THE ROLE OF PARTIAL LIMB BREAKS IN THE GROWTH AND PERSISTENCE OF ARROYO WILLOW (SALIX LASIOLEPIS)

Author: Boland, John

Source: Madroño, 71(2) : 71-83

Published By: California Botanical Society

URL: https://doi.org/10.3120/0024-9637-71.2.71

MADROÑO, Vol. 71, No. 2, pp. 71–83, 2024

THE ROLE OF PARTIAL LIMB BREAKS IN THE GROWTH AND PERSISTENCE OF ARROYO WILLOW (*SALIX LASIOLEPIS*)

JOHN BOLAND
3504 Louisiana Street, San Diego, CA 92104
johnboland@sbcglobal.net

ABSTRACT

This paper examines the occurrence of limb breaks in *Salix lasiolepis* Benth. (Arroyo Willow) in a natural riparian area, and it explores the morphological and ecological consequences of those breaks. Six *S. lasiolepis* stands of different ages (0.5–40 yr old) containing individuals of different average sizes (0.3–122 m^2 crown areas) were studied in the Tijuana River Valley, California. Results showed that limb breaks were common, and their numbers increased significantly with the size of the individual. Most limb breaks were partial, with sufficient vascular connection remaining for the broken limb to survive its break and fall. Each break was examined for the presence of included bark, i.e., a wedge of bark in the limb junction usually considered to be a defect because it weakens junctions and causes junctions to break easily. Included bark was observed in 76% of the limb-junction breaks, and its presence was associated with significantly lower xylem damage and higher survivorship of broken limbs. The ecological consequences of partial limb breaks were considerable. Most fallen limbs remained alive, touched the ground and produced vigorous new growth of epicormic shoots and adventitious roots. The fallen limbs allowed individuals to spread laterally, usurp space, and outcompete neighbors. Over time, repeated limb breaks changed the growth form of *S. lasiolepis* individuals from upright trees or shrubs to decumbent, clonal sprawlers. This study concludes that, in *S. lasiolepis*, limb breaks are an integral part of growth and maturation, included bark facilitates survivable limb breaks, and limb breaks are the unusual mechanism by which individuals spread laterally and achieve long-term persistence.

Key Words: Arroyo Willow, epicormic shoots, included bark, limb breaks, peramorphosis, *Salix lasiolepis*, shrub, sprawler.

A broken limb is usually considered a major setback for a tree. Such an injury can create an entrance point for bacterial, fungal, and insect attacks and can result in a loss of leaf area, resources, and competitive edge (Pokorny et al. 2003; Thomas 2014). In urban forests, broken limbs can injure people and damage property, so the focus of urban foresters has been on understanding and preventing breakages (Lonsdale 1999; Gilman 2011). One of the most common causes of limb breakage is the presence of included bark in the limb junction (Slater and Ennos 2015, 2016). Included bark is bark that remains in the junction as two limbs grow larger, and it forms a wedge that weakens the junction because bark has less supportive strength than wood (Slater and Ennos 2015). Urban foresters regard included bark as a serious junction defect, and they routinely conduct risk assessments identifying trees with included bark as hazardous and in need of pruning or bracing (Lonsdale 1999; Matheny and Clark 2009). Included bark has received little attention outside urban forests, however, so its importance in natural areas is unknown.

While working in a southern California riparian forest, I noticed that limb breaks were common on *Salix lasiolepis* Benth. (Arroyo Willow) and many of the broken junctions contained included bark. Most of the breaks were partial, with the broken limbs still partly attached at the break point, resting on the ground and producing epicormic shoots and adventitious roots (Fig. 1). This type of growth form had not been previously described for *S. lasiolepis* (e.g., Munz 1974, Hickman 1993). While elements of this growth form have been described in other species, e.g., limb breaks (Foster and Boose 1992; Walker et al. 1992; Gardiner 2021), epicormic shoots (Gartner 1989; Peterson and Pickett 1991; Del Tredici 2001), and adventitious roots (Woods 2008; Del Tredici and Orwig 2017), the abundance of broken, fallen, and surviving limbs, coupled with the extensive regrowth on the limbs, suggested that this growth form was of particular importance to *S. lasiolepis*.

This paper explores the occurrence of limb breaks on *S. lasiolepis* and the morphological significance of those breaks. It documents: (1) the types of breaks; (2) the timing of breaks; (3) the occurrence of included bark in breaks; and (4) the role of included bark in the survivorship of broken limbs. It further examines: (5) the vegetative resprouting on broken limbs; (6) the adventitious rooting of broken limbs; and (7) the overall effect of limb breaks on the *S. lasiolepis* growth form. The data presented support the conclusion that, for *S. lasiolepis*, limb breaks are an integral part of an individual's growth and maturation, and that, in *S. lasiolepis*, included bark is not a defect but, rather, an adaptive trait that facilitates survivable limb breaks and promotes lateral spread and longevity.

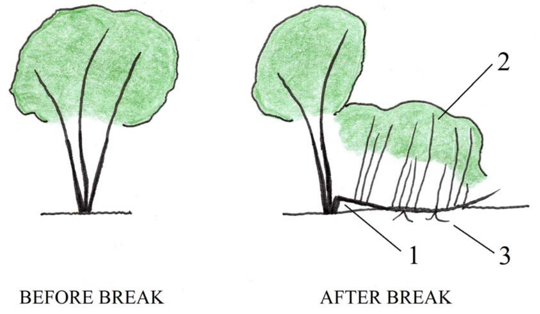

FIG. 1. Diagram of a partial limb break in *S. lasiolepis* illustrating the main features. BEFORE BREAK. The *S. lasiolepis* individual is a tall shrub. AFTER BREAK. Approximately 14 mo after the limb break, the same individual has become a sprawler. The fallen limb was only partially broken and remained alive (#1) and has produced a thicket of epicormic shoots (#2) and two sites of adventitious roots (#3).

METHODS

Study Site and Study Species

The Tijuana River Valley in San Diego County, California, is a coastal floodplain of approximately 1500 ha (Fig. 2). Most riparian habitats in the valley are relatively undisturbed and are preserved within three adjoining parks: the Tijuana River Valley Regional Park, the Border Field State Park, and the Tijuana Slough National Wildlife Refuge. The riparian habitats in the east are, however, frequently mowed by the International Boundary and Water Commission (IBWC). The riparian habitats are a patchwork of different aged stands that became established after various disturbance events with the oldest established in 1980. Riparian forests in the riverbed are numerically and structurally dominated by *S. lasiolepis* and *S. gooddingii* C.R.Ball (Goodding's Black Willow), and the surrounding riparian scrub is dominated by *Baccharis salicifolia* (Ruiz & Pav.) Pers. (Mule Fat; Boland 2014a). Recent research on these species in the valley includes studies of seed production (Boland 2014a), seed dispersal (Boland

