Plenary Session

Shrubland Ecosystems: Importance, Distinguishing Characteristics, and Dynamics

E. Durant McArthur[1]
Stanley G. Kitchen[2]

Abstract: The importance of shrub species and shrubland ecosystems gained considerable impetus about 30 years ago with the establishment of the USDA Forest Service Shrub Sciences Laboratory and a series of workshops and symposia that preceded and accompanied the establishment of the Laboratory. Since that time, the Shrub Research Consortium and other forums have addressed various aspects of wildland shrub ecosystem biology and management. Shrubs occur in most vegetation types but are dominants only in those habitats that place plants under considerable stress. Three primary, often interacting factors, that promote shrubby habitats are drought or aridity, nutrient-poor soils, and fire. Other stress factors that may also be interactive that contribute to the shrubby habitat are shade, poor soil aeration, winter cold, short growing season, and wind. Most of these conditions frequently occur in semi-arid, temperate, continental climates. The principal shrubland ecosystems of the western United States are sagebrush, chaparral, mountain brush, coastal sage, blackbrush, salt desert, creosote bush, palo verde-cactus, mesquite, ceniza shrub, shinnery, and sand-sage prairie. Similar as well as distinctively different shrubland ecosystems occur at other locations around the world. Shrubland ecosystems have different human and wildlife values and have, and are, subject to changing environmental conditions including different fire regimes. Fragmentations of these ecosystems, for example the sagebrush ecosystems, are of concern since some ecosystem components are at critical risk. Shrubland ecosystem changes have become more apparent in recent decades posing significant ecological and management problems. The challenge for land managers and ecologists is to understand the fluidity of the ecosystems and to be proactive and sensitive to the needs of healthy, productive landscapes.

Introduction

Shrubs and shrubland ecosystems are valued differently by natural resource professionals and pastoralists depending on their backgrounds, experience, geographical location, and the economic impact of those shrublands on their livelihood. The contrasting values or points of views about shrubs were stated by Everist (1972) in the context of Australian shrublands, which could be extrapolated generally: “wildland shrubs have greatest importance on … grazing lands, mostly as useful species but sometimes as invaders of and competitors with plants (more useful) … for animal … survival or productivity.” In North America, shrubs have been referred to as a neglected resource (McKell 1975; 1989) or contrastingly as an impediment to productive land use practice (Herbel 1979). In Africa and Asia, their value has long been appreciated and often over-exploited (Badresa and Moore 1982; Cloudsley-Thompson 1974). In Australia, shrubs have been recognized alternately as valuable, sustainable forage and as a system that is more productive when it is converted to a disclimax herbaceous state (Williams and Oxley 1979).

The importance of shrub species and shrubland ecosystems gained considerable impetus about 30 years ago with the establishment of the U.S. Forest Service Shrub Sciences Laboratory and a series of workshops and symposia that preceded and accompanied the establishment of the Laboratory (McKell and others 1972, Stutz 1976). Since its charter in 1983 (McArthur 2001; Tiedemann 1984), the Shrub Research Consortium (SRC), lead by the project leaders of the Shrub Sciences Laboratory, has sponsored a series of symposia on the biology and management of shrubland ecosystems. The SRC symposia have generally focused on the positive values of shrubs in shrubland ecosystems but have also addressed management issues where shrubs were considered as

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Table 1—Shrub Research Consortium Wildland Shrub Symposia series.

