Shrub Recruitment 10 Years Following Fire on Type-Converted and Native Chaparral Watersheds of San Dimas Experimental Forest, California[1]

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Abstract

Following the 1960 Johnstone wildfire, some areas on the San Dimas Experimental Forest, CA were type-converted from native chaparral to non-native grasses. In 2002, the Williams fire re-burned much of the same area. In 2012, vegetation was measured to document post-fire chaparral recruitment and recovery in the presence and absence of these previous type-conversions. Six 1-3 ha (2.5-7.5 ac) watersheds were studied: three type-converted and three native chaparral. Of 59 plant species identified, 49 were native. Mean cover values for sub-shrubs and grass were significantly greater in type-converted watersheds compared to native chaparral. In contrast, shrub, litter, total live and total cover values were significantly greater in native chaparral watersheds than type-converted. Tree, forb and bare soil cover values were similar among all watersheds. Shrubs and sub-shrubs combined provided 76 percent cover on type-converted watersheds and 114 percent on chaparral watersheds. Type-converted grass cover was mostly *Ehrharta calycina* with values between 4 and 40 percent compared to 6-8 percent in native chaparral watersheds. Over 52 years after type-conversion and 10 years following fire, results show that sub-shrubs and woody shrubs re-established in both type-converted and native chaparral watersheds. While all watersheds were mostly soft and hard chaparral species, two of three type-converted watersheds had a significant component of non-native grass cover. Future disturbances such as close interval wildfire or climate change may further contribute to non-native annual and perennial grass expansion, possibly changing the community recovery dynamics. Further research is needed to identify how and if these historical disturbances will continue to affect this unique landscape and its associated plant assemblages.

Keywords: hard chaparral, non-native plants, post-fire vegetation recovery, soft chaparral, type-conversion, watershed management, wildfire.

Introduction

Type-conversion of fire-adapted chaparral vegetation to non-native herbaceous grasslands has become a major concern in southern California, especially in wildland urban interface zones that burn frequently (Jacobson et al. 2004, Keeley et al. 2005). Non-native species dominate many areas previously occupied by chaparral shrublands (Keeley and Brennan 2012). Furthermore, climate change characterized

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by increased temperatures and erratic precipitation may favor proliferation of invasive species over native vegetation on disturbed sites (D'Antonio 2000). For these and other reasons, disturbances such as close-interval fire can threaten the ecological integrity of California chaparral by reducing native species distributions and diversity while altering ecosystem processes which favor non-native species.

Following fire, chaparral typically progresses initially from herbaceous forbs to "soft" chaparral (Conrad et al. 1986, Paysen et al. 1980) which is composed of shallow rooted, drought-deciduous, semi-woody (subligneous) sub-shrubs such as *Acmispon glaber* (deerweed), *Eriogonum fasciculatum* (California buckwheat), or *Salvia mellifera* (black sage). As time after disturbance increases, "hard" chaparral species composed of longer-lived, woody, deep-rooted sclerophyllous shrubs such as *Adenstoma fasciculatum* (chamise), *Ceanothus* spp. (California lilac), *Quercus* spp. (oak), and *Arctostaphylos* spp. (manzanita) normally dominate southern California chaparral ecosystems (Horton and Kraebel 1955). Generally, closed canopy conditions are associated with mature "hard" chaparral. However, close-interval fires or other disturbances such as mechanical manipulation of the vegetation have been known to change the trajectory of ecological processes where communities do not recover to a pre-disturbed state within typical succession time (D'Antonio and Vitousek 1992, Mack and D'Antonio 1998, Stylinski and Allen 1999). Hence, permanent type-conversion of native plant communities can occur.

Following the 1960 Johnstone wildfire, many watersheds on the San Dimas Experimental Forest (SDEF), Angeles National Forest, CA were type-converted from mixed chaparral shrublands to non-native annual and perennial grasses in order to study resource and watershed management alternatives. To aid the establishment of seeded grasses, various chemical (herbicide) and mechanical methods were used throughout SDEF to remove native shrubs during the first three years following the fire (Corbett and Green 1965, Rice et al. 1965). Species such as *Bromus mollis* (Blando brome), *Agropyron* spp. (pubescent and intermediate wheatgrass), *Lolium rigidum* (Wimmera ryegrass), *Phalaris tuberosa* var. *stenoptera* (Harding grass), *Poa ampla* (big bluegrass), and *Oryzopsis miliacea* (smilo grass) were deliberately seeded in many watersheds (nomenclature follows Corbett and Green 1965). Some objectives of chaparral landscape manipulation during that era included developing techniques to improve water yield, erosion control, wildlife forage, and to assist wildland fire management at the WUI by replacing extremely flammable native shrubs with fast growing, seeded non-native grasses (Bentley 1967).

