Altered Ecohydrologic Response Drives Native Shrub Loss under Conditions of Elevated Nitrogen Deposition

Yvonne A. Wood,* Thomas Meixner, Peter J. Shouse, and Edith B. Allen

ABSTRACT

Many regions of southern California's coastal sage scrub (CSS) are rapidly declining as exotic annual plants replace native shrubs. During this conversion, the subsurface hydrology of the semiarid hillslopes that support CSS may be altered. This could chronically suppress the ability of native shrubland to revegetate the landscape since ecosystem processes of nutrient availability and of seedling establishment rely on spatial patterns of available soil water. In this work, soil water and nutrient N regimes were compared over a 2-yr period between a southern California site where CSS has declined (approximately 5% shrub cover) with high additions of anthropogenic N, and one where CSS remains dominant (over 50% shrub cover) with predominantly background atmospheric additions of N. These two sites have similar climate, bedrock lithology, soils, and topography, and had the same vegetation type (Riversidean CSS) 30 years ago. We found that the depth and rate of rainwater percolation into wildland hillslope soils in response to early-season storm events has been greatly reduced after loss of CSS shrubs and vegetation type conversion to invasive grassland. With decreased rainwater redistribution to soil depths of 100 to 150 cm, the predominant zone of soil water has become the upper 25 cm. This shift exacerbates vegetation type conversion by (i) concentrating smog-produced nitrogenous (N) chemicals in the uppermost soil, where they become readily available, along with high soil water, to shallow-rooted exotic grasses early in the growing season and (ii) depriving adult and juvenile shrubs of deeper regolith water.

Native plants exert strong local control over the subsurface hydrology of arid and semiarid landscapes and the loss of a dominant vegetation type can dramatically alter soil water dynamics (Hill and Rice, 1963; Newman et al., 1997; Bhark and Small, 2003; Williamson et al., 2004a). The presence of woody shrubs fosters higher infiltration rates and focused percolation compared to lower stature grasses and forbs (Schlesinger et al., 1989; Schulze et al., 1998; Devitt and Smith, 2002; Bhark and Small, 2003; Williamson et al., 2004b). Shrub crowns funnel water to the soil surface as rainfall captured by leaf surfaces flows downward along woody stems (Mauchamp and Janeau, 1993; Gonzalez-Hidalgo and Bellot, 1997; Levia and Frost, 2003). The resulting spatial patterning of soil water across the landscape (Wood et al., 2005) controls important ecological processes, including nutrient availability (Schlesinger et al., 1996) and seedling establishment (Cione et al., 2002).

Many regions of coastal sage scrub (CSS), one of the dominant native shrub communities of southern California, are rapidly declining across low elevation hillslopes (Minnich and Dezzani, 1998) (Fig. 1). Coastal sage scrub, distinguished by nearly contiguous stands of aromatic subshrubs, grows in southern California's western regions under a Mediterranean-type climate with hot, dry summers and mild, rainy winter growing seasons. Minor components of herbaceous perennial and annual forbs occur beneath the 0.5- to 1.5-m-tall, shallow-rooted shrubs (Westman, 1981), and during occasional wet years produce a remarkable display of winter and spring wildflowers. Historical reports from the 1770s describe this unique shrubland as covering much of western Riverside County's lower elevation granitic foothills (Bolton, 1930). Now, in its stead, exotic annual grasses and forbs flourish across many of these same foothills due to a suite of environmental pressures from a burgeoning human population (Westman, 1981; Minnich and Dezzani, 1998).

In the 1970s, high concentrations of atmospheric oxidants, including both ozone and nitrogenous pollutants, were linked to CSS stand cover decline within southern California's South Coast Air Basin (SCAB) (Westman, 1979). Further work showed that nitrogenous air pollutants in particular appear to facilitate this decline (Allen et al., 1998; Padgett et al., 1999; Fenn et al., 2003). After settling out of the atmosphere, primarily during the dry summer smog season, nitrogen (N) containing compounds are held within the shrub canopy or atop the soil litter, or, as CSS stands thin, atop grass litter or the dry soil surface. Late fall and winter rains carry soluble N compounds into the soil where plants can utilize the nutrient-enriched water for vegetative growth. This early-season pulse of N-enriched soil water is hypothesized to favor non-native invasive herbs and grasses, which are overall phenologically earlier (Chiariello, 1989), and take up available soil nitrogen faster in greenhouse studies (Yoshida and Allen, 2004), than California native plants. During a 4-yr field fertilization study, annual exotic grasses responded to increased nutrient N with increased biomass during wet years (Allen et al., 1998). However, there were no long-term observable effects on native shrub cover during these field studies (Allen et al., 1998), suggesting a more complex mechanism in the type conversion of CSS than solely anthropogenic N conferring a competitive edge to exotic grasses and forbs (Allen, 2004).

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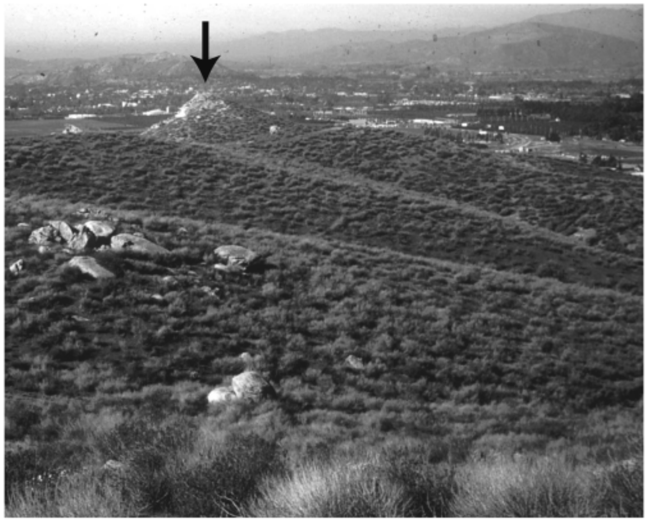
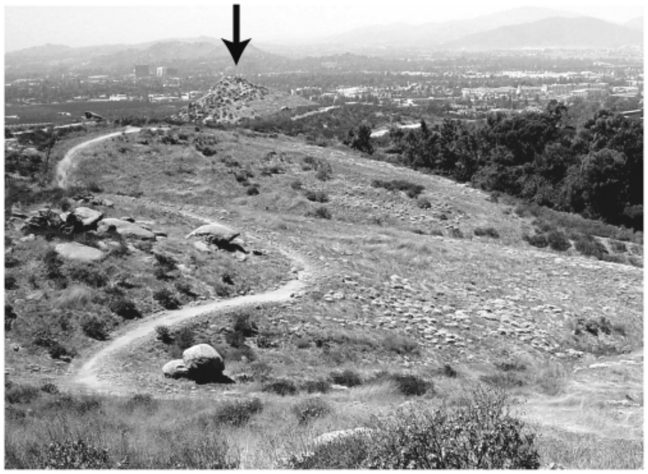
Abbreviations: CSS, coastal sage scrub; +CSS, healthy coastal sage scrub site at Lake Skinner; −CSS, degraded coastal sage scrub site at the base of the Box Springs Mountains; ET, evapotranspiration; RO, runoff; WBR, weathered bedrock.



(a)



(b)

Fig. 1. Repeat photographs of the foothills of the Box Springs Mountains illustrating the decline of coastal sage scrub (CSS). Arrows in each photograph point to same hill adjacent the UC Riverside campus. (a) Photograph taken in 1958, courtesy of the Botanic Gardens of UC Riverside (photograph taken by Dr. Frank Vasek). (b) Photograph taken in 2005 of the same site. Note distinctive textural differences across the landscape as shrub cover has been lost.

Elevated exotic grass biomass also fuels wildland fires, potentially on an annual basis during the dry, hot summers of southern California. As a result, increased frequency and greater areal extent of exotic grassland fires compared to those of the native shrubland, which occur on the order of decades, add momentum to the decline of CSS stands (D'Antonio and Vitousek, 1992; Minnich and Dezzani, 1998). For instance, the CSS plant community responds to disturbance due to fire largely through the recruitment of juveniles. After fire, burnt shrub stumps provide root channels to vector water to depth (Halvorson et al., 1997), suggesting a mechanism for fostering CSS seedling establishment across the burned landscape. However, type conversion to exotic grasslands is suggested to alter the availability of conduits capable of moving soil water to depth (Williamson et al., 2004b), which should alter the spatial patterning of both soil water and soluble anthropogenic N additions across the landscape. Thus, characterizing the timing and depth of movement of soil water, and soluble nutrient N, under native CSS stands compared to type-converted exotic grasslands is core to promoting the continued viability of southern California's endemic CSS plant community under the stress of urbanization.

STUDY GOALS AND OBJECTIVES

For this work, we designed a study to compare the ecohydrologic functioning of a site with native shrubland to that of a site where CSS had begun a rapid decline three decades earlier and been type converted to exotic grasslands. Our experimental design substitutes space-for-time to discern differences in patterns of water movement across the two landscapes. Landscape processes important to causing any differences can then be inferred from these patterns. While detailed understanding of these processes may require mechanistic studies under controlled conditions, this methodology allows the study of decades-long change in undisturbed wildland soils.

Our goals were to (i) determine if the subsurface hydrology of CSS foothill regions is altered when native shrub cover is lost, and, if so, (ii) consider if such ecohydrologic alterations, especially in a regime of high N deposition, prevent the reestablishment of native shrubs. Our objectives were to (i) determine seasonal vadose zone water distributions and fluxes in the soils of the two hillslope sites, (ii) relate them to seasonal subsurface nitrate N distributions, and (iii) compare ecosystem water use patterns between native shrub and invasive vegetation cover types.

Subsurface water dynamics were determined at the two sites using depth distributions of soil chloride concentrations as well as volumetric soil water content. The ocean is the major source of meteoric chloride, which is added to the land surface through summer dry deposition and winter rains (Junge and Werby, 1958). Since plants do not assimilate significant amounts of chloride, a micronutrient, depth distributions of this anion serve to trace soil water movement, indicating leaching depths (Scanlon, 1991; Allison et al., 1994; Phillips, 1994) reflective of both percolation and evaporation rates.

Volumetric soil water content, rather than soil matric potential, was measured to understand the spatial and temporal differences in plant available water between these two sites. This choice was based on determinations from pedotransfer models (Schaap et al., 1998, 2001; Ritchie et al., 1999) that (i) matric potentials for these two coarse-grained, low-organic-matter soils would be too low (less than -750 mb) during most sampling periods to be reliably measured in the field, and (ii) the range of plant available soil water would vary little with depth between the two sites, indicating that soil water content is an acceptable measure of plant available water (Ritchie and Amato, 1990).

