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Plant-soil biodiversity relationships and nutrient retention in agricultural riparian zones of the Sacramento Valley, California

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Abstract Forested riparian buffers in California historically supported high levels of biodiversity, but human activities have degraded these ecosystems over much of their former range. This study examined plant communities, belowground biodiversity and indicators of multiple ecosystem functions of riparian areas across an agricultural landscape in the Sacramento Valley of California, USA. Plant, nematode and soil microbial communities and soil physical and chemical properties were studied along 50-m transects at 20 sites that represented the different land use, soil and vegetation types in the landscape. Riparian zones supported greater plant diversity and nearly twice as much total carbon (C) per hectare compared to adjacent land managed for agricultural uses, but had generally lower soil microbial and nematode diversity and abundance. When woody plant communities were present in the riparian zone, plant diversity and species richness were higher, and soil nitrate and plant-available phosphorus levels were lower. Belowground diversity and community structure, however, appeared to depend more on plant productivity (as inferred by vegetation cover) than plant diversity or species richness. Greater plant species richness, nematode food web structure, total microbial biomass, woody C storage and lower soil nitrate and phosphorus loading were correlated with higher visual riparian health assessment scores, offering the possibility of managing these riparian habitats to provide multiple ecosystem functions.

Keywords Aboveground-belowground relationships · Carbon storage · Ecosystem function · Nematodes · PLFA

Introduction

Riparian corridors are well recognized as havens of biodiversity, but over 80% of the original riparian area has been lost from North America and Europe over the past 200 years (Naiman et al. 1993). Human activities, especially conversion of land to agricultural uses, have resulted in a loss of habitat and related biodiversity and ecosystem services (Balvanera et al. 2006; Millennium Ecosystem Assessment 2005). "Working landscapes"

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that include agriculture as well as riparian and other natural ecosystems may protect biodiversity and ecosystem functions while maintaining agricultural productivity (Jordan et al. 2007).

In a heterogeneous agricultural landscape, management of riparian buffer zones changes soil properties, plant and soil biodiversity, nutrient cycling, and erosion potential (Lovell and Sullivan 2006; Neher et al. 2005). Vegetated riparian buffers filter agricultural nutrients and pollutants, reduce erosion, improve water quality and provide reservoirs for biodiversity (Lovell and Sullivan 2006; Peterjohn and Correll 1984; Richardson et al. 2007). Multi-species riparian buffers that include herbaceous as well as woody species may result in higher total productivity, soil carbon (C) sequestration, and nitrogen (N) immobilization than monoculture plantings (Hill 1996; Marquez et al. 1999; Rowe et al. 2005; Tufekcioglu et al. 1998).

Soil microbial and nematode communities are important for ecosystem functions such as nutrient cycling and the stabilization of soil C from plant and microbial residues (Anderson 2000; Six et al. 2006), and soil biodiversity is thought to be essential for the maintenance of sustainable agricultural systems (Brussaard et al. 2007). Plant diversity and soil ecology are linked; greater diversity of plant species is often associated with greater plant productivity and soil microbial activity in field studies (Liu et al. 2008; Wardle et al. 2006; Zak et al. 2003). However, such studies have often been conducted at the field plot scale (Bardgett 2005; Ferris and Matute 2003; Porazinska et al. 2003), and thus have yielded little information on how these ecological phenomena extrapolate to the larger landscape scale where the collective effects of management decisions become evident (Swift et al. 2004; Tscharntke et al. 2005).

This study examined the relationship between above- and belowground biodiversity and ecosystem function of riparian areas in a heterogeneous agricultural landscape with different land use and soil types, located in the Sacramento Valley of California, USA. Land use varies in the degree of agricultural intensification, from non-irrigated rangelands to intensive, irrigated croplands, and management of canal and stream edges is largely under the control of individual landowners. Restoration of farm edges and riparian zones with native perennial plants has been a priority of some local stakeholders (Brodt et al. 2009; Robins et al. 2001).

Species-rich riparian forests once covered several million hectares (ha) in California's Sacramento Valley before clearing and draining by European settlers (Barbour et al. 1993; Roberts et al. 1980). Such forests are now restricted to narrow bands, typically 2–15 m wide, along streams and rivers, or have been eliminated. The following hypotheses were developed to compare ecosystem services of riparian areas with associated uplands over a gradient of land use intensity and physiographic conditions: (i) riparian areas support greater levels of plant and soil biodiversity, greater C stock per unit area and lower soil nutrient pools than adjacent agricultural land (crop fields or grazed grasslands); (ii) land use type affects these differences in biodiversity and nutrient pools; (iii) the presence of woody vegetation in the riparian zone increases the diversity and structure of above- and belowground communities and soil properties; and (iv) riparian zone health rating serves as an indicator of above- and belowground diversity and ecosystem functions.

Materials and methods

Site description

The study area is a 150-km^2 region of western Yolo County in the Sacramento Valley (northern Central Valley) of California, USA (38°N, 122°W) that ranges from 27 to 105 m in elevation. The area consists of upland annual grasslands and oak savanna in the Coast Ranges to the west (used for cattle grazing and dry farm grain rotations) and flat, lowland alluvial fans and plains to the east (used for intensive irrigated cropland, including walnut orchards and rotations of both conventional and organic corn, processing tomatoes, wheat, oats and barley). Average monthly temperatures range from about 6–29°C, and annual precipitation is 47 cm for this dry, Mediterranean climate, with rainfall mostly between November and April (WRCC 2009). Soils include the following great groups: Haploxeralfs, Haploxererts, Palexeralfs, Haploxerepts, and Xerorthents (Soil Survey Staff 2009). There are 212.9 km of waterways in the study area, which include both natural streams and constructed irrigation canals.

Twenty sites were sampled across the landscape, and were chosen to represent the range of soil and vegetation types found in the study area (see Culman et al. in press, *Landscape Ecol*, for details on site selection). Briefly, 2,049 points across the landscape were randomly selected within 50 m of a waterway. Then 14 spatial datasets on soil characteristics, land use, vegetation and topography were compiled in a Geographic Information System (GIS). Multivariate cluster analysis was used to classify the points into five clusters, from which 20 sites were chosen to represent the variation within each cluster, thus providing a systematic sampling regime for the entire landscape.

At each site, a 50-m transect was established perpendicular to the waterway, running from the channel edge into the adjacent field. Sampling plots were established at three positions along this transect at a distance of approximately 0.5, 9 and 50 m from the bankfull channel edge (Fig. 1). These positions are referred to as A (*a*gricultural field, which is either cropland or grazed grassland), B (floodplain *b*ench above the waterway), and C (*c*hannel edge). Position B was located on the edge of the floodplain bench, or in the case of irrigation canals, where permanent vegetation could potentially be established, and ranged from 4 to 24 m from the channel edge.

Characterization of vegetation communities, riparian health and woody carbon storage

Vegetation and riparian characterization were conducted at each site from May to June of 2007. For community-level vegetation assessment, the riparian greenline method was used on 40-m transects to classify communities into the appropriate vegetation series (Sawyer and Keeler-Wolf 1995; Winward 2000). At the species level, vegetation surveys used Braun-Blanquet style relevé plots of 15–100 m^2 for each of the three positions at each site (CNPS Vegetation Committee 2000); plants were identified according to Hickman (1993). Plants were classified into five main functional groups: (i) woody perennials, (ii) herbaceous natives, (iii) legumes, (iv) invasive/noxious weeds (USDA-NRCS 2009), and (v) other non-natives (excluding invasive/noxious weeds and legumes, but including crop species).

A quantitative visual assessment of riparian health was conducted along a 40-m reach at each site with a modification of the method for low gradient rangeland streams (Ward et al. 2003). Channel condition, access to the floodplain, bank stability, extent of natural riparian zone vegetation, macroinvertebrate habitat, pool variability and pool substrate were scored on a scale from 1 to 12. The riparian health score was calculated as a percentage for each of the 20 sites.