In 2002, the Williams fire burned about 16,000 ha (40,000 ac) of the Angeles National Forest, including both 42 year old native chaparral and type-converted watersheds on the SDEF. A Joint Fire Science Program study was funded in 2003 (JFSP Project Number 03-2-3-13) in part to investigate if the previously mentioned watershed management actions affected vegetation recovery after the 2002 Williams fire. In 2003, mean species richness by watershed was 35 in type-converted and 33 in native chaparral (Wohlgemuth et al. 2008). Four years post-fire, average species richness decreased for type-converted watersheds to 20 and native chaparral to 22. Initially, grass and forb cover dominated both watershed types, but the majority of cover shifted from herbaceous and grasses to sub-shrubs and shrubs by 2006. Four years post-fire, type-converted watersheds had a combined shrub and sub-shrub cover of 38 percent compared to 46 percent in native chaparral watersheds. In 2006, average grass cover for type-converted watersheds was 13 percent and 3 percent for native chaparral. Less shrub and forb cover and more sub-shrub and grass cover were found in type-converted compared to native chaparral watersheds. By the end of the

2006 measurement period, none of the watersheds had become woody, closed canopy chaparral.

In 2012, the six watersheds from the JFSP study were re-measured to determine whether shrub establishment and community development had changed in type-converted or native chaparral watersheds. More specifically, the intent of this re-assessment was to document if the overall cover of seeded non-native grasses or other non-native species had increased in type-converted watersheds or spread into native chaparral areas following the Williams fire, and if this grass cover corresponded to a decreased sub-shrub and woody shrub cover. Additionally, changes in species richness from 2003 to 2012 were compared between watershed types. Possible long-term vegetation disturbance scenarios in these burned native chaparral and type-converted watersheds include: 1) remain type-converted, 2) remain or return to chaparral, 3) become type-converted from native chaparral to weedy grassland, or, 4) become something in-between.

Methods

This study was conducted on the San Dimas Experimental Forest (SDEF), located in the San Gabriel Mountains, approximately 45 km (27 mi) northeast of Los Angeles, CA (figure 1). SDEF was established in 1933 and is administered by the U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station (Dunn et al. 1988). This reserve consists of over 7,000 ha (17,000 ac) and is centered at a latitude of 34^{o} 12’ N and longitude of 117^{o} 46’ W. It has a typical Mediterranean type climate with hot, dry summers and cool, moist winters. The area generally has southeast facing aspects with mean slopes of 68 percent and elevations between 450 and 1,700 m (1,500-5,500 ft.) (Dunn et al. 1988). The study area is underlain by crystalline metamorphic and intrusive igneous bedrock that typically produces steep slopes and poorly defined soil profiles with non-cohesive sandy loam soils (Wohlgemuth and Hubbert 2008). Soil depths ranged among all study watersheds from 0.15 to 0.24 m (0.39-0.78 ft.) (Unpublished data on file at Riverside, CA). Vegetation in SDEF is dominated by chamise-chaparral and mixed-chaparral, with woodland and riparian vegetation in canyon bottoms (Riggan et al. 1988).

This study documents post-fire vegetation growth 10 years following the 2002 Williams fire in six small watersheds (1-3 ha (2.5-7.5 ac)) which are located southeast of Glendora Ridge Road near Tanbark Flat and Forest Service Roads 1N14 and 1N10. Three of the watersheds were type-converted using herbicides and seeded with non-native grasses following the 1960 Johnstone wildfire (Corbett and Green 1965, Williamson et al. 2004). The other three had 42 year old mixed chaparral at the time of the 2002 Williams fire and served as untreated controls. Prior to the 2002 Williams fire, type-converted watersheds were predominantly *E. fasciculatum* and *S. mellifera* with a large component of the perennial non-native grass *Ehrharta calycina* (African veldt grass) (personal observations). All watersheds were mostly surrounded by native chaparral.

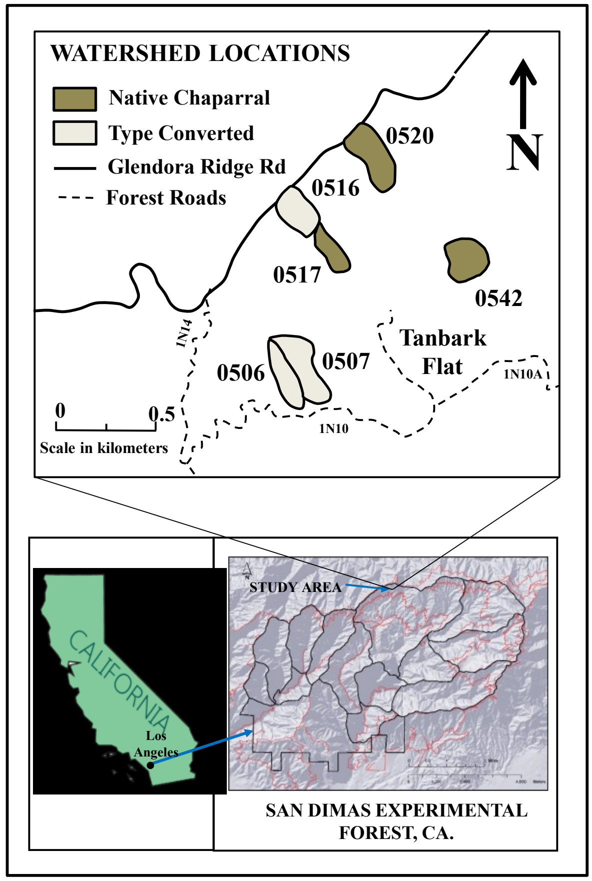

Figure 1—Study area location. The shaded relief map shows the perimeter of San Dimas Experimental Forest with major watershed boundaries, roads and trails within the Angeles National Forest, CA. Upper inset shows the relative locations of six small watersheds used for this study; three type-converted (0506, 0507 and 0516) and three native chaparral (0517, 0520, and 0542).