Patterns of movement of nitrogen additions into the vadose zone were examined by determining the depth distributions of soluble nitrate N and then comparing them to subsurface water movement as determined above. The anions chloride and nitrate have similar travel times through the regolith and should be translocated in similar patterns by infiltrating rainwater. However, soluble nitrate is a dynamic and mobile nonconservative macronutrient, with several biological, in addition to physical, processes controlling its distribution in soils and availability to native plant communities.

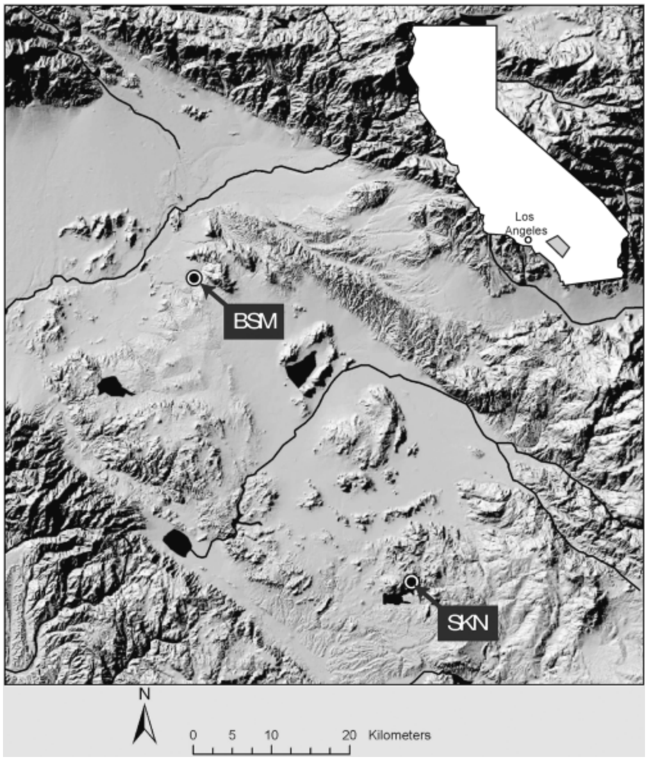


Fig. 2. Location of study sites. The generally trapezoidal-shaped Perris Plain is fault-bounded (strong linear features at the base of southern California mountain ranges) to the northeast and southwest. The Box Springs Mountains (shown in photographs of Fig. 1) have lost most of their coastal sage scrub (CSS) shrub cover. The site at Lake Skinner remains predominantly CSS.

MATERIALS AND METHODS

Study Sites

Two study sites were selected within southern California's Perris Plain, a vast north–south-trending, ancient granitic surface that comprises a majority of the western region of Riverside County (Fig. 2). They were chosen to have comparable climatic variables, bedrock lithology, topography, and soil characteristics, while having different vegetation types and anthropogenic N additions (Table 1).

During the 1970s, an inland association of CSS covered both sites (Minnich and Dezzani, 1998) (Fig. 1). This inland (Riversidean) association is dominated by California sagebrush (*Artemisia californica* Less.), California buckwheat (*Eriogonum fasciculatum* Benth.), laurel sumac [*Malosma laurina* (Nutt.) Nutt. ex Abrams], California encelia (*Encelia californica* Nutt.), and several species of sage (e.g., black sage, *Salvia mellifera* Greene, and white sage, *S. apiana* Jeps.) (Kirkpatrick and Hutchinson, 1980; Westman, 1981). Now, these two sites differ dramatically in both plant cover and anthropogenic N inputs (Minnich and Dezzani, 1998; Padgett et al., 1999) (Fig. 1; Table 1). The plant community at one site, Lake Skinner, remains predominantly CSS (+CSS), while at the other site near the Box Springs Mountains, the scrub has undergone a radical decline and non-native herbaceous vegetation dominates (−CSS) (Fig. 1; Table 1).

The −CSS site is located on granitic foothills of the Box Springs Mountains within a botanic preserve of the University of California, Riverside (Fig. 1 and 2). This site, 100 km east of Los Angeles at the northern end of the Perris Plain, is directly impacted by smog trajectories from the west that deliver large annual anthropogenic N inputs (Padgett et al., 1999). Vegetative cover at the −CSS site is predominantly invasive European grass and forb species such as ripgut brome [*Bromus diandrus* Roth var. *rigidus* (Roth) Sales], red brome (*Bromus rubens* L.), wild oat (*Avena fatua* L.), slender oat (*A. barbata* Pott ex Link), shortpod mustard [*Hirschfeldia incana* (L.) Lagrèze-Fossat], African mustard (*Brassica tournefortii* Gouan), Mediterranean split grass [*Schismus barbatus* (L.) Thell.], and filaree [*Erodium cicutarium* (L.) L'Hér.], with limited native shrub cover (5–10%).

The +CSS site is located approximately 70 km to the southeast of the first site, near Lake Skinner, within the Multi-Species Reserve. This site is shielded from smog trajectories by geographic barriers. Here, measured annual anthropogenic N inputs are minor (Padgett et al., 1999) and vegetative cover remains predominantly CSS (approximately 65% cover).

Both sites have a Mediterranean climate that is semiarid and hot (Fig. 3a). Limited rainfall (mean of approximately 250 mm yr^{-1}) occurs predominantly in the cool, winter months of November through April. The primary growing season is in late winter and spring after the soil has been moistened. Later, drought-deciduous CSS shrubs survive the hot, dry summers by shedding leaves to restrict water loss during transpiration and photosynthesis.

There is great interannual variability in southern California's rainfall patterns, and climatic indicators for both years of this study diverged from the norm. The first year (2001–2002) represents an extreme drought event for southern California, while the second (2002–2003) received slightly more than the mean annual precipitation, mostly due to a very rainy winter

Table 1. Site information for healthy (+CSS) and degraded (−CSS) coastal sage scrub stands.

	+CSS	−CSS
	Site characteristics	
Locale	Multi-Species Reserve, Lake Skinner	UCR Botanic Gardens, Box Springs Mountains
Location	33.608° N, 117.032° W	33.967° N, 117.320° W
NO_3–N additions†, kg ha^{-1} yr^{-1}	5	30
Cl additions‡, kg ha^{-1} yr^{-1}	4	2
Shrub cover, %	65	5
Bedrock lithology	granite	granite
	Soil characteristics	
Parent material	colluvium, granite with additions of gabbro	colluvium, granite
Usual depth to weathered granite, cm	150–175	100–125
Usual depth to fresh granite, cm	200	175
Texture		
Surface (0–25 cm)	sandy loam	sandy loam
Control section (50–100 cm)	sandy loam	loamy sand

† Based on values reported by Padgett et al. (1999).

‡ Based on measurements of chloride collected over a 2-yr period at both sites. The deposition of chloride at the Lake Skinner site is greater than that at the Box Springs Mountains site due to its closer proximity to the Pacific Ocean (Junge and Werby, 1958).

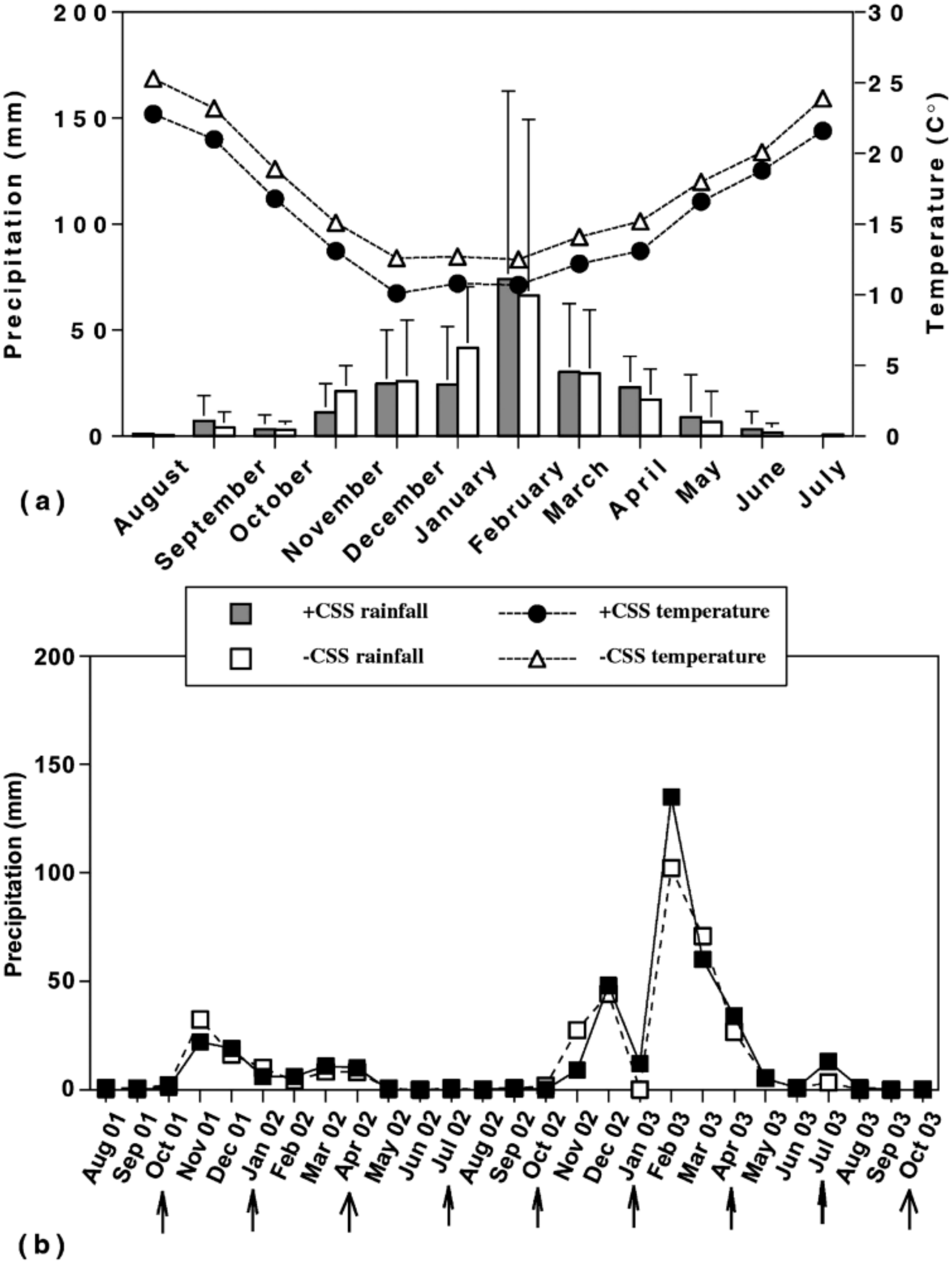


Fig. 3. (a) Mean monthly precipitation and air temperature based on data from California Irrigation Management Information System (CIMIS) stations within 3.2 km of each site (+CSS, healthy coastal sage scrub site at Lake Skinner; −CSS, degraded coastal sage scrub site at the base of the Box Springs Mountains). (b) Precipitation (from same sources) recorded over the two years of this study. Arrows indicate time of quarterly soil samplings.