To estimate woody C sequestration, the height, canopy dimensions and diameter at breast height (DBH) of all woody species 1.5 m or taller were recorded within the 40-m reach of the riparian zone (this zone varied in width from 14 to 40 m, depending on surrounding land use and topography) following the Forest Project Protocol (California Climate Action Registry 2007). Aboveground wood biomass of each tree species was calculated using allometric equations based on DBH (Jenkins et al. 2003). Belowground tree biomass at each site was estimated using an allometric equation based on the calculated aboveground biomass density (Cairns et al. 1997). Shrub above- and belowground biomass were calculated based on equations from Smukler et al. (*provisionally accepted, Agric Ecosyst Env*), which related the ellipsoid volume of each shrub canopy to biomass. Total woody biomass per ha was calculated as the sum of above- and belowground tree and shrub biomass divided by the area surveyed. Total woody C storage (Mg ha^{-1}) was calculated assuming a 50% C content for all species (California Climate Action Registry 2007).

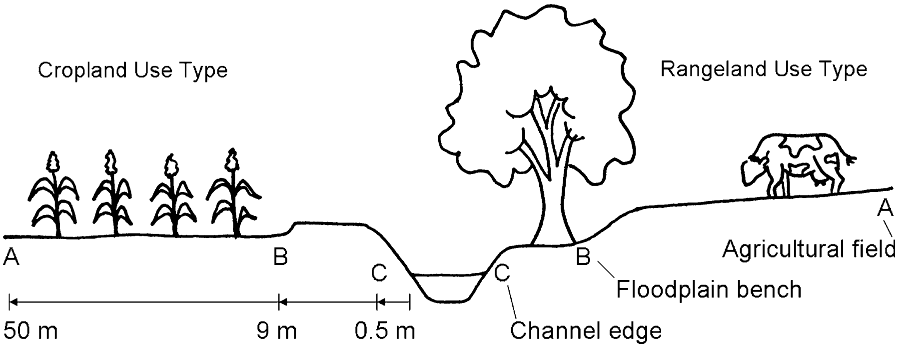

Fig. 1 Sampling positions relative to the waterway for the two land use types within the study area in the Sacramento Valley, California (not drawn to scale)

Soil sampling and profile descriptions

Soil profile characterization and sampling took place from late March to mid-April of 2007, when soil moisture was most similar across the landscape, and when soil temperatures were warm enough to facilitate soil microbial and nematode activity. Soil profiles (1 m × 1 m × 1 m) were dug at positions A, B and C at each site, but in three cases no soil pit could be dug at position B because the canal was incised within an agricultural field.

Profile descriptions were performed using standard soil survey techniques (Schoeneberger et al. 2002). Four semi-quantitative morphologic indicators of soil quality were measured: (1) A-horizon darkening (indicating the accumulation of soil organic matter (SOM)); (2) A-horizon thickness (indicating a lack of soil disturbance); (3) depth to redoximorphic features (indicating presence of water table during some portion of the year); and (4) depth to a potentially root-limiting horizon, defined by root-restrictive bulk density in any horizon (e.g., greater than 1.7 g m^{-3} for loams or greater than 1.5 g m^{-3} for silty clay loams; USDA 2001) and/or an extremely firm consistence or textural classes with greater than 60% coarse fragments (>2 mm in diam.). A-horizon darkening (in any A-, Ap-, AB- or BA-horizons) was considered significant when there was a decrease of at least one unit in the Munsell color value from the surface to the next underlying horizon.

Soil was sampled from each pit, and from two 7.5-cm diameter soil cores taken 2 m from the pit on either side, which were analyzed separately and treated as replicates. Depths were 0–15, 15–45, 45–75, and 75–100 cm. Each soil sample was homogenized, bagged, transported on ice, and stored at 4°C for less than 8 days before analysis for soil moisture, inorganic N, nematodes and PLFA (surface samples only), and air drying for other soil properties.

Characterization of soil biotic communities, physical properties and nutrients

Nematodes were extracted by a modified sieving and Baermann funnel method (Barker 1985; Ferris and Matute 2003). Nematodes were identified to genus or family level, assigned to trophic groups (Yeates et al. 1993) and functional guilds (Bongers and Bongers 1998), and used to calculate structure index (an indicator of soil food web length and connectance; Ferris et al. 2001).

For microbial community composition and biomass, phospholipid fatty acids (PLFA) were extracted and analyzed (Bossio and Scow 1998), and identified on a Hewlett Packard 6890 gas chromatograph (J&W Scientific, Folsom, CA). PLFA biomarkers were grouped into bacterial (actinomycetes, $Gram^{+}$ and $Gram^{-}$), fungal and unspecific origins following Potthoff et al. (2006).

Inorganic N was extracted with 2 M KCl, and analyzed colorimetrically for ammonium (NH_4^{+}) and nitrate (NO_3^{-}) on a Genesys 10VIS spectrophotometer (Thermo Fisher Scientific, Waltham, MA; Forster 1995; Miranda et al. 2001). Air-dried samples were crushed and sieved through a 2 mm screen. Particle size analysis was performed on a Coulter LS-230 Particle Size Analyzer (Beckman Coulter Inc., Miami, FL; Eshel et al. 2004). The Agriculture and Natural Resources Analytical Laboratory at the University of California at Davis analyzed soil for boron (B), total N and C, pH, Olsen phosphorus (P) and exchangeable cations as described at http://groups.ucanr.org/danranlab/Soil_Analysis_2/.

Two bulk density samples were collected from each soil pit at two depths (1–7 and 27–33 cm) using a brass ring (345 cm^3) to remove intact soil cores (Blake and Hartge 1986). Bulk density values of the bottom two soil layers were approximated based on the SSURGO data for the mapped soil type (Soil Survey Staff 2009). These values were used to calculate total soil C for the full 1-m profile using the percent soil C from each of the four sampled depth intervals.

Statistical analyses

Effects of land use and position from the channel edge on soil properties and plant, nematode and microbial diversity, richness and functional group abundance were analyzed using a mixed model ANOVA (based on repeated measures) with land use type as the between-subject factor (two levels: rangeland and cropland), and position from the channel edge as the within-subject factor (three levels: A, B and C). This and all other tests were considered significant at $P < 0.05$. One-way ANOVAs examined the simple effects of position for each land use type when there was a significant interaction, as well as for sites where woody-dominated communities (defined as narrowleaf willow series, blue oak series, Fremont cottonwood series, and valley oak series) were either absent or present in the riparian area. Mixed model three-way ANOVAs were used to analyze soil properties by depth, position from waterway and land use type. Data were normalized using log ($x + 1$) or square root transformations when necessary to meet ANOVA assumptions. All ANOVAs were performed in SAS v9.1 (SAS Institute, Cary, NC) using the Tukey HSD test to determine differences between least square means.

Pearson's product moment correlations between riparian health rating, diversity measures, soil properties and soil profile indicators were run in R 2.7.2 (R Development Core Team 2008). Shannon's diversity index (H′) and species richness were calculated with the *diversity* function in the *vegan* package in R. Pairwise comparisons of each group of biota were performed with Mantel tests to test the null hypotheses that no relationship exists between the two datasets (Mantel 1967). The test was performed in R with the *mantel* function in the *vegan* package using Bray-Curtis distance measures.

An indicator species analysis identified plant species that were indicators of good versus poor riparian health, based on species abundance (cover) and frequency (Dufrêne and Legendre 1997). A perfect score (1.0) indicates a species is both faithful (always present) and exclusive to a given category (McCune and Grace 2002). Indicator values were calculated using the *duleg* function in the *labdsv* package in R, and significance was tested with 1,000 randomizations in a Monte Carlo test. For this purpose, the riparian health ratings were divided into four equally weighted health classes: poor (19.6–34.5%), fair (34.6–49.4%), moderate (49.5–64.3%), and good (64.4–79.2%).

Results

Diversity and structure of plant, nematode and microbial communities

A total of 114 plant species were identified (Appendix Table 6), and classified into five main functional groups: California state-listed invasive/noxious weeds (33 species), other herbaceous non-natives (excluding legumes and invasive/noxious weeds; 31 species), herbaceous natives (29 species), woody perennials (15 species), and non-native legumes (6 species). Of the total, 62 were annual species while 52 were perennials.