During July and August 2012, vegetation composition and cover were measured in each of six watersheds using 30 or 40 previously established 10 m (32 ft.) transects (Wohlgemuth et al. 2008). Line intercept sampling (Canfield 1941) was used to quantify plant cover and species richness along each transect (figure 2). Plants were identified to species (nomenclature follows Baldwin et al. 2012). Each species was assigned to a physiognomic growth form (tree, shrub, sub-shrub, forb or grass). The shrub category refers to deep-rooted, evergreen “hard” chaparral species (Sawyer and Keeler-Wolf 1995). Sub-shrubs include drought-deciduous, semi-woody plants sometimes referred to as “soft” chaparral (Conrad et al. 1986, Paysen et al. 1980). Forbs included herbaceous plants other than grasses or grass-like plants. All species were classified as native or non-native (USDA, NRCS Plants Database 2013).

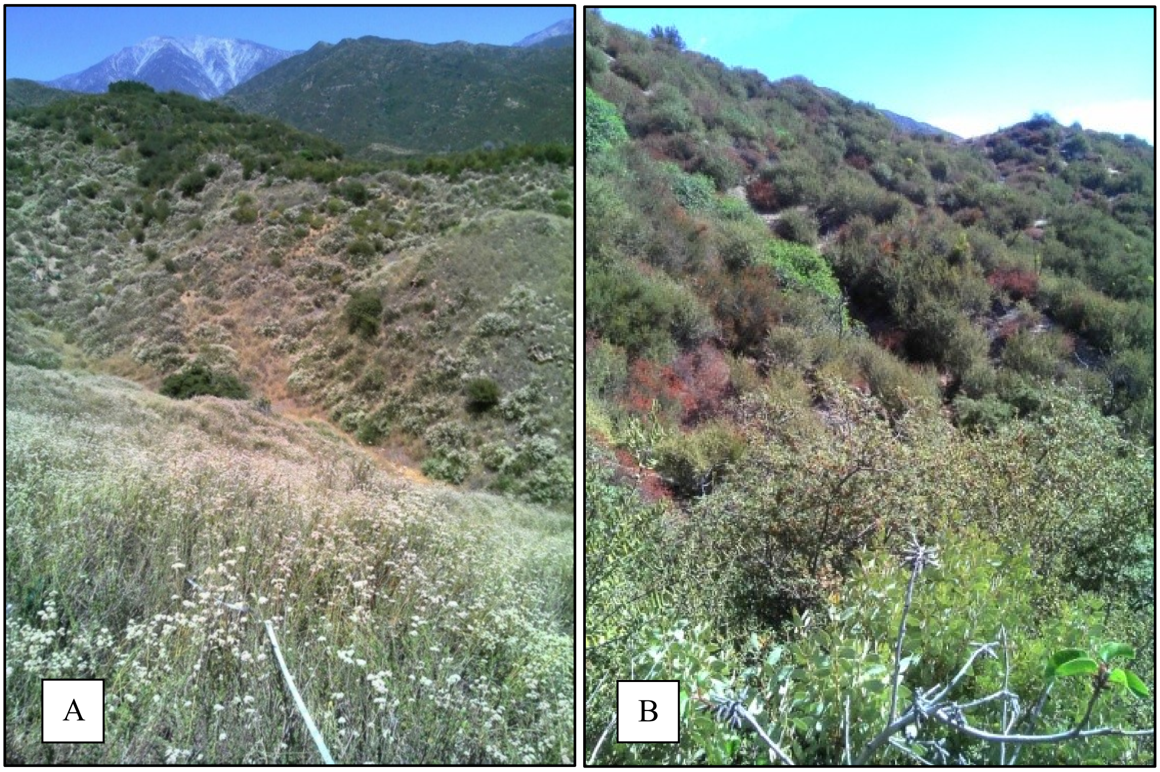

Figure 2—Vegetation for two watershed types were measured in 2012, 10 years after the 2002 Williams fire in the San Dimas Experimental Forest, CA. (A). Dominant live plant cover in type-converted watersheds included the sub-shrub *Eriogonum fasciculatum*, the non-native perennial grass *Ehrharta calycina* and some native shrubs: *Ceanothus crassifolius, Adenostoma fasciculatum,* and *Quercus berberidifolia.* (B). Native chaparral watersheds had an overlapping live plant cover that was predominately shrubs: *A. fasciculatum, C. crassifolius, Arctostaphylos glandulosa* and *Q. berberidifolia*. Photos: USDA Forest Service.

Areas without live vegetation were recorded as cover categories of plant litter or bare soil--which included rocks. If litter was observed in the understory, then litter cover was recorded as well as the plant cover above it. Additional species observed outside designated line transects were documented to identify future seed sources and overall species richness. Species not encountered along line transects (but within 20 m) were noted as “nearby” species. However, cover of these “nearby” species was not measured.