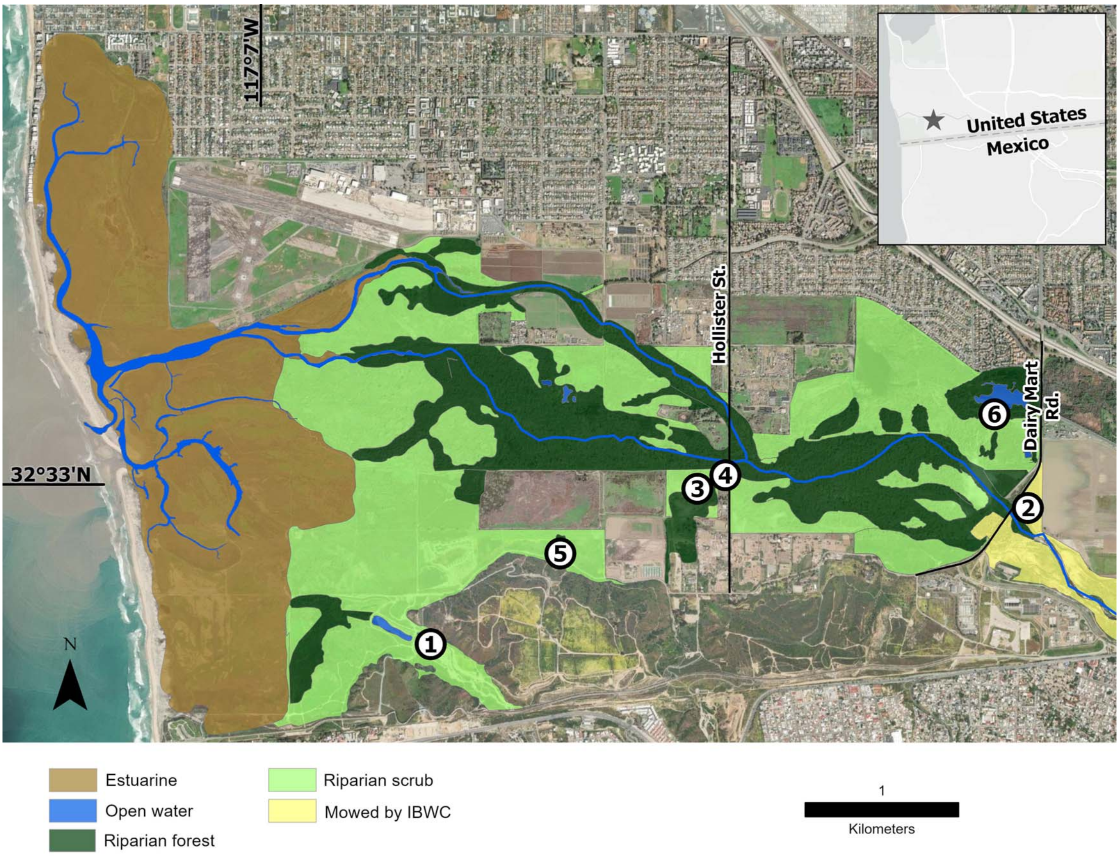

FIG. 2. Map of the Tijuana River Valley showing the vegetation types and locations of the six study sites. The sites were in willow stands of different ages, from 0.5 yr old (Site 1) to 40 yr old (Site 6).

2014b), seedling recruitment (Boland 2014a; Boland 2017), zonation of seedlings and adults (Boland 2014a), and impacts of the Kuroshio Shot Hole Borer (*Euwallacea kuroshio* Gomez and Hulcr, sp. nov.; KSHB; Boland 2016; Boland and Woodward 2019, 2021).

Salix lasiolepis is the most common willow species in California (Ritter 2018). It is a shade-intolerant pioneer species found near fresh water, and in San Diego County it forms stands along streams from 6500 ft to the coast (Lightner 2011). In the Tijuana River Valley, *S. lasiolepis* occurs in even-aged, single-species stands at the riparian forest/riparian shrub transition. Six stands of different ages were chosen for study (Fig. 2). Individuals in the selected stands ranged from small saplings in the two younger stands to large, mature individuals in the four older stands. The ages of the two youngest stands (0.5 and 3.5 yr) were known, as I had witnessed their establishment, whereas the ages of the four older stands (13, 16, 23, and 40 yr) were estimated from historical photos on Google Earth and elsewhere (Safran et al. 2017). These stands had not experienced destructive flooding in the past 25 yr, therefore individuals within them had not been damaged by unusual storm flows. Also, these stands had not been heavily impacted by the KSHB invasion that occurred in the valley from 2015 to 2017 (Boland 2016; Boland and Uyeda 2020). Fieldwork for this study was conducted on 601 d between January 2020 and November 2023.

Limb Breaks

To describe and quantify limb breaks, a transect line of 75 m was laid in a randomly chosen direction in each of the six stands, and the first 20 live *S. lasiolepis* individuals along each transect were labeled (n = 120 trees total). The labeled individuals were examined and breaks on all live major and minor branches down to 2 cm in diameter were counted. Each break point was examined for the presence of included bark, and the percentage of cross-sectional area broken was recorded as an estimate of xylem damage, or break severity. Each broken limb, i.e., the distal part of the limb beyond the break, was recorded as alive or dead and whether it was touching the ground. The type of break was recorded as either a limb split, base break, snap, or shear crack following the nomenclature of Slater and Ennos (2015) and Mattheck (1998). These surveys of limb breaks were conducted during summer 2020. Additionally, the site with the most limb breaks (Site 4; 16 yr old), was visited monthly for 2 yr, January 2020 to December 2022, to track the timing of additional, new breaks on the 20 labeled individuals.

New Growth After a Limb Break

The extensive new growth of epicormic shoots that occurred after a limb break (Fig. 1) was described in three ways. First, in three canopy gaps created by limb breaks, epicormic shoots that sprouted from fallen limbs were followed for 14 mo to determine how quickly they filled the gaps. The three gaps (named A, B, and C) were on three individuals in Site 4. Each gap had formed naturally from a limb break that occurred between September 2020 and June 2021. Data recorded within a week after each break included the type of break, number of limbs involved, broken limb size (circumference and length), area impacted beyond previous canopy, plant species impacted by the fallen limb, gap size (area of missing crown), and gap aspect. The regrowth was observed regularly over the following year during which time a thicket of epicormic shoots developed. Data recorded 14 mo after the break included the number, lengths, and origins of all epicormic shoots; the area over which new epicormic shoots arose; and the percent canopy cover in the gap using dot planimetry on three vertical canopy photographs taken from 1 m height within the gap. The second method of describing the new growth was to compare the growth rate of epicormic shoots with that of outer canopy twigs. The average length of all the epicormic shoots (n = 53) in one gap (Gap C) at 10 mo after the break was compared to that of 11-mo-old outer canopy twigs (n = 100) on the same individual and four nearby individuals. Finally, the overall contribution of epicormic shoots to *S. lasiolepis* canopies was estimated as the percent cover of the crown derived from epicormic shoots in each of the 20 labeled individuals in each of the six stands.

Adventitious Rooting of Fallen Limbs

The 20 labeled individuals in each stand were also examined for production of adventitious roots (Fig. 1). For each individual, the number of limbs on the ground and the number of rooting locations were recorded, as well as the maximum distance that adventitious roots were found from the original rooting site. Points of rooting on the horizontal limbs were not difficult to find with some shifting of accumulated leaf litter and minor digging. In addition, the influence of adventitious rooting on survivorship was studied in the oldest stand (40 yr old; Site 6). In a 5.1 ha area within the stand, all living and dead *S. lasiolepis* individuals (n = 30) were categorized as either having adventitious roots or not, and survivorships of individuals with and without adventitious roots were compared. Similarly, all living and dead major limbs (n = 153) on the same individuals were categorized as either having adventitious roots or not, and survivorships of limbs with and without adventitious roots were compared.

Change in Growth Form with Age and Size

The growth form of the 20 labeled individuals in each stand was noted as either a tree, a shrub or a sprawler and, for each stand, the percentage of each growth form was determined. A **tree** was defined as having a single erect limb with a single rooting site. A **shrub** was defined as having two to several erect limbs with a single rooting site and limbs that may touch but not lay on the ground. A **sprawler** was defined as an individual having one or more limbs with one or more limbs laying on the ground and, because limbs on the ground may produce adventitious roots, a sprawler may have more than one rooting site (Fig. 1). To generalize growth form in relation to size, the 120 labeled individuals were categorized as small, medium, or large based on crown area and, within each size class, the percentage of each growth form was determined. Crown areas used to categorize small, medium, and large individuals were <5 m^2, 5–50 m^2, and >50 m^2, respectively.

