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# The influence of stream channels on distributions of *Larrea tridentata* and *Ambrosia dumosa* in the Mojave Desert, CA, USA: patterns, mechanisms and effects of stream redistribution

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## ABSTRACT

Drainage channels are among the most conspicuous surficial features of deserts, but little quantitative analysis of their influence on plant distributions is available. We analysed the effects of desert stream channels ('washes') on *Larrea tridentata* and *Ambrosia dumosa* density and cover on an alluvial piedmont in the Mojave Desert, based on a spatial analysis of transect data encompassing a total length of 2775 m surveyed in 5 cm increments. Significant deviations from average transect properties were identified by bootstrapping. Predictably, shrub cover and density were much reduced inside washes, and elevated above average levels adjacent to washes. Average *Larrea* and *Ambrosia* cover and density peaked 1·2–1·6 m and 0·5–1·0 m from wash edges, respectively. We compared wash effects in runon-depleted (−R) sections, where washes had been cut off from runon and were presumably inactive, with those in runon-supplemented (+R) sections downslope from railroad culverts to help identify mechanisms responsible for the facilitative effect of washes on adjacent shrubs. Shrub cover and density near washes peaked in both +R and −R sections, suggesting that improved water infiltration and storage alone can cause a facilitative effect on adjacent shrubs. However, washes of <2 m width in +R sections had larger than average effects on peak cover, suggesting that plants also benefit from occasional resource supplementation. The data suggest that channel networks significantly contribute to structuring plant communities in the Mojave Desert and their disruption has notable effects on geomorphic and ecological processes far beyond the original disturbance sites. Copyright © 2010 John Wiley & Sons, Ltd.

KEY WORDS shrub cover and density; wash; alluvial fan; disturbance

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## INTRODUCTION

Although water is widely considered to be the primary driver of ecosystem processes in aridlands (Whitford, 2002), the role of edaphic factors is regarded a close second, as has been recognized since the earliest days of desert ecology (Cooper, 1922; Cannon, 1924). Soil surface characteristics, texture, horizonation, and macro- and micro-topography each modulate the effects of precipitation by locally controlling infiltration and soil water storage, as well as by interfering with plant establishment and root development (Miller *et al.*, 2009). The outward signs of edaphic controls are seen as a subtle—although sometimes not so subtle—spatial patterning in plant densities, species identities and canopy development (Parker, 1995; Lei and Walker, 1997; Hamerlynck *et al.*, 2002; Schenk *et al.*, 2003; Bedford *et al.*, 2009).

One of the most prominent surficial features of desert landscapes is their system of drainage channels, which is easily recognizable in aerial images (Figure 1). Drainage systems are self-organized landscape features that exhibit fractal characteristics of self-similarity across spatial scales (Rinaldo *et al.*, 2006). Drainages collect and conduct storm runoff and sediment and are hydrologically and biogeochemically distinct from surrounding soils. For example, drainage channels ('washes') generally have a lower N and P content due low organic inputs (Titus *et al.*, 2002), but higher water storage after flow events (Atchley *et al.*, 1999). In addition, water infiltrates more rapidly in washes, because wash sediments lack a vesicular A horizon (Miller *et al.*, 2009). Large drainages or arroyos are reported to have positive effects on the water status of plants that grow in their vicinities (Schlesinger *et al.*, 1987; Ehleringer and Cooper, 1988; Atchley *et al.*, 1999), although the episodic nature of channel flow also predispose near-channel populations to exaggerated boom-bust cycles (Hamerlynck and McAuliffe, 2008).

Superficial inspection of aerial images seems to support the idea that even minor washes affect perennial plant distributions, with larger than average and perhaps a greater number of shrub canopies apparently adjacent to the washes. Although these patterns may seem obvious

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to the human eye, to date there has been no rigorous quantification of the spatial relationships between shrubs and washes. The purpose of this study was to do just that, as well as to examine the possible mechanisms involved in favouring shrub development near drainages. In addition, we examined the effects of altered wash flow caused by long-term redistribution along a railroad.

Three mechanisms could contribute to the positive effect of drainages on nearby shrubs. The most obvious mechanism results from the function of washes as water conduits. Episodically, wash sediments receive infiltration from runon water originating upslope, providing a resource subsidy to nearby shrubs with roots in or near wash sediments. However, larger drainages on the alluvial fans in Mojave Desert rarely run, on the order of only once in 2·6–7·3 years on average (Griffiths *et al.*, 2006), arguably not often enough to produce a persistent effect on vegetation.

A second possible mechanism involves the high infiltration rate of the coarse wash deposits. The infiltration rate of wash deposits can be orders of magnitude higher than that of older deposits close by (Miller *et al.*, 2009). This, and the fact that washes are slightly lower and can thus collect water from surrounding surfaces if there is local runoff, promotes water storage in the wash sediments that may allow plants near washes to remain well-hydrated for longer after rain events. The cumulative effect of even a few more days of positive carbon balance per year may well produce measurable and persistent effects on average canopy sizes.

Third, washes are corridors of reduced shrub density, thus shrubs near washes should have fewer neighbours to compete with, at least to one side, than plants that grow farther away from washes. The apparent effect of washes on nearby shrubs could simply be the result of compensatory growth because of reduced competition. Of course, all three mechanisms (resource subsidy, improved infiltration and storage, and reduced competition) could contribute jointly to the apparent positive effects of drainages on adjacent vegetation.

Our approach to quantifying and explaining wash effects on shrubs was to map shrub cover, density and geomorphic surface type along two extended transects, approximately perpendicular to the drainage channel network, on a gently sloped alluvial fan in the Mojave National Preserve near the Kelso Depot, California. The two transects had a combined length of 2775 m and were mapped in increments of 5 cm over the course of 3 days in the spring of 2007. One transect lay upslope from and parallel to the Kelso Cima road and adjacent railroad line, and purposely was positioned far enough from the road to represent an undisturbed condition to serve as a ‘control’. The second transect lay downslope from and parallel to the railroad at a distance where disturbances to the channel network because of the railroad’s culverts were still clearly in effect. This transect intersected several runon-supplemented regions (+R) in the fan areas of railroad culverts and runon-depleted (−R) regions between the fans (Figure 1). In the +R sections, washes were wider and presumably more active (because of the consolidation of runon from upland areas) than their counterparts above the road. In the −R sections, washes were still clearly recognizable but presumably had not channelled runon water from upland areas for the century since the railroad’s completion in 1905.

Our first goal was to simply quantify the spatial relationships between washes and shrubs by expressing shrub cover and density as a function of distance from the wash margin, and determining the statistical significance of the observed patterns through comparison with bootstrap confidence intervals for average shrub cover and density. Secondly, we attempted to evaluated the mechanism behind the facilitative effect of washes on adjacent vegetation by comparing wash-plant spatial relationships in the +R and −R areas below the railroad, using the transect above the railroad as a control representing an undisturbed drainage network. We presumed that finding a stronger facilitative effect of washes in +R and control areas than of washes in −R areas would identify resource subsidy by runon as a significant mechanism. Furthermore, finding a facilitative effect of washes on shrubs in −R areas would indicate that plants also benefit from improved infiltration and water storage in wash sediments, independent of runon. Finally, finding a negative relationship between shrub densities inside and outside the wash could be taken as evidence that the reduced density of competitors inside the wash also contributes to the positive effect of washes on adjacent plants.