Cover was calculated separately by species and physiognomic growth form for each transect. Mean species cover and richness were compared in the presence and absence of the historic type-conversions for all watersheds and between watershed types to determine the extent of plant community development since the 2003-2006 JFSP study (Wohlgemuth et al. 2008).

To identify significant differences in cover of physiognomic growth forms between watershed types, a linear mixed model analysis was performed using SAS with watersheds a random variable and transects a sub-sample within watersheds. Least-squares means (the mean of the watershed means) were estimated for each watershed type. F-tests were used to test for equality of means between the three native chaparral and three type-converted watersheds. Furthermore, physiognomic growth form cover differences were compared among all watersheds with both watershed and watershed type fixed to identify if there were any significant differences within watersheds irrespective of watershed type. Values were considered significant at $P < 0.05$.

Results

In 2012, 10 years following the Williams fire, a total of 59 species of plants were identified on line transects and "nearby" areas for all six watersheds. As reported in table 1, 44 species were tallied on all transects which included 3 trees, 14 shrubs, 8 sub-shrubs, 13 forbs and 6 grasses.

Of species measured on transects, 80 percent were native. Non-native species included 1 tree (out-planted), 2 forbs, and 6 grasses. Type-converted watershed transects had 9 non-native species compared to 4 in native chaparral. Species richness on type-converted transects was 35 in 2012 and included 2 trees, 10 shrubs, 8 sub-shrubs, 9 forbs, and 6 grasses. Native chaparral watersheds had a species richness of 30 in 2012 and included 1 tree, 11 shrubs, 8 sub-shrubs, 6 forbs, and 4 grasses. Five tree species were observed in total, but very little tree cover was encountered on line transects in any watershed.

Species composition and cover varied between watershed types (table 1; table 2). Of all native species observed, 34 occurred in type-converted watersheds and 35 in native chaparral. Of all non-native species observed, 10 occurred in type-converted and 6 occurred in native chaparral watersheds. Three tree, 4 shrub, 1 sub-shrub, and 7 forb species were found in the type-converted watersheds that were not found in native chaparral. One tree, 6 shrub, and 7 forb species were found in the native chaparral watersheds, but not the type-converted.

In 2012, non-native species cover in type-converted watersheds was predominately the non-native perennial grass, *E. calycina*, followed by *Festuca myuros* (rattail fescue) (table 1). Two type-converted watersheds had 33 and 39 percent *E. calycina* cover, while the third had less than 2 percent (unpublished data on file at Riverside, CA). For native chaparral watersheds, non-native species cover consisted of 5 percent *Bromus madritensis* ssp. *rubens* (red brome) and 2 percent was *E. calycina*. Trace occurrences of six other non-native species in both watershed types included *Avena fatua* (wild oats), *Bromus diandrus* (ripgut brome), *Bromus tectorum* (cheat grass), *Centaurea melitensis* (tocalote), and *Hirschfeldia incana* (short pod mustard). Non-native species and cover were measured on 76 percent of transects in type-converted watersheds and observed "nearby" 52-100 percent of the time (unpublished data on file at Riverside, CA). This contrasts with native chaparral watersheds which had non-native species cover occurring on an average of 45 percent of transects and non-native species were observed "nearby" between 47 and 67 percent of the time.

Table 1—Mean percentage live cover on line-transects by species for three type-converted and three native chaparral watersheds 10 years following the 2002 Williams fire in the San Dimas Experimental Forest, CA. Mean values are averages over all transects within a watershed type. Physiognomic growth forms are defined in Methods section of text. Note: (n) = number of 10 m transects; (--) indicates zero plant cover; (*) indicates non-native species.