Additional Stand Features

Additional supporting data were recorded to further describe features of the *S. lasiolepis* stands, individuals, and limbs. In each stand, tree density was measured by counting the individuals within 1 m of one side of the transect line, giving the number per 75 m^2. Lateral spreading rate of the canopy was measured by placing five stakes at a stand's edge and revisiting after 1 and 2 yr to calculate average rates of annual lateral growth at the canopy edge (at Sites 2, 4, and 5 only). Light penetration through the canopy was measured at Sites 2 through 6 at midday on a cloudless day at ten points along a 20 m transect using a light meter (Extech Instruments Model 401025; Extech Instruments Corporation, Nashua, NH). Light outside the canopy was measured at three points before entering the stand and three points after exiting the stand. Light intensity under the canopy was calculated as the average under-canopy measure divided by the average outside-canopy measure and expressed as a percentage (Harper 1977). Light penetration was also measured before and after the break in one canopy gap (Gap C in Site 4). Maximum heights of the 20 labeled individuals in each stand were measured. The crown of each labeled individual was mapped to scale on quadrille paper using the spoke method (Blozan 2006) and, from these maps, crown area and maximum crown width were measured. For each labeled individual, major live limbs were counted; limb size (circumference) was measured at breast height or, for horizontal limbs, at 1.37 m along the limb; and angle of inclination of each major live limb relative to horizontal was measured at 1.37 m along the limb with a Pitch & Slope Locator 750 (Johnson Level & Tool Mfg. Co., Inc., Mequon, WI).

RESULTS

Limb Breaks

Limb breaks were common on *S. lasiolepis* in the Tijuana River Valley, and most of the broken limbs remained alive. In the survey of 120 individuals, a total of 119 limb breaks were found. The limb breaks were on 38 individuals, with a maximum of ten breaks on one individual. The limb breaks were found in the four older stands only; in two of these sites (Sites 4 and 6) 60% of the individuals had live breaks (Table 1). The number of limb breaks increased significantly with the size of individual based on crown area for both total breaks ($r^2 = 0.580$; $P < 0.01$; $n = 120$) and live breaks ($r^2 = 0.636$; $P < 0.01$; $n = 120$).

Limb breaks were of four types: limb splits, base breaks, snaps, and shear cracks (Fig. 3). Limb splits are breaks or cracks at a limb junction, and base breaks are breaks or cracks at the junction of an epicormic shoot and a larger limb. Snaps are transverse fractures, and shear cracks are longitudinal fractures, and both occur between branch junctions. Of the 119 breaks observed, limb splits were the most common (55%), followed by snaps (20%), base breaks (19%) and shear cracks (6%; Table 2). The average circumferences of the four types of broken limbs ranged from 33 cm (snaps; $n = 24$) to 77 cm (base breaks; $n = 22$). Most of the breaks were partial, i.e., there was still vascular tissue connection, and survivorship of broken limbs was high for all break types except snaps; the percentages of broken limbs still alive at limb splits, base breaks, and sheer cracks were 79%, 91% and 100%, respectively, whereas at snaps it was only 33% (Table 2). Altogether, 73% of the broken limbs remained alive ($n = 119$). The low survivorship of snaps was consistent with the high average percentage of xylem damaged in that type of break (72%; $n = 24$). Overall, survivorship of a broken limb was strongly linked to the severity of the break; broken limbs that remained alive averaged xylem damage of only 13% (±15%; $n = 87$), whereas those that had died averaged xylem damage of 87% (±19%; $n = 32$). These percentages were significantly different (t-test, $t = 21.9$, df = 117, $P < 0.001$).

Included bark was observed in 76% of the breaks at limb junctions, i.e., at 79% of the limb splits and at 68% of the base breaks (Table 2). Included bark was not observed in any of the snaps or shear cracks. Included bark usually appeared as a large intrusion of bark at the site of the limb failure, as shown in Figs. 3A and 3B. At breaks with included bark, xylem damage averaged 22% (±30%) and branch survivorship was 85% ($n = 67$), whereas at breaks with no included bark, xylem damage averaged 47% (±40%) and branch survivorship was only 58% ($n = 52$). The presence of included bark at a break was therefore associated with significantly lower xylem damage (t-test, $t = 4.0$, df = 117, $P < 0.001$) and significantly higher survivorship of the broken limb (G-test of independence; $G = 11.2$, df = 1, $P < 0.01$).

Most broken limbs came to rest on the ground regardless of break type, a noteworthy result because live *S. lasiolepis* limbs touching moist ground can readily form adventitious roots. Among those broken in limb splits, base breaks, and shear cracks,

TABLE 1. CHARACTERISTICS OF *S. LASIOLEPIS* OF DIFFERENT AGES IN THE SIX STUDY SITES. Means are for n = 20 unless otherwise indicated, nd = no data.

	Site					
Characteristic	1	2	3	4	5	6
Stand age (years)	0.5	3.5	13	16	23	40
Limb breaks						
# Live	0	0	4	49	12	22
# Dead	0	0	0	18	8	6
# Total	0	0	4	67	20	28
Percent of individuals with live breaks	0	0	15	60	20	60
Epicormic shoots (e.shoots)						
Percent of individuals with e.shoots	0	0	15	65	85	100
Percent of crown composed of e.shoots (mean ± std deviation)	0 ± 0	0 ± 0	8 ± 19	44 ± 42	58 ± 37	84 ± 27
Adventitious roots (a.roots)						
Percent of individuals with a.roots	0	0	0	60	10	95
Maximum distance from origin (m)	0	0	0	7.7	7	13.5
Growth form						
Percent Tree	100	100	10	10	10	0
Percent Shrub	0	0	75	30	45	25
Percent Sprawler	0	0	15	60	45	75
Shape						
Limb angles (degrees) (mean ± std deviation)	80 ± 5	80 ± 7	60 ± 14	39 ± 25	49 ± 19	20 ± 17
Percent of individuals with limbs on ground	0	0	15	80	40	80
Height of crown (m) (mean ± std deviation)	1.8 ± 0.3	5.5 ± 1.1	7.7 ± 1.2	8.6 ± 1.6	7 ± 1.2	6.9 ± 1.0
Width of crown (m) (mean ± std deviation)	0.6 ± 0.2	1.7 ± 0.6	7.4 ± 4.0	14.6 ± 5.1	9 ± 4.3	14.3 ± 4.4
Area of crown (m^2) (mean ± std deviation)	0.3 ± 0.2	2.2 ± 1.2	36 ± 56	122 ± 91	35 ± 32	95 ± 68
# Major limbs (mean ± std deviation)	1 ± 0	1 ± 0	3.4 ± 2.5	4.8 ± 3.2	2.3 ± 1.1	2.4 ± 1.7
Stand characteristics						
Density (#/75 m^2)	820	146	15	4.2	13	2
Percent light reaching ground	nd	6	4	2	5	4
Lateral growth (m/yr; mean ± std deviation; n = 5)	nd	1.3 ± 0.5	nd	0.8 ± 0.2	0.2 ± 0.2	nd

88% to 90% were in contact with the ground, as were 75% of those broken in snaps (Table 2). Overall, of the 119 broken limbs observed, 102 (86%) were fully on or touching the ground and, importantly, 75 (63%) of these were still alive.