Plant diversity (H') was greater in the riparian positions, B and C, than in the agricultural position, A (Table 1). Rangeland H' was greater than in the cropland land use type, and had an average of almost twice as many species. Positional differences were more pronounced in the rangeland than the cropland sites, with more species near the waterway in both cases.

Both woody perennial cover and native herbaceous species cover were greater in the riparian positions (B and C) than in position A in both land use types. Mean percent cover of total vegetation and legumes were both greater in rangeland than cropland. In the croplands, invasive/noxious weed cover was greater in riparian positions (B and C) than position A, while rangeland sites had greatest invasive/noxious weed cover at position B. The arable croplands had much greater cover of non-native species in the agricultural fields than in the riparian zone, but non-native species cover did not vary with position in the rangelands.

Nematode H′ and richness did not vary by position from the waterway or land use type (Table 1). There were 43 different nematode taxa (either genera or families), of which 14 were plant feeders or associates, 13 were bacterivores, six were fungivores, five were omnivores and four were predators. There were 10 common nematode taxa (found in over half of the samples), and 15 rare nematode taxa (found in less than 5% of the samples) (data not shown). Total nematode abundance and abundance of fungivores and plant feeders were greater at position A than at position C on the channel edge (Table 1). Both omnivores and predators were rare, but they were more abundant in agricultural fields and floodplain benches (positions A and B), than at the waterway edge (position C). Bacterivores were the only trophic group that varied between land use types, and were two times more abundant in cropland than rangeland sites.

Nematode structure index, a measure of soil food web length and connectance, ranged from 0 to 93.9 (on a scale of 0–100). In rangeland sites, it was greater in the field and riparian bench positions (56.5 ± 5.0 and 48.4 ± 3.6 for positions A and B, respectively) than at position C near the channel edge (30.1 ± 5.4, $P < 0.001$). However, structure index did not differ by position in the cropland, and averaged 34.8 ± 3.3 for all sites.

Diversity of microbial PLFA biomarkers was greater in the agricultural position (A) than at position C at the edge of the channel (Table 1). Both the diversity and richness of the microbial biomarkers were greater for rangelands than croplands. There were 72 different PLFA biomarkers identified across the landscape: bacterial (18 biomarkers, composed of

Table 1 Distribution of plant, nematode and microbial communities according to position from waterway (A = agricultural field, B = floodplain bench, C = channel edge) and two land use types in the Sacramento Valley, California

	Position from waterway				Land use type			P*LU
	A	B	C	Sig[a]	Cropland	Rangeland	Sig	Sig
Plants	(n = 20)	(n = 20)	(n = 20)		(n = 36)	(n = 24)		
Shannon's diversity index	0.8 ± 0.1 b	1.5 ± 0.1 a	1.5 ± 0.1 a	***	1.1 ± 0.1	1.5 ± 0.1	**	NS
Species richness					7.5 ± 0.8	14.2 ± 1.3	***	*
Cropland	4.5 ± 0.9 b	8.4 ± 1.2 ab	9.6 ± 1.4 a	**				
Rangeland	8.8 ± 0.8 b	13.8 ± 1.0 b	20.0 ± 2.5 a	***				
Total cover (%)[b]	46.5 ± 7.5	61.3 ± 7.8	62.2 ± 6.9	NS	45.9 ± 5.8	72.7 ± 4.7	*	NS
Woody perennials	1.9 ± 1.9 b	16.4 ± 6.0 a	19.1 ± 7.9 a	**	9.4 ± 3.5	17.0 ± 6.8	NS	NS
Herbaceous natives	0.6 ± 1.9 b	2.1 ± 0.6 a	5.1 ± 1.5 a	***	2.9 ± 0.8	2.0 ± 0.7	NS	NS
Legumes	1.4 ± 0.8	2.9 ± 0.9	5.0 ± 1.8	NS	0.6 ± 0.3	6.9 ± 1.5	***	NS
Invasive/noxious weeds					23.2 ± 4.5	56.0 ± 5.2	***	*
Cropland	5.8 ± 3.8 b	29.7 ± 8.9 a	34.0 ± 7.9 a	*				
Rangeland	59.0 ± 7.6 ab	69.2 ± 9.0 a	39.8 ± 8.2 b	*				
Other non-natives[c]					10.8 ± 3.6	3.3 ± 1.7	NS	**
Cropland	26.8 ± 9.0 a	3.8 ± 1.9 b	2.0 ± 0.8 b	**				
Rangeland	0.7 ± 0.4	2.0 ± 1.2	7.2 ± 4.8	NS				
Nematodes	(n = 20)	(n = 18)	(n = 20)		(n = 34)	(n = 24)		
Shannon's diversity index	1.8 ± 0.1	1.9 ± 0.1	1.8 ± 0.1	NS	1.8 ± 0.1	1.9 ± 0.1	NS	NS
Taxa richness	16.0 ± 0.7	16.0 ± 0.8	15.4 ± 1.3	NS	15.3 ± 0.7	16.5 ± 0.9	NS	NS
Total abundance (100 g^{-1} soil)	592 ± 59 a	431 ± 68 ab	309 ± 58 b	**	478 ± 58	397 ± 42	NS	NS
Bacterivores	143 ± 24	125 ± 30	80 ± 12	NS	144 ± 20	75 ± 11	*	NS
Fungivores	272 ± 35 a	158 ± 25 b	110 ± 22 b	***	195 ± 28	161 ± 19	NS	NS
Plant feeders	142 ± 19 a	120 ± 23 ab	101 ± 30 b	*	106 ± 20	142 ± 18	NS	NS
Omnivores + predators	34.7 ± 7.1 a	28.9 ± 5.2 a	17.4 ± 4.8 b	*	32.6 ± 5.2	18.9 ± 3.4	NS	NS
PLFA biomarkers	(n = 19)	(n = 18)	(n = 17)		(n = 33)	(n = 21)		
Shannon's diversity index	3.1 ± 0.0 a	3.1 ± 0.0 ab	3.1 ± 0.0 b	***	3.1 ± 0.0	3.1 ± 0.0	*	NS
PLFA richness	39.9 ± 1.2	39.6 ± 1.2	36.0 ± 1.3	NS	36.5 ± 0.9	42.0 ± 1.1	**	NS
Total abundance (nmol g^{-1} soil)	40.9 ± 5.1	41.8 ± 5.1	29.9 ± 3.9	NS	29.6 ± 2.7	50.5 ± 4.7	***	NS
Actinomycetes	2.4 ± 0.3	2.3 ± 0.3	1.8 ± 0.2	NS	1.8 ± 0.1	2.9 ± 0.3	***	NS
Gram$^+$ bacteria	8.7 ± 1.0	8.2 ± 0.9	6.1 ± 0.8	NS	6.3 ± 0.5	10.0 ± 0.9	***	NS
Gram$^-$ bacteria	6.0 ± 0.8	6.2 ± 0.8	4.3 ± 0.5	NS	4.5 ± 0.4	7.2 ± 0.7	**	NS
Fungi	5.4 ± 0.8	5.8 ± 0.8	4.1 ± 0.6	NS	3.8 ± 0.4	7.2 ± 0.7	***	NS

Mean ± SE

[a] Significance for each main effect in the 2-way ANOVA, and the interaction of the two terms (position by land use type, P*LU): $P \leq 0.001$ = ***; ≤ 0.01 = **; ≤ 0.05 = *. For significant interactions, simple effects are described instead of main effects for position. Means with the *same lower-case letter* within each row are not significantly different in Tukey comparisons at $\alpha = 0.05$ level

[b] Cover does not necessarily total 100% as there may be canopy overlap or bare ground

[c] Non-native, herbaceous species excluding legumes and invasive/noxious weeds

seven Gram$^+$ bacteria, five Gram$^-$ bacteria, three actinomycetes, and three unspecific bacterial biomarkers), fungal (three biomarkers), and 51 unspecific biomarkers. Mean bacterial PLFA abundance was about three times higher than fungal PLFA abundance at each position from the waterway.