		Mean percentage live cover by species		
Genus and species	**Common name**	**Type-converted n=99**	**Native chaparral n=100**	**Physiognomic growth form**
Acmispon glaber	Deerweed	1.50	0.70	sub-shrub
Adenostoma fasciculatum	Chamise	3.88	18.40	shrub
Arctostaphylos glandulosa	Eastwood manzanita	0.68	0.90	shrub
Arctostaphylos glauca	Bigberry manzanita	--	0.20	shrub
*Avena fatua**	Wild oats	0.14	0.40	grass
Baccharis salicifolia	Mule fat	0.46	--	shrub
*Bromus diandrus**	Ripgut brome	0.10	0.10	grass
Bromus madritensis ssp. *rubens**	Red brome	0.78	4.30	grass
*Bromus tectorum**	Cheat grass	0.02	--	grass
Calochortus splendens	Splendid Mariposa lily	0.11	--	forb
Ceanothus crassifolius	Hoaryleaf ceanothus	10.84	35.70	shrub
Ceanothus integerrimus	Deer brush	0.20	0.40	shrub
*Centaurea melitensis**	Tocalote	0.05	--	forb
Cercocarpus betuloides	Mountain mahogany	--	0.40	shrub
Cryptantha intermedia	Common cryptantha	0.02	--	forb
Cuscuta sp.	Dodder species	0.02	--	forb
Ehrendorferia chrysantha	Golden ear-drops	--	0.10	forb
*Ehrharta calycina**	African veldt grass	23.39	1.10	grass
Erigeron sp.	Fleabane	0.02	--	forb
Eriodictyon trichocalyx	Smooth leaf yerba santa	7.96	4.20	sub-shrub
Eriogonum fasciculatum	California buckwheat	44.01	18.80	sub-shrub
Eriophyllum confertiflorum	Golden yarrow	0.69	0.50	sub-shrub
*Festuca myuros**	Rattail fescue	1.32	--	grass
Garrya veatchii	Silktassel bush	--	0.20	shrub
Hazardia squarrosa	Sawtooth goldenbush	0.37	0.30	sub-shrub
Helianthemum scoparium	Common rush rose	2.26	0.90	sub-shrub
Helianthus gracilentus	Slender sunflower	0.12	0.30	forb
Hesperoyucca whipplei	Chaparral yucca	0.38	0.30	sub-shrub
Heteromeles arbutifolia	Toyon	0.29	0.20	shrub
*Hirschfeldia incana**	Short pod mustard	0.09	0.40	forb
Malacothamnus fasciculatus	Bush mallow	--	0.10	shrub
Malosma laurina	Laurel sumac	1.03	--	shrub
Marah macrocarpus	Wild cucumber	--	0.70	forb
Mimulus cardinalis	Scarlet monkeyflower	0.06	--	forb
Pellaea mucronata	Cliff brake	--	0.01	fern/forb
Phacelia cicutaria	Caterpillar phacelia	0.01	--	forb
Pinus sp.*	Pine species	0.06	--	tree
Prunus ilicifolia	Hollyleaf cherry	0.42	--	shrub
Pseudognaphalium biolettii	Bioletti's everlasting	--	0.02	forb
Quercus agrifolia	Coast live oak	--	0.30	tree
Quercus berberidifolia	Scrub oak	0.36	4.00	shrub
Rhus ovata	Sugar bush	0.75	12.80	shrub
Salix gooddingii	Black willow	0.06	--	tree
Salvia mellifera	Black sage	5.05	15.10	sub-shrub
Total Number of Species:	44	35	30	

Table 2—Species observed "nearby" (within 20 m), but not on the 10 m line transects for three type-converted (TC) and three native chaparral (NC) watersheds 10 years following the 2002 Williams fire in the San Dimas Experimental Forest, CA. Physiognomic growth forms defined in Methods section of text. Note: (n) = number of 10 m transects; (*) indicates non-native species; (+) indicates species presence "nearby"; (--) indicates species absence "nearby".

Genus and species	Species occurring nearby Common name	TC n=99	NC n=100	Physiognomic growth form
Calystegia macrostegia	California morning glory	--	+	forb
Camissoniopsis bistorta	California suncup	--	+	forb
Ceanothus oliganthus	Hairy ceanothus	+	+	shrub
*Cirsium vulgare**	Bull thistle	--	+	forb
Ericameria parishii	Parish's goldenbush	+	--	shrub
Penstemon sp.	Penstemon species	+	+	forb
Plantanus racemosa	Western sycamore	+	--	tree
Pseudognaphalium californicum	California everlasting	+	+	forb
Quercus chrysolepis	Canyon live oak	+	+	tree
Rhamnus ilicifolia	Holly-leaf redberry	--	+	shrub
Rhus aromatica	Basket bush	--	+	shrub
Salvia columbariae	Chia	+	+	forb
*Spartium junceum**	Spanish broom	+	+	shrub
Toxicodendron diversilobum	Poison oak	+	--	sub-shrub
Trichostema lanatum	Woolly bluecurls	--	--	sub-shrub
Total number "nearby" species:	15	9	11	

F-tests showed significant differences in mean cover of some growth forms between the two watershed types (table 3). Means for shrub, forb, litter, and total cover were significantly less in type-converted watersheds compared to native chaparral. Mean live cover for type-converted watersheds included a combined shrub and sub-shrub cover of 76 percent (table 3). Live cover in type-converted watersheds was predominately *E. fasciculatum* and *E. calycina*, followed by *A. fasciculatum*, *C. crassifolius*, *Eriodictyon trichocalyx* (smooth leaf yerba santa) and *S. mellifera* (table 1). In contrast, mean live cover for native chaparral watersheds contained an

Table 3—Percentage of mean cover by physiognomic growth form between three type-converted and three native chaparral watersheds 10 years following the 2002 Williams fire on the San Dimas Experimental Forest, CA. P-values from F-tests show whether mean cover values between watershed types were significantly different at the 0.05 percent level. Note: (n) = number of watersheds.

	Mean percentage of growth forms between watershed types		
Physiognomic growth Form	Type-converted n=3	Native chaparral n=3	*P-value*
Tree	0.10	0.27	0.5966
Shrub	19.35	72.66	0.0018
Sub-shrub	56.59	41.16	0.1315
Forb	0.51	1.55	0.0152
Grass	26.66	6.64	0.1561
Litter	15.13	44.04	0.0420
Bare/Soil	15.82	16.24	0.8878
Total Live	102.59	122.42	0.0945
Total Cover	133.74	182.69	0.0380

overlapping shrub and sub-shrub cover totaling 114 percent (table 3). Predominant cover for native chaparral watersheds included *Ceanothus crassifolius* (hoaryleaf ceanothus), followed by *E. fasciculatum* and *A. fasciculatum.* Additional shrub cover in native chaparral watersheds also included *S. mellifera*, *Rhus ovata* (sugar bush), *Quercus berberidifolia* (scrub oak) and *E. tricocalyx* (table 1).