As for the timing of breaks, 20 new limb breaks occurred during the 2-yr period of observation of labeled trees in Site 4. These breaks occurred in 11 different months spread over the 2 yr indicating that they were not caused by a single extreme wind event. The breaks were not evenly spread throughout the year; significantly more than expected (13 of 20) occurred during the fall months (September to November; G-test of goodness of fit; $G = 14.4$, $df = 3$, $P < 0.01$). Of the 20 new breaks observed, limb splits were the most common (60%), followed by snaps (25%), base breaks (15%) and shear cracks (0%). These frequencies were similar to those seen among the 119 breaks discussed above, i.e., 55%, 20%, 19% and 6%, respectively (Table 2).

Salix lasiolepis breaks remained open for many years and did not show obvious degradation from bacteria, fungi or insects. Break injuries were not covered by resins, gums or latex, but instead were slowly covered by wound wood that grew from the living cambium around the edge of the injury and rolled over the injury. Wound wood covered the cambium and phloem first and then gradually enclosed the exposed xylem with new wood and bark, thereby sealing the injury. In many cases, the cambium around the included bark contributed to the wound wood.

New Growth After a Limb Break

The three canopy gaps studied were created by limb splits and base breaks, and four of the five limbs involved survived their breaks and falls (Table 3). Lengths of broken limbs ranged from 4.4 m to 9.4 m, and circumferences ranged from 17 to 60 cm (i.e., diameters of approximately 5 to 19 cm). The canopy gaps ranged in size from 8.7 to 20.3 m^2 and represented 3% to 16% of each individual's original crown area. The other species directly impacted by these fallen limbs were *B. salicifolia* and *Ricinus communis* (11 and 2 individuals, respectively). Within a few weeks of the breaks, abundant epicormic shoots developed. The shoots grew from the fallen limbs and from nearby limbs on the same individual, and they filled each canopy gap with new growth. Notably, growth was not from an individual's outer canopy, from neighboring individuals, or from other species. Also, all the shoots filling the gap were

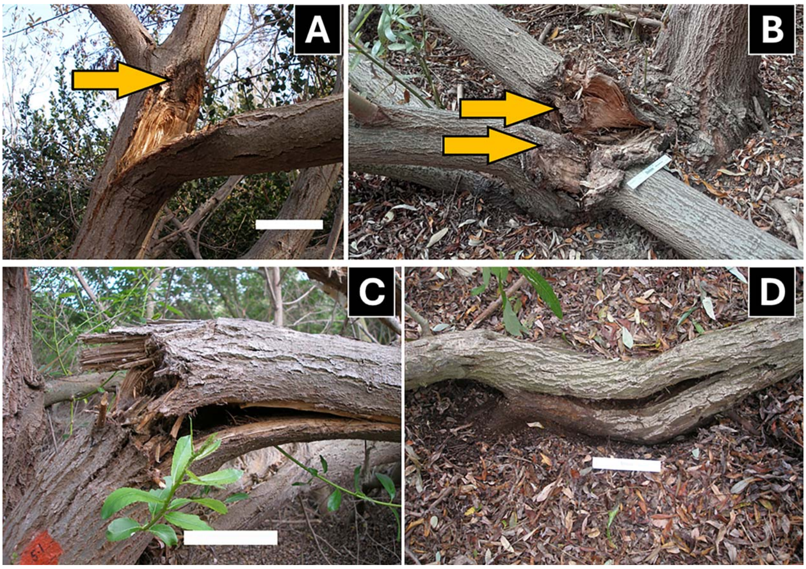

FIG. 3. Types of limb breaks found in *S. lasiolepis*. A. Limb split. B. Base break (three are shown here). C. Snap. D. Shear crack. These examples were all partial breaks and in these cases all the broken limbs survived. Arrows point to included bark. The white ruler is 16 cm long.

epicormic shoots; no root sprouts or root suckers were ever seen on *S. lasiolepis*.

After 14 mo, vigorously growing, dense thickets of epicormic shoots had developed along the fallen limbs in the three gaps. Thicket areas ranged from 11.3 to 43 m^2, i.e., 1.3 and 2.1 times larger than their respective missing crown areas (Table 3). By this time, epicormic shoots were tall and dense and occupied 92% to 97% of the space within the gap. Average 14-mo shoot lengths ranged from 1.6 m to 2.8 m, and shoot densities ranged from 1.5 shoots per m^2 to 9.8 shoots per m^2. Shoot growth could be remarkably fast; for example, one shoot, the most successful in Gap C, grew 4.58 m in 429 d, averaging more than 1 cm/d. Shoots tended to be very dense initially and less dense later as shorter shoots were shaded out and died; for example, a 1 m section of broken limb in Gap C had 28 short shoots at 8 mo and only three tall shoots at 14 mo.

In two of the three canopy gaps, limb breaks and epicormic regrowth led to what was essentially instant lateral expansion of the canopies because the limb breaks extended the canopies at Gaps B and C by 2 m and 5 m, or by 10 m^2 and 23 m^2, respectively (Table 3). This substantial, albeit episodic, lateral spread via broken limbs and epicormic regrowth was in sharp contrast to the usual slow rate of lateral spread of canopies as measured at stakes placed at canopy perimeters, which averaged only 0.2 to 1.3 m/yr in the three stands measured (Table 1).

Epicormic shoots that filled the light gaps looked and grew differently to the leafy, outer canopy twigs at the tips of branches. Epicormic shoots grew from dormant buds on large limbs, started growing at any time of the year, had indeterminate annual growth, were primarily orthotropic (i.e., erect with radial symmetry), and were similar in appearance to seedlings. In contrast, canopy twigs grew from axillary buds on small twigs from the previous year, started growing in January, had determinate annual growth (which virtually ceased in June), were primarily plagiotropic (i.e., horizontal with dorsiventral symmetry), and did

TABLE 2. CHARACTERISTICS OF THE FOUR TYPES OF LIMB BREAKS FOUND IN *S. LASIOLEPIS*.

	At branch junction		Not at branch junction	
Characteristic	Limb split	Base break	Snap	Shear crack
# of breaks	66	22	24	7
Frequency of occurrence (percent)	55	19	20	6
Limb circumference (cm) (mean ± std deviation)	50 ± 27	77 ± 28	33 ± 16	63 ± 15
Percent survivorship	79	91	33	100
Percent xylem damaged (mean ± std deviation)	26 ± 34	17 ± 26	72 ± 27	11 ± 22
Percent with included bark	79	68	0	0
Percent touching the ground	88	90	75	88

TABLE 3. CHARACTERISTICS OF THE THREE CANOPY GAPS STUDIED. Information was gathered at the time of gap creation (a–c) and 14 mo afterwards (d). LS is a limb split, BB is a base break, BASA is *Baccharis salicifolia* and RICO is *Ricinus communis*.

