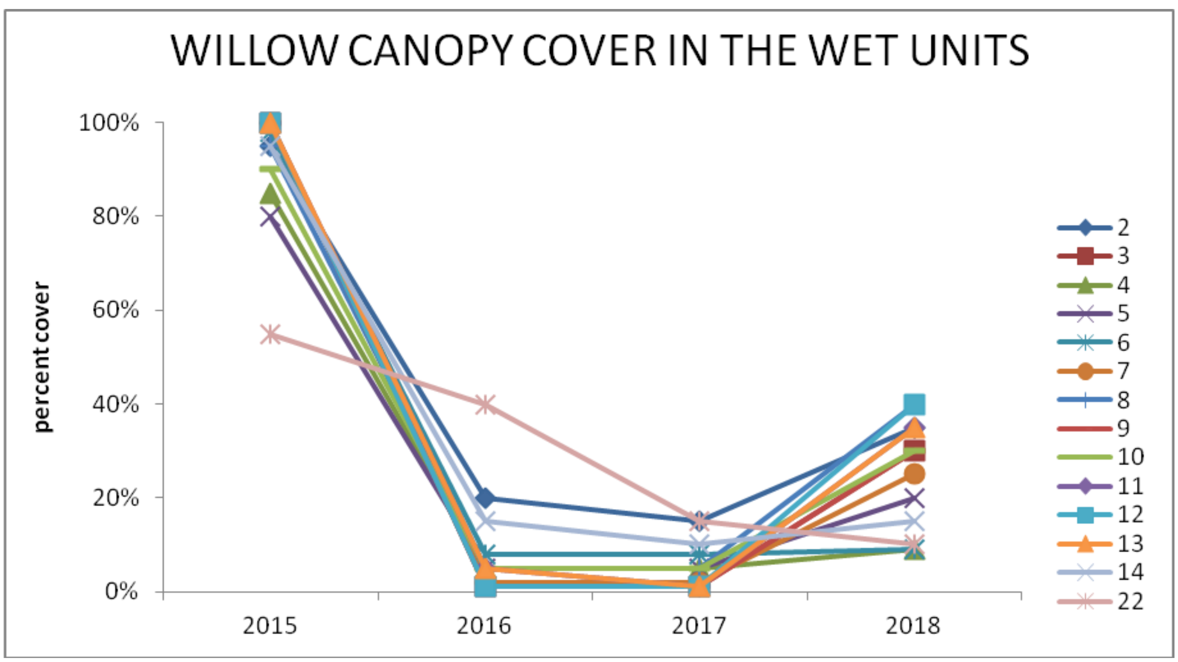


Figure 17. Willow canopy cover in the Wet Forests from 2015-18.

Discussion

The KSHB attack in 2015-16 caused most of the willows in the Wet Forests to lose their upper trunks and branches, so that in 2016 and 2017 there was virtually no canopy in the Wet Forest units (Boland 2016, 2017b). Since then, through the production of resprouts and seedlings, the willows have started to create a new canopy. The young, shrub-sized canopy developing in the recovering Wet Forests appears to provide good breeding habitat for the endangered least Bell's vireo. This vireo is known to require dense, young forests for breeding (Kus 2002) and the valley, including the Wet Forests, appears to be meeting this requirement at the moment.

5.6. ABUNDANCES OF THE WORST INVASIVE SPECIES, INCLUDING *ARUNDO DONAX*

The invasive species of greatest concern in the valley are arundo (*Arundo donax*), castor bean (*Ricinus communis),* and tamarisk *(Tamarix ramosissima).* These 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). Arundo and castor bean were particularly abundant in the KSHB-damaged riparian forests in 2017 (Boland 2018), and in 2018 I asked the question:

- **What is current distribution and abundance of the worst invasive species in the valley?**

Methods

In winter 2018-19, I estimated the percent cover of arundo, castor bean and tamarisk in each of the survey units, by making observations from as many accessible places as possible. In addition, because arundo can be identified in aerial photos, I estimated the percent cover of arundo in each of my survey units from Google Earth (imagery date = 8/13/2018); I averaged the two arundo estimates (field surveys and Google Earth surveys) to make the final percent cover estimate.

Results

- Both arundo and castor bean were abundant in the riparian forests in 2018 (Figures 18 and 19). Tamarisk, on the other hand, was rare in all survey units – usually less than 2% cover and always less than 10% cover.
- Arundo and castor bean were most abundant in the heavily-damaged eastern forests, particularly in Units 4 – 9, where arundo reached 55% cover and castor bean reached 60% cover (Figures 18 and 19).
- Arundo dominated the vegetation in many sites, especially those immediately downstream of the Dairy Mart bridge (Figures 20 and 21).

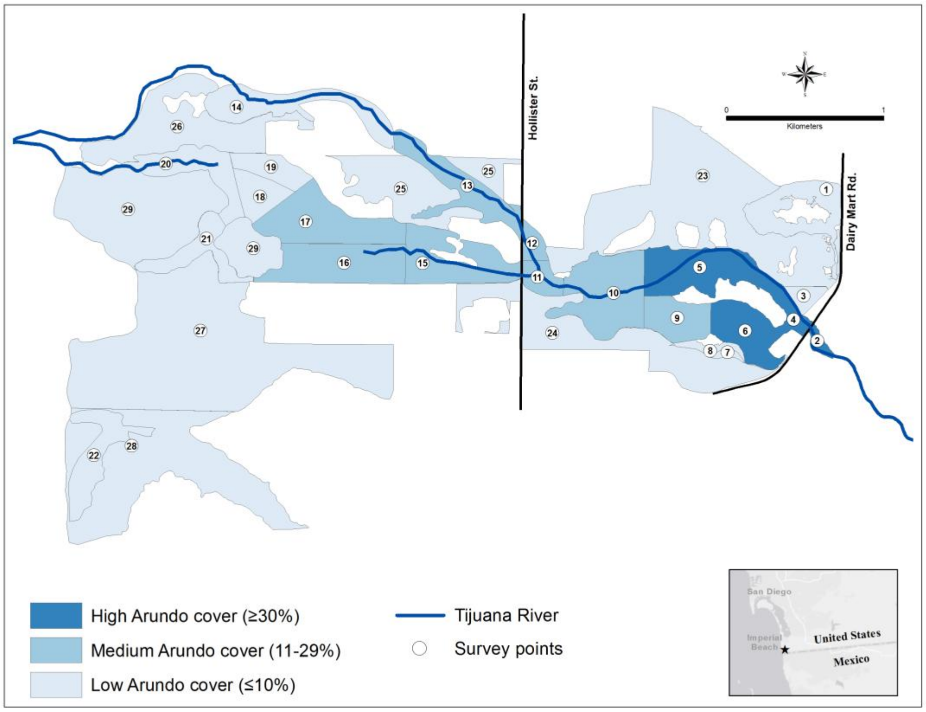


Figure 18. Percent cover of arundo in the riparian survey units, as of winter 2018-19. [Map created by John Boland and Monica Almeida, February 2019.]