When group abundances were adjusted for total PLFA abundance, the relative abundance of fungi was still greater in rangelands than croplands (14.0 ± 0.2 vs. 12.5 ± 0.3%, respectively; $P < 0.01$). The response for Gram$^+$ and Gram$^-$ bacteria was opposite, with relative abundance less in rangelands than croplands (19.9 ± 0.4 vs. 21.6 ± 0.3%, respectively, $P = 0.01$ for Gram$^+$; 14.1 ± 0.3 vs. 15.2 ± 0.2%, respectively, $P < 0.01$ for Gram$^-$). Actinomycetes had an average relative abundance of 6.1 ± 0.2% and did not vary with land use type or position.

Soil properties

Soil surface samples (0–15 cm depth) were on average 34% lower in total soil C at position C near the channel edge than at position A (i.e., fields or grasslands managed for agricultural production) (Table 2). The percentage of fine particles (silt and clay) was lower at the channel edge than at position A. Rangeland sites had larger pools of NH_4^+–N, total soil C and exchangeable Ca in the surface layer, and smaller pools of NO_3^-–N and Olsen-P than the cropland sites. Total C was almost 50% higher in rangelands than croplands, and rangelands had a higher soil C to N ratio. In general, stronger positional gradients occurred for soil properties in rangelands than croplands, e.g. total soil N. Rangeland sites had higher pH and greater B concentration near the edge of the channel than in grazed fields. Weighted averages of soil nutrients for the four sampling depths from 0 to 100 cm showed similar trends for position and land use as for the 0–15 cm surface layer (Appendix Table 7). However, differences in weighted average values tended to be smaller.

Depth explained from 4% (NO_3^-–N) to 42% (total C) of the variance in the three-way ANOVA model (data not shown). Total C and N, NH_4^+–N, NO_3^-–N, Olsen-P and exchangeable K decreased with depth, while pH and exchangeable Na, Ca and Mg increased with depth (data not shown). Effects of depth on total C and N were especially pronounced, with differences of about 50% between surface (0–15 cm) and deepest (75–100 cm) samples (data not shown).

Linking aboveground and belowground biota and soil properties

Vegetation and nematodes shared the greatest correlative structure out of the three biological communities, with a standardized Mantel statistic (*r*, analogous to a correlation coefficient) of 0.24 ($P < 0.001$). PLFA communities were only weakly related to nematodes ($r = 0.11$, $P < 0.01$) and vegetation ($r = 0.08$, $P < 0.05$) in Mantel tests. Using Pearson's correlation tests, total percent plant cover correlated positively with nematode diversity and richness, as well as PLFA biomarker richness and abundance (Table 3). Vegetation species richness was also positively correlated with total PLFA abundance, which can be used as a proxy for total microbial biomass. Diversity of PLFA biomarkers was positively correlated with nematode diversity ($r = 0.29$, $P < 0.05$) and PLFA richness was positively correlated with nematode richness ($r = 0.32$, $P < 0.05$).

The presence of woody-dominated plant communities in the riparian zone increased total plant species diversity and richness (Fig. 2a, b). Nematode diversity and richness showed no differences (Fig. 2c, d), while PLFA diversity decreased in the riparian zone regardless of the presence of woody communities (Fig. 2e, f). Soil concentrations of NO_3^-–N and Olsen-P in the riparian positions were lower in sites with woody communities (1.7 ± 0.7 vs. 7.4 ± 2.0 μg NO_3^-–N g^{-1}, $P = 0.01$, and 14.1 ± 1.4 vs. 20.8 ± 2.2 μg Olsen-P g^{-1}, $P = 0.01$, for presence versus absence of woody communities, respectively). Total soil C, however, did not vary in the presence of woody communities at either position B or C (data not shown).

Riparian health and ecosystem functions

Riparian health scores for the 20 sites ranged from 19.6% to 79.2%, with an average score of 41.3 ± 4.2%. At position C near the channel edge, riparian health scores correlated positively with plant diversity and richness, and with soil NH_4^+–N and C concentrations for the surface 0–15 cm (Table 4). In contrast, the riparian health scores were negatively correlated with soil NO_3^-–N and Olsen-P at position C. Both PLFA and nematode richness were positively correlated with riparian health scores at position B on the floodplain bench. Riparian health rating also correlated positively with nematode structure index at position B, but showed a trend in the opposite direction at the more disturbed position C.

Total C storage per ha (sum of soil C to 1-m depth and woody C), was greater in the riparian zones of the rangelands than croplands or agricultural fields used for crops or grazing (Fig. 3). This difference was largely due to greater wood C, as total soil C storage for the full 1-m profile did not vary between positions

Table 2 Soil properties in top 15 cm layer according to three positions from waterway (A = agricultural field, B = floodplain bench, C = channel edge) and two land use types in the Sacramento Valley, California

	Position from waterway				Land use type			P*LU
	A ($n = 20$)	B ($n = 20$)	C ($n = 20$)	Sig[a]	Cropland ($n = 36$)	Rangeland ($n = 24$)	Sig	Sig
NO_3^-–N (μg g^{-1})	5.7 ± 1.5	4.2 ± 1.2	4.2 ± 1.8	NS	7.6 ± 1.2	0.4 ± 0.1	***	NS
NH_4^+–N (μg g^{-1})	1.6 ± 0.2	1.7 ± 0.3	1.2 ± 0.2	NS	1.1 ± 0.2	2.0 ± 0.2	**	NS
Total N (%)					0.09 ± 0.00	0.11 ± 0.01	NS	**
Cropland	0.11 ± 0.01 a	0.09 ± 0.01 ab	0.08 ± 0.01 b	*				
Rangeland	0.13 ± 0.01 a	0.13 ± 0.01 a	0.06 ± 0.01 b	***				
Total C (%)	1.1 ± 0.1 a	1.1 ± 0.1 a	0.8 ± 0.1 b	**	0.9 ± 0.0	1.2 ± 0.1	***	NS
C:N ratio	9.4 ± 0.3	10.3 ± 0.4	11.9 ± 0.9	NS	9.7 ± 0.4	11.9 ± 0.6	**	NS
Olsen-P (μg g^{-1})	22.3 ± 3.4	19.6 ± 1.8	14.6 ± 1.8	NS	21.8 ± 1.5	14.3 ± 2.6	**	NS
B (μg g^{-1})					0.5 ± 0.1	0.1 ± 0.0	***	***
Cropland	0.7 ± 0.1	0.3 ± 0.1	0.4 ± 0.1	NS				
Rangeland	0.0 ± 0.0 b	0.0 ± 0.0 ab	0.1 ± 0.1 a	*				
Exchangeable K[b]	0.7 ± 0.1 ab	0.8 ± 0.0 a	0.5 ± 0.1 b	*	0.7 ± 0.1	0.7 ± 0.1	NS	NS
Exchangeable Na[b]					0.2 ± 0.0	0.3 ± 0.1	NS	***
Cropland	0.2 ± 0.0 a	0.1 ± 0.0 b	0.2 ± 0.1 ab	*				
Rangeland	0.1 ± 0.0 b	0.1 ± 0.0 b	0.6 ± 0.2 a	***				
Exchangeable Ca[b]	13.3 ± 1.0 ab	13.3 ± 0.8 b	15.0 ± 0.9 a	*	12.6 ± 0.4	15.9 ± 1.1	*	NS
Exchangeable Mg[b]	6.6 ± 0.6	5.6 ± 0.4	6.6 ± 0.4	NS	6.3 ± 0.3	6.1 ± 0.5	NS	NS
pH					7.1 ± 0.1	7.1 ± 0.2	NS	**
Cropland	6.5 ± 0.1	7.0 ± 0.2	7.3 ± 0.2	NS				
Rangeland	6.5 ± 0.2 b	6.9 ± 0.2 b	7.8 ± 0.1 a	***				
Clay (%)	17.9 ± 0.9 a	14.9 ± 1.0 b	14.1 ± 0.8 b	***	16.1 ± 0.6	14.9 ± 1.0	NS	NS
Silt (%)					54.4 ± 1.1	50.4 ± 2.1	NS	*
Cropland	57.3 ± 1.6	53.4 ± 1.9	52.5 ± 2.0	NS				
Rangeland	58.0 ± 2.4 a	49.9 ± 3.7 ab	43.5 ± 3.4 b	*				
Sand (%)	24.5 ± 1.8 b	33.1 ± 2.7 a	37.0 ± 2.6 a	***	29.5 ± 1.6	34.7 ± 3.0	NS	NS

Mean ± SE

[a] Significance for each main effect in the 2-way ANOVA, and the interaction of the two terms (position by land use type, P*LU): $P \leq 0.001$ = ***; ≤ 0.01 = **; ≤ 0.05 = *. For significant interactions, simple effects are described instead of main effects for position. Means with the *same lower-case letter* within each row are not significantly different in Tukey comparisons at $\alpha = 0.05$ level

[b] Exchangeable cations are given in meq 100 g^{-1} soil

or land use types (data not shown). Woody C storage in the riparian zone was positively correlated with riparian health scores ($r = 0.58$, $P < 0.01$).