Characteristic	Gap A	Gap B	Gap C
a) Fallen limbs			
Date of break(s)	Sept '20	Mar '21	June '21
# Limbs involved	2	2	1
Type of break	LS, LS	BB, BB	BB
Circumference of limb at break (cm)	17, 36	29, 54	60
Length of limb from break to tip (m)	4.4, 4.5	7.3, 6.5	9.4
Limb survivorship	alive, dead	alive, alive	alive
b) Canopy gap created			
Missing crown area (m^2)	9.3	8.7	20.3
Crown area of whole individual (m^2)	123	266	129
Missing crown area as percent of total	8	3	16
Aspect of canopy gap (facing)	north	south	south
c) Impact of fallen limb			
Species (and #) impacted	0	BASA (4)	BASA (7), RICO (2)
Extension of canopy (m)	0	2	5
Extension of canopy (m^2)	0	10	23
d) Epicormic shoots (14 mo after break)			
Area of live shoot thicket (m^2)	18.5	11.3	43
Percent of canopy closed (mean ± std deviation) (n = 3)	92 ± 4	93 ± 3	97 ± 1
Total number of live shoots in thicket	28	111	216
# of live shoots on fallen limbs	6	86	134
# of live shoots on nearby limbs	22	25	82
Length of live shoots (mean ± std deviation) (n)	2.8 ± 1.0 (28)	1.8 ± 0.9 (111)	1.6 ± 1.1 (216)
Density of live shoots in thicket (#/m^2)	1.5	9.8	5.0

not resemble seedlings. The average lengths of 10-mo-old epicormic shoots and 11-mo-old outer canopy twigs were significantly different ($t = 15.5$, $df = 151$, $P < 0.001$); epicormic shoots averaged 166.5 cm (±90.6 cm, $n = 53$), whereas canopy twigs averaged only 22.3 cm (±15.4 cm, $n = 100$).

The percentage of epicormic shoots in the crown of *S. lasiolepis* individuals increased with age of the stand and the size of the individual. The average percent of epicormic shoots making up the crown of individuals ranged from 0% in the younger stands to 84% in the oldest (Table 1). The canopies of older, larger individuals were largely derived from epicormic shoots due to repeated limb falls and regrowth over time, with epicormic shoots comprising 100% of the canopy in many of these individuals. Overall, the percentage of epicormic shoots in the crown increased significantly with the size of individual, based on crown area ($r^2 = 0.184$; $P < 0.01$; $n = 120$).

Photos of the same *S. lasiolepis* individual taken before and after three limb breaks show several important aspects of limb breaks and epicormic growth (Fig. 4). First, the photos show the impact limb breaks had on the light regime. Before the breaks only 2% (±3%; $n = 10$) of ambient sunlight reached the lower limbs, whereas after the breaks 66% (±40%; $n = 13$) of ambient sunlight reached the fallen limbs. These light conditions were significantly different ($t = 5.0$, $df = 21$, $P < 0.001$). Second, the photos show how quickly thickets of epicormic shoots developed after a limb break. The after photo (Fig. 4B) was taken just 14 mo after the first break, and already the thicket growing from fallen limb #2 had 216 shoots, including one that was 4.58 m tall. Third, they show the impact limb breaks had on the structure of the individual. This individual changed from having mainly vertical limbs to having mainly horizontal ones, and its crown area spread from 129 m^2 to 216 m^2, a 67% increase.

Adventitious Rooting of Fallen Limbs

Adventitious rooting, or layering, was common on older, larger *S. lasiolepis* individuals. In the survey of 120 labeled individuals, a total of 135 adventitious rooting sites were found. These sites were on 28 individuals, with a maximum of 14 rooting sites per individual. Individuals with adventitious roots were found only in the three older stands, with the greatest percentage (95%) in the 40-yr-old stand (Site 6; Table 1). Adventitious roots were regularly found 7 m from the original rooting site, with 13.5 m being the maximum distance found (Table 1). Overall, the number of adventitious rooting sites increased significantly with the size of individual, based on crown area ($r^2 = 0.405$; $P < 0.01$; $n = 120$).

Adventitious rooting was correlated with high survivorship. In the examination of live and dead individuals in the oldest site (Site 6), individuals with limbs on the ground that had adventitious roots had 100% survivorship ($n = 24$; all alive), while those

FIG. 4. The same *S. lasiolepis* individual before and after limb breaks. A. Before photo (4/22/2021) shows four major upright limbs (#1–4). B. After photo (9/22/2022) shows only one limb (#4) remained upright after three base breaks occurred over a 6-mo period (6/2021 to 11/2021). Broken limbs #1 and #3 are visible; #2 is obscured by a thicket of epicormic shoots. The photos show the change in light regime, the rapid growth of epicormic shoots, the increase in crown area and the changes in the structure of the individual. For scale, the number 4 in both photos is at 2.5 m above the ground.

without limbs on the ground and without adventitious roots had only 50% survivorship ($n = 6$; 3 alive). Similarly, in the examination of large limbs, limbs on the ground with adventitious roots had 100% survivorship ($n = 57$; all alive) while those in the air and without adventitious roots had 56% survivorship ($n = 96$; 54 alive). Survivorship of limbs with adventitious roots was significantly higher than those without (G-test of independence; $G = 48.2$, df = 1, $P < 0.01$).

Change in Growth Form with Age and Size

Percentages of the tree, shrub, and sprawler forms of *S. lasiolepis* individuals varied among the six stands, with the tree form dominant in the youngest stand (100% in Site 1) and the sprawler form dominant in the oldest (75% in Site 6; Table 1). Changes in other structural features were consistent with these changing percentages. Limb angles relative to the horizontal plane declined with age of stand; average limb angles in the youngest and oldest stands were 80 and 20 degrees, respectively, indicating a shift from a vertical to a more horizontal individual and forest structure. The percentage of individuals with major limbs on the ground increased with age of stand; the average percentage in the youngest and oldest stands was 0% and 80%, respectively, again indicating a shift from a vertical to a more horizontal forest structure. Height of individuals reached an average maximum of 8.6 m in the 16-yr-old stand (Site 4), and older stands had slightly shorter average maximum heights of 7 m. While individuals ceased vertical growth, they continued to grow horizontally; crown widths of individuals in the youngest and oldest stands averaged 0.6 m and 14.3 m, respectively, and crown area averaged 0.3 m^2 and 95 m^2, respectively. Density of *S. lasiolepis* declined with age of stand; density in the youngest and oldest stands was 820 and 2 individuals per 75 m^2, respectively, indicating a considerable thinning of individuals over time (Table 1).

Grouping the 120 labeled individuals into small, medium and large size classes based on crown area generalized how growth form changed with size (Table 4, Fig. 5). Small individuals were mostly erect **trees** (95%); on average, they had one major limb, no limb breaks, and no limbs on the ground (Fig. 5A). Medium-sized individuals were mostly **shrubs** (58%); on average, they had 2.2 major limbs, 0.4 limb breaks, 0.5 limbs on the ground, and 0.3 adventitious rooting sites (Fig. 5B). Large individuals were mostly clonal **sprawlers** (74%); on average, they had 4.6 major limbs, 2.9 limb breaks, 2.3 limbs on the ground, and 3.5 adventitious rooting sites (Fig. 5C). Due to their years of lateral spread via limb breakage, large individuals were much wider (15.9 m) than tall (7.9 m). In general, the growth form of *S. lasiolepis* individuals changed over time from a vertical tree to a vertical shrub to a horizontal sprawler.

A sprawler had these growth characteristics: multiple limb breaks; horizontal limbs in contact with the ground; epicormic shoots growing from the horizontal limbs; multiple adventitious rooting locations; and a large crown that was wider than tall. A sprawler was therefore a laterally expanding, decumbent, clonal individual that had broken, horizontal limbs as its key underlying feature. A typical sprawler is illustrated in Fig. 6. This individual had five major limbs, all touching the ground. It had eight limb breaks (one break is visible in the photo at #2), and four of the five major limbs were on the ground due to breaks. This individual had more than 206 large epicormic shoots, many of which are visible in the photograph (e.g., at #4). It had nine adventitious rooting locations (one is shown at #5). The most distant adventitious rooting site was 5.7 m from the original rooting point. This individual was considerably wider (20.5 m) than tall (8.3 m) and occupied an area of 266 m^2.