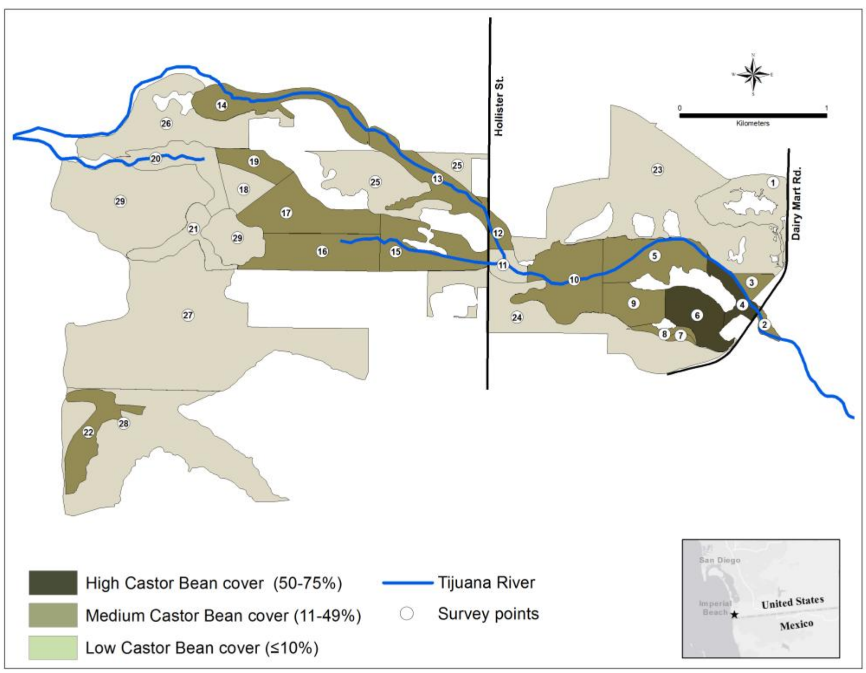


Figure 19. Percent cover of castor bean in the riparian survey units, as of winter 2018-19. [Map created by John Boland and Monica Almeida, February 2019.]

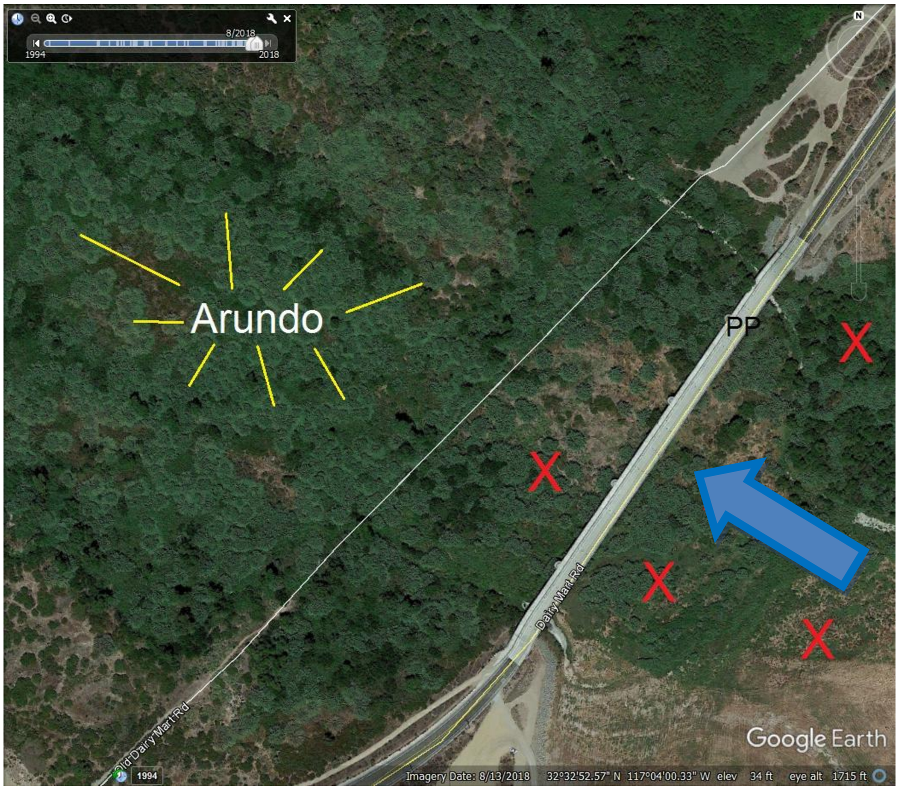


Figure 20. Abundant arundo (light green clumps) in the Dairy Mart bridge area (Units 4 and 6), as seen on Google Earth. The many Xs show the IBWC property where arundo has been ploughed in the past. The arrow indicates the direction of the river flow. PP indicates the photo point from which Figure 21 was taken.

Figure 21. Abundant arundo in the Dairy Mart bridge area (Unit 4). Photo taken looking west on 14 August 2017 from position 'PP' on the bridge (Figure 20).

Discussion

Both arundo and castor bean have benefited from the increased light that followed the KSHB-damage to the willow canopy, and both species are now growing strongly in the heavily-damaged Wet Forests. Tamarisk, on the other hand, has not become particularly abundant in the riparian forests over the past few years. [Tamarisk remains a problem in the saltier soils elsewhere in the valley (Whitcraft et al. 2007).]

The KSHB attack has had ecosystem-wide impacts. The KSHB's preference for the two willow trees, the dominant trees in the Tijuana River Valley (Boland 2014b), has drastically altered the canopy architecture, understory microclimate, and ecosystem processes such as productivity and water balance within the forest units (Ellison et al. 2005). Also the KSHB attack has resulted in arundo, one of the worst invasive species in California (Cal-IPC 2006), becoming abundant in the damaged forests. The KSHB is therefore affecting not only its preferred host species but also the structure and function of the entire ecosystem.

Arundo is the most persistent and difficult invasive plant in the valley. It is spread mainly by bulldozers and other heavy equipment; bulldozers break-up rhizomes and make the rhizomes available for downstream spread by water flows (Boland 2008). That is the reason why arundo is most abundant in the eastern forests immediately downstream of where the International Boundary and Water Commission (IBWC) has been bulldozing, disking, and mowing the arundo on its property for decades (Boland unpublished data).

The herbicidal treatment of arundo would greatly reduce the abundance of arundo in the valley and thereby greatly assist the recovery of the native forests. As shown in Section 5.3 above the willows are adept at reestablishing themselves in open spaces and will do so abundantly if given the chance. Therefore the treatment of arundo should be the highest priority for all managers of properties in the Tijuana River Valley in order to restore these valuable riparian forests.

5.7. CONCLUSIONS

The second of the three main storylines coming out of the KSHB's invasion of the Tijuana River Valley is that the vegetation in the damaged forests is responding rapidly. **Willows have responded in three ways: by the healing of old KSHB-infested trees; by the resprouting of old KSHB-damaged trees; and by the seeding of new trees.** All of these ways have been documented here. The healing and resprouting of KSHB-infested willows is important because it means that the old notion that a KSHB infested tree is as good as dead is not correct. While some trees do die as a result of KSHB infestation, many do not. This is important to keep in mind when deciding whether or not to cut down an infested tree.