## METHODS

### *Site characteristics and study species*

The transects were located in the Mojave National Preserve, California, USA, along opposite sides and parallel to the railroad and Kelso–Cima highway, about 6 km northeast of the Kelso Depot. Exact coordinates are provided in Figure 1. Alongside the Kelso–Cima highway runs a Union Pacific railroad line, built in 1905, connecting Los Angeles and Salt Lake City. The railroad is protected by culverts spaced about 300–500 m apart. Above the railroad, washes are consolidated and guided towards the culverts by a system of levees and excavations. Below the railroad, deeply cut washes at the culvert outlets branch out downstream into distributary channels and fans, dividing the areas just below the railroad into regions of channel flow depletion and addition (Figure 1). Remnants of the old channel network are still clearly visible in the runon-depletion zones, but one can assume that washes in this region did not receive flow from upslope during the 100+ years that the railroad existed. The lower transect was located approximately 250 m downslope from the road, cutting through several runon supplemented and depleted zones. Depletion zones would have received runoff from the highway, but almost certainly not enough to produce channel flow at a distance of 250 m. The upper transect was located 250 upslope from the road, well outside

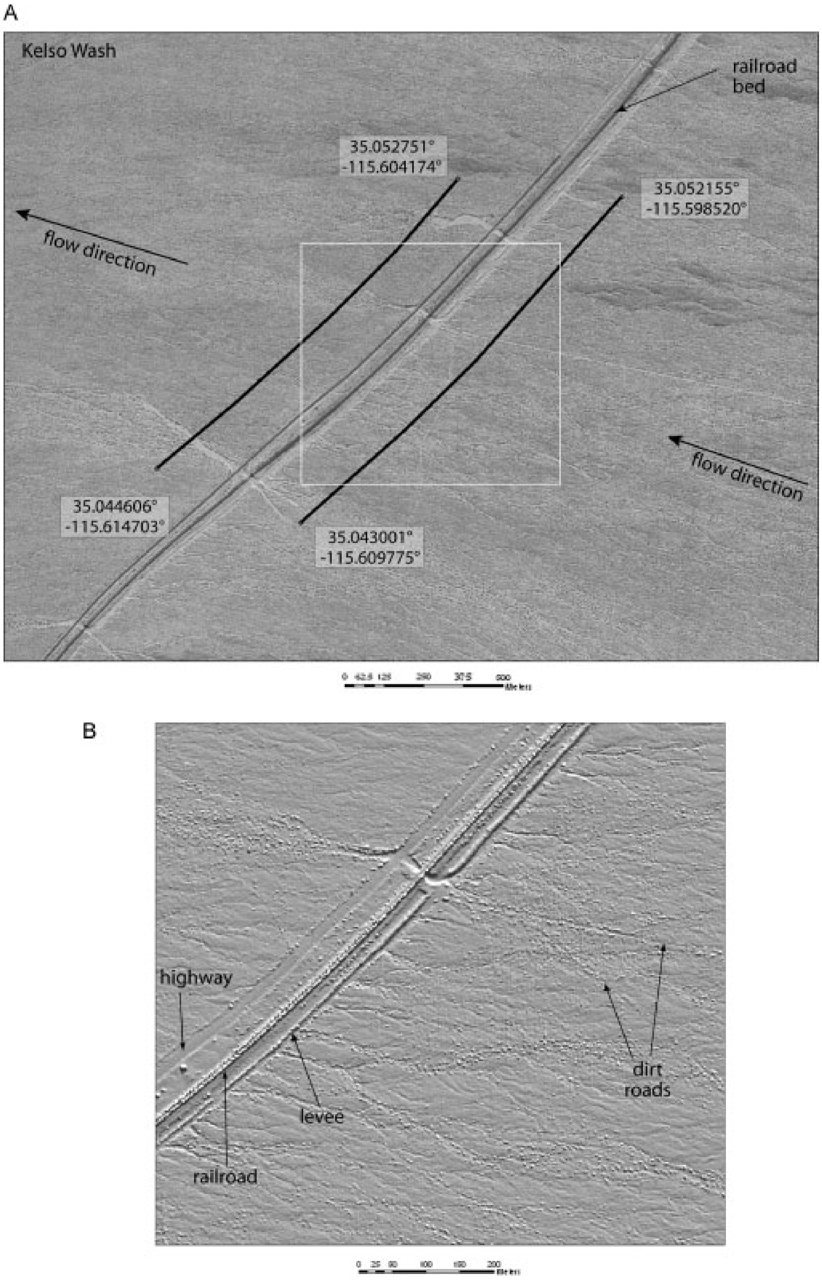

Figure 1. (A) Aerial photograph with faint hillshade from topography superimposed. Higher part of alluvial fan is in lower right corner; Kelso Wash visible in upper left is at the lower end of the alluvial fan. Two transect lines traverse the lower part of the fan. The transect below the railroad is divided into runon depleted (−R) and runon-supplemented (+R) regions. White box shows inset area of (B). (B) Inset of a hillshade calculated from 1-m LiDAR data. Note that drainage channels are more deeply incised above and below the railroad diversion structures, and the plant canopy sizes in the runoff-added and runoff-deprived areas below the railroad are distinctly different.

the zone of railroad construction and soil movement for the purpose of channel consolidation. Thus, from the viewpoint of runon redistribution, we considered the transect above the road a ‘control’.

The railroad and the two transects cross the lower part of a broad alluvial fan extending from the Providence Mountains to the valley centre, which is occupied by Kelso Wash. The fan is composed of granitic rock types varying in size from cobbles to silt, and exhibits a complex mosaic of fan upland surfaces and intervening washes (Figure 1). Different ages of deposits lie within the complex of upland surfaces, as shown by our unpublished geologic mapping, so we designed long transects to cross representative numbers of the washes, uplands of varying ages, and also disturbed and undisturbed sites.

Our assessment of shrub cover and density concentrated on the two co-dominant species of Mojave Desert basins: the evergreen long lived (possibly >1000 years; Vasek, 1980; McAuliffe, 1988) *Larrea tridentata* (DC.) and the much shorter-lived (*ca* 30 years; Sandquist *et al.*, 1993) drought-deciduous *A. dumosa* (Grey).

### *Data collection*

Data were collected in March 2007 along two transects of 1450 m above the railroad and 1325 m length below the

Table I. Classification of surface features and criteria used.

| | Criteria |
|---|---|
| A: Geological distance features | |
| Qya1 | Surface deposits composed of lose sand, chiefly inside washes or fans. No Av horizon. |
| Qya2 | Surface deposits mostly lose sand, but outside active channels. Early stages of varnish development. No Av horizon. |
| Qya3 | Weakly developed Av horizon. Weak varnish or incipient pavement development. |
| Qya4 | Weak pavement. Well developed Av horizon about 3 cm thick. |
| B: Biological distance features: | |
| *L. tridentata* | Surface is covered by living *L. tridentata* branches directly overhead. |
| *A. dumosa* | Surface is covered by living *A. dumosa* branches directly overhead. |
| C: Biological point features: | |
| *L. tridentata*—active | Live leaves indicate present or recent physiological activity. |
| *L. tridentata*—live but inactive | No live leaves but stems still hydrated. |
| *L. tridentata*—dead | Only dead stems. |
| *A. dumosa*—active | Live leaves indicate present or recent physiological activity. |
| *A. dumosa*—alive but inactive | No live leaves but stems still hydrated. |
| *A. dumosa*—dead | Only dead stems. |

railroad. Transects were slightly offset to match up geologic parent materials and wash flow patterns (Figure 1). Two teams of two recorded either the biological (*Larrea* or *Ambrosia* cover) or geological features (surface type) in 5 cm increments. Definitions used for identifying geomorphic- and plant cover-type are summarized in Table I.

Four stages of soil development were distinguished, based on Miller *et al.* (2009). Surfaces characterized as Qya1 were channels comprized chiefly of sandy or silty deposits with no soil development and lacking a vesicular A (Av) or B horizon. Qya2 surfaces were the next older channel terrace deposit, still featuring bar and swale topography and very little horizon development, but with higher clay content because of the accumulation of aeolian dust. Qya3 surfaces had a weakly developed Av horizon with weak varnish and incipient desert pavement and reddened Bw horizons, while Qya4 had moderately developed Av horizons with weak pavement development, noticeably reddened Bw horizons, and cemented Bk horizons. For the analysis we regarded all Qya1 surfaces as 'washes'. Surface type was mapped by recording start and end points of geomorphically homogeneous segments to the nearest 5 cm. Where the deposit type was difficult to identify, especially in distinguishing between Qya3 and Qya4, the Av horizon was probed with a trowel close to but not directly on the transect for definitive assignment to one of the categories. A previous study determined that the four surface types varied by about an order of magnitude in near-surface saturated hydraulic conductivity with the Qya1 surface having the highest, and the Qya4 surface the lowest conductivity (Table II).