DISCUSSION

This study reveals several new aspects of the growth of *S. lasiolepis*, and it sheds light on the

TABLE 4. CHARACTERISTICS OF *S. LASIOLEPIS* INDIVIDUALS BASED ON SIZE. A.rooting = Adventitious rooting sites; e.shoots = epicormic shoots. Mean and std deviation are given where applicable.

Characteristic	Small	Medium	Large
Crown area (m^2)	<5	5 to 50	>50
# of individuals	42	43	35
Growth form			
Percent Tree	95	12	3
Percent Shrub	5	58	23
Percent Sprawler	0	30	74
Average crown size			
Height (m)	3.7 ± 2.1	7.3 ± 1.4	7.9 ± 1.4
Width (m)	1.2 ± 0.8	8.0 ± 2.9	15.9 ± 4.3
Area (m^2)	1.3 ± 1.3	24.6 ± 12.5	133.6 ± 75.4
Volume (m^3)	7 ± 9	160 ± 101	894 ± 544
Average limb breaks			
# Live	0 ± 0	0.3 ± 0.7	2.1 ± 2.3
# Dead	0 ± 0	0.2 ± 0.5	0.8 ± 1.3
# Total	0 ± 0	0.4 ± 0.8	2.9 ± 3.0
Average shape			
# Major limbs	1.1 ± 0.2	2.2 ± 1.0	4.6 ± 3.0
Limb angle (degrees)	80 ± 6	49 ± 23	32 ± 22
# Limbs on ground	0 ± 0	0.5 ± 0.7	2.3 ± 2.2
# A.rooting sites	0 ± 0	0.3 ± 0.9	3.5 ± 4.4
Percent of crown composed of e.shoots	0 ± 0	43 ± 46	59 ± 36

dynamic processes that shape a natural *S. lasiolepis* forest by linking limb breaks to new growth, lateral spread and, ultimately, increased survivorship.

Limb Breaks and Included Bark

Of the four types of limb breaks in *S. lasiolepis*, the two of ecological significance are limb splits and base breaks. Because these two breaks occur at limb junctions and are usually only partial breaks, they result in fallen limbs that survive and give rise to new growth in the form of epicormic shoots and adventitious roots. The other two types of limb breaks, snaps and sheer cracks, are less consequential; they occur between limb junctions and appear to have no obvious positive nor negative effects on growth or survivorship. In the following discussion, the term limb breaks will refer primarily to limb splits and base breaks.

Limb breaks in *S. lasiolepis* have none of the negatives typically associated with normal limb break injuries. The breaks do not result in obvious bacterial, fungal or insect attacks nor cause individuals to suffer from loss of canopy and leaf area. Indeed, the partial limb breaks so common in *S. lasiolepis* have positive benefits, the main one being that they enable large live limbs to come into contact with the ground and therefore allow an individual to spread laterally, usurp space, and outcompete neighbors.

Included bark appears to play a key role in the breaking of *S. lasiolepis* limbs. In other species, included bark has been shown to weaken a typical tree branch junction by an average of 24% (Slater and Ennos 2015). In this study of *S. lasiolepis*, included bark was present in 76% of the limb junction breaks and its presence was associated with lower levels of xylem damage and higher levels of survivorship of broken limbs. Furthermore, included bark helped form the wound wood that covered the break injury. Together these factors suggest that, in *S. lasiolepis*, included bark is an adaptive trait. Adaptive traits are those that provide a fitness advantage in a particular environment (Keeley et al. 2011). For example, North American conifers subject to frequent fires self-prune their lower dead branches, and the subsequent gap in fuels between the surface litter and the live canopy reduces canopy fires and promotes individual survivorship. Self-pruning is an adaptive trait under those conditions (Keeley et al. 2011). Similarly, included bark in *S. lasiolepis* in riparian habitats weakens a junction so that it *will* fail when the load is high, it facilitates survivable limb breaks, and it promotes lateral spread and longevity. Included bark provides a fitness advantage to *S. lasiolepis* individuals in this riparian environment. This view of included bark as beneficial in *S. lasiolepis* contrasts with the conventional view, especially among urban foresters, that included bark is always a branch defect (Lonsdale 1999; Matheny and Clark 2009).

With this ecological role in mind, other species that exhibit included bark in their limb junctions in urban forests should be examined in their native habitat to determine whether limb breakage provides an ecological advantage to them as well. Species to examine would include: *Sorbus aucuparia* L. (Rowan), *Fraxinus pennsylvanica* Marshall (Green Ash), *Acer ginnala* Maxim. (Amur Maple), *A. saccharinum* L. (Silver Maple), *Fagus sylvatica* L. (European Beech), *Robinia*

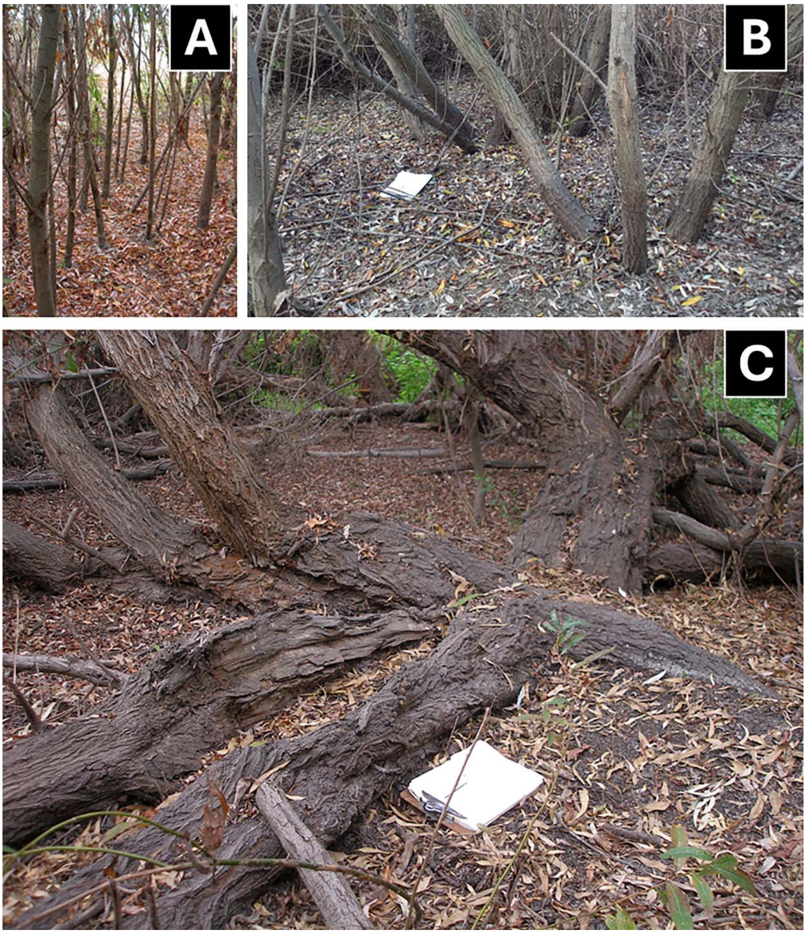

FIG. 5. The three growth forms of *S. lasiolepis* individuals. A. Small individuals are vertical trees. B. Medium-sized individuals are vertical shrubs. C. Large individuals are horizontal sprawlers. For scale, the clipboard is 31 cm long, 23 cm wide.

pseudoacacia L. (Black Locust), and *Tilia tomentosa* Moench (Silver Linden; Pokorny et al. 2003; Drenou et al. 2020).

Epicormic Shoots and Adventitious Roots

If a partial limb break is the first step in an individual's horizontal spread, then the rapid growth on the fallen limb is the next. Soon after a limb breaks and falls, epicormic shoots sprout from dormant buds along the entire length of the fallen limb and, later, adventitious roots tap into the soil below it.