The spread of the KSHB within the Tijuana River Valley has been similar to a wildfire in chaparral and the recovery of the vegetation after the KSHB impact has also been similar to the recovery of chaparral after a wildfire (Rundel and Gustafson 2005). In both cases the vegetation recovers through the production of resprouts from surviving old stumps and through the establishment of new plants via seeds. In the Tijuana River Valley the seedlings have included willows as well as native ground cover that have not been observed in the valley before. The fire analogy reminds us that the KSHB-impacted habitats have not been 'destroyed' or 'lost'. By attacking the willows the KSHB has set back the competitively dominant trees, opened up the forests and let sunlight in for other species. Some 'new' plant species have become established. The valley used to be a continuous willow forest (Boland 2014b) but now is a mosaic of willow forests at different stages of infestation and recovery. The KSHB has therefore increased the habitat diversity and plant diversity within the valley.

The recovering willows in the Wet Forests are generally not being reattacked by the KSHB, which is remarkable for two reasons. **First**, the KSHB is abundant in the nearby Dry Forests and presumably could easily reinvade the Wet Forests. **And second**, many of the resprouting trees and seedlings are of the size that was attacked during the initial KSHB attack in 2015-16. Predictions have been made that all of resprouts larger than one inch in diameter would be attacked by the KSHB (Eskalen in Sahagun 2017). However, that prediction has not come true – 72% of the resprouts were larger than one inch in 2018 and were not being infested (Figure 15). This situation begs the question: Why are the recovering willows not being attacked by the KSHB? Successfully answering this question could provide essential information about willows and about the KSHB. One explanation could be that the infested willows have changed their chemistry as a result of the borer attack, and this has increased the resistance of the plant to further borer attacks; this herbivore-induced change in chemistry is common and called an "induced response" (Karban and Myers 1989).

Unfortunately some invasive species are also thriving in the recovering Wet Forests in the Tijuana River Valley. Arundo in particular degrades the forest and reduces the value of the habitat for native species. The best way for a manager in one of the parks in the Tijuana River Valley to manage the KSHB invasion is to treat arundo with herbicides thereby greatly assisting the natural restoration of the native forests in the valley.

6. KSHB INFESTATION IN OTHER PARTS OF SAN DIEGO COUNTY

The third storyline coming out of this research on the KSHB in the Tijuana River Valley is that the KSHB's impacts along the polluted Tijuana River are far greater than its impacts anywhere else in San Diego County (Boland 2018). In this section I will describe surveys conducted in other parts of San Diego County to determine whether this is still true.

6.1. KSHB IN THE SAN DIEGO COUNTY STUDY SITES

In 2017 I surveyed willows in several other sites in San Diego County outside the influence of the Tijuana River and found that they were either not infested or only lightly infested. No other site had the KSHB-infestation rates of the Tijuana River Valley. In 2018, I asked the following questions:

- **What is the current extent of KSHB infestation and KSHB-induced willow mortality rates within each site?**
- **Has the KSHB infestation spread in these sites?**

Methods

The nine sites outside the influence of the polluted Tijuana River were in open space parks with established riparian forests comparable to those in the Tijuana River Valley (Table 7). Two of these sites were within 5 km of the KSHB-infested Tijuana River Valley, others were up to 40 km away. During winter 2018-19 each site was visited and the condition of as many willows as could be examined in two hours was recorded. The tagged trees that had been sampled in 2017 and had their wood characteristics measured were of particular interest. For KSHB infestation rate, each willow was examined and classified as 'currently infested' if it had evidence of active tunneling by the KSHB, such as extrusion of sawdust or recent gumming out of sap from KSHB holes. For KSHB-induced mortality rate, each willow was classified as alive, recently dead from KSHB attack if it had KSHB holes, or dead from some other cause if it had no KSHB holes. KSHB infestation rates and KSHB-induced mortality rates were calculated for each site as the percent of the total number of willow trees examined.

Results

- This year KSHB was infesting willows at two of the study sites, whereas last year it was present at just one (Table 8).
- The KSHB was not abundant at the infested sites – it occurred in 11% of the trees in Florida Canyon (OUT-4) and 1% of the trees in Cottonwood Grove, San Diego River (OUT-6; Table 8).
- The KSHB had caused some willow mortality in Florida Canyon (OUT-4). Three arroyo willows appeared to have been killed by the KSHB.
- None of the tagged trees had been infested in any of the sites.

Table 7. Locations of the San Diego County survey sites. All of these sites are outside the influence of the polluted main channel of the Tijuana River (TJR).

Site name	Watershed	Preserve Name	Dominant trees	Dist. to TJR. (km)
OUT-1	isolated (near Goat Canyon)	Border Field State Park	willows	1.4
OUT-2	Otay River	Otay Valley Regional Park	willows	3.7
OUT-3	Tijuana River tributary	Pacific Gateway Park	willows	6.2
OUT-4	Florida Canyon	Balboa Park	willows	19.4
OUT-5	Sweetwater River	San Diego National Wildlife Refuge	Old diverse stand	22.5
OUT-6	San Diego River	Mission Valley Preserve	willows + cottonwood	24.1
OUT-7	San Diego River	Mission Trails Regional Park	Old diverse stand	31.5
OUT-8	Penasquitos Creek	Torrey Pines State Natural Reserve	willows + cottonwood	40.2
OUT-9	Penasquitos Creek	Los Penasquitos Canyon Preserve	Young diverse stand	42.2

Table 8. Willow KSHB infestation rates and KSHB-induced mortality rates within the San Diego County sites. INF = infested with KSHB.

Site	WILLOW INFESTATION RATES				MORTALITY	% INF of
	2017-18	2018-19			%	TAGGED
	% INF	# INF	TOT	% INF		TREES
OUT-1	0%	0	39	0%	0%	0%
OUT-2	0%	0	61	0%	0%	0%
OUT-3	0%	0	62	0%	0%	0%
OUT-4	9%	18	157	11%	2%	0%
OUT-5	0%	0	86	0%	0%	0%
OUT-6	0%	1	81	1%	0%	0%
OUT-7	0%	0	75	0%	0%	0%
OUT-8	0%	0	46	0%	0%	0%
OUT-9	0%	0	56	0%	0%	0%
mean	1%			1%	0%	0%
Total		19	663			

Discussion

The KSHB is spreading: in 2017 it was in only one of my San Diego County sites and now it is at two. However, the KSHB's spread has two interesting components. **First**, the KSHB has not spread to the two sites that are within 5 km the Tijuana River Valley. As the KSHB's population has exploded in the Tijuana River Valley one would expect the KSHB to have arrived in these sites in large numbers and to have quickly attacked the willows in these sites. Instead it has appeared in sites that are far from the Tijuana River Valley. **Second**, the spread has been relatively slow. At Florida Canyon, 9% of the trees were infested in 2017-18, and 11% of the trees were infested in 2018-19. This is not the devastatingly fast spread rates seen in the Wet Forests in the Tijuana River Valley in 2015-16 (Boland 2016).