Table II. Hydraulic conductivities of near-surface soil for the four surface types in Table I. Values summarized from Nimmo *et al.* (2009) for experiments conducted near the study site.

| | Qya1 | Qya2 | Qya3 | Qya4 |
|---|---|---|---|---|
| Mean $k_{sat}$ (cm h$^{-1}$) | 9 | 6 | 3 | 1·0 |
| Range | 3–30 | 5–8 | 1–7 | 0·5–2·5 |

*Larrea* and *Ambrosia* cover directly over the transect line were also recorded in terms of start and end points in 5 cm increments; however, we did not record whether the cover was comprized by a single canopy or two or more overlapping canopies. For each continuous segment of shrub cover, the height of the tallest canopy point directly over the transect line was also recorded.

In addition, we collected shrub density data inside a 1-m wide strip centred on the transect line for the entire transect lengths. If the midpoint of central trunks fell within the strip, their location perpendicular to the transect line was recorded to the nearest 5 cm.

The transect line cut across the dominant direction of channel network at an oblique angle that we estimated to be 60° on average based on aerial photographs. This means that the average perpendicular distances from a point on the transect to the nearest wash margin may have been only 87% (i.e. the sine of 60°) of the average distance along the transect line. Thus, the distances we report here should be regarded as distance proxies, not to be interpreted as the shortest distance.

### *Statistical approach*

Throughout, we used resampling statistics (bootstrapping; Efron, 1981) to determine confidence limits around average transect properties to identify statistically significant deviations from the mean. The general approach was to randomize the spatial relationships of transect characteristics (type of shrub cover, soil surface type) and the associations between them without changing the frequency of each type within the transect or transect segment analysed. Thus, confidence intervals represent expectations of random distribution and assortment of transect characteristics with identical mean occurrence.

In general, booststrap 90-percentile confidence intervals were derived by resampling 1000 times, calculating the mean variable of interest for each sample (e.g. *Larrea*

Table III. Comparison of the average properties of the two transects.

| | Above railroad (control) | Below railroad overall | Below railroad runon depleted (−R) | Below railroad runon added (+R) |
|---|---|---|---|---|
| Total transect length (m) | 1450 | 1325 | 945 (71%) | 380 (29%) |
| Geomorphic characteristics | | | | |
| Qya1 cover (%) | 19·4 | 12·9 | 8.0 | 25.3 |
| Qya2 cover (%) | 26·2 | 23·7 | 11.7 | 53.6 |
| Qya3 cover (%) | 29·8 | 35·8 | 43.7 | 16.2 |
| Qya4 cover (%) | 24·6 | 27·6 | 36.7 | 5.0 |
| *Larrea* characteristics: | | | | |
| Density (plts $m^{-2}$) | 0·087 | 0·093 | 0.083 | 0.118 |
| Cover (%) | 11·7 | 11·9 | 10.5 | 15.1 |
| Mean max height (cm) | 104·7 | 103·7 | 95.5 | 122.9 |
| Est. canopy diameter (m)[a] | 1·33 | 1·23 | 1.14 | 1.45 |
| Est. canopy diameter (m)[b] | 1·31 | 1·28 | 1.27 | 1.28 |
| *Ambrosia* characteristics: | | | | |
| Density (plts $m^{-2}$) | 0·218 | 0·294 | 0.322 | 0.223 |
| Cover (%) | 4·59 | 6·65 | 6.75 | 6.39 |
| Mean max height (cm) | 33·7 | 35·5 | 34.9 | 37.9 |
| Est. canopy diameter (m)[a] | 0·58 | 0·53 | 0.50 | 0.61 |
| Est. canopy diameter (m)[b] | 0·52 | 0·54 | 0.52 | 0.60 |

[a] This estimate is equivalent to the average size of continuous canopy-covered sections over the transect line.
[b] This estimate is based on dividing the estimated canopy cover by the estimated density and transforming canopy area to canopy diameter.

cover), sorting the means from the highest to the lowest value, and selecting the lowest of the highest 50 and the highest of the lowest 50 for the upper and lower confidence limits. Details on specific resampling proceedures are further described below.

### *Calculation of average transect properties*

Using a remote image, the transect below the railroad was visually divided into segments of runon addition below the culvert outlets (+R) and segments of runon depletion (−R; Figure 1). The transect above the railroad served as a control in so far as it represented conditions where runon was not artificially redirected. Average cover, density and height data were calculated for the whole transects above and below the railroad as well as for the two subsections of the lower transect (Table III).

Percent cover for geomorphic type and shrub species was calculated by summing the length of all 5-cm segments of a given type and dividing by entire transect length. Density data were calculated by dividing the total stem count inside the 1-m wide belt transect by the length of the transect. Mean maximal shrub heights were estimated from maximal height data collected in conjunction with the plant cover data. Mean shrub diameter was estimated by two methods. The first estimate was obtained by calculating the average segment length of continuous shrub cover over the transect line. This estimate is prone to underestimating canopy size, as most canopies would not have been cut through their midsections by the transect line (if transects line cut through at random, the true average diameter would have been greater by 1·575, based on the assumption of a circular canopy). On the other hand, some canopies may have been overlapping, leading to an overestimation of individual canopy size. The second diameter estimate assumed a circular canopy, and was obtained by dividing the shrub cover estimate by the density estimate and then dividing by Pi, taking the square root and multiplying by 2. This method will tend to overestimate the diameter because we estimated a square term (area) from the average of the root term (radius). In the end, both estimates yielded fairly close values (Table III).

### *Distance from wash analysis*

To determine the effect of washes on shrub distributions, we examined trends in average shrub cover and density with distance from the wash edge. For this analysis, all surfaces categorized as Qya1 were considered 'wash'. From 2 m into the wash to 5 m beyond the wash margin, cover characteristics (geomorphic type, canopy cover and density by species) were extracted for both sides of the wash (Figure 2). The 2 m side of this 7 m segment, which pointed into the wash, was given negative coordinates (−2 to 0 m) and the side pointing away from the wash positive coordinates (0 to +5 m), so that the zero coordinate always coincided with the wash margin. Then, average cover and density values were calculated in 5 cm increments as a function of distance from the wash margin.

For the analyses involving either the +R or −R portions of the transect below the railroad, a wash and its associated 7 m segment was considered inside a given runon type if its bank (the zero coordinate) was inside. In all cases, both banks of a wash fell within the same runon category.

To derive 90-percentile bootstrap confidence intervals for cover data, we resampled at random from any transect element inside the respective transect segment (above the road, +R or −R, below the road), including 'wash' elements. Each of the 1000 bootstrap samples was