Significant site-specific differences in mean cover by physiognomic growth form were found among the six watersheds regardless if type-converted or native chaparral (table 4). Shrub cover in all type-converted watersheds was significantly lower than in all native chaparral. Sub-shrub cover in one type-converted watershed was significantly higher than another type-converted watershed. No significant differences were found for sub-shrub cover among native chaparral watersheds. Between watershed types, sub-shrub cover was significantly higher in two of three type-converted watersheds compared to two of three native chaparral watersheds. Mean grass cover (predominately *E. calycina*) in one type-converted watershed was similar to native chaparral. Litter cover did not vary among type-converted watersheds, and two of three native chaparral watersheds had significantly greater litter cover compared to type-converted. Total live cover among type-converted watersheds and one native chaparral did not differ significantly. The two remaining native chaparral watersheds had significantly greater live cover overall compared to type-converted. This same trend was also observed for total cover. There were no significant differences found among all watersheds for tree, forb, or bare ground cover.

Discussion

Over 52 years after type-conversion and 10 years since the 2002 Williams fire, the most widespread plant growth forms in native chaparral watersheds were shrubs and sub-shrubs. In contrast, there was a significant component of the non-native perennial grass *E. calycina* in two of the three type-converted watersheds, and “hard” chaparral shrub cover was significantly less in all type-converted watersheds compared to native chaparral (table 3). The substantial proportion of perennial grass cover in these watersheds raises concerns for the passive recovery of native plants and associated habitat, especially if the grass component continues to increase. Chaparral shrublands are important for the preservation of ecosystem services such as wildlife habitat, hydrological function, carbon storage, oxygen production, and hillslope stability, especially in southern California’s WUI. Loss of resilient chaparral ecosystems due to type-conversion could jeopardize the ecological integrity of California’s unique natural landscape (Allen-Diaz 2000, Lambert et al. 2010).

Native shrub and sub-shrub recruitment and success is an essential part of the post-disturbance recovery process for chaparral. After the 2002 Williams fire, mean shrub and sub-shrub cover increased in type-converted watersheds from 38 percent in 2006 (Wohlgemuth et al. 2008) to 76 percent six years later in 2012. In comparison, native chaparral watershed mean shrub and sub-shrub cover increased from 46 percent in 2006 (Wohlgemuth et al. 2008) to 114 percent in 2012. The substantial sub-shrub cover with increasing woody shrub cover suggests that these watersheds may be in transition to becoming a closed-canopy mixed-chaparral community given more time. However, non-native perennial grass cover is still persisting in over one third of the landscape in two type-converted watersheds compared to about 6 percent in native chaparral (table 4).

Table 4—Tukey test comparisons among all watersheds showing statistical significance of differences in physiognomic growth form cover means. Cover values were analyzed using both watershed type and watershed as fixed effects. Means for the same variable (shrub, sub-shrub, grass, litter; total live, and total cover) with the same letter are not significantly different from each other at the five percent level. No significant differences were found among watersheds for tree, forb, or bare/soil cover (not shown). Note: (n) = number of 10 m transects sampled; (TC) indicates type-converted; (NC) indicates native chaparral; (-) indicates no significant differences; (*) indicates significant differences (P<0.05).

	Significant differences of mean percentage cover among watersheds								
Physiognomic growth form			Type-converted			Native chaparral			
	Watershed	% Cover	0506 n=29	0507 n=30	0516 n=40	0517 n=30	0520 n=40	0542 n=30	Tukey significance
Shrub			-	-	-	*	*	*	a
	TC 0507	19.38	-	-	-	*	*	*	a
	TC 0516	25.49	-	-	-	*	*	*	a
	NC 0517	69.47	*	*	*	-	-	-	b
	NC 0520	64.69	*	*	*	-	-	-	b
	NC 0542	84.83	*	*	*	-	-	-	b
Sub-shrub	TC 0506	59.04	-	-	-	*	-	-	ab
	TC 0507	44.30	-	-	*	-	-	-	bc
	TC 0516	65.83	-	*	-	*	-	*	a
	NC 0517	31.92	*	-	*	-	-	-	c
	NC 0520	49.46	-	-	-	-	-	-	abc
	NC 0542	41.53	-	-	*	-	-	-	bc
Grass	TC 0506	39.92	-	-	*	*	*	*	a
	TC 0507	36.33	-	-	*	*	*	*	a
	TC 0516	3.94	*	*	-	-	-	-	b
	NC 0517	5.62	*	*	-	-	-	-	b
	NC 0520	7.79	*	*	-	-	-	-	b
	NC 0542	6.50	*	*	-	-	-	-	b
Litter	TC 0506	12.36	-	-	-	*	*	*	a
	TC 0507	16.47	-	-	-	-	*	*	ab
	TC 0516	16.54	-	-	-	-	*	*	ab
	NC 0517	26.95	*	-	-	-	*	*	b
	NC 0520	44.58	*	*	*	*	-	*	c
	NC 0542	60.58	*	*	*	*	*	-	d
Total Live	TC 0506	111.67	-	-	-	-	-	*	ab
	TC 0507	100.51	-	-	-	-	*	*	a
	TC 0516	96.09	-	-	-	-	*	*	a
	NC 0517	107.98	-	-	-	-	-	*	ab
	NC 0520	124.06	-	*	*	-	-	-	bc
	NC 0542	135.10	*	*	*	*	-	-	c
Total Cover	TC 0506	138.31	-	-	-	-	*	*	ab
	TC 0507	136.88	-	-	-	-	*	*	ab
	TC 0516	126.22	-	-	-	*	*	*	a
	NC 0517	154.82	-	-	*	-	*	*	b
	NC 0520	184.49	*	*	*	*	-	*	c
	NC 0542	208.72	*	*	*	*	*	-	d