The role of epicormic shoots in *S. lasiolepis* is to quickly fill a light gap and thereby to repair and spread the canopy. Most tree species repair damage to their crowns by producing epicormic shoots that replicate the original architectural model of the species; this process is called reiteration (Halle et al. 1978, Tomlinson 1983, Ishii et al. 2007). In many species, the new epicormic shoots appear as miniature versions of the tree growing on a cut stump or damaged trunk (Tomlinson1983). The importance of reiteration is that it promotes tree longevity by resetting the "aging clock" to an earlier developmental phase (Bon et al. 1994; Del Tredici and Orwig 2017), and it promotes crown productivity by reducing the respiration-to-photosynthesis ratio (Ishii et al. 2007). The fast-growing epicormic shoots that fill light gaps in *S. lasiolepis* are an example of such reiteration and rejuvenation.

Adventitious rooting by limbs touching the ground, also called layering, occurs in many tree, shrub, and herbaceous species, particularly those growing in wet habitats (Woods 2008; Thomas 2014; Del Tredici and Orwig 2017). The ability to layer can be important in the rapid invasion of a site by invasive species (Sigg 2000; Boland 2006). In *S. lasiolepis*, the growth of adventitious roots on fallen branches consolidates the spreading individual's foothold and allows the individual to tap into multiple areas for water and nutrients. The adventitious rooting also increased the lifespan of the limbs, as *S. lasiolepis* limbs with

FIG. 6. A typical *S. lasiolepis* sprawler showing the key features of the growth form. Numbers indicate: (1) original rooting site; (2) a major limb break; (3) a major limb that is horizontal due to a break; (4) vertical epicormic shoots on the horizontal limb; and (5) adventitious rooting of the horizontal limb 2.5 m from the original rooting site. This individual was 266 m^2 in crown area, 20.5 m wide and 8.3 m tall. For scale, the numbers are 9.5 cm tall, 10.3 cm wide.

adventitious roots had significantly higher survivorship than those without.

From Tree to Sprawler

As documented in this study, the growth form of *S. lasiolepis* changes with age and size. The changes—from tree to shrub to sprawler—appear to be adaptations to the pressures and opportunities an individual experiences as its stand ages. The initial growth form of a **tree** appears to be in response to competition for light. Seedlings of *S. lasiolepis* and *B. salicifolia* establish together in suitable clearings in early spring, and seedling density can be as high as 1300 per m^2 (Boland 2014a). A fast-growing upright tree form is essential to keep an individual's canopy in the light and not be outcompeted by the thousands of other young plants nearby. The tree form is generally considered the best when resources are abundant and there is competition for light (Koch et al. 2004; Thomas 2014). The second growth form of a **shrub** appears to be brought about by the surviving trees exploiting their opportunities. At about 5 yr of age, *S. lasiolepis* trees reach the maximum height for the species in the area (7–9 m) and, as individual deaths lead to thinning of the canopy, surviving individuals send up basal epicormic shoots to exploit the new light gaps. The deaths of neighbors therefore allow the tree to become a tall, multi-limbed shrub. The third growth form of a **sprawler** appears to be the result of the largest individuals imposing themselves on their neighbors. After a few years, limbs growing vigorously in the sun become too heavy for their branch junctions and break, crushing neighboring plants as they fall. Fallen limbs, now horizontal, remain partly connected at the break point and rapidly produce fast-growing, vertical epicormic shoots and, later, adventitious roots, thus transforming the shrub into a large, decumbent sprawler. Eventually, all original upright limbs of the shrub fall or die, leaving only rooted horizontal limbs on a widely spreading plant. Over time, the largest epicormic shoots will, in turn, break, fall, resprout and root, resulting in further spread and persistence. The change from a shrub to a sprawler usually involves a reduction in the individual's height and a considerable increase in its crown area (Fig. 4). Because the surviving limbs usually remain connected to each other, the production of horizontal limbs and adventitious roots appears to be less about vegetative reproduction and more a method of individual persistence (Bond and Midgley 2001; Clarke et al. 2015). In summary, the changes in growth form represent an effective strategy for *S. lasiolepis* to grow larger under the changing conditions as they age. Each change in form is an increase in crown area, and each likely results in an increase in flower production and an increase in fitness. Indeed, plant size is frequently used as a proxy for plant fitness (Younginger et al. 2017).

In the Tijuana River Valley, *S. lasiolepis* is a multi-trunked riparian forest edge species that occupies the zone between the taller, single-trunked *Salix gooddingii* in the lower, wetter areas and the shorter *B. salicifolia* shrub in the higher, dryer areas (Boland 2014a). The relative positions of these three species are determined at the time of seedling establishment (Boland 2014a), and the *S. lasiolepis* recruitment zone is often very narrow, sometimes less than 3 m wide (Boland 2017). Remarkably, the *S. lasiolepis* sprawling growth form allows individuals, over time, to spread beyond the seedling establishment zone, form adventitious roots higher on the bank, outcompete the neighboring *B. salicifolia*, and expand its edge dominance. Limb breakage and adventitious rooting therefore allow *S. lasiolepis* to invade and occupy sites that were not suitable for establishment from seeds.

The Tijuana was an excellent site for this study because it has *S. lasiolepis* stands of various ages and sizes. The Tijuana River, however, is polluted by sewage flows from Mexico (Boland and Woodward 2019) presenting the possibility that *S. lasiolepis* in the valley grows differently to how it grows in less nutrient-enriched areas. Additional surveys of *S. lasiolepis* conducted during 2022 at six other sites in San Diego County dismissed that possibility, however, and confirmed that the main features of *S. lasiolepis* growth observed at the Tijuana River Valley were in fact present at riparian areas throughout the County (Boland unpublished data). That is, small *S. lasiolepis* individuals were trees or shrubs, and large individuals were sprawlers that had limb breaks, horizontal limbs, epicormic shoots and adventitious roots, as observed in the Tijuana River Valley.

All trees undergo phasic development, i.e., they pass through a juvenile, non-flowering phase and an adult, flowering phase, followed by senescence and death (Zimmermann and Brown 1971). In *S. lasiolepis*, it appears that the tree and shrub forms represent the juvenile and adult phases, respectively. The flowering sprawler form therefore represents an added, post-adult phase in which there is die-back of the upright limbs but continued growth and regrowth of any horizontal limbs on the ground. The addition of a post-adult phase is a phenomenon known as peramorphosis (Dobreva et al. 2021). By developing into a sprawler, an individual *S. lasiolepis* postpones senescence and extends its life, reproductive output, and overall fitness. The characteristics brought to light and described in this study—included bark, partial limb breaks, epicormic shoots, and adventitious roots—comprise the unusual mechanism by which *S. lasiolepis* becomes a sprawler and flourishes as a long-lived pioneer species.

ACKNOWLEDGMENTS

I thank Deborah Woodward for helpful discussions, assistance in the field, and improvements to the manuscript. I also thank Monica Almeida at Tijuana River National Estuary Research Reserve for producing the map; the San Diego County Parks and Recreation Department for preserving the Tijuana River Valley woodlands; and two anonymous reviewers for valuable comments on early drafts.

LITERATURE CITED

BLOZAN, W. 2006. Tree measuring guidelines of the eastern native tree society. Bulletin of the Eastern Native Tree Society 1:3–10.

BOLAND, J. M. 2006. The importance of layering in the rapid spread of *Arundo donax* (Giant Reed). Madroño 53:303–312.