Indicator species analysis for riparian health classes at position C at the channel edge revealed that Johnsongrass (*Sorghum halepense*, a perennial state-listed noxious weed) was an indicator of poor riparian health (Indicator Value (IV) = 0.63, $P < 0.05$), while dogstail grass (*Cynosurus echinatus,* an annual non-native) and pale spikerush (*Eleocharis macrostachya*, a perennial native) were strong indicators of good riparian health (IV = 0.75, $P < 0.01$ for both). At position B on the floodplain bench, no plant species was an indicator of poor riparian health, but hairy vetch (*Vicia villosa*, a non-native legume) and Fremont cottonwood (*Populus fremontii*, a native tree) were both indicators of good riparian health (IV = 0.56, $P < 0.05$ and IV = 0.50, $P < 0.05$, respectively).

Of our four indicators of soil quality based on soil profile characteristics, only A-horizon darkening correlated with riparian health scores (Table 5).

Table 3 Pearson's correlation coefficients between aboveground and belowground biotic diversity, richness and abundance at sites in the Sacramento Valley, California ($n = 60$)

	Vegetation Shannon's diversity	Vegetation species richness	Vegetation total % cover
Nematodes			
Shannon's diversity	0.02	0.16	**0.38**
Taxa richness	0.06	0.08	**0.34**
Total abundance	−0.04	−0.23	−0.08
PLFA biomarkers			
Shannon's diversity	−0.20	−0.08	0.03
Biomarker richness	0.17	0.22	**0.29**
Total abundance	0.25	**0.28**	**0.31**

Bold values are statistically significant at $P \leq 0.05$

A-horizon darkening also correlated positively with plant species richness and nematode H′. Thus, a change in soil surface color was the most informative soil quality indicator of biodiversity and riparian health.

Discussion

Riparian gradient and land use types

Riparian zones are often reservoirs of native plant diversity (Richardson et al. 2007), and indeed riparian positions here were richer in plant diversity than adjacent fields managed for agricultural purposes. However, native plant diversity in the riparian positions in this landscape was lower than in historical or remnant stands elsewhere in the Central Valley (Roberts et al. 1980; Sawyer and Keeler-Wolf 1995). This lower native plant diversity could be the legacy of historic land use change, including drainage of wetlands, clearing of forests, and tillage and land

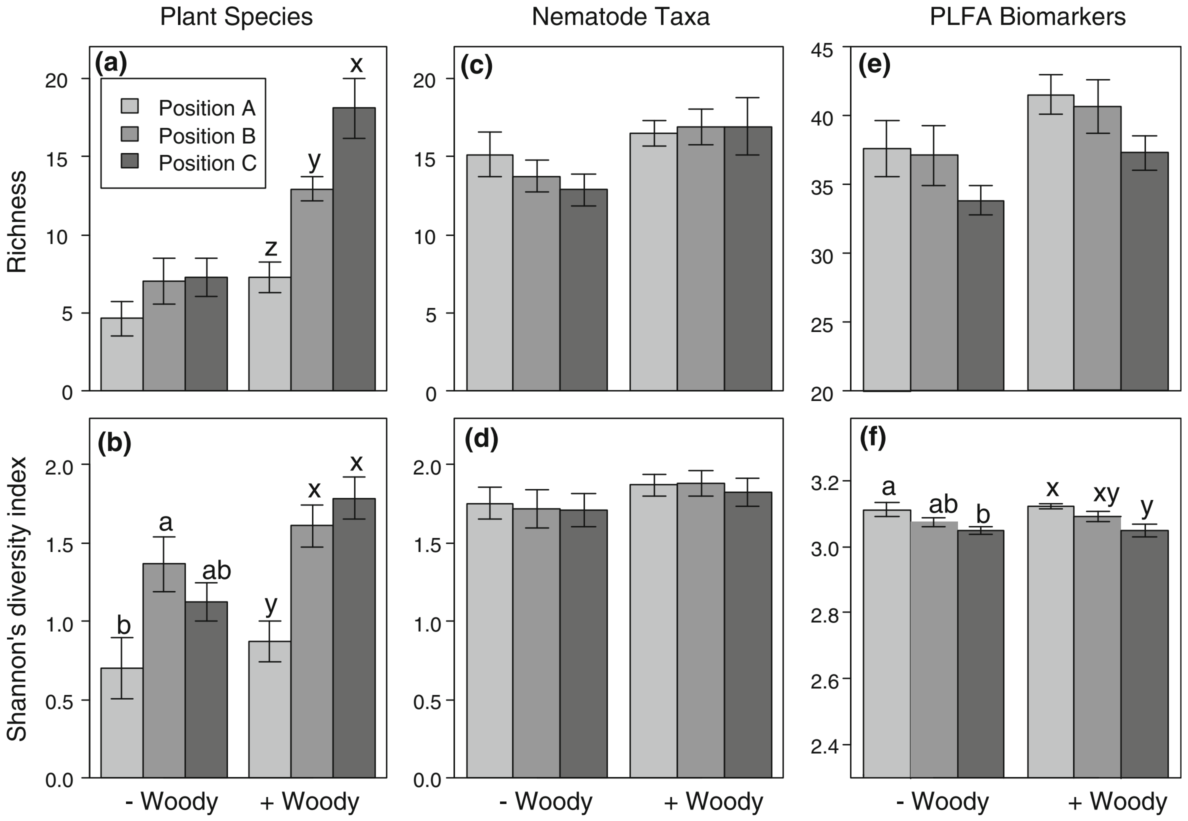

Fig. 2 Richness and diversity of plants (**a**, **b**), nematodes (**c**, **d**) and microbes (PLFA biomarkers) (**e**, **f**) in sites without (− Woody, $n = 8$) or with (+ Woody, $n = 12$) woody riparian communities in the Sacramento Valley, California. Position A = agricultural field, Position B = floodplain bench, Position C = channel edge. Means ± SE with the same *lower-case letter* within each group of biota are not statistically different in Tukey means comparisons at $\alpha = 0.05$ level

Table 4 Pearson's correlation coefficients between riparian health scores and biotic and soil properties at two positions within the riparian zone (B = floodplain bench, C = channel edge, $n = 20$ for each) at sites in the Sacramento Valley, California

	Riparian Health Scores	
	Position B	Position C
Plants		
Shannon's diversity	0.13	0.52*
Species richness	0.58**	0.70***
Nematodes		
Shannon's diversity	0.23	0.27
Taxa richness	0.50*	0.09
Total abundance	−0.15	0.10
Structure index	0.49***	−0.29
PLFA biomarkers		
Shannon's diversity	0.30	0.01
Biomarker richness	0.55*	0.45
Total abundance	0.57*	0.54*
Soil (0–15 cm)		
NO_3^-–N (μg g^{-1})	−0.49*	−0.53*
NH_4^+–N (μg g^{-1})	0.61**	0.64**
Total N (%)	0.36	−0.35
Total C (%)	0.61**	0.60**
Olsen-P (μg g^{-1})	−0.43	−0.69***