(Fig. 3b). Both sites received nearly identical amounts of precipitation in nearly identical temporal patterns over the two years of the study (Fig. 3b). However, the amount of meteoric chloride deposited at the two sites differs (Table 1) due to differing distances from the Pacific Ocean (Junge and Werby, 1958). The +CSS site is approximately 40 km inland from the Pacific Ocean and received approximately twice the amount of naturally deposited chloride as the −CSS site, which is approximately 70 km inland from the Pacific Ocean.

Field Techniques

Regolith samples (approximately 250 g each) were collected over a 2-yr period, beginning in October 2001 through October 2003, using a 6.35-cm-diameter bucket auger to hand-drill cores. Since seasonality of rainfall is important to ecosystem function in Mediterranean climates, triplicate samples were collected quarterly for each site during October, January, April, and July resulting in 27 cores at each site. Soils were sampled intensively within the near surface (2-, 5-, 10-, 15-, and 25-cm depths) and then at every 25-cm depth increment until fresh granite prevented deeper coring. Sample locations were chosen to resemble each other as closely as possible for both sites (predominantly north aspect, slopes of approximately 30%, and the presence of bedrock outcrops of granite). The upslope contributing runoff area for the +CSS is slightly larger than that for the −CSS site. However, even during the intense winter storms of 2002–2003, negligible runoff was observed in the field at either site.

Laboratory Analyses

Regolith samples were stored in sealed plastic containers, placed in coolers, and then frozen on return from the field. Field samples were sieved to remove material larger than 2 mm and subsamples (10 g) were removed for gravimetric water content measurements (Gardner, 1986). Bulk density values, determined using 5.4-cm-diameter cores, were then used to calculate the percent soil water by volume. Soil textures were determined by the hydrometer method (Gee and Bauder, 1979) for samples from three cores for each site.

Extracts from the field samples were analyzed for chloride and nitrate N using ion colorimetry, a robust, reliable, and well-tested methodology for soil chemical measurements (Frankenberger et al., 1996; Clesceri et al., 1998). Using standard operating conditions, spike recoveries are 98 to 102% with minimum detection limits of 0.07 mg L^{-1}, values that were considered acceptable for this comparative study. Gravimetric water content (determined as described above) was used to adjust measured chloride and nitrate N concentrations of extracts to an oven-dry soil weight basis (μg g^{-1}).

Chloride concentrations were measured in extracts made by combining 30 g of soil with 30 mL of double distilled deionized water. The resulting slurries were allowed to equilibrate (with occasional stirring) for 48 h at room temperature. They were then centrifuged at 1500 rpm for 10 min, filtered through disposable 0.2-μm filters, and stored at -20°C until analyzed for chloride on an Alpkem (Clackamas, OR) RFA/2 320 ion colorimeter continuous flow analyzer (CFA).

Nitrate N concentrations were measured by combining 10 g of soil with 50 mL of KCl (Maynard and Kalra, 1993). [Nitrate N was extracted using KCl rather than water, as was chloride, to allow concurrent measurement of soil ammonium for other studies (Keeney and Nelson, 1982).] The resulting slurries were shaken on a mechanical shaker (low speed) for 60 min at room temperature and allowed to settle for 15 min. Extracts were then filtered through disposable 0.4-μm filters and stored at -20°C until analyzed colorimetrically on a Technicon (Tarrytown, NY) Autoanalyzer II CFA.

Calculations

Annual Soil Water Dynamics

Soil water enters the subsurface through two predominant modes: matrix flow and preferential flow (Beven and Germann, 1982). Matrix flow occurs as the slow diffusion of water, both as a fluid and in the vapor phase, through the matrices of unsaturated soil. Matrix flow is predominantly controlled by spatial differences in water potential between moist soil regions and nearby drier ones. In comparison, preferential flow occurs as the nonuniform, rapid movement of water and solutes from the soil surface to subsurface horizons and weathered bedrock (Bouma, 1991). Preferential flow is spatially concentrated, being focused along preexisting pathways through unsaturated soil, often along continuous channels such as animal burrows, plant roots, or surface cracks, and usually occurs during rain events following periods of dry, warm weather (Beven and Germann, 1982).

Within wildland soils, the relative contribution of preferential flow and matrix flow determines the timing and depth of accessible plant available water, as well as its chemical composition, including soluble nutrients carried to depth from the soil surface. To estimate the relative contribution of each type of flow across the studied hillslopes, the following equations were used.

Total annual water flux [q_{total} (mm yr^{-1})] was estimated using a modification of the chloride ratio method (Wood et al., 1997; Sukhija et al., 2003). Here:

$$q_{\text{total}} = (P \times \text{Cl}_{\text{p}})/\text{Cl}_{\text{gw}} \qquad [1]$$

where P = annual rainfall (mm yr^{-1}), Cl_{p} = average chloride concentration of the infiltrating rainwater (mg L^{-1}), and Cl_{gw} = chloride concentration of the ground water (mg L^{-1}). For this study, Cl_{gw} is approximated using the lowest concentrations of regolith water chloride at depth. To estimate the flux for a year, data from soil cores extracted in October, the driest sampling period, were used for these calculations.

The relative contribution of preferential flow to annual flux through a specific soil depth was estimated as the difference between the total annual water flux and the mean annual matrix water flux:

$$q_{\text{pref}} = q_{\text{total}} - q_{\text{m}} \qquad [2]$$

The mean annual matrix flux to a specific soil depth can be estimated as the water flux [q_{m} (mm yr^{-1})] passing through that depth using the equation:

$$q_{\text{m}} = (P \times \text{Cl}_{\text{p}})/\text{Cl}_{\text{sw}} \qquad [3]$$

where P = annual rainfall (mm yr^{-1}), Cl_{p} = average chloride concentration of the infiltrating rainwater (mg L^{-1}), and Cl_{sw} = average chloride concentration of soil water for the studied depth (mg L^{-1}) (Scanlon, 1991; Wood et al., 1997).

Ecosystem Water Usage

To understand the continued viability of ecosystems under the stress of aridity, it is necessary to understand their water dynamics. In the vadose zone of wildland plant communities, water mass conservation for a given period of time requires:

$$\text{rainfall} = \text{evapotranspiration} + \text{percolation} + \text{runoff} + \Delta\text{soil water} \qquad [4]$$

We used this equation to determine the relative importance of percolation, evapotranspiration, and soil water storage to the CSS and exotic grassland plant communities. Soil water storage (Δsoil water) was calculated annually based on measured soil water values (Table 2). Percolation was assumed to be equal to the total soil water flux (q_{total}) as described above, and runoff was assumed to be approximately zero based on field observations. This equation assumes no lateral entry or outlet of water to or from the soil.

Although this study's sites are located on hillslopes, lateral water flow through the two soils was assumed to be comparable due to the similarities of the sites. Their locations on the studied hillslopes were chosen to minimize differences in available upslope contribution to run-on. Additionally, subsurface downslope water flow was assumed to occur predominantly beneath the soil portion of the regolith, within the weathered and fractured granitic bedrock (Jones and Graham, 1993; Sternberg et al., 1996). The extent of bedrock outcrops was matched as closely as possible between the two hillslopes. This was done to equalize the potential for bedrock runoff, as well as to equalize the availability of any bedrock fractures open to the atmosphere, which could act as direct conduits for rainwater movement to subsurface weathered bedrock.

Seasonal Movement of Nitrate Nitrogen to Below the Coastal Sage Scrub Root Zone

Due to its solubility and ease of translocation by soil water, nitrate N added to the soil in excess of plant removal can be-

Table 2. Soil water content of the sites: near surface 25 cm, underlying soil to the weathered bedrock (WBR), and within the WBR for the healthy coastal sage scrub site at Lake Skinner (+CSS) and the degraded coastal sage scrub site at the base of the Box Springs Mountains (−CSS).

	Soil water content†							
	Soil depth							
	0 to 25 cm		25 cm to WBR‡		>WBR‡ depth		Total	
Sample date	+CSS	−CSS	+CSS	−CSS	+CSS	−CSS	+CSS	−CSS
	cm							
October 2001	1.1 (0.8)	1.0 (0.3)	8.6 (1.8)	3.8 (0.7)	10.3 (–)	3.3 (1.3)	20.1 (2.6)	8.0 (2.3)
January 2002	3.1 (1.0)	1.5 (0.2)	13.8 (2.6)	4.6 (0.8)	5.6 (1.9)	1.9 (0.1)	22.5 (5.5)	8.0 (1.1)
April 2002	1.1 (0.2)	0.9 (0.1)	11.5 (0.6)	3.9 (0.7)	2.3 (–)	1.9 (0.3)	14.9 (0.8)	6.6 (1.0)
July 2002	0.6 (0.3)	0.5 (0.0)	12.4 (1.4)	3.8 (0.8)	7.0 (0.6)	0.5 (0.5)	20.0 (2.2)	4.8 (1.4)
October 2002	0.6 (0.2)	0.4 (0.1)	9.6 (0.8)	3.4 (1.1)	1.4 (–)	4.7 (0.4)	11.6 (1.0)	8.5 (1.6)
January 2003	3.6 (0.3)	1.8 (0.1)	12.4 (1.2)	4.2 (1.4)	2.3 (–)	3.3 (0.8)	18.3 (1.5)	9.3 (2.3)
April 2003	5.6 (0.9)	4.8 (0.3)	15.9 (2.7)	7.7 (1.7)	5.6 (–)	5.6 (0.9)	27.1 (3.7)	18.1 (2.9)
July 2003	0.8 (0.3)	0.5 (0.1)	12.9 (1.1)	3.8 (0.5)	2.3 (–)	2.8 (0.2)	16.0 (1.4)	7.1 (0.7)
October 2003	0.6 (0.1)	0.4 (0.1)	10.5 (1.1)	3.8 (0.7)	0.8 (–)	2.0 (0.3)	12.0 (1.2)	6.2 (1.1)
Average	1.9	1.3	11.9	4.3	4.2	2.9	18.0	8.5
Median	1.1	0.9	12.4	3.8	2.3	2.8	18.3	8.0

† Mean of triplicate samples for each site; values within parentheses represent average deviation.