Differences in species composition between watershed types was observed (table 1; table 2). Average species richness on type-converted transects increased from 20 in 2006 (Wohlgemuth et al. 2008) to 22 in 2012. Native chaparral watersheds had an average species richness of 22 in 2006, which decreased to 20 in 2012. Chaparral species community composition can be related to stand age (Keeley 1992, Patric and Hanes 1964). In addition, micro-site differences may support different community compositions among the various watersheds. The seed sources of native trees and woody shrubs identified on transects and "nearby" show that native species abundance and cover has the potential to increase over time in these watersheds.

Non-native cover (grasses and forbs) was much higher on type-converted watersheds compared to native chaparral (table 1). Schultz et al. (1955) showed that non-native annual grasses can competitively exclude chaparral seedlings. It is unknown what role the perennial grass *E. calycina* may play in possible future colonization of "hard" chaparral species. Additional monitoring of physiognomic growth form cover and diversity, especially non-native herbaceous and perennial grass cover at these sites, could determine if type-converted watersheds remain mixed "soft" chaparral and grasses, or if species composition will shift towards a predominately "hard" chaparral shrub community given more time. Furthermore, it would be informative to know if non-native grass cover will continue to increase or if it will move into intact native chaparral watersheds given the close proximity to type-converted areas.

In 2012, mean non-native grass cover in type-converted watersheds was 27 percent, almost four times greater than the 7 percent found in native chaparral (table 3). This was a two-fold increase in grass cover for both watershed types since 2006 as reported by Wohlgemuth et al. (2008). Interestingly, of the three type-converted watersheds, the one with the lowest grass cover also had the highest cover of shrubs and sub-shrubs. Keeley et al. (2005) found that the most critical factor influencing non-native plant population dominance in chaparral is the rapid return of the sub-shrub and woody shrub cover. Because the cover of the perennial grass *E. calycina* has increased considerably from 2006 to 2012, and it was accompanied by less shrub and sub-shrub cover in the watersheds where it was abundant, its presence, a remnant of the type-conversion manipulations that occurred in the 1960s, may be an enduring component in the chaparral ecosystems of SDEF.

Relationships between native and non-native plant species diversity have been suggested to play a determining role in non-native plant invasions (Elton 1958). The perennial grass *E. calycina* has successfully persisted in SDEF since it was introduced in the 1960s. This grass, and other non-native species observed, could serve as potential seed sources for future expansion of non-native plant populations. Shifts in vegetation assemblages of native chaparral species to non-native annual and perennial grasses may increase fire return intervals, affect soil water availability, alter carbon storage, and change community population dynamics (D' Antonio 2000, Facelli and Pickett 1991, Jacobson et al. 2004, Keeley et al. 2005, Keeley and Brennan 2012).

Shallow, fibrous root masses of many non-native grasses are believed to inhibit native shrub seedling establishment (Eliason and Allen 1997). In SDEF, the size and distribution of root masses in the soil profile under non-native grasses have been shown to vary considerably from that of native chaparral plant species (Williamson et al. 2004). Non-native forbs and grasses can alter soil-water utilization because root depth, root number and root size are different from native species (Holmes and Rice 1996, Perkins and Nowak 2013, Williamson et al. 2004). Compared to chaparral vegetation, soil temperatures under the perennial grass *E. calycina* have been shown to be warmer from September to March and cooler from June to September (Williamson 2004). In addition, organic matter in soils under *E. calycina* grass tussocks was greater, A-horizons were thicker, and water content was less compared to under chaparral, indicating that pedogenic processes have been altered under type-converted vegetation compared to chaparral (Williamson et al. 2004). Effects of the perennial grass *E. calycina* on soil water availability and soil formation could perturb chaparral population dynamics, particularly if this perennial grass cover continues to increase. This is of further concern when considering unknown future climatic changes such as erratic rainfall and higher temperatures.