6.2. KSHB IN THE FLORIDA CANYON STUDY SITE

Florida Canyon (OUT-4) is an interesting site because it was one of the few sites outside the Tijuana River Valley where the trees were infested with KSHB in 2017 (Boland 2018). Here I take an in-depth look at the KSHB in Florida Canyon and ask the question:

- **Are there any patterns in KSHB infestation within Florida Canyon?**

Methods

The Florida Canyon trees are unusual because they receive all of their water from urban runoff; most of the water flows into the forests from a single storm drain that discharges water from a residential area of North Park, City of San Diego (Figure 22). During several visits to the canyon in summer and fall 2018, I examined all of the arroyo willows in the forests for KSHB, tagged and GPSed each tree, and determined the distance of each from the point of discharge. To determine whether the infested arroyo willows were equally distributed in the forest, I divided the trees into either 'close to the point of discharge' (< 300m) or 'far from the point of discharge' (> 300m) and did a Chi-squared test on the results.

Results

- The KSHB attack in Florida Canyon showed an interesting pattern: all of the arroyo willows that were infested with KSHB were growing relatively close to the storm drain's point-of-discharge, whereas none of the arroyo willows growing far (>300 m) from the point-of-discharge was infested (Figures 22 and 23). There was a significant relationship between number of infested willows and distance from point-of-discharge (Chi-squared test, X^2 (2, N = 157) = 31.7, $p < 0.001$).

Discussion

The forest in Florida Canyon is a remnant forest, containing many old willows and oaks. Because the forest is surrounded by urban development and receives water only via a storm drain it can also be considered a "treatment wetland" that filters pollutants from the storm water that flows through the forest on its way to San Diego Bay. Typical pollutants in urban storm water are nutrients (e.g., nitrogen and phosphorus from lawn fertilizers, automobile exhaust, animal waste, and household detergents), pathogens, petroleum hydrocarbons, metals and synthetic organics (Davis 2005).

The local distribution of the KSHB-infested willows was not random – all of the KSHB-infested willows were near the storm drain outfall where, presumably, they were exposed to the highest nutrient levels. This pattern suggests that when searching for KSHB-infested trees in other riparian systems in San Diego County it would be a good idea to search near storm drain outfalls.

Figure 22. The storm drain outfall that sends flows into the Florida Canyon riparian forests. Flows were so large during winter 2018-19 that they eroded one bank.

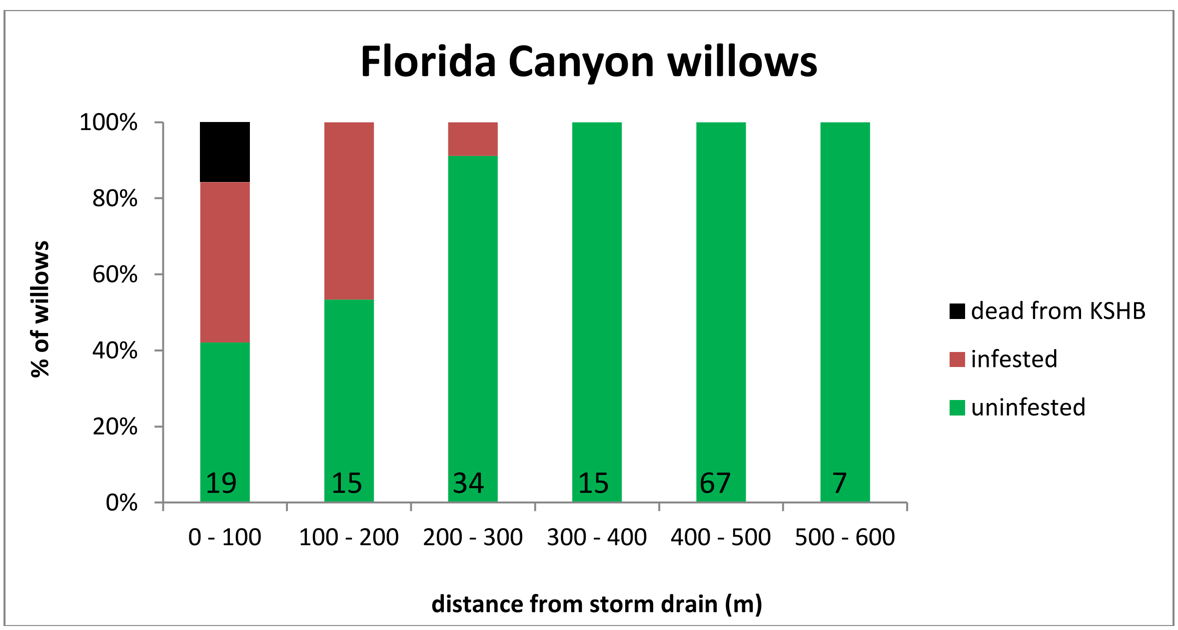


Figure 23. The condition of the arroyo willows in Florida Canyon with distance from storm drain pictured in Figure 22. The percent of willows that were killed by KSHB, infested with KSHB and uninfested in each 100 m segment along the stream in Florida Canyon. The number on each column is the number of willows in each 100 m segment of stream (N_{tot} = 157).

6.3. CONCLUSIONS

The surveys of KSHB infestation rates and KSHB-induced mortality rates conducted within the Tijuana River Valley and elsewhere in San Diego County continue to show that the **KSHB's impacts along the polluted Tijuana River are far greater than its impacts anywhere else in San Diego County**. The KSHB has infested several other sites in San Diego County, e.g., patchy areas along the San Luis Rey River, Escondido Creek and Sweetwater River (Eric Porter, USFWS personal communication 6 March 2018) and the two sites examined here, but none has been as severely hit as the Tijuana River Valley. The Tijuana River Valley must be regarded as an extreme case.

7. KSHB IN SPECIES OTHER THAN WILLOWS

7.1. KSHB INFESTATION OF SYCAMORES IN THE TIJUANA RIVER VALLEY

In a recent article on ISHB, it was claimed that '*if uncontrolled, the beetle "will kill all the sycamores in California," says Akif Eskalen, a plant pathologist at the University of California, Riverside*' (Raver 2018). Here I take a look at sycamores in the Tijuana River Valley and ask the question:

- **Is there any evidence that the Tijuana River Valley sycamores are being killed by the KSHB?**

Methods

There are only a few sycamores (*Platanus* spp.) growing in the Tijuana River Valley. Unlike the willows, which have recruited naturally, the sycamores have all been planted, either in riparian restoration projects or for shade. I found all of the sycamores – living and dead – in and around Units 15 and 25 and examined them for cause of death and level of KSHB infestation. I classified each as either 'alive', 'recently dead from KSHB attack', or 'dead from some other cause'. The live trees were further counted as 'currently infested' if it showed evidence of active tunneling by the KSHB, i.e., extrusion of sawdust or recent gumming out of sap from KSHB holes, or as 'not currently infested' if it had no evidence of KSHB attack or had only old, non-active KSHB holes. These surveys were conducted in June 2018.

Results

- There were no dead sycamores in the study area.
- There were 24 live sycamores and they occupied habitats that ranged from wet Forest to dry Scrub (Figure 24).
- Only two of the 24 trees were infested with KSHB (8% of the trees) and both of these trees were only lightly infested.
- The KSHB attack on the sycamores showed the following pattern: the sycamores that were infested with KSHB were growing relatively close to the polluted flows in the wetter forest rather than in the drier scrub (Figure 25).

Discussion

As far as I can tell, the KSHB has not killed any of the sycamores growing in the Tijuana River Valley – the site where the ISHB has had its greatest impact – and therefore there is no evidence to support the idea that the ISHB will kill all of the sycamores in California.