‡ Depth to weathered bedrock (WBR) for +CSS site is taken to be greater than 175 cm; for −CSS site is taken to be greater than 125 cm.

come a source of ground water pollution. Excess nitrate N leached beneath the root zone of plants represents a significant hazard, since it is beyond the region of biological uptake and can be moved toward underlying aquifers during wet years. High rates of addition of nitrogenous smog pollutants atop wildland soils adjacent the Los Angeles Basin suggest that underlying aquifers may be at risk of nitrate N pollution similar to those beneath agricultural fields.

Studies investigating the magnitude of risk associated with agricultural fertilizer N contamination of underlying aquifers have relied on an inexpensive analytical method developed by Pratt et al. (1978) for estimating the amount of nitrate leached beneath the crop root zone (Al-Jamal et al., 1997). In this method, the ratio between the chloride added to the soil in the irrigation water (kg ha^{-1}) and the measured concentration of soil chloride (mg g^{-1}) below the root zone is used to estimate the leaching fraction. The leaching fraction is then used to calculate the amount of nitrate N (kg ha^{-1}) moved to this depth based on the measured concentration of the soil nitrate N (mg g^{-1}) below the root zone.

Although the assumption of steady state conditions used to derive the equations for this method (Pratt et al., 1978) cannot be met under natural conditions, this method was selected to provide a comparative assessment of nitrate N (kg ha^{-1}) leaching beneath the native shrub root zone on a seasonal basis. Surface additions of chloride were measured using rainwater collectors located on each site and should introduce little error in the accuracy of these methods. Since both sites are close to the ocean, the amount of dry atmospheric deposition of chloride should be very low compared to the addition of chloride in rainwater (Junge and Werby, 1958).

Nitrate N (kg ha^{-1}) present beneath the root zone of native shrubs was estimated using the following equation (Pratt et al., 1972, 1978) for the sampled depth of 150 to 175 cm at each site:

$$\mathrm{NO}_{3\mathrm{RZ}} = \mathrm{Cl}_{\mathrm{TOT}} \times (\mathrm{NO}_{3\mathrm{s}}/\mathrm{Cl}_{\mathrm{s}}) \qquad [5]$$

where $\mathrm{Cl}_{\mathrm{TOT}}$ = total amount of meteoric chloride (kg ha^{-1}) added during a specific time period, $\mathrm{NO}_{3\mathrm{s}}$ = measured nitrate N (mg g^{-1}) for the soil beneath the root zone, and Cl_{s} = measured chloride (mg g^{-1}) for the soil beneath the root zone.

RESULTS

Vadose Zone Physical Characteristics

Both sites have relatively thin soils with sandy loam textures that have formed atop moderately steep hillslopes (Table 1). The soils of the −CSS site are 60 to 100 cm deep with weathered granitic bedrock encountered at approximately 75 to 125 cm, and fresh granite encountered at approximately 150 to 200 cm. The soils of the +CSS site are deeper (75–125 cm) with depth to weathered granitic bedrock at approximately 150 to 175 cm, and fresh granite at approximately 175 to 225 cm. The soil–weathered granitic rock contact was obvious due to changes in the feel during hand augering, and to a distinct color change in the extracted regolith material. The thinner soils of the −CSS site are most likely due to surface sediment losses during vegetation type conversion (Rice and Foggin, 1971; Gabet and Dunne, 2002). We have not attempted to quantify such losses from the −CSS site, but note that they could play an important role in the continued viability of the native shrub community by decreasing the depth of soil available to store water on a seasonal basis.

Vadose Zone Water

As described below, the measured seasonal regolith water distributions and fluxes reflect changes in the subsurface hydrology of the vegetation type converted landscape compared to the native shrubland (Fig. 4 and 5; Tables 2, 3, and 4). The depth and rate of rainwater percolation into wildland hillslope soils in response to early-season storm events has been greatly reduced after the loss of CSS shrubs and vegetation type conversion to invasive grassland. With decreased water flow to depth in the altered vegetation landscape, the upper 25 cm has become the predominant zone of soil water. Here, redistributed rainfall is utilized by fast-growing herbaceous invaders, instead of being moved to depth within the rooting zone of the native shrubs. (Throughout the presentation of results and discussion that follows, differences in means between the two sites were tested using a two-tailed *t* test for samples with unequal variance. Statements of significance indicate a $p = 0.05$.)

Patterns of Regolith Water Depth Distributions

On average, the subsurface of the +CSS site held more than twice the amount of soil water as the −CSS

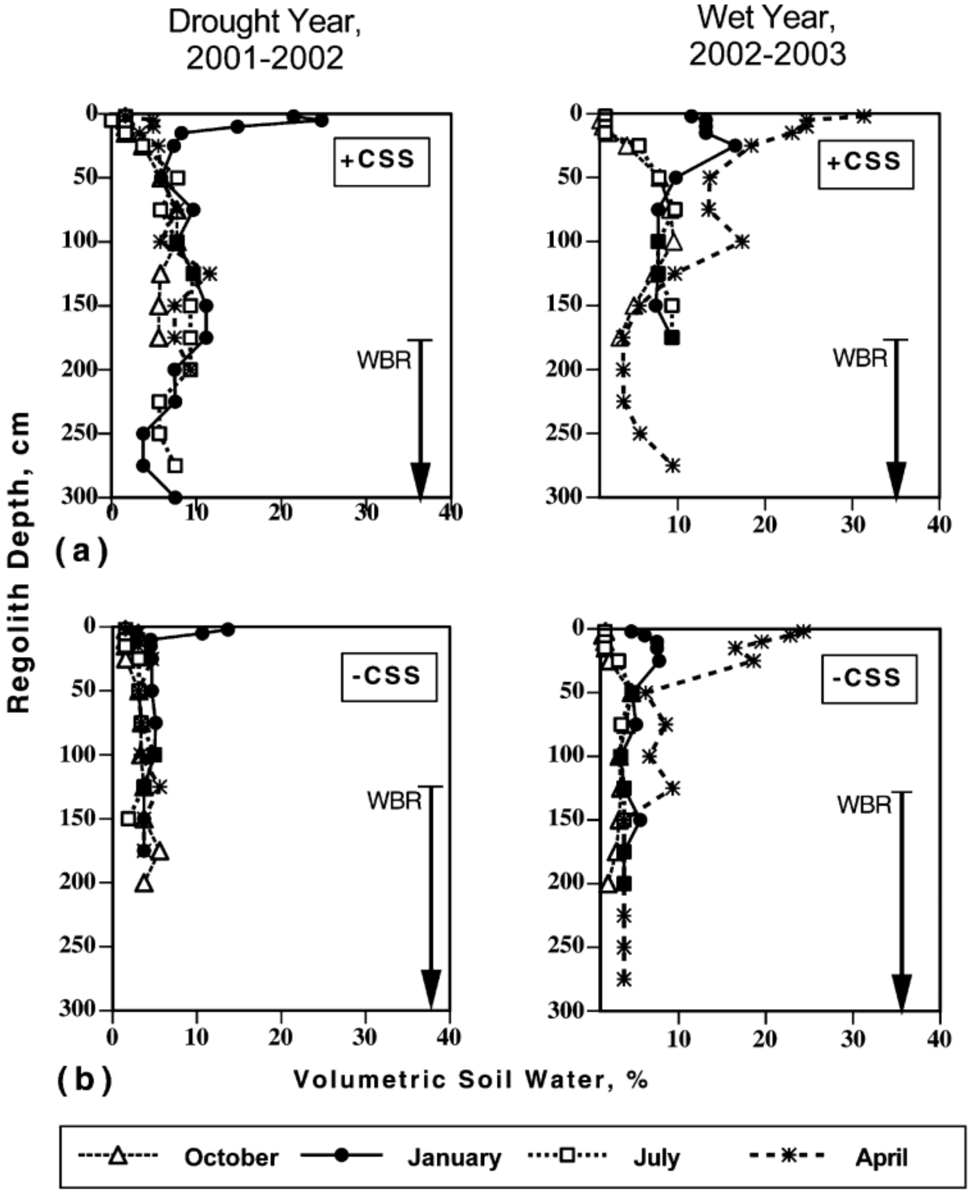


Fig. 4. Percent regolith water, by volume, for quarterly soil cores taken in the extreme drought of 2001–2002, and the following wet year of 2002–2003. An arrow indicates the region of the regolith (on average) that is weathered bedrock (WBR) at each site. (a) Data from the healthy coastal sage scrub site at Lake Skinner (+CSS). (b) Data from the degraded coastal sage scrub site at the base of the Box Springs Mountains (−CSS).

site over the two years of study (Table 2), even though these two sites received nearly the same amount of precipitation in the same temporal patterns (Fig. 3b). While the deeper soils of the +CSS site are expected to hold more water than the −CSS soils, the observed difference in plant available water is proportionally more (2.5 times more water at the +CSS site) than the difference in soil depth (1.3 times more soil at the +CSS site). This suggests that factors other than available water storage capacity are important in causing these differences.

Soil Water Within the Near Surface Zone (≤25-cm Depth)

The top 25 cm of soil at both sites held nearly the same amount of water (mean of 1.3 cm compared to 1.9 cm, Table 2). Here, within the predominant rooting zone of exotic annual grasses (Holmes and Rice, 1996), volumetric soil water values at both sites varied dynamically with wide extremes over the 2-yr period (Fig. 4). With the effects of weather directly impacting the land surface, soil water content after fall and winter storm events was as much as 31%, increased from a minimum of 1% during hot and dry summers (Fig. 4).