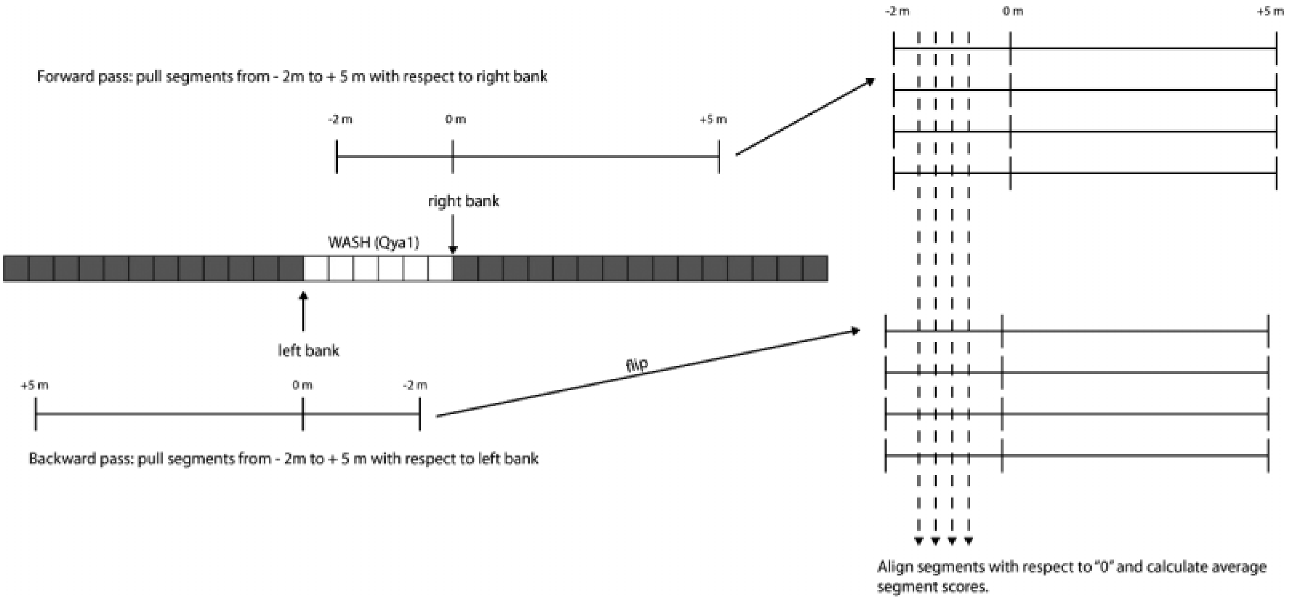

Figure 2. Schematic to explain the numerical procedure used to generate Figures 3–5. The boxes symbolize 5 cm increments along the transect line (not drawn to scale). Left and right banks were identified as the two outer limits of a continuous Qya1 deposit. The forward pass pulls out 7 m segments from 2 m before to 5 m past the 'right' bank. The backward pass pulls out 7 m segments surrounding the 'left' bank. Points on the segment pointing towards the opposite bank are assigned negative coordinates. They include points in the wash but may also go beyond the opposite bank for washes <2 m in diameter.

composed of as many individual draws as there were 7 m segments in the analysis. For the distance analysis of density, we used the 10-element running average of density to smooth out some of the spatial variability. Accordingly, each sample in the bootstrap analysis was composed of 10 times the number of 7 m segments in the analysis.

In the analysis of shrub size as a function of distance from wash, we divided the 7 m segments into 12 distance classes, in 0·4 m increments from 0 to 4·8 m (ignoring greater distances). The diameters (along the transect line) of each *Ambrosia* or *Larrea* canopy in the segment were determined and assigned to one of the distance bins according to the position of the diameter midpoints. Mean diameters were calculated on the basis of all canopies associated with a particular bin. Bootstrap confidence intervals were derived individually for each bin using the respective sample sizes and resampling canopy diameters from the entire transect segment, irrespective of position.

All calculations were automated using customized C++ programs coded in Microsoft Visual Studio 2005. The output was checked against the data input and manual calculations to ascertain that the programs worked as intended.

## RESULTS

The transect below the railroad had 34% less transect length classified as Qya1 ('wash') and 20% more transect length classified as Qya3 compared with the transect above the railroad (Table III). Younger geomorphic surface types (Qya1 and Qya2) were less abundant in −R zones and more abundant in +R zones, while an opposite trend was observed for older geomorphic types (Qya3 and Qya4). Because the transects were not replicated, it is impossible to say whether these as well as other differences were statistically significant. They were, however, based on a very large number of observations at the scale of 5 cm.

Above and below the railroad, *Larrea* cover averaged about 12%, whereas *Ambrosia* cover averaged 5–6% (Table III). *Larrea* cover was almost identical for the two transects overall, but cover and density were, respectively, 44% and 43% higher in +R than in −R areas. *Larrea* canopies were also taller on average in the +R zones. Cover and density of *Ambrosia* were, respectively, 45% and 35% higher below the railroad than above the railroad. However, in contrast to *Larrea, Ambrosia* cover and density were higher in the −R zones than in the +R zones. By one estimate of average canopy size, *Ambrosia* individuals were larger and plants were taller in the +R zones.

In all three transect categories (above the railroad, +R and −R below the railroad), shrub cover rose above the 90-percentile confidence limit at some distance away from the wash margin (Figure 3). These cover peaks were not associated with a corresponding trend in average geomorphic surface characteristics (data not shown), but were pure distance-from-wash effects. *Larrea* cover consistently peaked between 1·5 and 2·5 m away from the wash margin, whereas *Ambrosia* cover peaked at 0·55 m (above railroad), 0·3 m (−R below railroad) and 1·25 m (+R below railroad). Thus, in all but the +R sections, *Ambrosia* cover peaked considerably closer to the wash than *Larrea* cover. In the +R areas, the peak densities of the two shrubs were offset by only 0·1 m.

There was a second peak density for *Ambrosia* at a distance of approximately 4 m in the −R areas (Figure 3C).

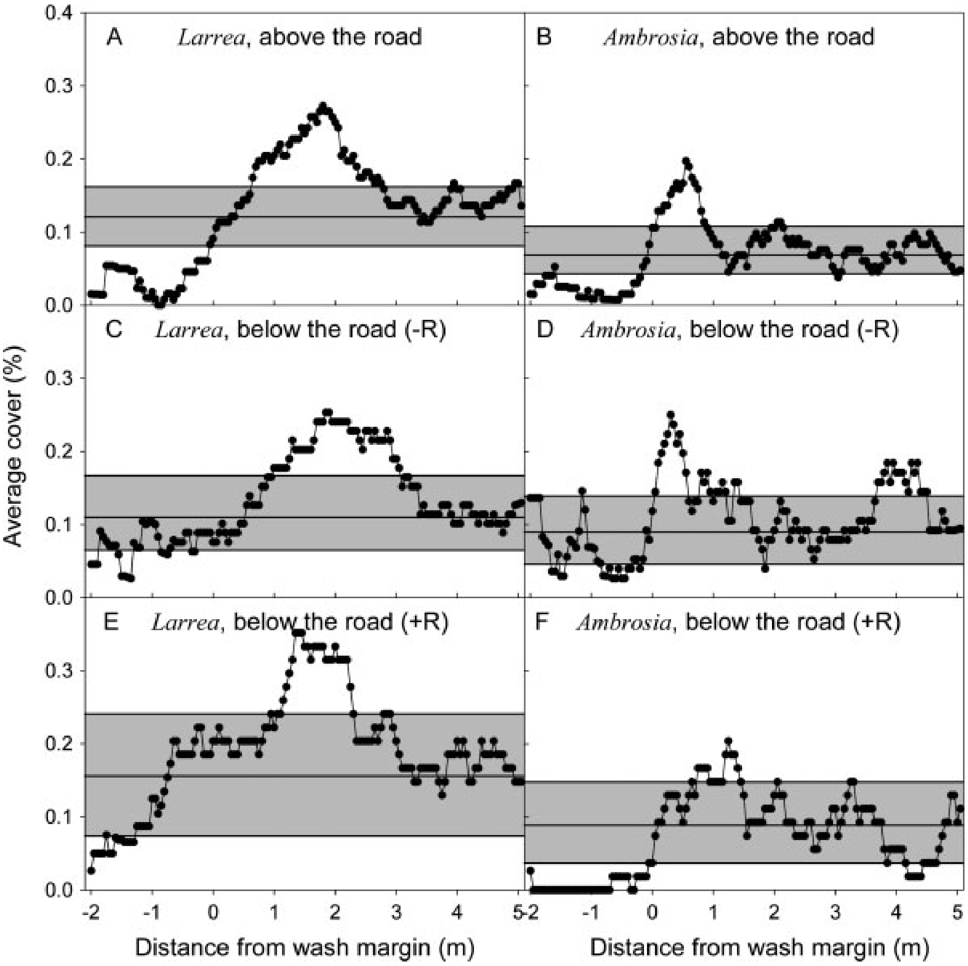

Figure 3. Average *Larrea* and *Ambrosia* cover (in %) drawn in 5 cm increments as a function of distance from the wash margin. (A), (B): for the transect above the railroad ($n = 148$). (C), (D): for the runon-deprived sections of transect below the read ($n = 108$), (E), (F): for the runon-supplemented sections of the transect below the road ($n = 54$). The wash margin is located at 0 on the x-axis and distances pointing away from the wash are positive, distances pointing into the wash are negative. Distances are measured along the transect line and do not represent the shortest distance between a transect element and the nearest wash. The shaded band indicates the 90-percentile bootstrap confidence interval and the midline indicates the average density across the entire transect.