Significance levels: $P \leq 0.001$ = ***; ≤ 0.01 = **; ≤ 0.05 = *

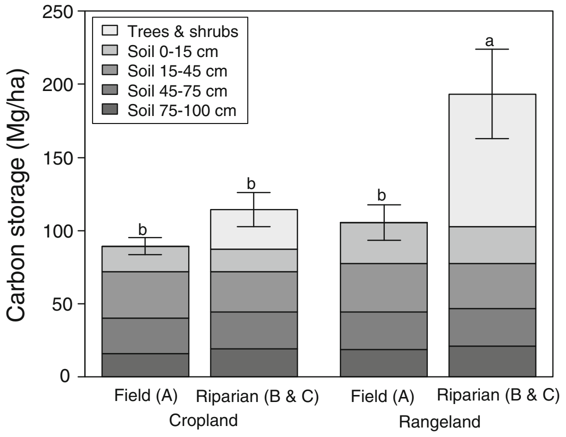

Fig. 3 Carbon storage in the top 1 m of soil and in woody biomass in the field (Position A) versus riparian zone (mean of Positions B and C) according to two land use types in the Sacramento Valley, California. Total mean C storage ± SE denoted by the same *lower-case letter* is not statistically different in Tukey means comparisons at $\alpha = 0.05$ level ($n = 12$ for cropland and $n = 8$ for rangeland)

planing for agriculture, dating back to the late 1800s (Barbour et al. 1993).

Soil fungi and fungivorous nematodes often decrease with disturbance and/or wetter soils (Holland and Coleman 1987; Neher et al. 2005; Six et al. 2006). Thus, the greater abundance of fungivorous nematodes in position A may reflect drier and less disturbed soil conditions more conducive to fungal decomposition pathways further from the waterways. Most of the grazed rangelands were not tilled, and some of the irrigated cropland had not received spring tillage, whereas waterways had experienced substantial water and soil movement during the fall and winter rainy season. Surprisingly, abundance of PLFA fungal biomarkers did not vary according to position from the waterway, but the trend was toward fewer fungi near the channel edge.

Position C in the active stream channel was subject to frequent erosion, deposition, and submergence due to seasonal flooding and irrigation events. Low values of C and N at this landscape position are likely due to the dynamic nature of stream channel processes. In this setting, deposition and erosion can inhibit SOM accumulation (and associated N mineralization) either by deposition of parent material low in organic matter or by episodic stripping of carbon-rich floodplain soils during flood events. The high level of soil disturbance along the active stream channel may also explain the lower overall abundance of nematodes (Bouwman and Zwart 1994; Ferris et al. 2001; Lenz and Eisenbeis 2000).

Land use type was an important factor in explaining variance in plant and microbial diversity and functional group distribution, as well as many soil nutrients. For example, cropland sites had a higher relative abundance of Gram$^+$ and Gram$^-$ bacteria, and bacterivorous nematodes were also nearly twice as abundant in croplands as rangelands. These trends likely reflect the effects of tillage and agrochemical application on soil community diversity and function, as opportunistic bacteria and bacterivorous nematodes are known to increase with ecosystem disturbance (Ferris et al. 2001; Minoshima et al. 2007).

The relatively low invasive/noxious weed cover near rangeland waterways suggests interactions with native perennial woody and herbaceous species. Disturbance along the channel edge, and more intensive grazing pressure from cattle accessing water, may have contributed to the increased plant species richness of

Table 5 Pearson's correlation coefficients[a] between soil quality indicators and measures of biotic diversity and riparian health at sites in the Sacramento Valley, California

Diversity measures	Depth to potential rooting barrier	Depth to redoximorphic features	A-horizon darkening	A-horizon thickness
Plants				
Shannon's diversity	0.01	−0.02	0.20	−0.05
Species richness	−0.07	−0.18	**0.25**	−0.17
Nematodes				
Shannon's diversity	0.14	−0.09	**0.29**	0.09
Taxa richness	**0.26**	0.01	0.16	0.00
PLFA biomarkers				
Shannon's diversity	−0.18	−0.18	0.25	0.07
Biomarker richness	−0.17	−0.09	0.16	0.07
Riparian health rating[b]	0.07	−0.17	**0.33**	−0.23

[a] *Bold values* are statistically significant at $P \leq 0.05$

[b] Riparian health correlations were run on data from positions B and C only ($n = 40$); all other correlations include data from all three positions from the waterway ($n = 60$)

riparian positions by reducing the competitiveness of weedier species, as has been reported of frequent flooding and mowing in European floodplain rehabilitation projects (Gerard et al. 2008). The higher invasive/noxious weed cover in cropland riparian zone positions than in the adjacent fields may be due to a lack of weed control measures in the riparian zone, whereas cultivation and herbicide applications are commonly practiced on the adjacent conventional crop fields planted with corn, tomatoes or grains (ARE-UC Davis 2008).

Plants, nematodes and soil microbes did not respond equally to differences in land use and the positional gradient from the waterway, reflecting different spatial and temporal scales of influence on these groups of organisms. While microbial communities in grasslands still show the effects of cultivation even 70 years after such practices have ceased (Steenwerth et al. 2003), plant communities can recover from such disturbance more quickly, especially when aided by active restoration (Giese et al. 2003; Richardson et al. 2007). Nematode communities, on the other hand, seemed to be most responsive to localized and seasonal resource availability and environmental conditions, instead of the larger landscape scale land use changes.

Aboveground-belowground relationships

Plant species richness and diversity increased where woody communities were present, possibly due to less disturbance by herbicide application, discing and scraping, mowing, grazing, burning and hand hoeing, all of which are riparian vegetation management practices commonly used in the region (Brodt et al. 2009). Nematode and PLFA diversity and richness were not affected by the presence of woody communities using ANOVA. However, another technique (data not shown), permutational multivariate analysis of variance (Anderson 2001), indicated that nematode communities appeared to be slightly responsive to woody plants, possibly due to changes in the quality and quantity of litter produced by different plant communities (Wardle et al. 2006). This statistical approach did not show any relationship between microbial community structure and the presence of woody communities, suggesting that land use and levels of disturbance may be more important than plant diversity (Drenovsky et al. 2009).

Woody plant communities also affected soil nutrient levels, as evident from lower concentrations of the readily available nutrients, NO_3^-–N and Olsen-P, in riparian positions containing woody communities. Where present, woody communities and their associated soil biota may have contributed to nutrient uptake and immobilization, as demonstrated for riparian forests in agricultural watersheds (Hill 1996; Lovell and Sullivan 2006; Peterjohn and Correll 1984). However, excess nutrients in riparian zones without trees may be an artifact of the scarcity of woody communities in croplands, where irrigated, fertilized fields may have been contributing these nutrients to the riparian zone via tailwater.

Plant, nematode and microbial communities were positively but weakly correlated with each other in Mantel tests, indicating that the three community datasets were related, but that the majority of structure in these data was not accounted for. Trophic interactions would be expected to influence the structure of the microbial, nematode and vegetation communities (Waldrop et al. 2006; Zak et al. 2003). The stronger correlation between nematode and microbial diversity and richness was probably due to the link between microbial-feeding nematodes (the most abundant group in the nematode community) and their food source. Although no direct synchrony exists between nematode and bacterial growth (Papatheodorou et al. 2004), abundance of bacterial-feeding nematodes depends on bacterial biomass (Zelenev et al. 2004).

Net primary productivity may have been important in shaping nematode and microbial diversity and richness, based on their correlations with total plant cover. Positive correlations between above- and belowground diversity have been observed (De Deyn and Van der Putten 2005; Zak et al. 2003), but net primary productivity or specific plant traits appear to be stronger drivers of microbial and nematode diversity than plant diversity (Sánchez-Moreno et al. 2008; Viketoft et al. 2009; Waldrop et al. 2006).