Soil Water at Depth (50 cm to the Weathered Bedrock)

Below the 50-cm depth, the +CSS site held on average nearly three times the soil water (11.9 cm) that the −CSS site held (4.3 cm) over the 2-yr period (Table 2). Within this region, which is the predominant rooting zone of native shrubs (Hellmers et al., 1955; Kummerow

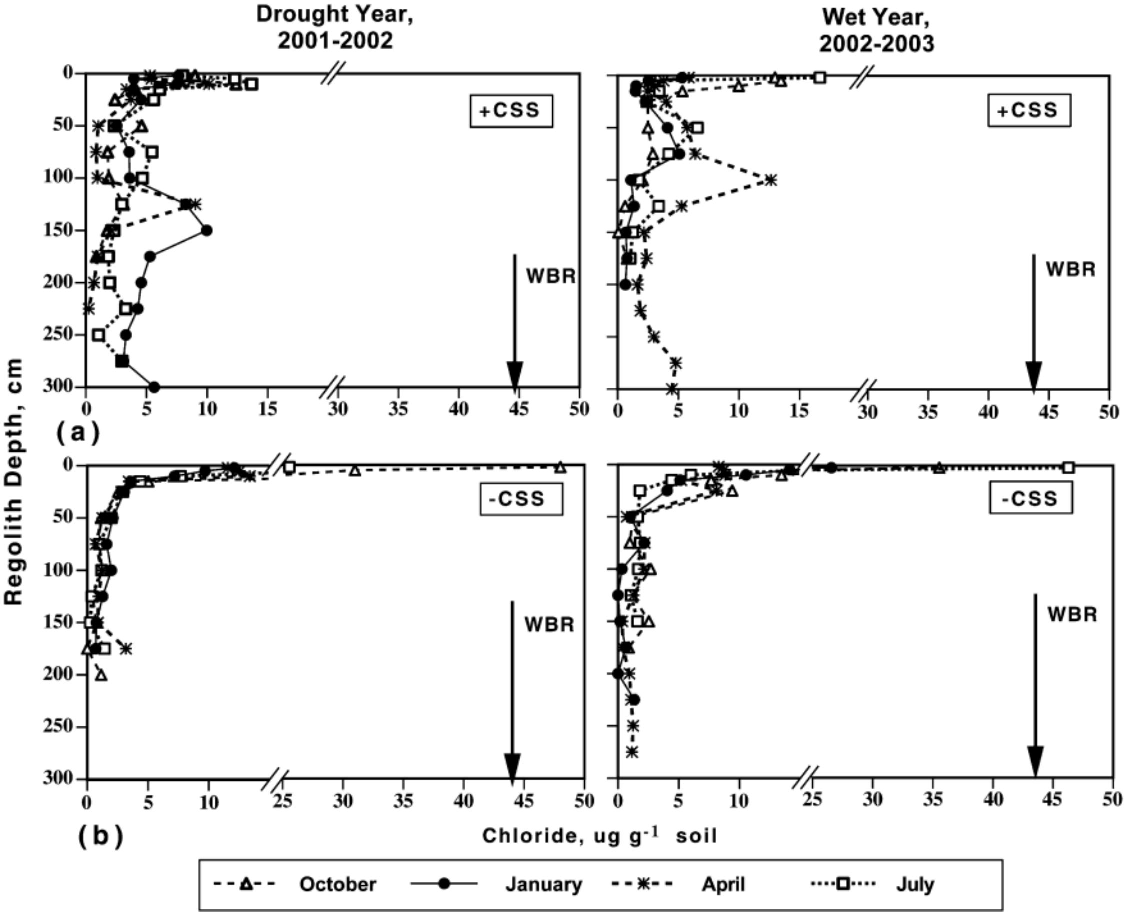


Fig. 5. Regolith chloride (μg g^{-1} based on oven dry soil weight) for quarterly samples taken in the extreme drought of 2001–2002, and the following wet year of 2002–2003. An arrow indicates the region of the regolith (on average) that is weathered bedrock (WBR) at each site. (a) Data from the healthy coastal sage scrub site at Lake Skinner (+CSS). Note the dynamic distribution over time of chloride throughout the regolith depth. (b) Data from the degraded coastal sage scrub site at the base of the Box Springs Mountains (−CSS). Note the L-shape to the curves indicating the strong stratification of soil chloride within the top 25 cm of the regolith, which overlies the static distributions over time of soil chloride beneath the 50-cm depth.

Table 3. Annual soil water dynamics below 25-cm depths: comparison of a coastal sage scrub covered hillslope compared to a hillslope type converted to invasive annual grass and forbs for the healthy coastal sage scrub site at Lake Skinner (+CSS) and the degraded coastal sage scrub site at the base of the Box Springs Mountains (−CSS).

			Soil water flux‡		
Site	Year†	Precipitation	Total§	Matrix¶	Preferential#
		mm yr^{-1}	mm yr^{-1}	% of total flux	% of total flux
+CSS	2001	155.0	2.9	49	51
	2002	75.0	3.2	45	55
	2003	318.0	21.9	56	44
−CSS	2001	166.1	1.7	59	41
	2002	82.4	1.5	91	9
	2003	280.8	2.3	100	0

† Water year measured from November through October.
‡ Based on chloride concentrations in soil water from samples collected at 50 to 125 cm (−CSS site) or to 175 cm (+CSS site). This excludes values from both the near surface and the weathered bedrock region of the regolith.
§ Calculated using the chloride ratio method as described in Materials and Methods.
¶ Calculated using the chloride mass balance method as described in Materials and Methods, and then represented as a percentage of the total flux.
# Difference between total and matrix fluxes, represented as a percentage of the total flux.

et al., 1977; Canadell and Zedler, 1994), plant available water depth distributions over time (Fig. 4) differed between the two sites at a statistically significant level ($p < 0.01$).

At the shrub-covered site (+CSS), regolith volumetric moisture values below the 25-cm depth varied dynamically over the 2-yr period, ranging between approximately 6% during hot, dry summers to upward of 17% in response to fall and winter storm events (Fig. 4a). Here, water represented at least 5% of the soil volume, even in the drought year of 2001–2002.

In contrast, where CSS cover has been greatly reduced for decades and the landscape has type converted to grassland (−CSS), redistribution of rainfall was primarily stratified within the uppermost soil with limited percolation deeper than 25 cm even after storm events. Plant available water was greatly reduced at depth compared to the +CSS site, with measured volumetric soil water remaining nearly static at a value of 3.5% over the two years of this study (Fig. 4b). Higher values occurred only twice, with a small increase (to 5.5%) occurring in response to the storms during the fall of 2001 (January 2002 sampling) and a larger increase (9%) following the substantial winter rainfall (193 mm) before the April 2003 sampling.

Table 4. Annual soil water budget: comparison of a coastal sage scrub covered hillslope to one type converted to invasive annual grass and forbs for the healthy coastal sage scrub site at Lake Skinner (+CSS) and the degraded coastal sage scrub site at the base of the Box Springs Mountains (−CSS).

			Actual distribution of precipitation			Relative distribution of precipitation			
Site	Year†	Precipitation	Recharge‡	Soil storage§	ET and RO¶	Recharge	Soil storage	ET and RO	Growth period#
		mm yr^{-1}				% of incoming precipitation			
+CSS	2001	155.0	2.9	–	–	1.9	–	–	
	2002	75.0	3.2	0.3	71.5	4.2	0.4	95.3	1 Dec.–8 Jan.
	2003	318.0	21.9	0.9	295.1	6.9	0.3	92.8	1 Dec.–11 Apr.
−CSS	2001	166.1	1.7	–	–	1.0	–	–	
	2002	82.4	1.5	−1.0	81.8	1.9	0.0	99.3	1 Dec.–8 Jan.
	2003	280.8	2.3	0.4	278.1	0.8	0.1	99.0	1 Dec.–22 Mar.

† Water year measured from November through October.

‡ Calculated total annual flux from Table 3.

§ Storage value calculated from Table 2 data.

¶ ET, evapotranspiration; RO, surface runoff. Field observations indicate that surface runoff was a very minor component of the soil water budget during the period of this study.

Potential period for plant growth determined from calculated ET (this study) and average measured monthly ETo (nearest CIMIS stations; http://www.cimis.water.ca.gov/cimis/welcome.jsp [verified 19 Aug. 2005]). The term ETo represents the evapotranspiration of a specific reference crop at a specific weather station based on a modified version of the Penrod equation. At CIMIS stations, ETo is measured for complete cover by closely clipped grass. For more information, see http://www.cimis.water.ca.gov/cimis/infoEtoOverview.jsp;jsessionid=A4BD699462854502882265203987534D (verified 19 Aug. 2005).

The difference in soil water movement to the shrub rooting depth between the two sites is illustrated by the following observation. The +CSS soil held 9% water by volume between the depths of 150 to 175 cm after 47 mm of rain (January 2002 sample). In contrast, the −CSS soil required more than four times as much rainfall to attain the same amount of plant available water at the depth of 125 cm following the wet winter of 2003 (April 2003 sample) (Fig. 2 and 4).

Weathered Bedrock Water

This region of the regolith is important for providing stored water to Mediterranean ecosystems during dry summers (Arkley, 1981). The CSS shrubs, whose roots have been observed within weathered bedrock (Knecht, 1971), are expected to utilize plant available water held there (Rose et al., 2003). Between 3 and 10% soil water by volume was measured within the weathered bedrock beneath the +CSS. However, the amount of soil water held in the weathered bedrock at the −CSS site (2–5% soil water by volume) differed significantly ($p < 0.05$) from that at the +CSS site. Over the course of this study, the weathered bedrock at the +CSS site held on average 4.2 cm of water, and at the −CSS site, 2.9 cm of water (Table 2).

Seasonal Differences between Soil Water

The two sites had significant differences between their depth distributions of soil water content for all sampling periods ($p \ll 0.05$) except for samples taken at the end of the driest year (2001–2002) (sampled October 2002) ($p = 0.16$) and samples taken after the wettest 3-mo period (April 2003) ($p = 0.213$). Under these extreme weather conditions, the two sites did not differ significantly in their depth distributions of soil water. At the end of the drought year, the soils at both sites were at their driest, and at the end of the wet winter, the soils at both sites held at least 7% water by volume (Fig. 4).

Soil Chloride and Vadose Zone Water Flux

Patterns of soil chloride depth distributions over time differed significantly within certain regions of the subsurface of the two sites (Fig. 5): the 0- and 5-cm depths ($p < 0.005$) and the 25- to 125-cm depths ($p < 0.05$). No significant differences were noted for chloride distribution patterns within the weathered bedrock.