In this zone only, *Ambrosia* peak cover flanked both sides of the *Larrea* cover peak.

Inside the washes (plotted in negative distances), shrub cover was below the 90-percentile confidence limits in the transect above the railroad and the +R areas below the railroad, indicating significantly reduced shrub cover inside active washes. By contrast, inside the −R washes, shrub cover was not different from average.

To examine whether some of the variation in the location of peak cover was as a result of variation in wash size (e.g. washes were much wider in the +R portions than in the other two transects), we pooled all transect segments and redistributed them in three wash diameter bins. Observed peak densities clearly increased with wash diameter in both species, but peak location with respect to the wash margin did not appear to be influenced by wash diameter (Figure 4). *Larrea* cover peaked consistently between 1·5 and 2·5 m and *Ambrosia* cover between 0·35 and 0·85 m.

We also analysed average shrub densities as a function of distance from the wash margin. Because densities were much more variable than cover, we show the 10-element (50 cm) running average in Figure 5. Consistent with the cover data, we found significantly elevated shrub densities near washes. *Larrea* densities peaked closest to the wash margin (at 1 m) in the +R zone and the furthest away (at 2·6 m) in the −R zone of the lower transect. Peak densities for *Ambrosia* were more closely spaced between 0·35 and 0·85 m from the wash margin.

The observed increases in shrub cover near the wash could be caused by increased shrub density alone, but aerial photographs suggest that individual canopies may have also been larger near washes. We found the diameters (measured along the transect line) of *Larrea* canopies to be significantly above the 90-percentile confidence in the distance class 1·2–1·6 m (measured from the canopy midpoint) above the railroad and in the −R areas, but not different in the +R areas (Figure 6A). Canopies at this distance were on average 2 m wide, so their edges would be located 20–60 cm from the wash, consistent with the aerial image (Figure 1). Canopies in the same distance class were of similar size in the +R zone, but they were not significantly above average, because canopies were overall larger in this zone (Table III). We detected

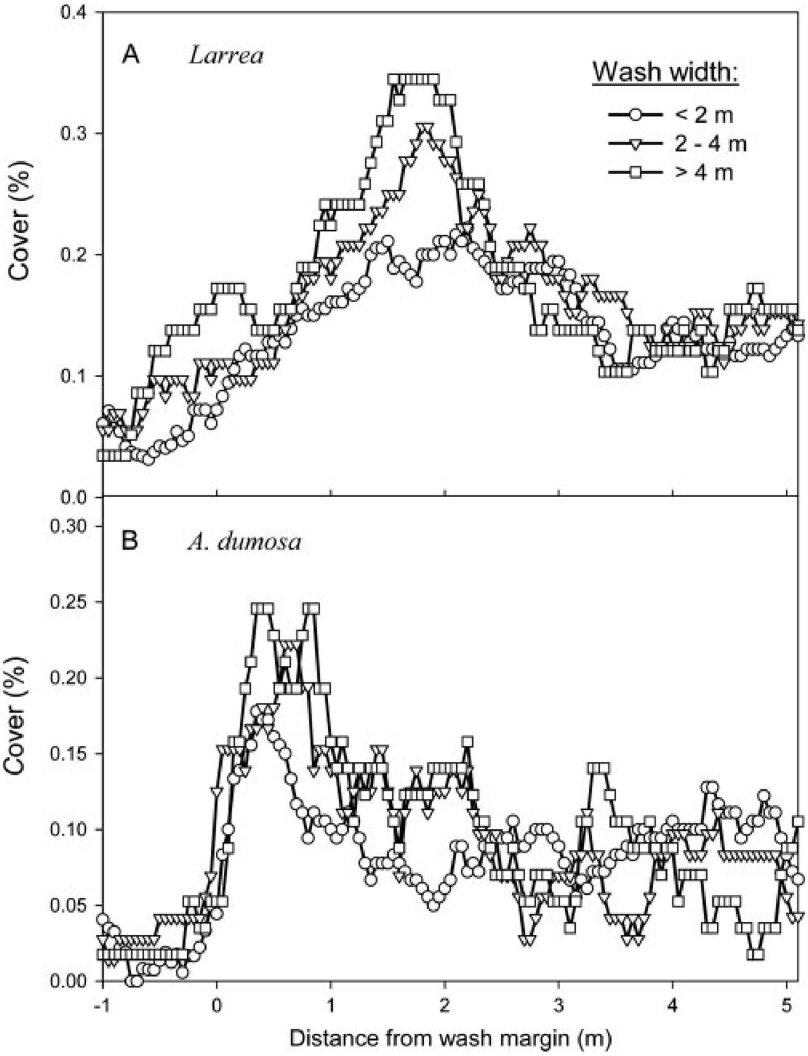

Figure 4. *Larrea* (A) and *Ambrosia* (B) cover (in %) as a function of distance from the wash margin, pooled across both transects and binned by the size class of the wash, where wash size was assessed as the distance along the transect line. There were 180 washes <2 m, 72 washes between 2 and 4 m and 58 washes >4 m in diameter.

another significantly larger than average canopy width in the 2·4–2·8 m distance class, although this average was based on only four individuals, so this peak may have been spurious. *Larrea* individuals closest to the wash tended to be below the 90-percentile confidence interval. Significant distance-size relationships were not detected for *Ambrosia* canopies (Figure 6B).

### *The question of causation*

We suggested three explanatory hypotheses (resource subsidy, improved water infiltration and storage and reduced competition) to explain the observed differences in shrub cover and density near washes. Although these hypotheses are not mutually exclusive, it may be possible to exclude some as dominant factors based on our data. We performed a final analysis to examine if the magnitude of the positive effect of washes on shrub cover was more strongly associated with runon condition, wash size or competitor density. For example, if the positive effect of washes on shrub cover was primarily because of resource subsidies from upslope areas, average near-wash cover should have been greatest in +R areas, intermediate above the railroad and much reduced in −R areas. If, on the other hand, improved infiltration and water storage was primarily responsible for increasing shrub cover at a distance, then runon condition should have had no significant effect, and instead, the wash effect should have increased with wash diameter. In trying to distinguish between these two explanations, we must consider that the +R zone had wider washes, so the effects of runon condition on shrub cover should be compared across washes of similar sizes. In the following analysis, peak shrub cover was taken to be the average cover from 1·75 to 2·00 m for *Larrea* and from 0·4 to 0·6 m for *Ambrosia*.