On the other hand, these results do provide more support for the Enriched Tree Hypothesis (Section 8.2 below) – the sycamores growing closest to the sewage-polluted Tijuana River flows were the most infested sycamores in the study area.

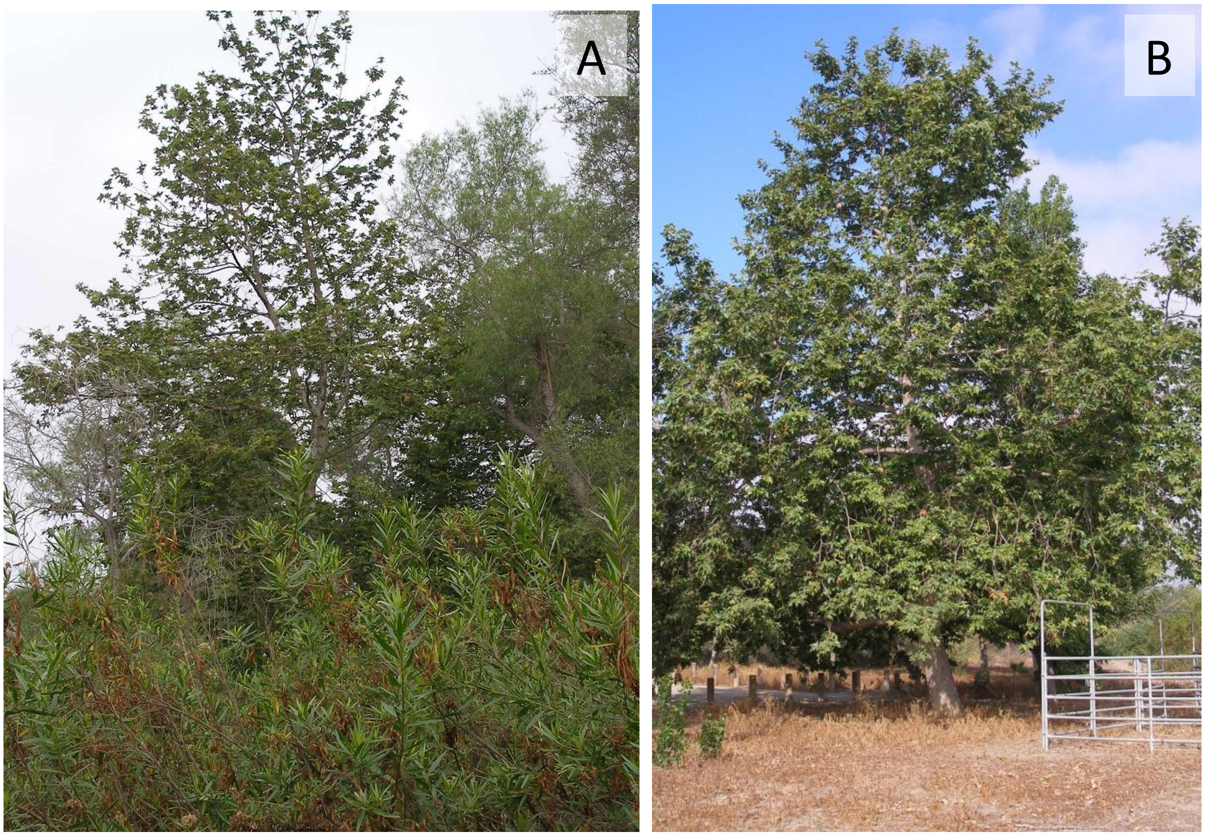


Figure 24. Two of the surveyed sycamores showing their large size and habitats: (A) in riparian forest; and (B) in dry scrub.

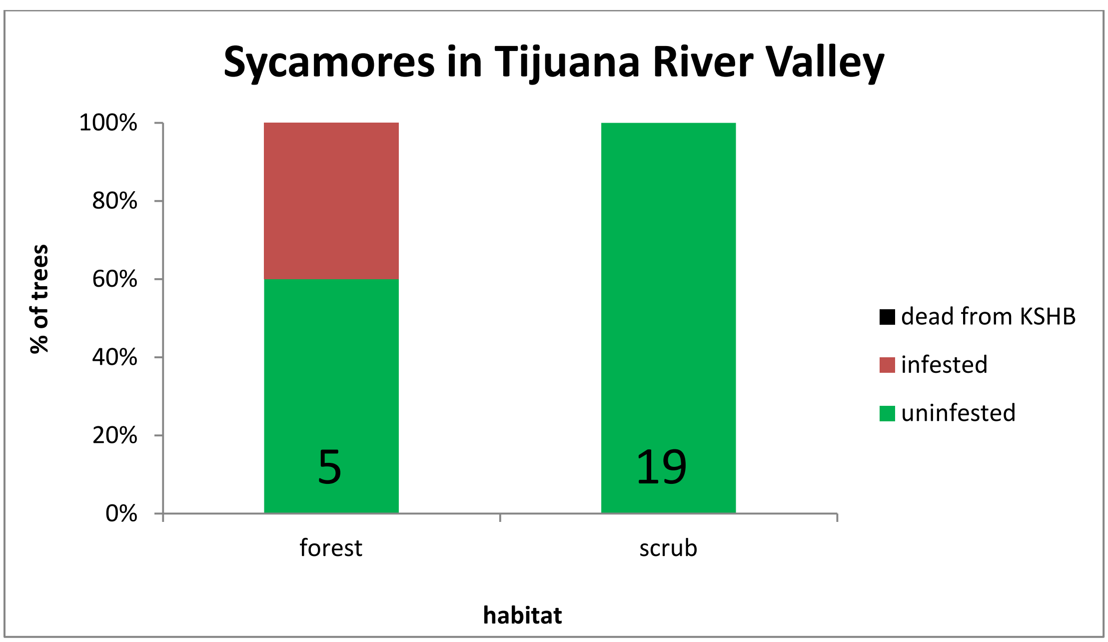


Figure 25. The condition of the sycamores in Units 15 and 25. The percent of trees that were killed by KSHB, infested with KSHB and uninfested in the forest and scrub habitats. [None of the sycamores were killed.] The number on each column is the number of sycamores surveyed in each habitat (N_{tot} = 24).

8. PARADIGM SHIFT

8.1. NEW FINDINGS REQUIRE CHANGE TO OLD WAY OF THINKING

My studies of the KSHB in the Tijuana River Valley and at sites outside the valley have produced new findings that advance the understanding of ISHB spread and impact in the natural habitats of southern California. The new findings can serve to update certain old ecological ideas held by the plant pathology research community, as some of the old ideas are at odds with the new data. Listed below are some of the most important new findings, with an explanation of why the old idea no longer is accurate.

<u>1. New Finding</u>: Not all sites are equally susceptible to infestation; the Wet Forests in the Tijuana River Valley are an exceptional case. The Wet Forests of the Tijuana River Valley have been by far the most severely affected of any site in the county. As the degree of KSHB infestation and impact has been significantly correlated with the level of sewage pollution and the Wet Forests are the most polluted in southern California, all lines of evidence indicate that the Wet Forests of the Tijuana River Valley are exceptional in the region. [See Boland and Woodward (*in press*), and Sections 4 and 6 of this report.]