At the +CSS site, soil chloride was distributed throughout the studied regolith depths with two regions of notable increase over time (Fig. 5a). Within the top 5 cm, soil chloride concentrations ranged from 2 to 17 $\mu g\ g^{-1}$. The low values reflect the leaching of chloride during surface wetting, and the high values represent the concentration of chloride due to evaporation. These dynamic hydrologic processes of wetting and drying of the near surface soil were also seen in the plant available water values (Fig. 4). Similar variance in chloride concentrations occurred at the +CSS site between the 100- to 150-cm depths, reflecting subsurface hydrology as dynamic as that near the surface. In this region, where woody shrub roots are predominantly found (Hellmers et al., 1955; Canadell and Zedler, 1994), quarterly soil chloride concentrations ranged from 1 to 13 $\mu g\ g^{-1}$, again reflecting processes of anion leaching or accumulation.

In contrast, at the −CSS site, soil chloride was highly stratified in its distribution, with most found within the top 25-cm depth. Wide variations in soil chloride concentrations indicate dynamic fluxes in near surface water over time, and concomitant anion leaching and accumulation, similar to the top 5 cm of the +CSS site (Fig. 5b). In this region, where exotic grass roots are predominantly found (Holmes and Rice, 1996), quarterly chloride concentrations ranged from 3 to 48 $\mu g\ g^{-1}$ by soil weight. These values were statistically different than those at the +CSS site ($p < 0.005$). Here, maximum chloride concentrations were nearly three times greater than at the +CSS site, even though the −CSS received about half the chloride additions at its surface.

With depth below 25 cm, variance in soil chloride at the −CSS site was nearly static over the 2-yr period with minimum values near 0 $\mu g\ g^{-1}$, and maximum values of 4 $\mu g\ g^{-1}$. In this region, the variations in chloride concentration were minor, and the depth patterns were statistically different from those at the +CSS ($p < 0.05$)

where extremes were pronounced. This pattern supports limited water movement to depth beneath the invasive grassland landscape, as suggested by the volumetric soil water data discussed above (Fig. 4). This pattern also suggests that during surface wetting episodes when leaching of chloride occurs, soil water may be carrying soluble anions downslope in the near surface rather than moving them to depth as at the +CSS site.

Seasonal Differences

Following the wet winter of 2003 (sampled in April 2003) there was a statistically significant difference ($p = 0.005$) between the soil chloride data collected at the +CSS site compared to the −CSS site. No difference was observed between the depth distributions of plant available water, as reported earlier, indicating that the soil had wetted at both sites during the winter. However, the differences in the depth distributions of soil chloride reflect dissimilar patterns of water flux into the subsurface of the two sites.

Estimates of Preferential versus Matrix Flow

Wetting fronts translocate soluble chloride from the soil surface to depth following fall and winter rainstorms. Then, as water evaporates, chloride concentrates during dry and hot summer months. The resulting patterns of soil chloride distribution with depth form the basis for estimating flux through wildland soils. Patterns of soil water flux differ between the two sites (Table 3). Estimates calculated using seasonal soil chloride profiles from three water years (2001, 2002, and 2003) indicate that annual soil water fluxes at the −CSS site were generally dominated by matrix flow (representing 58–99% of the total flux). In contrast, at the +CSS site, preferential flow consistently accounted for about half (44–53%) of the total flux (Table 3).

Differences in the water flux patterns between the two sites were underscored by their responses to the average water year of 2003 that followed the drought years of 2001 and 2002. During the drought, total soil water fluxes were calculated to be relatively low at both sites (approximately 3 mm yr^{-1} at +CSS versus approximately 2 mm yr^{-1} at −CSS) and both sites had nearly the same amount of soil water moved by matrix flow (between 1 and 1.4 mm yr^{-1}). However, even under conditions of drought, preferential flow at the +CSS site continued to account for half the total water flux for both years (52 and 53%), while at −CSS, preferential flow represented only 6 to 40% of the total water flux.

During the wetter year of 2003, differences between soil water fluxes for the two sites were striking: more than eight times the total water flux occurred at the +CSS site compared to the −CSS site (Table 3). At the +CSS site, total water flux increased to 22 mm yr^{-1}, with 44% of the flux due to preferential flow and 56% due to matrix flow. Increases in the flux due to both types of flow through the shrub-covered hillslope suggest a positive feedback between increased preferential flow and increased matrix flow. Indeed, if root channels offer pathways for preferential flow, they would concurrently offer increased surface area for the initiation of matrix flow.

In contrast, at the −CSS site, the calculated total soil water flux of 2.3 mm yr^{-1} for water year 2003 was estimated to be all matrix flow. While this flux is the fastest estimated for all three years at the −CSS site, it is barely one-tenth the flux estimated for water year 2003 at the +CSS site (21.9 mm yr^{-1}). Since both sites were wetted during the winter of 2003 year based on depth distributions of soil volumetric water (sampled April 2003) ($p = 0.22$), the effect of the faster flux at the +CSS site was to distribute rainwater carrying chloride significantly differently with depth than at the −CSS site ($p = 0.005$). At the +CSS site, most chloride was concentrated in the shrub root zone, with an additional region of concentration in the weathered bedrock (Fig. 5). This suggests that faster preferential flow, representing 44% of the total annual flux of 21.9 mm yr^{-1} beneath the native shrubland, promoted ready soil water transmission into the shrub root zone as well as into the underlying weathered bedrock (Fig. 4). At the −CSS site, most chloride remained stratified in the near surface soil, even after the wet winter of 2003 (Fig. 5), reflecting the limited transmission of rainwater through the soil (Table 3).

Ecosystem Water Usage

Water budgets indicate that greater than 90% of rainfall was removed by evapotranspiration (ET) at both sites with minor amounts converted to storage or drainage (Table 4), which is expected for semiarid plant communities. At the −CSS site, nearly all (99%) of the incoming precipitation for both years was calculated to be removed through ET (or occurred as minor amounts of surface runoff [RO]). At the +CSS site, more water was available for regolith storage or drainage, with 95% of the water for 2002 and 93% during 2003 being removed through ET.

While soil water storage was virtually nil (<<1%) at both sites over the 2-yr study (Table 4), any drainage should be available to be added to stores of water in the weathered bedrock. Drainage below the soil–weathered granitic rock interface represented 4% of the water budget for +CSS during the drought year, and 7% during the average water year, while at the −CSS it represented only 1% for either year. Thus, at the +CSS site, increased soil water flux, including increased preferential flow, promoted four to seven times more drainage into the weathered granitic bedrock region than calculated for the −CSS site. Water within the weathered bedrock should move downslope carrying soluble chloride and nitrate (Jones and Graham, 1993; Sternberg et al., 1996; Tsujimura et al., 2001) and become available to deep-rooted vegetation during dry periods (Arkley, 1981; Rose et al., 2003), be added to ground water, or reappear at the surface through one of the several springs nearby.

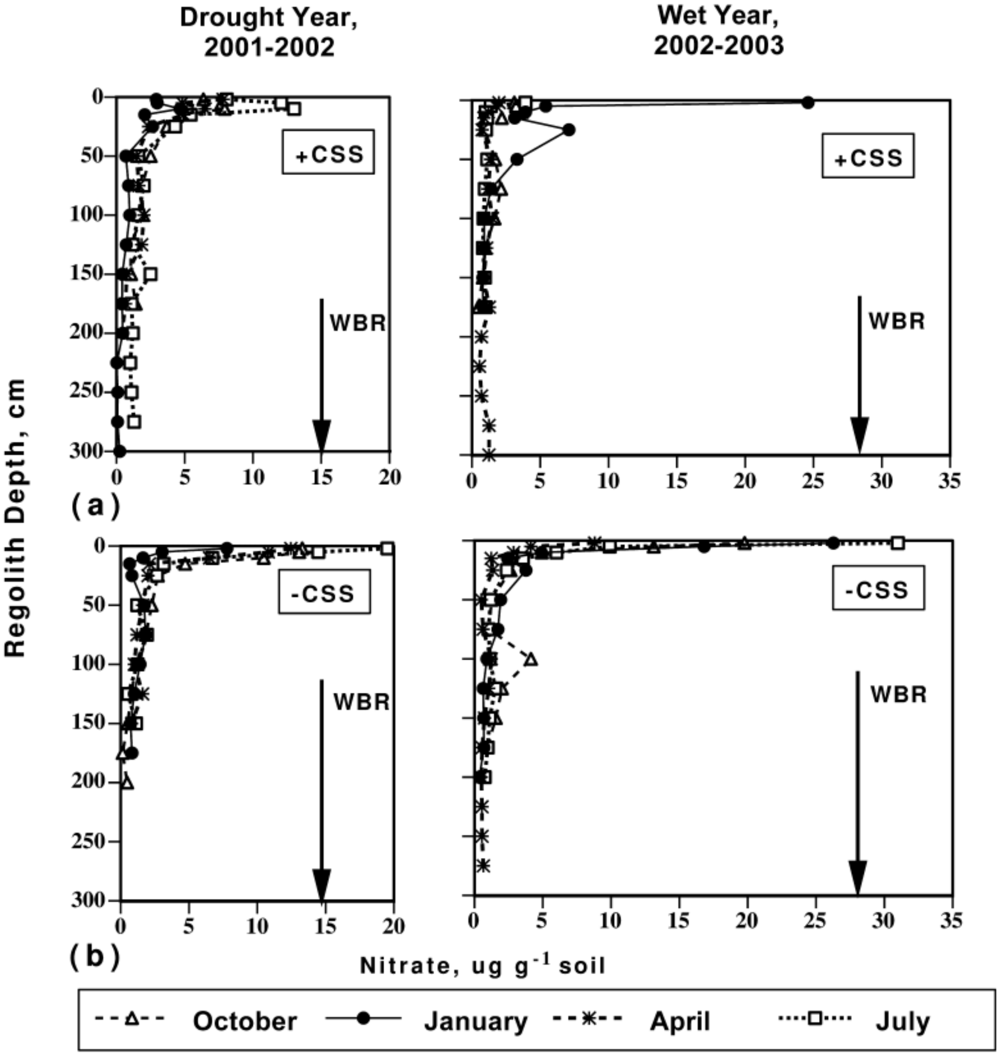


Fig. 6. Regolith nitrate N (μg g^{-1} based on oven dry soil weight) for quarterly soil cores taken in the extreme drought of 2001–2002, and the following wet year of 2002–2003. An arrow indicates the region of the regolith (on average) that is weathered bedrock (WBR) at each site. (a) Data from the healthy coastal sage scrub site at Lake Skinner (+CSS). Note the distribution of nitrate N that is mainly concentrated within the surface 25 cm. However, there is not as strong an L-shape to the distribution as is evident at the −CSS site. (b) Data from the degraded coastal sage scrub site at the base of the Box Springs Mountains (−CSS). Note the L-shape to the curves indicating the strong stratification of nitrate N within the top 25 cm of the regolith.