Changes to soil properties that are caused by plants, which in turn influence the performance of microbiota and soil fauna populations as well as other plants, are termed plant-soil feedbacks (e.g. allelopathy or carbon fixation) (Ehrenfeld et al. 2005, Perkins and Nowak 2013, Van der Putten et al. 2013). Physical, chemical, and biological changes to the soil environment by non-native plant species can profoundly alter many ecosystem processes (Ehrenfeld 2010, Vitousek et al. 1990). Through changes in the demography of plant and microbiota populations, and/or the physiological activity of individuals, non-native species can influence the dynamics of coexistence, invasion, and the restoration success of an ecosystem (Ehrenfeld 2003, Van der Putten et al. 2013). Consequences of different mycorrhizal fungi diversity associated with grasses compared to shrubs on plant-soil feedback mechanisms have been shown to influence plant biodiversity, productivity, variability, and stability, all of which are critical for ecosystem functioning (Egerton-Warburton and Allen 2000, Eliason and Allen 1997, van der Heijden et al. 1998). Therefore, it is possible that non-native grasses in type-converted watersheds may be adversely affecting successional trajectories by changing the most basic building blocks of the trophic system, thereby altering the natural transition toward "hard" chaparral species dominance by displacing the native flora as a result of competition for light, nutrients, and water (Dahlin et al. 2013, Eliason and Allen 1997). Further examination into whether there is some threshold density of cover by non-native grasses in chaparral ecosystems at which ecosystem function breaks down would be informative.

The perennial grass component in type-converted watersheds may be even more problematic if future disturbances such as close-interval fire occur. *E. calycina* accumulates a large and persistent seed bank, readily resprouts after fire, and has been associated with severe soil water repellency (Smith et al. 1999, Williamson 2004). Once established in an area, non-native grasses may shorten fire return intervals by providing highly ignitable flashy fuels (Keeley and Brennan 2012, Zedler et al. 1983). Absence of fire for long periods of time is necessary for obligate seeders to reproduce in chaparral ecosystems (Jacobsen et al. 2004). Air pollution (nitrogen deposition) effects on "soft" chaparral vegetation can decrease cover and biomass of native sub-shrubs, forbs and mycorrhizal fungi while increasing cover and biomass of non-native grass species (Allen et al. 2005, Egerton-Warburton and Allen 2000, Perkins and Nowak 2013). Alteration of disturbance regimes can have profound effects on a functional group of species (Mack and D'Antonio 1998), threatening the resilience of a healthy ecosystem. Some or all of these factors may have contributed to the differences found in watershed species composition, which included significantly higher grass and lower shrub cover in type-converted compared to native chaparral watersheds.

Mean litter cover was significantly greater in native chaparral compared to type-converted watersheds (table 3). Litter plays a critical role in plant species composition which can mediate nutrient, water, and carbon cycling within and among different populations of flora and fauna (Dahlin et al. 2013, Ehrenfeld 2003, Facelli and Pickett 1991). The importance of the type, as well as the amount, of litter present can also affect chaparral seedling survival (Keeley 1992, Patric and Hanes 1964). Differences in litter composition, structure, and mass associated with grasses compared to shrubs may contribute to chaparral germination success or failure. In native chaparral watersheds, the robust litter layer may provide a more suitable seedbed for germination and seedling survival for many native chaparral species compared to the grass and sub-shrub litter of type-converted watersheds.

Mean forb cover was greater in native chaparral compared to type-converted (table 3), but very low values were observed in both watershed types. The low cover and low species richness of forbs measured may have been due to time since fire, the presence of grasses, or perhaps timing of sampling in late summer (Beyers et al. 1998, Hubbert et al. 2012, Keeley and Keeley 1989, Muller et al. 1968, Williamson 2004). Sampling during the active growing season may increase the detection of forbs.

Bare ground cover was similar among all watersheds and it has not changed since 2006 as reported by Wohlgemuth et al. (2008). Canopy gaps are important for insolation stimulation of germination and growth of some native species (Baskin and Baskin 1998). These gaps of bare soil may allow different species to expand their distributions into available spaces. Keeley (1992) found that in arid, open landscapes, fire-persisters (*Quercus, Rhamnus, Heteromeles*) do poorly and fire recruiters (*Adenostoma, Arctostaphylos,* and *Ceanothus*) dominate. In time, as these watersheds age and litter accumulates in bare gaps, the potential exists for a greater variety of chaparral species to re-establish and flourish.

Conclusions

Ten years after fire were sufficient for native chaparral watersheds on the San Dimas Experimental Forest to return to shrub dominated conditions, although they were not yet closed-canopy. In contrast, live plant cover in type-converted watersheds was substantially different, in that it was predominately sub-shrubs and non-native grasses with some shrubs. Less “hard” chaparral shrub cover and more grass cover in type-converted compared to native chaparral watersheds is an enduring effect of the deliberate type-conversion that occurred 52 years prior to this study. These differences in vegetation growth form cover demonstrate how unaided post-fire chaparral species recovery has occurred in previously type-converted and native chaparral watersheds in southern California. Additional monitoring would document whether past type-conversion permanently shifted the plant community to a new, stable species composition consisting of sub-shrubs and the non-native perennial grass *E. calycina*, or if “hard” chaparral species can recolonize and eventually establish dominance in these grassy watersheds. Site-specific conditions may affect both chaparral species composition and re-establishment success and possibly the time interval required for succession to occur following disturbance. Effective resource and watershed management of deliberately type-converted shrublands at the wildland-urban interface may require pro-active management interventions to eradicate non-native species in order to maintain the rich native plant diversity unique to southern California’s chaparral.

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