<u>Old thinking</u>. This means that the old idea that other riparian sites are going to be attacked as severely as the Tijuana River Wet Forests (e.g., Greer et al. 2018) does not reflect the current data.

<u>2. New Finding</u>: Infestations follow different trajectories at different sites. In the Wet Forests, the KSHB infestation progressed rapidly over the course of a few months from barely noticeable to heavy infestation, high mortality, and dramatic canopy collapse, i.e., the infestation had a steep trajectory. In the drier forests, the KSHB infestation is taking a different course; infestation rates have climbed slowly over several years, mortality has remained low, and the canopy has so far remained mostly intact, i.e., the infestation has displayed a shallow trajectory. In the very dry willow stands in the Scrub, infestation and mortality rates have remained extremely low, i.e., the infestation has a very shallow trajectory. [See Figure 7 and Section 4 in this report.]

<u>Old thinking</u>. This means that the old idea that all infestations will have the same trajectory, i.e., start in a few trees, quickly spread to all trees in the stand, and eventually progress to a severe infestation, does not reflect current data. Furthermore the old idea that a light infestation must be a recent (early-stage) infestation while a heavy infestation must be an old (later-stage) infestation, is simply incorrect; a light infestation can be either recent or old, and a heavy infestation can be either recent or old. These old ideas misinterpret the situation.

<u>3. New Finding</u>: Not all individuals of a tree species are the same and not all individuals are equally susceptible to a KSHB attack. Among individuals of a given tree species (e.g., arroyo willow), morphology and physiology varied from site to site. Arroyo willow trees could be tall and fast-growing at one site, and short and slow-growing at another; and wood characteristics varied, from low density/high moisture content to high density/low moisture content. Most importantly, the KSHB responded to these morphological and physiological differences; KSHB infestation and mortality rates were highest in fast-growing trees with low density/high moisture content wood, while they were lowest in slow-growing trees with high density/low moisture content wood. [See Boland and Woodward (*in press*), Section 4 of this report, and Boland (2018).]

Old thinking. The old idea that all trees of a given species are essentially the same and all are equally likely to be infested by ISHB does not reflect current science. The old idea and logic was used by McPherson et al. (2017) to predict that nearly 12 million urban trees were at risk in coastal southern California. It was also used by Eskalen when he predicted that, if uncontrolled, the beetle "will kill all the sycamores in California" (Raver 2018). The old way of thinking incorrectly presumes that all individuals of an ISHB host species are the same and, by extrapolating from the worst-case scenario, it greatly overstates the possible negative impacts of the ISHB.

4. New Finding: Not every tree infested with ISHB will die.
In the Tijuana River Valley, I have followed many individual, tagged trees, and I have found that many can survive a KSHB infestation. Even a heavily-attacked and heavily-damaged tree can survive and recover. Trees can heal an existing trunk and/or resprout new branches and trunks. [See Sections 5.1 and 5.2 in this report, and Figures 3, 7 and 10 in Boland 2018.]

Old thinking. This means that the old idea that all trees infested with ISHB will die does not reflect current science. The old way of thinking overstates the negative impacts of the ISHB.

5. New Finding: KSHB impacts are correlated with nutrient enrichment.
In the Tijuana River Valley, willows growing closest to sewage pollution had, on average, higher KSHB-induced willow mortality rates than those growing farther away. Also a comparison of willows in the Tijuana River Valley with similar, but less polluted, San Diego County riparian sites supported the link between sewage pollution and high KSHB infestation rates. Finally at a lightly-infested site outside the Tijuana River Valley (Florida Canyon), willows growing closest to the storm drain outfall, and most exposed to nutrient-laden urban runoff, were the most infested willows in the canyon. In all cases, KSHB impacts were significantly correlated with sewage pollution/nutrient enrichment. [See this report (Section 6.2), Boland (2016, 2018), and Boland and Woodward (*in press*).]

Old thinking. Previously there was no explanation for the disparate distribution patterns of the KSHB in San Diego County or the ISHB in southern California. Finding a link to sewage pollution – or more generally to nutrient enrichment – is an important advance and is explained further below.

8.2. A NEW WAY OF THINKING – THE ENRICHED TREE HYPOTHESIS

My studies of the KSHB in the Tijuana River Valley and other San Diego County sites have led me to develop a new hypothesis – the Enriched Tree Hypothesis – to explain the observed patterns in ISHB distribution and impact (Boland and Woodward *in press*). The hypothesis is as follows:

A. *Riparian trees subject to nutrient enrichment from frequent sewage pollution grow quickly, and their fast growth results in wood of low density and high moisture content. If attacked by the KSHB, the trunks and branches of these nutrient-enriched trees provide an environment conducive to the fast growth of the symbiotic fungi upon which the KSHB feeds. With an abundant food supply, the KSHB population increases rapidly and the trees are heavily damaged by thousands of KSHB galleries in their trunks and branches (Figure 26A).*

B. *Riparian trees not subject to frequent sewage pollution grow more slowly and have denser, drier wood. Conditions in their trunks and branches are not conducive to the fast growth of the KSHB's symbiotic fungi. The KSHB generally ignores, or has low abundances in, these slow-growing trees (Figure 26B).*

The exact mechanism underlying the rapid growth of ambrosia beetles in nutrient enriched trees is not known, but it could be as simple as the enriched tree having sap that supplies the borer's symbiotic fungi with plentiful sugars and nutrients. In a nutrient enriched tree, the phloem sap is likely loaded with plentiful sugars from the fast-growing, photosynthesizing leaves, and the xylem sap is likely loaded with plentiful nitrogen and phosphorus from the enriched soil and water. High nutrient conditions in the trunks and branches of enriched trees would no doubt promote the growth of the symbiotic fungi and, ultimately, promote the growth of the borer population.

The Enriched Tree Hypothesis is discussed in detail in Boland and Woodward (*in press*). We examined wood densities, wood moisture contents, KSHB infestation rates, and KSHB-induced mortality rates in two willow species (black willow and arroyo willow) at sites near and far from sewage input. Comparisons were made on two spatial scales: broadly among sites within San Diego County; and locally among sites within the Tijuana River Valley. In brief, results showed that there was a significant link between high sewage pollution and high KSHB infestation rates, and the Enriched Tree Hypothesis describes that link.

The Enriched Tree Hypothesis explains current patterns of KSHB impact in San Diego County, and it highlights the Tijuana River Valley as an extremely unusual site due to its high sewage inputs. No other natural riparian site in San Diego County is as nutrient enriched as the Tijuana River Valley, so no other natural riparian site in San Diego County would be expected to experience the relatively severe KSHB impacts observed in the Wet Forests of the Tijuana River Valley. Other sites are likely to experience only mild impacts if they become infested.