Riparian health as an indicator of biodiversity and ecosystem function

Riparian zone health scores from visual assessments were highly correlated with many biodiversity and soil properties, e.g., total soil C, A-horizon darkening and nematode structure index. The mechanism by which healthier riparian zones increase SOM accumulation and soil food web structure is not clear, but disturbance is apparently a factor, since there were fewer correlations at the channel edge than on the floodplain bench.

Riparian health scores were negatively correlated with soil NO_3^-–N and Olsen-P, which may reflect the generally degraded state of the riparian zones in more intensive cropland sites where these nutrients were applied as fertilizers. Vegetation cover in these degraded riparian zones was mostly weedy, with Johnsongrass emerging as an indicator species. Greater riparian health scores, on the other hand, may indicate nutrient immobilization by more productive plant communities, where Fremont cottonwood and hairy vetch were found to be indicator species. The strong association between riparian health scores, soil quality, diversity measures and noxious weed distribution suggests that this simple visual scoring approach may prove useful for assessments by landowners and resource agencies. For example, local conservation and restoration programs led by non-governmental organizations (e.g., Audubon California) and governmental agencies (e.g., the Resource Conservation District and the USDA Natural Resources Conservation Service) are in need of inexpensive monitoring and evaluation tools.

Conclusions

In this complex agricultural landscape in a Mediterranean climate, riparian vegetation was a key element in management strategies to provide multiple ecosystem benefits. Healthier riparian zones, especially those with woody communities, provided more ecosystem functions, acting as C reservoirs, nutrient buffer strips to protect water quality, and habitat for above- and belowground biodiversity. The visual rating of riparian health, plant indicator species, and soil color differences were associated with indicators of biodiversity and ecosystem functions, and thus could serve as rapid assessment tools for land managers and restoration professionals. Maintaining or restoring native woody plant communities along these agricultural waterways appears to be a key element in improving the services they provide.

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Appendix

Table 6 Mean plant species cover, arranged by functional groups, for three positions (A = agricultural field, B = floodplain bench, C = channel edge) in two land use types (cropland and rangeland) in the Sacramento Valley, California

Classification	Species	Common Name	Habit	Cropland			Rangeland		
				A	B	C	A	B	C
				Mean % cover					
Woody perennial[a]	*Alnus rhombifolia*	White alder	Perennial						1.3
	Ceanothus griseus var. *horizontalis*	Carmel ceanothus	Perennial		1.7				
	Frangula californica	California coffeeberry	Perennial		0.8				
	Heteromeles arbutifolia	Toyon	Perennial						1.3
	Juglans californica var. *hindsii*	Northern CA black walnut	Perennial		0.0	5.2		0.1	0.1
	Juglans regia	English walnut	Perennial	3.1	6.0	3.1			
	Populus fremontii	Fremont cottonwood	Perennial					9.4	22.2
	Prunus dulcis	Almond	Perennial					2.5	0.1
	Quercus douglasii	Blue oak	Perennial				0.1	0.4	
	Quercus lobata	Valley oak	Perennial		3.1	0.2		4.7	0.3
	Quercus wislizeni	Interior live oak	Perennial					0.1	
	Salix exigua	Narrow-leaved willow	Perennial		0.0	3.1			
	Salix laevigata	Red willow	Perennial						0.1
	Salix lasiolepis	Arroyo willow	Perennial					3.8	5.0
	Sambucus mexicana	Blue elderberry	Perennial		1.7				
Herbaceous native	*Amaranthus blitoides*	Prostrate pigweed	Annual	0.1	0.3	0.9			
	Artemisia douglasiana	California mugwort	Perennial		0.2	1.0			
	Asclepias fascicularis	Mexican whorled milkweed	Perennial					0.1	0.1
	Aster subulatus	Slender aster	Annual			0.0			
	Carex senta	Swamp carex	Perennial			0.2			
	Chamaesyce serpyllifolia	Thyme-leafed spurge	Annual		0.3	0.3			
	Conyza canadensis	Horseweed, Canada fleabane	Annual		0.0	0.0			
	Croton setigerus	Dove weed	Annual		0.0	0.0			0.1
	Cyperus eragrostis	Tall flatsedge	Perennial	0.1		0.5			1.3
	Datisca glomerata	Durango root	Perennial						0.3
	Eleocharis macrostachya	Pale spikerush	Perennial						0.4
	Elymus glaucus	Blue wildrye	Perennial		0.2		0.3	0.3	0.1
	Epilobium brachycarpum	Panicle willoweed	Annual		0.3	0.7	0.1	0.4	0.1
	Glycyrrhiza lepidota	Wild licorice	Perennial						0.1

Table 6 continued

Classification	Species	Common Name	Habit	Cropland			Rangeland		
				A	B	C	A	B	C
				Mean % cover					
	Helenium puberulum	Sneezeweed	Annual			0.3			
	Heliotropium curassavicum	Seaside heliotrope	Perennial						0.1
	Hemizonia congesta ssp. *luzulifolia*	Hayfield tarweed	Annual					0.1	
	Juncus arcticus ssp. *littoralis*	Mountain rush	Perennial						0.1
	Juncus xiphioides	Irisleaf rush	Perennial						0.3
	Leymus triticoides	Beardless wildrye	Perennial		0.8	0.8			
	Nassella pulchra	Purple needlegrass	Perennial		0.2		0.6	0.1	0.1
	Navarretia sp. (prob. N. tagetina)	Marigold navarretia	Annual					0.1	
	Phyla nodiflora var. *nodiflora*	Mat lippia	Perennial						0.1
	Schoenoplectus californicus	California bulrush	Perennial		0.2				
	Schoenoplectus maritimus	Cosmopolitan bulrush	Perennial			0.8			0.1
	Schoenoplectus pungens	Common threesquare	Perennial						0.3
	Triteleia laxa	Ithuriel's spear	Perennial					0.1	
	Typha angustifolia[c]	Narrowleaf cattail	Perennial						0.3
	Xanthium strumarium	Common cocklebur	Annual	0.0	0.3	0.2			0.5
Leguminous non-native	*Medicago sativa*	Alfalfa	Perennial	0.1		0.1			
	Melilotus indica	Indian sweetclover	Annual		0.2			0.4	0.8
	Trifolium fragiferum	Strawberry clover	Perennial	0.0					1.3
	Trifolium hirtum	Rose clover	Annual				1.9	3.3	3.5
	Vicia sativa	Common vetch	Annual		0.2	0.9		0.3	0.1
	Vicia villosa	Hairy vetch	Perennial	0.0	0.2		1.4	2.3	5.4
Invasive/noxious weed	*Aegilops triuncialis*	Barb goatgrass	Annual				16.6	10.0	2.9
	Avena barbata	Slender oat	Annual	1.7	1.3	0.2	5.7	2.1	1.5
	Brassica nigra	Black mustard	Annual		0.0	0.1			
	Bromus diandrus	Ripgut	Annual		7.7	3.2	0.1	9.8	2.6
	Bromus hordeaceus	Soft chess	Annual		0.3	0.0	3.6	3.3	1.4
	Carduus pycnocephalus	Italian thistle	Annual		0.1	0.5	0.1	2.0	0.9
	Centaurea solstitialis	Yellow starthistle	Annual	0.2	0.9	0.2	13.3	6.7	6.9
	Convolvulus arvensis	Field bindweed	Perennial	0.7	2.0	5.3	0.4	0.1	
	Cynodon dactylon	Bermuda grass	Perennial		0.4	0.6		3.1	9.1