Vadose Zone Nitrate Nitrogen

Temporal Patterns of Nitrate Nitrogen Depth Distributions

Even though the −CSS site received six times more atmospheric nitrogen inputs at its surface than the +CSS site (Table 1; Padgett et al., 1999), nitrate N depth distributions over time were relatively similar between the two sites (Fig. 6). The only significant difference ($p < 0.05$) was found in the very near surface soil between 0 and 5 cm, due to the very high concentrations of nitrate N stratified there at the −CSS site (Fig. 6). Here, nitrate N concentrations were dynamic, ranging between 3 and 31 μg g^{-1} by soil weight. This 10-fold range in values is reflective of an active hydrologic zone close to the soil–atmosphere interface where large amounts of anthropogenic N were deposited and made readily available for uptake by shallow-rooted plants. Below the 25-cm depth there was minimal change in soil nitrate N concentrations over time at either site.

At the −CSS site, the depth distribution of soil nitrate N correlated with that of chloride ($r^2 = 0.80$; Fig. 5b and 6b), suggesting that primarily water movement determined the patterns of occurrence of both anions throughout the soil. Limited water moves to depth at this site (Fig. 4), suggesting leaching and accumulation of both chloride (Fig. 5) and nitrate N (Fig. 6) primarily within the surface 25 cm of the soil. Both anions become concentrated through ET in the root zone of the invasive annuals. Here, however, the proportion of nitrate N remaining from soil surface additions is greatly reduced compared to the proportion of surface chloride additions remaining. That is, roughly 90% of the incoming nitrate N was removed before its concentration during ET. Proposed mechanisms responsible for its removal include rapid uptake during the growth of invasive annu-

Table 5. Seasonal nitrate N available to be leached to ground water: water years 2002–2003 for the healthy coastal sage scrub site at Lake Skinner (+CSS) and the degraded coastal sage scrub site at the base of the Box Springs Mountains (−CSS).

	Cumulative rainfall		Nitrate N leached beneath CSS root zone	
Sample date	+CSS	−CSS	+CSS	−CSS
	mm		kg ha^{-1}	
October 2001	1	3	0.0	0.0
January 2002	47	59	0.0	0.4
April 2002	27	20	0.3	0.1
July 2002	0	1	0.0	0.0
October 2002	1	2	0.0	0.0
January 2003	69	72	1.0	2.1
April 2003	229	200	1.7	2.8
July 2003	19	9	0.3	0.0
October 2003	1	0	0.0	0.0
Estimated nitrate N leached, kg ha^{-1} yr^{-1}			1.7	2.7

als and grasses, storage in the soil as a solute during slow matrix flow through the subsurface, or rapid downslope leaching in the near surface soil following the initial storm events of each year.

In contrast, at the +CSS site, subsurface patterns of nitrate N and chloride were dissimilar, showing little correlation when compared by depth increments (r^2 = 0.16). This suggests that processes in addition to subsurface water movement (most likely biological) control the depth distribution of soluble nitrate N. In the very dry year of 2001–2002, nitrate N increased at depth within the soil of +CSS after the onset of the drought (April, July, and October, 2002 samples), perhaps added to the soil through the death of fine roots. During the wetter year of 2002–2003, soil nitrate N values remained nearly the same for all soil depths during the winter (April, 2003) and spring (July, 2003). The only notable increase in nitrate N at the +CSS site (Fig. 5a) occurred within the soil surface (especially at the 0- to 2-cm depths) after fall rains (January, 2003), an event noted during other average rain years by researchers at this site (Padgett et al., 1999). If this higher concentration of surface nitrate N (26 μg g^{-1}) was moved to depth by the rapid soil water flux, as was chloride, it must have been used by the native shrubs for growth, leaving little left to be concentrated in the soil at depth.

Seasonal Patterns of Nitrate Nitrogen Accumulation at Depth

Large surface additions of nitrate threaten water quality when they are in excess of plant requirements and are translocated beneath the depth of biological removal, that is, beneath the root zone of the dominant vegetation (Schepers et al., 1991). Then nitrate becomes available to be leached through preferential flow paths within the weathered bedrock, and on to ground water or surface stream systems.

Overall, twice the amount of nitrate N was moved beneath the shrub root zone (150–175 cm) at the −CSS site than at the +CSS site (Table 5). During the drought year of 2001–2002, neither site accreted appreciable amounts of nitrate N in this region (<0.5 kg ha^{-1}), reflecting low soil water fluxes incapable of moving soluble anions to depth (Table 3). In contrast, during the wet fall and winter months of 2002–2003 (October 2002 and January 2003 samples) both sites had increased nitrate N movement to beneath the rooting depth of shrubs. At the shrub-covered site, three times the amount of nitrate N moved during the wet winter compared to the preceding drought year (approximately 1.7 kg ha^{-1}). At the −CSS, the increase was sixfold between these time periods (approximately 2.8 kg ha^{-1}). This suggests that either site can present a hazard to water quality if sufficient nitrate N accumulates within its soil before wet years.

DISCUSSION

After nearly three decades of vegetation type conversion (Fig. 1), the depth and rate of rainwater percolating into the soil of wildland hills covered by invasive grasslands has been greatly reduced compared to those covered with native California coastal sage scrub. The predominant zone of plant available soil water beneath invasive grasslands is within the surface 25 cm of soil. In contrast, where native shrubs remain, water moves readily down-solum in response to early-season storm events (Fig. 3). These contrasting patterns of subsurface hydrology drive two different soil–plant interactions, each of which support the continued viability of their current vegetation type.

Loss of Native Shrubs Alters Subsurface Hillslope Hydrology

The subsurface hydrology of relatively pristine granitic hillslopes across cismontane California is strongly influenced by the presence of CSS. Native shrubs foster faster infiltration (Fierer and Gabet, 2002), greater regolith water at depth (Table 2), and the presence of soil water earlier in the season than do exotic grasses and forbs (Fig. 3 and 4). Loss of coarse, deep woody shrub roots and their replacement by dense, fine shallow grass roots (Holmes and Rice, 1996) alters soil macropore structure to one that moves water downward as slow, diffuse, matrix flow (Williamson et al., 2004b) as seen at the −CSS site (Table 3). Slow percolation concentrates most incoming precipitation in the region of the shallow roots of exotic grasses and forbs (0- to 50-cm depths), where it is available for their growth, rather than in the rooting zone of native shrubs (125- to 175-cm depths). As a result, the average water stored in the soil beneath 25 cm to the weathered bedrock region of the −CSS site was about one-third that stored at the +CSS site (Table 2). Additionally, downward flux to the zone of weathered granitic bedrock is reduced at the −CSS site, with annual water fluxes to this depth nine times faster at the +CSS site than at the −CSS site during the wetter year of 2002–2003 (Table 3). During the average water year 2002–2003, only 1% of the −CSS soil water budget percolated to weathered bedrock, compared to 7% for the +CSS site (Table 4). As a result, the average water stored in the weathered bedrock region of the −CSS site was three-fourths that stored at the +CSS site (Table 2).

Soil Water Patterns across the Landscape and Coastal Sage Scrub Ecosystem Processes

Native shrubs respond with new growth within days of early rain events, suggesting that rapid movement of rainwater along preferential flow paths (Table 3) provided by root channels (Halvorson et al., 1997; Schulze et al., 1998; Burgess et al., 2000; Devitt and Smith, 2002) plays a core role in the ecosystem functioning of these plant communities. The resulting patterns of temporal and spatial soil water distributions across CSS landscapes drive important ecosystem processes (Kirkpatrick and Hutchinson, 1980).

Native Shrub Seedling Establishment Following Disturbance

Where invasive grasses become established, early-season preferential flow to below soil depths of 25 to 50 cm is reduced (Fig. 4b). This compromises shrub juvenile recruitment after disturbance since seedling taproots cannot acquire adequate soil water (Eliason and Allen, 1997). Available opportunities for CSS seedling establishment across these grasslands are then reduced to late in wet years (Cione et al., 2002), or a series of wet years such as El Niño events, when there is sufficient precipitation to increase soil water at depth (Fig. 4b) through matrix flow (Table 3). Such a reduction in the number of years, as well as months per year, available for successful seedling establishment decreases the rate of recruitment of new shrubs across the degrading landscape, especially as fewer shrubs become available to produce viable seed (Cione et al., 2002).

Coastal Sage Scrub Loss and Reduced Surface Soil Water

Additionally, temporal patterns of plant available water within the near surface, where it is required by many shrub species for germination, is altered when grass invades. Loss of contiguous shrub cover decreases shade, and increases soil temperatures and shallow soil water evaporation across these hills (Breshears et al., 1998) during warm days. At the same time, early germinating invasive grasses require water for their seedlings. The surface 25 cm of soil at the +CSS site, where shrubs provided shade and invasive annuals were few, held more water than at the −CSS sites (Table 2). This was especially notable after fall rains (Fig. 3b and 4a) when +CSS soil ($\leq$25-cm depth) held twice the plant available water as the −CSS soil (Fig. 4). Relatively less of the incoming precipitation was utilized for ET (Table 4) at the +CSS site (95%) compared to the −CSS site (99%). Beyond differences in water requirements between the grasses and the native shrubs, this is probably an effect of cooler soil surface temperatures due to increased shade (Breshears et al., 1998) and of the ready movement of water deeper into the soil (Fig. 4) where temperature ranges are attenuated.

Coastal Sage Scrub Loss and Reduced Soil Water with Depth

The soil region represents an important seasonal store of water for the +CSS site (Fig. 5), whereas the amount of water held within the soil of the −CSS site is three times less than that at the +CSS site (Table 2). The loss of woody shrub root channels available to transmit water as preferential flux is an important mechanism in this reduction, as is the loss of available soil depth (Table 1). Not only do thinner soils provide fewer matrixes for storing water, they also will have higher mean subsurface temperatures as air temperatures increase, which will increase ET demand. Thus, the loss of soil due to vegetation type conversion (Gabet and Dunne, 2002) is a phenomenon that should be addressed during attempts to restore CSS plant communities across southern California hills.