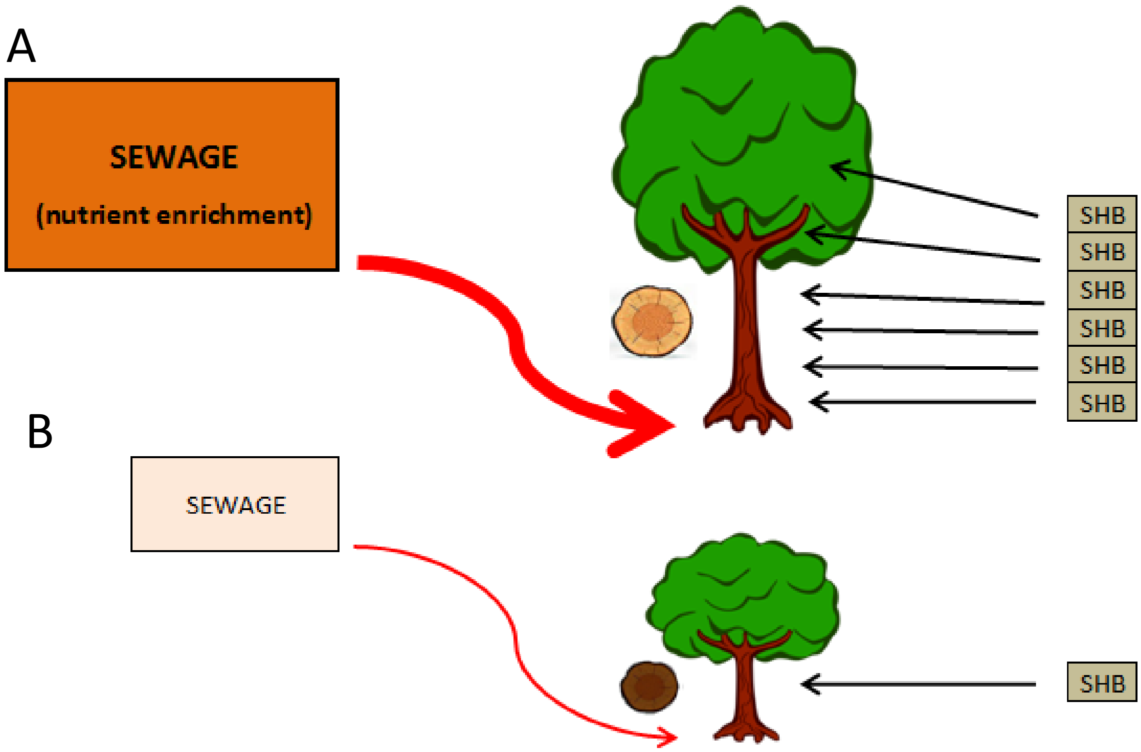


Figure 26. The Enriched Tree Hypothesis illustrated. A: When excessive sewage flows into a site it stimulates the growth of trees and the trees are susceptible to a mass attack by Shot Hole Borers (SHBs). B: At other sites not influenced by excessive sewage, trees grow more normally and the trees are not abundantly attacked by SHBs. Figure from Boland (2018).

The Enriched Tree Hypothesis focuses on site condition (specifically nutrient level) and tree condition as the factors that determine the severity of ISHB impact. It was generally thought that the environment and condition of the trees should play roles in the shot hole borer's choice of site and trees, but no one had worked out the mechanism. As recently as 2017, Hulcr and Stelinski (2017, page 296), wrote that "*in ambrosia beetle research, the role of the environment and preexisting conditions of the trees has not yet been well appreciated, even though it appears to determine the impact of these beetles.*" The Enriched Tree Hypothesis recognizes the importance of the roles of the environment and preexisting tree condition, and it also identifies the underlying mechanism of nutrient enrichment. Notice that, according to the hypothesis, ISHB may disperse widely but it is expected to establish and thrive only where suitable enriched trees occur.

The Enriched Tree Hypothesis can direct future searches for ISHB infestations. Because the hypothesis identifies sewage pollution – or nutrient enrichment – as a major risk factor for KSHB impacts, it ratchets down the KSHB-threat level for most natural riparian sites in southern California, where nutrient pollution levels are lower. Instead, the hypothesis directs attention to other nutrient-enriched sites where the water might be polluted and the trees might be over-fertilized, e.g., near storm drain outfalls, in treatment wetlands, on golf courses, etc.

The Enriched Tree Hypothesis can suggest future research on ISHB. The hypothesis shifts the focus from the current emphasis on the symbiotic fungi and the list of tree host species to the key roles of the environment and preexisting conditions of trees in determining the extent and severity of KSHB impact. It therefore directs future research to studies of the nutrients in the soils and nutrients in the trees; a better understanding of these factors will be essential for predicting the occurrence and outcome of future shot hole borer attacks in southern California.

The Enriched Tree Hypothesis is a major new idea that can be used as a much-needed framework to significantly improve our understanding of and response to the invasion of shot hole borers in southern California.

9. RECOMMENDATIONS

9.1. RESEARCH RECOMMENDATIONS

The research and data presented in this report suggest the following areas for valuable future research:

<u>A. Willow's induced response.</u>
The recovering willows in the Wet Forests were generally not being reinfested by the KSHB, even though (a) the KSHB was abundant in the nearby Dry Forests and presumably could easily reinvade the Wet Forests, and (b) many of the resprouting trees and seedlings had stem diameters that were attacked during the initial KSHB invasion of the valley (Section 5). **Hypothesis**: The infested willows have changed their chemistry as a result of the borer attack, and this has increased the resistance of the plant to further borer attacks; this change in chemistry is common and called an "induced response" (Karban and Myers 1989). **Study:** Examine the chemistry of the bark and wood of resprouting host plants before, during and after an ISHB attack; and test whether ISHB are less likely to infest the changed bark and wood.

<u>B. KSHB dispersal by air.</u>
I suggest that ISHB dispersal within southern California is most likely through the air. If willow seeds can land in abundance in suitable sites using the wind (Boland 2014a, 2017a) then the ISHB can too. The borers have brains, small bodies, and functional wings – all characteristics that make dispersal by wind very likely. **Hypotheses:** Their brains can choose the best time to fly from their natal tree into favorable above the forest canopy; their light weight can allow them to be carried by winds high above the ground at many kilometers per hour; and their brains and wings can allow them to search for a suitable tree at their new location. **Study:** I suggest two tests. First, determine whether KSHB flights from trees are random or non-random, and whether the flights are linked to some meteorological feature, like wind speed; this would involve

short-period trapping (e.g., hourly) near a heavily-infested tree. Second, determine whether KSHB are present in the winds high above infested trees; this would involve the use of nets attached to aircraft or hot-air balloons, or traps tethered to drones or balloons (e.g., Milius 2019).

C. Nutrients inside enriched trees.
Understanding the mechanism underlying the rapid growth of ambrosia beetles in enriched trees would reveal the central mechanism of the Enriched Tree Hypothesis and could be a very promising area of future research. **Hypothesis.** As fungi require sugars and nutrients (such as nitrogen and phosphorus) for growth (Kendrick 1992) I suggest that in enriched trees the phloem sap is loaded with sugars from the very productive leaves, and the xylem sap is loaded with nutrients (such as nitrogen and phosphorus) from the enriched soil. Together these extremely high nutrient conditions in the trunks and branches promote the fast growth of the symbiotic fungi and, ultimately, the fast growth of the beetles (Boland and Woodward *in press*). **Study:** These ideas can be tested with measurements of the sugars and nutrients (both concentrations and loading rates) in trees subject to differing amounts of sewage or fertilizers, followed by controlled trials in the lab on the growth response of ISHB's fungal symbionts to various sugar and nutrient concentrations and loading rates (Boland and Woodward *in press*).