Table 6 continued

Classification	Species	Common Name	Habit	Cropland			Rangeland		
				A	B	C	A	B	C
				Mean % cover					
	Cynosurus echinatus	Dogstail grass	Annual		0.0				0.3
	Dactylis glomerata	Orchard grass	Perennial						0.1
	Festuca arundinacea	Tall fescue	Perennial				0.1		
	Hordeum marinum ssp. *gussonianum*	Mediterranean barley	Annual	0.2	0.4	0.0	0.3	2.8	2.0
	Hordeum murinum ssp. *leporinum*	Hare barley	Annual					0.1	0.1
	Hypochaeris glabra	Smooth cat's-ear	Annual		0.0				
	Lepidium latifolium	Perennial pepperweed	Perennial		0.2	0.2			
	Lolium multiflorum	Italian ryegrass	Annual	2.5	5.5	12.6	1.1	6.1	4.9
	Lythrum hyssopifolium	Hyssop loosestrife	Annual						0.2
	Malvella leprosa	Alkali mallow	Perennial		0.2		0.1	0.1	0.3
	Marrubium vulgare	Horehound	Perennial		0.0	0.1		0.4	0.1
	Medicago polymorpha	California burclover	Annual	0.3	0.3	0.0	1.6	0.4	0.5
	Nicotiana glauca	Tree tobacco	Perennial			0.0			0.1
	Picris echioides	Oxtongue	Annual	0.0	0.1	0.3	0.1	0.1	0.4
	Piptatherum miliaceum	Smilo grass	Perennial		1.0	0.9		0.3	
	Raphanus sativus	Radish	Annual	0.0					
	Rubus discolor	Himalayan blackberry	Perennial		3.1	1.9			
	Rumex acetosella	Red sorrel	Perennial			0.0			0.1
	Rumex crispus	Curly dock	Perennial	0.1	0.1		0.1	0.1	0.1
	Sinapis arvensis	Charlock mustard	Annual	0.1	5.7	3.5			
	Sorghum halepense	Johnsongrass	Perennial		0.2	4.3			
	Taeniatherum caput-medusae	Medusahead	Annual				16.1	21.3	5.1
	Torilis arvensis	Hedgeparsley	Annual			0.1	0.1	0.6	0.3
	Tribulus terrestris	Puncturevine	Annual		0.0				
Herbaceous non-native[b]	*Amaranthus albus*	Tumble pigweed	Annual	0.2	0.0	0.0			
	Anagallis arvensis	Scarlet pimpernel	Annual		0.0	0.0			0.1
	Anthemis cotula	Mayweed chamomile	Annual		0.0	0.0			
	Avena sativa	Oat cv.	Annual	7.3					

Table 6 continued

Classification	Species	Common Name	Habit	Cropland			Rangeland		
				A	B	C	A	B	C
				Mean % cover					
	Brachypodium distachyon	Purple false brome	Annual						0.1
	Bromus madritensis ssp. *madritensis*	Foxtail chess	Annual		1.0	0.8		1.6	0.2
	Capsella bursa-pastoris	Shepherd's purse	Annual				0.3		
	Chenopodium album	Lambsquarters	Annual	0.0	0.9	0.3			
	Euphorbia serpens	Creeping spurge	Annual						0.3
	Galium murale	Tiny bedstraw	Annual	0.0		0.0			
	Galium parisiense	Wall bedstraw	Annual				0.1		0.3
	Geranium molle	Dovefoot geranium	Annual		0.0	0.2		0.1	0.1
	Gnaphalium luteoalbum	Everlasting cudweed	Annual			0.0			0.1
	Hordeum vulgare ssp. *vulgare*	Barley cv.	Annual	1.7	0.8				
	Lactuca serriola	Prickly lettuce	Annual				0.2	0.1	0.2
	Lycopersicon esculentum	Tomato cv.	Annual	7.7					
	Malva nicaeensis	Bull mallow	Annual	0.2	0.3	0.2			
	Polygonum arenastrum	Common knotweed	Annual				0.1		
	Polygonum argyrocoleon	Silversheath knotweed	Annual	0.0	0.0	0.0			
	Polypogon monspeliensis	Annual rabbitsfoot grass	Annual			0.0			5.3
	Portulaca oleracea	Common purslane	Annual	0.0	0.2				
	Rumex dentatus	Toothed dock	Annual				0.1	0.1	
	Rumex obtusifolius	Broadleaf dock	Perennial						0.1
	Silene gallica	English catchfly	Annual						0.1
	Sonchus oleraceus	Annual sow thistle	Annual	0.3	0.3	0.1		0.1	0.1
	Torilis nodosa	Knotted hedgeparsley	Annual						0.1
	Tragopogon porrifolius	Salsify	Annual						0.1
	Triticum aestivum	Wheat cv.	Annual	7.3					
	Verbena litoralis	Seashore vervain	Perennial						0.1
	Veronica persica	Persian speedwell	Annual	0.0		0.0			
	Zea mays	Corn cv.	Annual	1.9					

[a] All are native except *J. regia* and *P. dulcis*

[b] Excluding legumes and noxious weeds

[c] Native to Canada, but possibly naturalized in California (Hickman 1993; USDA-NRCS 2009)

Table 7 Weighted average soil properties for top 100 cm according to position from waterway (A = agricultural field, B = floodplain bench, C = channel edge) and two land use types in the Sacramento Valley, California

	Position from waterway				Land use type			P*LU
	A (n = 20)	B (n = 20)	C (n = 20)	Sig.	Cropland (n = 36)	Rangeland (n = 24)	Sig.	Sig.
NO_3^-–N (μg g^{-1})	3.85 ± 1.07	3.83 ± 1.12	2.68 ± 1.05	NS	5.44 ± 0.88 a	0.48 ± 0.18 b	***	NS
NH_4^+–N (μg g^{-1})	0.66 ± 0.07 ab	1.02 ± 0.29 a	0.63 ± 0.07 b	*	0.57 ± 0.05 b	1.08 ± 0.24 a	**	NS
Total N (%)	0.08 ± 0.00 a	0.07 ± 0.00 ab	0.06 ± 0.01 b	**	0.07 ± 0.00	0.06 ± 0.01	NS	*
Total C (%)	0.69 ± 0.04	0.67 ± 0.04	0.66 ± 0.04	NS	0.62 ± 0.03 b	0.74 ± 0.04 a	*	NS
C:N ratio	9.32 ± 0.61 b	10.38 ± 0.59 ab	12.41 ± 1.53 a	**	9.54 ± 0.42	12.46 ± 1.28	NS	**
Olsen-P (μg g^{-1})	11.85 ± 2.81	11.82 ± 1.67	10.44 ± 1.31	NS	12.69 ± 1.07 a	9.40 ± 2.39 b	*	NS
B (μg g^{-1})	0.39 ± 0.10	0.22 ± 0.05	0.28 ± 0.05	NS	0.46 ± 0.05 a	0.06 ± 0.03 b	***	***
Exch-K (meq/100 g)	0.47 ± 0.03	0.49 ± 0.03	0.43 ± 0.03	NS	0.46 ± 0.02	0.47 ± 0.03	NS	*
Exch-Na (meq/100 g)	0.38 ± 0.08 ab	0.20 ± 0.04 b	0.51 ± 0.16 a	*	0.33 ± 0.05	0.41 ± 0.13	NS	**
Exch-Ca (meq/100 g)	15.18 ± 1.10	14.42 ± 0.72	15.56 ± 0.83	NS	13.48 ± 0.35 b	17.41 ± 1.01 a	**	NS
Exch-Mg (meq/100 g)	7.45 ± 0.59	6.46 ± 0.56	7.43 ± 0.39	NS	7.26 ± 0.28	6.90 ± 0.63	NS	NS
pH	6.96 ± 0.10 b	7.12 ± 0.14 b	7.50 ± 0.13 a	***	7.14 ± 0.09	7.27 ± 0.14	NS	**
Clay (%)	21.1 ± 0.9 a	17.3 ± 1.0 b	16.7 ± 0.9 b	***	18.9 ± 0.7	17.6 ± 1.1	NS	**
Silt (%)	58.4 ± 1.1 a	53.8 ± 1.8 b	53.2 ± 2.3 b	**	57.6 ± 1.2	51.4 ± 1.7	NS	*
Sand (%)	20.6 ± 1.8 b	28.8 ± 2.7 a	30.1 ± 3.1a	***	23.5 ± 1.8	31.1 ± 2.7	NS	*

Mean (±SE) significance is indicated for each main effect in the 2-way ANOVA, and the interaction of the two terms: $P \leq 0.001$ = ***; ≤ 0.01 = **; ≤ 0.05 = *. Means with the *same letter* are not significantly different in Tukey comparisons at $\alpha = 0.05$ level

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