The peak cover of *Larrea* near small washes in the +R areas fell above the 90-percentile confidence interval of the pooled sample, and below it near large washes the −R zone (Figure 7A). Thus, small, enhanced-flow washes had a larger than expected effect on *Larrea* cover and large, diminished-flow washes had a smaller than expected effect. For *Ambrosia* in the +R areas (Figure 7B), both small and medium washes had a larger than expected effect on cover, whereas in the transect

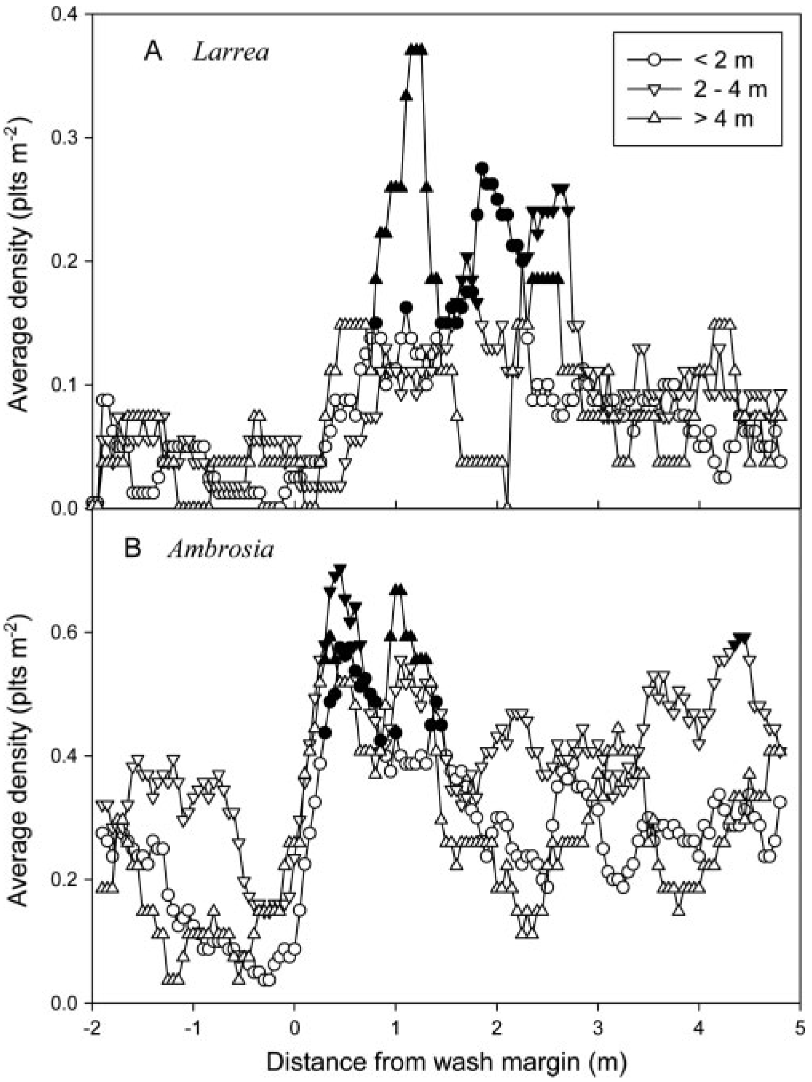

Figure 5. Average *Larrea* (A) and *Ambrosia* (B) density drawn as a function of distance from the wash margin. Densities were first averaged by distance across the individual 5 cm by 1-m survey elements following the procedure explained in Figure 2 and then smoothed by calculating the 10-element running averages. Averages that fell significantly above the 90-percentile bootstrap confidence interval (based on a sample size of $10 \times N$, the number of segments in sample) were drawn as filled symbols. $N = 148$ for above the road, $N = 108$ for −R transects and $N = 54$ for +R transects.

above the railroad, small washes had a smaller than expected effect.

Overall, the effect of wash size on *Larrea* cover was statistically insignificant, since the 90-percentile confidence intervals for the three wash size classes broadly overlapped (Figure 7A). For *Ambrosia* the effect of wash size was more pronounced than for *Larrea*; when pooled across all runon conditions (above the railroad, +R and −R areas), cover was significantly higher near large washes than near small washes (Figure 7B). For *Ambrosia* near large washes, runon condition did not seem to matter.

Finally, to test the reduced competition hypothesis, we tested if there was a negative correlation between *Larrea* density inside the wash and peak *Larrea* and *Ambrosia* cover outside the wash. When washes of all sizes were pooled within each runon class, *Larrea* cover weakly increased with *Larrea* density inside the wash (Figure 7C), contrary to expectation. There was no correlation between *Ambrosia* cover outside the wash and *Larrea* density inside the wash. Grouping by wash size class yielded essentially the same result, either no or a weak positive correlation (data not shown).

## DISCUSSION

Predictably, we found that channel flow consolidation led to a higher percentage of recently deposited sediments classified as Qya1 ('wash') and Qya2 in the +R sections of the lower transect, indicating that new channels developed and old channels widened over the last 100 years, replacing some of the Qya3 and Qya4 surfaces in the process (Table III). The −R areas of the lower transect were less affected, because soil maturation takes many centuries to millennia (Miller *et al*. 2009). Any difference in the geomorphic cover between the −R section of the lower transect and the transect above the railroad is probably because of elevation and other factors influencing surficial geologic processes such as position in the alluvial fan.

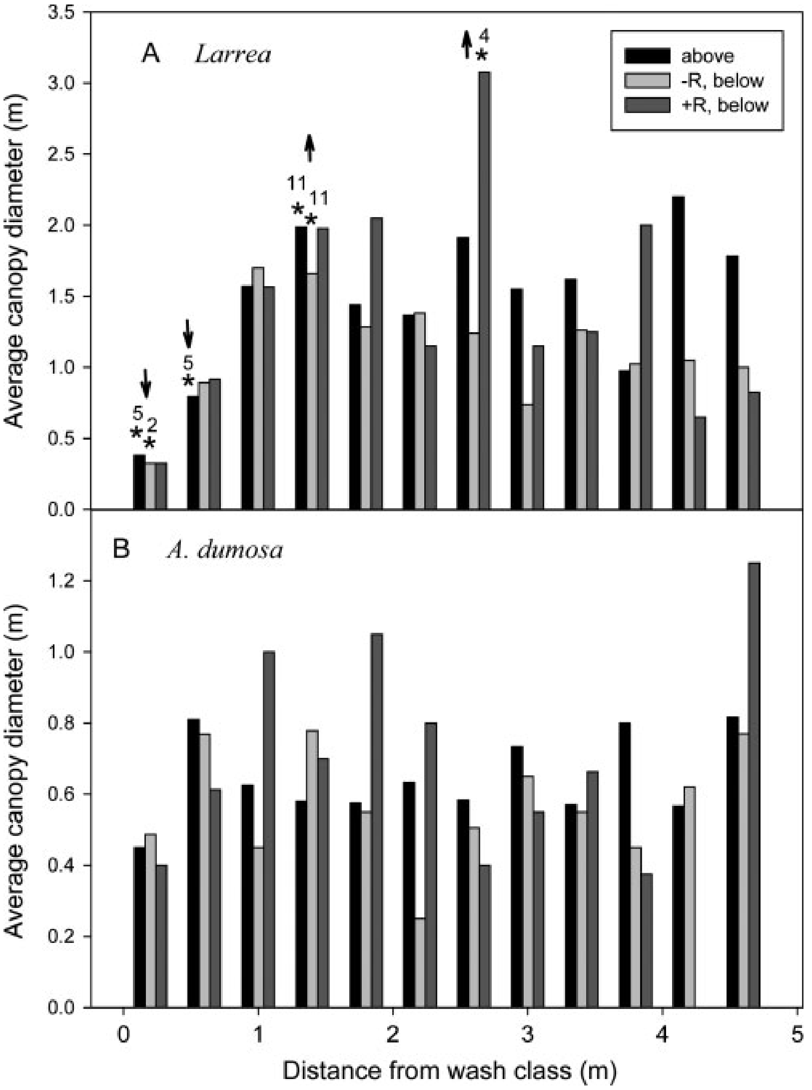

Figure 6. The average canopy diameter (across the transect line) of *Larrea* (A) and *Ambrosia* (B) within distance classes (in 0·4 m increments) as measured along the transect line between the canopy centre and the wash margin. Bars are grouped by transect. Canopy diameters significantly above (arrow pointing up) or below (arrow pointing down) the 90-percentile bootstrap confidence interval are marked by an asterisk with the corresponding sample size in brackets above.

Our results provided clear evidence that washes affect the growth and density of shrubs inside the wash and up to 3 m away from the wash. Although this was no surprise, the study provided a detailed quantification of the spatial relationships between washes and shrubs and some insights into the mechanisms involved.