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

BOLAND, J. M. 2014b. Secondary dispersal of willow seeds: sailing on water into safe sites. Madroño 61:388–398.

BOLAND, J. M. 2016. The impact of an invasive ambrosia beetle on the riparian habitats of the Tijuana River Valley, California. PeerJ 4:e2141.

BOLAND, J. M. 2017. Linking seedling spatial patterns to seed dispersal processes in an intermittent stream. Madroño 64:61–70.

BOLAND, J. M. AND K. A. UYEDA. 2020. The ecology and management of the Kuroshio Shot Hole Borer in the Tijuana River Valley 2019–20 (year 5). Final report for US Navy, US Fish and Wildlife Service and Southwest Wetlands Interpretive Association. 70 pages. Website: https://trnerr.org/wp-content/uploads/2020/05/KSHB-TRValley2020.pdf (accessed 10 January 2024).

BOLAND, J. M. AND D. L. WOODWARD. 2019. Impacts of the invasive shot hole borer (*Euwallacea kuroshio*) are linked to sewage pollution in southern California: the Enriched Tree Hypothesis. PeerJ 7:e6812.

BOLAND, J. M. AND D. L. WOODWARD. 2021. Thick bark can protect trees from a severe ambrosia beetle attack. PeerJ 9:e10755.

BON, M. C., F. RICCARDI, AND O. MONTEUUIS. 1994. Influence of phase change within a 90-year-old *Sequoia sempervirens* on its *in vitro* organogenic capacity and protein patterns. Trees 8:283–287.

BOND, W. J. AND J. J. MIDGLEY. 2001. Ecology of sprouting in woody plants: the persistence niche. Trends in Ecology and Evolution 16:45–51.

CLARKE, P. J., D. M. BELL, AND M. J. LAWES. 2015. Testing the shifting persistence niche concept: plant resprouting along gradients of disturbance. The American Naturalist 185:747–755.

DEL TREDICI, P. 2001. Sprouting in temperate trees: a morphological and ecological review. The Botanical Review 67:121–140.

DEL TREDICI, P. AND D. A. ORWIG. 2017. Layering and rejuvenation in *Tsuga canadensis* (Pinaceae) on Wachusett Mountain, Massachusetts. Rhodora 119:16–32.

DOBREVA, M. P., J. CAMACHO, AND A. ABZHANOV. 2021. Time to synchronize our clocks: connecting developmental mechanisms and evolutionary consequences of heterochrony. The Journal of Experimental Zoology Part B: Molecular and Developmental Evolution 338:87–106.

DRENOU, C., D. RESTREPO, AND D. SLATER. 2020. Demystifying tree forks: vices and virtues of forks in arboriculture. Journal of Botany Research 3:100–113.

FOSTER, D. R. AND E. R. BOOSE. 1992. Patterns of forest damage resulting from catastrophic wind in central New England USA. Journal of Ecology 80:79–98.

GARDINER, B. 2021. Wind damage to forests and trees: a review with an emphasis on planted and managed forests. Journal of Forest Research 26:248–266.

GARTNER, B. L. 1989. Breakage and regrowth of *Piper* species in rain forest understory. Biotropica 21:303–307.

GILMAN, E. 2011. An illustrated guide to pruning. Delmar Publishers, Albany, NY.

HALLE, F., R. A. A. OLDEMAN, AND P. B. TOMLINSON. 1978. Elements of tree architecture in tropical trees and forests. Springer-Verlag, New York.

HARPER, J. L. 1977. Population biology of plants. Academic Press, London, UK.

HICKMAN, J. C. (ed.) 1993. The Jepson manual – higher plants of California. University of California Press, Berkeley, CA.

ISHII, H. T., E. D. FORD, AND M. C. KENNEDY. 2007. Physiological and ecological implications of adaptive reiteration as a mechanism for crown maintenance and longevity. Tree Physiology 27:455–462.

KEELEY, J. E., J. G. PAUSAS, P. W. RUNDEL, W. J. BOND, AND R. A. BRADSTOCK. 2011. Fire as an evolutionary pressure shaping plant traits. Trends in Plant Science 16:406–411.

KOCH, G. W., S. C. SILLETT, G. M. JENNINGS, AND S. D. DAVIS. 2004. The limits to tree height. Nature 428: 851–854.

LIGHTNER, J. 2011. San Diego County native plants. San Diego Flora, San Diego, CA.

LONSDALE, D. 1999. Principles of tree hazard assessment and management. Stationery Office Ltd, Publications Centre, London.

MATHENY, N. AND J. CLARK. 2009. Tree risk assessment: what we know (and what we don't know). Arborist News 18:28–33.

MATTHECK, C. 1998. Design in nature: learning from trees. Springer-Verlag, Berlin.

MUNZ, P. A. 1974. A flora of southern California. University of California Press, Berkeley, CA.

PETERSON, C. J. AND S. T. A. PICKETT. 1991. Treefall and resprouting following catastrophic windthrow in an old-growth hemlock-hardwoods forest. Forest Ecology and Management 42:205–217.

POKORNY, J. D., J. O'BRIEN, R. HAUER, G. JOHNSON, J. ALBERS, P. BEDKER, AND M. MIELKE. 2003. Urban tree risk management, a community guide to program design and implementation. Minneapolis, MN: USDA Forest Service Northeastern Area State and Private Forestry.

RITTER, M. 2018. California plants: a guide to our iconic flora. Pacific Street Publishing, San Luis Obispo, CA.

SAFRAN, S., S. BAUMGARTEN, E. BELLER, J. CROOKS, R. GROSSINGER, J. LORDA, T. LONGCORE, D. BRAM, S. DARK, E. STEIN, AND T. MCINTOSH. 2017. Tijuana River Valley historical ecology investigation. Report prepared for the California State Coastal Conservancy. 216 pages. Website: https://www.sfei.org/sites/default/files/biblio_files/Tijuana%20River%20Valley%20Historical%20Ecology%20Investigation%20-%20medium%20resolution_0.pdf (accessed 10 January 2024).

SIGG, J. 2000. *Cotoneaster* spp. Pp. 133–136 *in* C. Bossard, J. Randall, and M. Hoshovsky (eds.), Invasive plants of California's wildlands. University of California Press, Berkeley, CA.

SLATER, D. AND A. R. ENNOS. 2015. The level of occlusion of included bark affects the strength of bifurcations in Hazel (*Corylus avellana* L.). Arboriculture & Urban Forestry 41:194–207.

SLATER, D. AND A. R. ENNOS. 2016. An assessment of the remodeling of bifurcations in Hazel (*Corylus avellana* L.) in response to bracing, drilling, and splitting. Arboriculture & Urban Forestry 42:355–370.

THOMAS, P. A. 2014. Trees: their natural history. Cambridge University Press, Cambridge, UK.

TOMLINSON, P. B. 1983. Tree architecture. American Scientist 71:141–149.

WALKER, L. R., J. VOLTZOW, J. D. ACKERMAN, D. S. FERNANDEZ, AND N. FETCHER. 1992. Immediate impact of Hurricane Hugo on a Puerto Rican rain forest. Ecology 73:691–694.

WOODS, K. D. 2008. Living long by staying small: stem layering as an adaptive life-history trait in shade-tolerant tree seedlings. Canadian Journal of Forest Research 38:480–487.

YOUNGINGER B. S., D. SIROVÁ, M. B. CRUZAN, AND D. J. BALLHORN. 2017. Is biomass a reliable estimate of plant fitness? Applications in Plant Sciences 5: apps.1600094.

ZIMMERMANN, M. H. AND C. L. BROWN. 1971. Trees: structure and function. Springer-Verlag, New York, NY.