Coastal Sage Scrub Loss and Reduced Weathered Bedrock Water

Fall and winter rainfall moved to depth by vertical preferential flow and then stored within weathered granitic bedrock is important to this Mediterranean-type shrubland during hot and dry periods (Arkley, 1981; Jones and Graham, 1993; Sternberg et al., 1996; Rose et al., 2003). At the +CSS site, where ET demand was less than at the −CSS site, more water was available for transmission to depth and weathered bedrock replenishment represented 4% of incoming precipitation compared to 2% at the −CSS site during the drought of 2001–2002 (Table 4). Wetting and drying cycles below the soil–weathered granitic rock interface at the +CSS site (Fig. 4a and 5a) suggest utilization of this reservoir by shrubs whose woody roots have been observed to extend to such depths (Knecht, 1971).

Subsurface preferential flow pathways do not only move water vertically along root channels. Hillslope gradients also play an important role in determining the subsurface pathways of soil water and shallow ground water (Hewlett, 1961). After movement of water to depth, subsurface features that roughly parallel the surface topography, such as the soil–bedrock interface, control preferential flow downslope at depth (Freer et al., 1997). Thus, the reduction of water flow to the weathered bedrock zone under the type-converted hills may impact nearby native plant communities that rely on baseflow, such as those within riparian zones or near ephemeral spring systems.

Coastal Sage Scrub Loss, Nutrient Nitrogen Dynamics, and Water Management Concerns

The movement of soluble nitrate N to pollute freshwater systems is a concern associated with anthropogenic additions of nitrogenous compounds to native hillslope ecosystems (Riggan et al., 1985; Fenn et al., 2003). Estimates of the relative apportionment of nitrate within and through the soils of the two sites allow comparisons of their nutrient N dynamics and subsequent potential to degrade freshwater systems.

Nitrate Nitrogen Dynamics Across +CSS Hillslopes

At the +CSS site, approximately 1.7 kg ha^{-1} yr^{-1} of the annual atmospheric load (5 kg ha^{-1} yr^{-1}) of nitrate

N (Table 1) moves to within the soil–weathered bedrock contact (Table 5). Assuming that all remaining surface additions of nitrate N are consumed by the native shrub system, then approximately 3.3 kg $\mathrm{ha^{-1}\ yr^{-1}}$ is utilized during growth at the +CSS site. This approximation is based on the assumption that very little nitrate N moves downslope in the near surface soil as a solute. These estimates suggest that CSS naturally contributes excess nitrate N to neighboring lower elevation plant communities, flushed during rainy seasons through the weathered bedrock to be made available to very deep-rooted plants, or to be added to freshwater stream systems, nearby springs, or ground water.

Accretion of elevated levels of nitrate within the root zone of native chaparral shrubs was suggested by Riggan et al. (1985) to be responsible for the heightened nitrate concentrations in streams draining the mountains that ring the smoggy Los Angeles Basin. This raises concerns that if smog levels increase near the relatively pristine +CSS site, then the deeper subsurface hydrology could readily carry excess anthropogenic nitrogen from the soil surface to depth beneath the shrub root zone along preferential flow pathways. Elevated levels of nitrate N could accumulate within weathered bedrock, becoming available to be moved to freshwater streams or ground water during wet years. Similar concerns were raised by Walvoord et al. (2003) after their discovery of very large reservoirs of nitrate N deep within arid alluvial fan systems in the Great Basin Desert that had been added naturally following Holocene climate change to drier conditions.

Nitrate Nitrogen Dynamics Across −CSS Hillslopes

At the −CSS site, approximately 2.7 kg $\mathrm{ha^{-1}\ yr^{-1}}$ of the annual atmospheric load (30 kg $\mathrm{ha^{-1}\ yr^{-1}}$) of nitrate N (Table 1) moves to within the soil–weathered bedrock contact (Table 5). Thus, an estimated approximately 27 kg $\mathrm{ha^{-1}\ yr^{-1}}$ of nitrate N remains available in the uppermost soil of the −CSS site to either support invasive grassland biomass accumulation or to be translocated downslope to lower elevations. Invasive grasses utilize, at a very rough estimate, four to seven times more nitrate N than native CSS (Yoshida and Allen, 2004). Based on a consumption of 3.3 kg $\mathrm{ha^{-1}\ yr^{-1}}$ by native CSS (as suggested above), the invasive grassland biomass production would utilize between 13 and 23 kg $\mathrm{ha^{-1}\ yr^{-1}}$.

Between 4 and 14 kg $\mathrm{ha^{-1}\ yr^{-1}}$ would then be available to be translocated downslope in the upper 25 cm of soil. High near surface fluxes during the first rains of the season, when biotic N demand is lowest, also predisposes the −CSS hillslopes to N loss. Here less water moves to depth early in the season (Fig. 4). However, the high concentrations of nutrient N within the very near surface (0–5 cm) of soil at the grassland site are reduced to zero after fall rains, suggesting not only its utilization by grasses but also its transmission downslope before its utilization by invasive grasses.

This scenario suggests that −CSS hills produce seasonal flushes of nitrate N within two regions of their soil, which are available to impact ecological processes on a landscape scale. Stratified within the uppermost surface 25 cm of soil, large amounts of soluble nitrate N are translocated downslope to basin sediments, surface stream systems, or to nearby plant communities (native or wildland). Within the weathered bedrock, a smaller amount of nitrate N is available to be translocated downslope (Freer et al., 1997) during El Niño and be added to stream systems, nearby springs, or to the much deeper regional aquifers.

Conceptual Ecohydrologic Model of Coastal Sage Scrub Loss

We propose that the interaction of high anthropogenic nitrate N additions and loss of deep shrub roots as conduits for preferential flow initiates a feedback mechanism fostering the health of invasive annual plants at the expense of the native CSS plant community (Fig. 7). The CSS decline across hillslopes probably begins as invading annual plant species establish in regions with high anthropogenic N additions to the soil surface (Yoshida and Allen, 2004). As early-season exotic annual grasses increase in cover within CSS stands, their dense, fibrous, shallow root systems (Holmes and Rice, 1996) act to limit the movement of soil water to depth. This further fosters their growth by concentrating anthropogenic N additions in an increasingly shallower depth of moistened soil. At the same time, both adult and juvenile native shrubs, which rely on the availability of soil water below 50 cm early in the growing season, are disadvantaged (Hellmers et al., 1955; Kummerow et al., 1977; Canadell and Zedler, 1994; Eliason and Allen, 1997).

Eventually the decline of CSS stands is further ensured as their response to fire is compromised. With CSS cover diminished, fewer root channels are available from charred stumps to carry water deep into the burned hillslope (Halvorson et al., 1997), reducing the success of shrub seedling establishment across a landscape with a decreasing shrub species seed-bank (Cione et al., 2002). Then, a highly fertilized soil solution in the top 25 cm of soil, resulting from high anthropogenic N additions, further supports invading annual grasses and forbs after fire. The increased frequency and greater extent of grassland fires add momentum to the decline of native shrubs (D'Antonio and Vitousek, 1992; Minnich and Dezzani, 1998) as the time available to reestablish healthy, contiguous CSS cover is greatly reduced.

Implications for Coastal Sage Scrub Restoration

Southern California's CSS is among the most intensively human-impacted vegetation types in the United States (Westman, 1981; Minnich and Dezzani, 1998) and has become a focus for mitigation and restoration efforts (Bowler, 1990). Our results suggest that, in addition to other established techniques (Allen, 2004), such efforts should focus on reinstating a subsurface hydrologic regime that moves water below the 50-cm soil depth. The successful reestablishment of a healthy belowground ecosystem may be core to ensuring the long-term stability

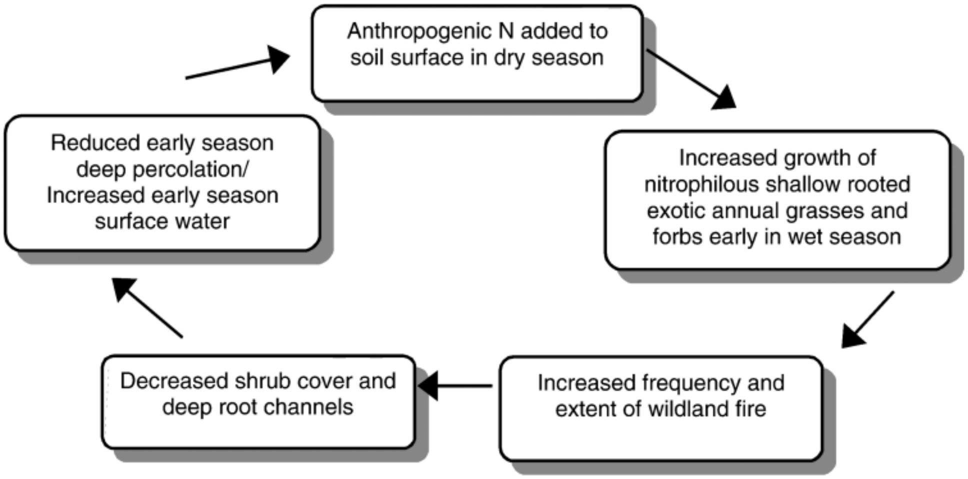


Fig. 7. Schematic of the negative feedback between physical and biotic processes associated with additions of anthropogenic nitrogen that drives coastal sage scrub (CSS) decline over time.

of restored CSS vegetation across hillslopes previously invaded by exotic annual grasses. Mechanical methods should be investigated to offer vertical preferential flow pathways that mimic natural root channels or animal burrows, especially after grassland fires. Additionally, plantings of native shrubs should take advantage of spatial patterns of subsurface water movement controlled by the landscape's geomorphology. For instance, just below bedrock exposures, especially those with significant fracture systems, rainwater will be transported to greater depth than beneath the grass-covered soil.

CONCLUSIONS

Our results suggest a major shift in the hydrologic response of degraded CSS ecosystems as mature shrubs, and their root conduits, decrease in number. As a result, the top 25 cm of the soil becomes the predominant zone of water movement, with increasing amounts of exogenous nitrogen being concentrated in a shallow depth of the upper soil. Such a shift in hydrologic response should increase the rate of CSS ecosystem loss in these regions as shrub seedling establishment rates decline and the infiltration of rain to depth slows. This will limit the growth of mature shrubs and favor early-season exotic plants due to increased water and nutrient N concentrations in a shallower depth of soil.

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