### *Wash effects on Larrea*

*Larrea* growth and establishment was clearly stimulated by proximity to washes and was depressed inside them (Figure 3). The analysis in Figure 7A suggests that the resource subsidy mechanism is involved, confirming results of an earlier study demonstrating that runon-depletion results in reductions of average *Larrea* cover (Schlesinger and Jones, 1984). The mechanism of improved infiltration and storage also seems to play a role, because *Larrea* cover also peaked near inactive washes in the −R sections (Figure 3C). This effect was unlikely to be the remnant of former vegetation patterns, i.e. because of the survival of large plants that developed where active washes used to be. Even though *Larrea* plants can be extraordinarily long lived, canopy sizes are more dynamic, dying back when the hydrologic regime changes (Hamerlynck and McAuliffe, 2008).

Peak cover of *Larrea* tended to increase with wash width (Figure 4), although this trend may not have been significant (Figure 7A). Larger washes potentially provide greater resource benefits to nearby *Larrea* shrubs than smaller washes, because wider washes have more surface area to facilitate infiltration and storage, and *Larrea* roots are known to grow preferentially into regions where more resource is available (Brisson and Reynolds, 1994). However, the distance between the wash margin and peak *Larrea* cover was not affected by wash width or wash activity (Figures 3 and 4). We measured elevated *Larrea* cover and density (relative to the transect average) consistently between 1 and 3 m from the wash margin.

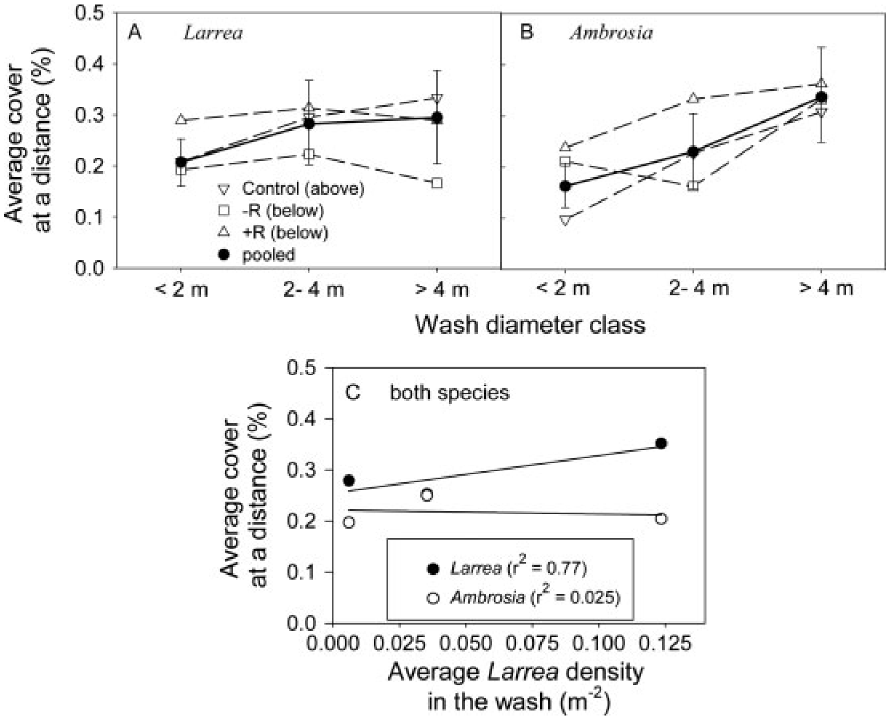

Figure 7. Graphical analysis to test for the effects of runon condition (A), (B), wash size (A), (B) and cover inside the wash (C) on peak plant cover adjacent to washes. For details, see text.

Because of the oblique angle between the transect line and the main direction of the channels (Figure1A), the perpendicular distance was perhaps closer to 0·9–2·6 m. Cover peaked at between 1·4 and 1·9 m (or 1·2–1·6 m perpendicular), and canopies were widest at an average distance of 1·4 m (or 1·2 m perpendicular; Figure 7A). Furthermore, canopies that were closer to the wash, e.g. from 0–0·4 m from the wash, were smaller than average. Thus, the overall pattern of Larrea near washes resembled a conspicuously non-random 'pearl string' lineup with the edges of canopies aligned with the wash margin, consistent with the appearance of aerial images (Figure 1).

What does this pattern suggest about the interactions of washes and *Larrea* shrubs? First, given the extensive lateral root system of *Larrea*, it is no surprise that shrubs at a distance of 1·6 m can access water stored underneath wash sediments. Brisson and Reynolds, (1994) determined an average horizontal extension of major structural roots in *Larrea* between 0·5 and 1 m with a maximum of 2 m. Gile *et al.* (1998), in the Chihuahua Desert, traced some lateral *Larrea* roots more than 4 m out from the central stem of the plant, although most laterals were shorter. Lateral roots are commonly found at a depth of 15–30 cm, which would likely place them below the silty wash sediments, where most water infiltrating through wash sediments would be stored. Given the longevity of some *Larrea* shrubs it is possible that some roots underneath washes even preceded the establishment of the wash. Shrubs at distances of 2 m or more would probably be too distant to reliably intersect with the wash, explaining why shrubs at this distance are of average size (Figure 6A), and why cover and density return to average as well (Figures 3–5).

More difficult to understand is why shrubs closer than 1 m to the wash margin appeared to have less benefit than shrubs at 1·5 m and even average *Larrea* shrubs (Figure 6A). The lower than average cover and density *inside* the wash is commonly explained by channel flow, which periodically uproots or buries new recruits. If this is in fact the limiting factor, *Larrea* shrubs should have begun to invade wash sediments of inactive washes in −R areas. There is some evidence that this is what happened, as *Larrea* cover inside −R washes was higher than in control washes and not significantly different from average *Larrea* cover (Figure 3C). Cover inside +R washes also averaged up to 1·2 m in the wash (Figure3E), but this probably had other causes, including overall larger shrubs overhanging wash margins.

The effective gap in *Larrea* density inside active washes would tend to reduce cover near the wash margin, explaining in part why cover is not maximized immediately adjacent to the wash but slowly built up to peak cover at about 2 m (Figure 3). However, this effect does not explain why shrubs with central stems close to the wash were smaller than average (Figure 6A). One possibility is that lateral root formation is suppressed by immediate proximity to a wash, giving an individual less soil space to explore. Alternatively, plants near washes could have shorter live spans, being perhaps intolerant to occasional bank overflow, flooding and erosive events. *Larrea* roots are known to be intolerant of excessive soil moisture (Lunt *et al.*, 1973). Yet another explanation turns the causation around: younger, smaller *Larrea* are less likely to have formed mounds (e.g. Lee, 1986) to divert the pathway of washes during their formation. Thus, there is a greater probability of finding washes next to small and presumably younger *Larrea* shrubs than next to larger, older shrubs. The latter explanation seems most likely where relatively small washes (e.g. <1 m width) are concerned.

### *Wash effects on Ambrosia*

At a population level, *Ambrosia* and *Larrea* responded in opposite ways to runon redistribution. Whereas *Ambrosia* density was maximized in −R areas and minimized in control areas, *Larrea* densities were maximized in +R areas and minimized in −R areas (Table III). This result is in contrast to Schlesinger and Jones' (1984) study which found both *Ambrosia* and *Larrea* cover reduced in runon-depleted areas, although by a lesser amount for *Ambrosia* (9%) than for *Larrea* (17%). A likely explanation for this discrepancy is that runon contributed a greater amount to the water budget in earlier study. In general, negative associations between *Ambrosia* and *Larrea* are quite commonly observed (Parker and Bendix, 1996), consistent with the understanding of *Larrea* as a superior competitor to *Ambrosia* (Mahall and Callaway, 1992, Schenk *et al.*, 2003). Improvements in resource supply likely strengthen the competitive effect of *Larrea* on *Ambrosia*, while reduced resource supply weakens this interaction.