9.2. MANAGEMENT RECOMMENDATIONS

The results reported here and in previous reports (Boland 2017b, 2018) support the following management actions.

A. Restoration projects

- **Continue to plant willows in new riparian restoration sites if the water quality is good.** Willows are not being attacked in most sites and the worst willow attacks have occurred only where the worst sewage pollution occurs, so willows can and should be planted in most new restoration sites, particularly in sites where the water quality is known to be good.

- **Use natural restoration methods to restore riparian sites**. Natural restoration is superior to the more commonly conducted horticultural restoration because it produces a forest community with a high density of trees, in which the species are in the appropriate down-slope zonation, and the trees are of the appropriate sex ratios and genetic diversity (Briggs 1996, Boland 2014a).

B. Parks in the Tijuana River Valley

- **Treat arundo.** Arundo is flourishing in the valley partly because the KSHB is attacking willows, arundo's main competitor. Arundo substantially degrades a site and reduces the value of the habitat. The best way for park managers in the valley to manage the KSHB problem is to treat arundo with herbicides and to allow the natural restoration of the riparian forests.

C. Trees currently infested with KSHB

- **Do not cut down infested trees thinking that they are going to die.** Both infested and heavily-damaged trees can recover by producing resprouts and/or by growing over the KSHB galleries. An infested tree is not necessarily a dead tree.

D. Urban forests

- **Do not over-fertilize or overwater trees.** Park rangers and city managers can lower the risk of KSHB infestation by not over-fertilizing or overwatering their landscape trees. Nutrient-enriched trees are more vulnerable to KSHB infestation.

E. Searching for KSHB impacts in other parts of San Diego County

- **Search in nutrient-enriched areas.** When searching for KSHB-infested trees in other riparian systems in San Diego County it is imperative that one search the trees in sites where the water might be polluted, e.g., near storm drain outfalls.

10. ACKNOWLEDGEMENTS

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11. PHOTOGRAPH DETAILS AND CREDITS

Here are the particulars for each photo used in the report.

Figure 3A	
Date	August 24, 2018
Location	Unit 11, Tijuana River Valley
Subject/activity	Trees in the Wet Forest
Names of people	None
photographer	John Boland
Figure 3B	
Date	August 27, 2016
Location	Unit 18, Tijuana River Valley
Subject/activity	Trees in the Dry Forest
Names of people	None
photographer	John Boland
Figure 3C	
Date	June 30, 2016
Location	Unit 28, Tijuana River Valley
Subject/activity	Trees in the Riparian Scrub habitat
Names of people	None
photographer	John Boland
Figure 4A	
Date	October 29, 2015
Location	Unit 8, Tijuana River Valley
Subject/activity	Sawdust tubes coming out of KSHB holes
Names of people	None
photographer	John Boland
Figure 4B	
Date	December 20, 2015
Location	Unit 14, Tijuana River Valley
Subject/activity	Arroyo willow infested with KSHB and broken by winds
Names of people	None
photographer	John Boland
Figure 9A	
Date	February 4, 2016
Location	Unit 3, Tijuana River Valley
Subject/activity	Heavily damaged willows
Names of people	None
photographer	John Boland

Figure 9B	
Date	September 12, 2018
Location	Unit 15, Tijuana River Valley
Subject/activity	Lightly damaged willows
Names of people	None
photographer	John Boland
Figure 11A	
Date	May 15, 2015
Location	Unit 2, Tijuana River Valley
Subject/activity	The forest before the KSHB infestation
Names of people	None
photographer	John Boland
Figure 11B	
Date	February 4, 2016
Location	Unit 2, Tijuana River Valley
Subject/activity	The forest after the KSHB infestation
Names of people	None
photographer	John Boland
Figure 11C	
Date	March 23, 2018
Location	Unit 2, Tijuana River Valley
Subject/activity	The forest during recovery
Names of people	None
photographer	John Boland
Figure 11D	
Date	April 27, 2019
Location	Unit 2, Tijuana River Valley
Subject/activity	The forest during recovery
Names of people	None
photographer	John Boland
Figure 12	
Date	November 1, 2018
Location	Unit 13, Tijuana River Valley
Subject/activity	Excavation of trunk showing growth over KSHB tunnels
Names of people	None
photographer	John Boland

Figure 14A	
Date	March 8, 2016
Location	Unit 13, Tijuana River Valley
Subject/activity	Growth of resprouts on R1
Names of people	John Boland
photographer	Elizabeth Onan
Figure 14B	
Date	October 7, 2016
Location	Unit 13, Tijuana River Valley
Subject/activity	Growth of resprouts on R1
Names of people	John Boland
photographer	Elizabeth Onan
Figure 14C	
Date	November 7, 2017
Location	Unit 13, Tijuana River Valley
Subject/activity	Growth of resprouts on R1
Names of people	John Boland
photographer	Elizabeth Onan
Figure 14D	
Date	September 21, 2018
Location	Unit 13, Tijuana River Valley
Subject/activity	Growth of resprouts on R1
Names of people	John Boland
photographer	Elizabeth Onan
Figure 16A	
Date	January 19, 2018
Location	Unit 2, Tijuana River Valley
Subject/activity	Recruitment of stand of seedlings
Names of people	John Boland
photographer	Deborah Woodward
Figure 16B	
Date	October 20, 2018
Location	Unit 2, Tijuana River Valley
Subject/activity	Survival and growth of stand of seedlings
Names of people	Deborah Woodward
photographer	John Boland

Figure 16C	
Date	May 22, 2017
Location	Unit 3, Tijuana River Valley
Subject/activity	Recruitment of stand of seedlings
Names of people	John Boland
photographer	Deborah Woodward
Figure 16D	
Date	October 20, 2018
Location	Unit 3, Tijuana River Valley
Subject/activity	Survival and growth of stand of seedlings
Names of people	John Boland
photographer	Deborah Woodward
Figure 16E	
Date	September 9, 2017
Location	Unit 12, Tijuana River Valley
Subject/activity	Recruitment of stand of seedlings
Names of people	Deborah Woodward
photographer	John Boland
Figure 16F	
Date	October 20, 2018
Location	Unit 12, Tijuana River Valley
Subject/activity	Survival and growth of stand of seedlings
Names of people	Deborah Woodward
photographer	John Boland
Figure 20	
Date	August 13, 2018
Location	Unit 4, Tijuana River Valley
Subject/activity	Abundant Arundo
Names of people	None
photographer	Google Earth
Figure 21	
Date	August 14, 2017
Location	Unit 4, Tijuana River Valley
Subject/activity	Abundant Arundo
Names of people	None
photographer	John Boland

Figure 22	
Date	January 11, 2019
Location	Florida Drive, Balboa Park, San Diego
Subject/activity	Storm drain
Names of people	None
photographer	John Boland
Figure 24A and B	
Date	June 15, 2018
Location	Units 15 and 25, Tijuana River Valley
Subject/activity	Sycamores
Names of people	None
photographer	John Boland

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