Interactions between *Larrea* and *Ambrosia* are probably best understood by considering both long- and short-term processes. Long-term resource depletion results in density decreases for *Larrea* by changing the balance between growth and mortality (Schlesinger and Jones, 1984). In the short-term, lower *Larrea* densities slow soil water consumption after rain and leave relatively more water for *Ambrosia* to exploit (Fonteyn and Mahall 1981, Schlesinger *et al.* 1989). Unlike *Larrea, Ambrosia* has an opportunistic pattern of fine root growth, e.g. fine root production is stimulated in wet soils (Wilcox *et al.*, 2004). Although there were fewer *Ambrosia* shrubs in +R areas than in the −R areas, shrubs in the +R areas were larger on average (Table III), demonstrating that *Ambrosia* does benefit from enhanced resource levels, given an opportunity to access them.

Wash effects on *Ambrosia* were qualitatively and quantitatively very different from wash effects on *Larrea*. Although both *Ambrosia* and *Larrea* cover peaked at a distance away from wash margins in all three transect types (Figure 3), the distance between the wash margin and *Ambrosia* peak cover was generally shorter than the distance for *Larrea* (between 0·59 and 1·26 m along the transect line, thus closer to 0·5–1·0 m in perpendicular distance vs 1·4–1·9 m and 1·2–1·6 m, respectively for *Larrea*). *Ambrosia* density also peaked closer to the wash, between 0·36 and 0·45 m away from the wash (vs 1·2–2·6 m for *Larrea*). Wash width had a less pronounced effect on *Ambrosia* peak density (Figure 4B) and there was no significant relationship between distance from wash and *Ambrosia* canopy size (Figure 6B). That said, there were also similarities: shrub cover and density of both species were significantly below average in control and +R washes, but not so in −R washes, suggesting that both species had establish on the sediments of (inactive) washes since the flow disruption.

Many of these differences can be explained by the smaller size of *Ambrosia* canopies and the more restricted lateral extent of their root systems. *Ambrosia* roots normally do not protrude far beyond the canopy edge (McAuliffe, 1995) at a depth of 20–30 cm (Schwinning and Hooten, 2009). In the present study, average canopy diameters for *Ambrosia* were between 0·5 and 0·6 m, thus, individuals probably needed to be closer to the wash for roots to reach below the wash sediments. Furthermore, washes of >4 m width appeared no more useful than washes of 2–4 m width (Figure 4B), suggesting that restrictions of lateral root length remained in effect even in a resource enriched soil environment. Unlike for *Larrea*, there was no significant tendency for *Ambrosia* shrubs to be smaller when growing right next to a wash. *Ambrosia* has a far shorter life span than *Larrea*, and the disturbance regime near washes may not be of a magnitude to impact shrub sizes. In terms of *Ambrosia*'s ability to redirect overland flow, *Ambrosia* shrubs also form mounds (e.g. Schenk and Mahall, 2002), but as a result of the shorter life span and smaller canopy size, *Ambrosia* mounds are not as developed as those of large *Larrea* plants, which, according to one study, rise 15 cm above the surrounding surface (Lee, 1986). Thus the mounds associated with even large *Ambrosia* plants and small *Larrea* plants maybe equally ineffective at influencing the pathway washes take during formation.

In −R washes, *Ambrosia* also showed a clearly identifiable second peak centred at a (transect) distance of 4 m, both in cover (Figure 4B) and density (Figure 7B). This cannot be a direct wash effect, given the distance from the wash and the rooting habit of *Ambrosia.* One possibility is that this pattern is the result of a nurse plant effect, with *Larrea* facilitating the survival and growth of *Ambrosia* at its canopy edge. Walker *et al.* (2001) found no evidence that transplanted *Ambrosia* seedlings gained a net benefit from growing under shrubs; however, neither did this study, as the facilitation was most likely associated with being on the edge of a *Larrea* canopy rather than under it. Perhaps growing on the edge of the taller canopy allows *Ambrosia* to benefit from the 'fertile island' effect (Bolling and Walker, 2002), while avoiding limiting light levels. The fact that we did not observe a second *Ambrosia* peak in transects above the railroad or in +R areas may indicate that net-facilitation between desert shrubs can only be observed at certain resource levels. Recall that the −R zone of the lower transect was most conducive for *Ambrosia* and least so for *Larrea* populations (Table III). Thus, *Ambrosia* had a subtle advantage in the −R zone, that may have allowed a weak facilitative effect to surface.

### *Implications for the future of Larrea–Ambrosia shrublands*

The Mojave Desert, as all other extensively used or protected ecosystems in the western United States, is undergoing rapid changes resulting from global warming and increasing demands for access, including for the development of alternative energy projects (wind, solar) and recreation (e.g. off-road vehicles). Current climate models predict that the Mojave Desert is going to be drier, perhaps with an increased frequency of intense, runoff-producing storm events (Hereford *et al*., 2006). According to the data presented here, the overall drier conditions could favour the frequency of *Ambrosia* and other drought-deciduous species, but increased occurrence of channel flow could enhance the dominance of *Larrea* near streams. Thus, climate change could impact overall species abundances and their spatial distributions. Such changes could ultimately influence long-term geologic surficial processes, as these are increasingly understood as the result of interactions between plants and sediment-transport dynamics (McAuliffe *et al*. 2007, Miller *et al*. 2009), where plant communities affect spatial patterns of sediment erosion and deposition and changes in channel flow will in turn feed back into plant communities.

The demand for increased access will necessitate more transportation infrastructure, including roads, railroads, transmission lines and pipelines. These are often built along the contours of hillslopes above the base of the alluvial fans that are a widespread feature of the Mojave Desert. As this study demonstrated, these linear features disrupt the distributary channels in desert landscapes far beyond the actual construction sites (Figure 1), impacting downhill stream channel morphology and distribution, as well as the distribution of plants and the animals they support. Ironically, actions taken to mitigate the effects of climate change, such as the construction of alternative energy plants, have their own ecological costs, which in some may cases exacerbate the direct effects of climate change, for example, by creating runon-deprived landscape elements solely dependent on declining local precipitation inputs.

## CONCLUSION

The spatial analysis of shrub cover in relation to drainages provided a new perspective on the structure and function of *Larrea–Ambrosia* shrublands of the Mojave Desert. The analysis clearly showed that shrub growth and establishment is not only dependent on surface conditions at the original germination site, but also influenced by edaphic distance effects. Furthermore, distance effects were distinct for *Larrea* and *Ambrosia*, most likely caused by the species' distinct above- and below-ground morphologies, as well as differences in rooting strategies and life expectancies. For example, consistent with the species' more compact root habit, *Ambrosia* cover and density peaked closer to washes than *Larrea* cover and density. Postulated relationships between life history characteristics and spatial patterns in relation to washes need to be corroborated by direct observation, including by root excavations below washes and resource addition experiments.

Areas of the piedmont that were cut off from runon as a result of the construction of a railroad line had higher densities and cover of *Ambrosia* than areas with undisturbed channel flow or areas where runon was enhanced by channel consolidation. In contrast, *Larrea* cover and density was highest in areas with enhanced runon, in line with the common understanding of *Larrea* as a superior competitor for soil resources.

Comparison of wash effects on shrubs in runon depleted, control, and runon-enhanced areas suggest at least two mechanisms through which washes enhance the growth of nearby shrubs: First, infiltration occurring during channel flow events provides water subsidies from upland areas. Second, enhanced infiltration into wash sediment allows more locally generated rainwater to be stored below wash sediments. It is very likely that the reduced shrub density inside active washes also leads to some degree of compensatory growth beyond the wash margin.

The ecohydrology of deserts is increasingly understood as the result of intricate interactions between its biota (biological crust, plants and animals), climate, and surficial geologic processes, playing out over time scales of decades to millennia. Therefore, the enduring health and resilience of these ecosystems depend on the protection, not just of their biota, but also of their surfaces and drainage system integrity.

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