Number	Date held	Title and location	Proceedings publication
1	1982	Research and Management of Bitterbrush and Cliffrose in Western North America —Salt Lake City, Utah	Tiedemann and Johnson 1983
2	1983	The Biology of Atriplex and related Chenopods—Provo, Utah	Tiedemann and others 1984
3	1984	The Biology and Management of Artemisia and Chrysothamnus—Provo, Utah	McArthur and Welch 1986
4	1985	Plant—Herbivore Interactions—Snowbird, Utah	Provenza and others 1987
5	1987	Shrub Ecophysiology and Biotechnology—Logan, Utah	Wallace and others, 1989
6	1989	Cheatgrass Invasion, Shrub Die-off, and other Aspects of Shrub Biology and Management—Las Vegas, Nevada	McArthur and others 1990
7	1991	Ecology and Management of Riparian Shrub Communities—Sun Valley, Idaho	Clary and others 1992
8	1993	Wildland Shrub and Arid Land Restoration— Las Vegas, Nevada	Roundy and others 1995
9	1995	Shrubland Ecosystem Dynamics in a Changing Environment—Las Cruces, New Mexico	Barrow and others 1996
10	1998	Shrubland Ecosystem Ecotones—Ephraim, Utah	McArthur and others 1999
11	2000	Shrubland Ecosystem Genetics and Biodiversity—Provo, Utah	McArthur and Fairbanks 2001
12	2002	Seed and Soil Dynamics in Shrubland Ecosystems—Laramie, Wyoming	Hild and others 2004
13	2004	Shrub Dynamics: Fire and Water—Lubbock, Texas	Sosebee and others—this proceedings

ecological or management problems (table 1). The two symposia that focused more on shrub control management issues rather than positive values were numbers 9 and 13 in the series which were held in the Southwest where shrubs have displaced grasses in historic time over large acreages (Barrow and others 1996; Herbal 1979, Sosebee and others—this proceedings). A series of wildland shrub workshops, each emphasizing various shrub taxa and communities (especially for land management professionals), were held in both Wyoming (1972-1988) and Utah (1981-1991)—see Fisser (1990), Johnson (1990), and McArthur (2001) for lists of these proceeding publications and more details on the process.

Although shrubs are an important and widespread life form, they are difficult to circumscribe. Individual species may be shrubs in some circumstances and trees in other circumstances. Other species may alternatively be shrubs or herbaceous plants depending on certain circumstances, for example, climate or soil fertility (Francis 2004). Shrubs do not comprise a cohesive phylogenetic unit, but derive from many lineages (McArthur 1989; Stebbins 1972; 1976). The shrub habit is more of a growth form than a phylogenetic unit. However, some taxonomic lines are wholly shrubby as might be expected depending upon the point of establishment of the shrub growth habit (table 2). Simmonds (1976) identified 168 principal crop plants of which 12 are shrubs. These 12 crop shrubs (tea, hazel, blueberries, cassava, currants and gooseberries, wattles, roselle, guava, pomegranate, raspberries and blackberries, coffees, and peppers) represent 12 different families (McArthur 1989). Francis (2004) analyzed the Natural Resources Conservation Service (USDA 2003) "Plants" database and determined that there were 5,281 species in the United States and territories that carry the growth habit designations "shrub" or "sub-shrub." These species represent 166 families (table 3). Note that the West (especially the Southwest), Southeast, Hawaii, Puerto Rico, and Virgin Islands are more species-rich than other areas, such as Alaska, the North Central States, and New England.

Shrubs occur in many vegetation types. Shrubs ordinarily have more than one main stem caused by branching below or above ground level, are perennial, and are lignified (Francis 2004). Often shrubs are thought of as midway between a tree and herb with adaptive advantages of both life forms that sustain the shrub habit in some unique situations (Stutz 1989). Shrubs have near relatives that are herbs and/or trees (table 2). Shrubs are dominant, but for the most part, only in habitats that place plants under considerable stress such as drought or aridity, nutrient-poor soils, fire, shade, poor soil aeration, winter cold, short growing seasons, and wind (McArthur 1989; Stebbins 1972; 1975). Many of these conditions are met in semi-arid continental climates (McArthur 1989; McKell and others 1972). For example, shrubs are widely distributed in the United States (fig. 1), but are dominants from a continental-scale perspective in the semiarid west (McArthur 1984). Table 4 is an analysis of shrub importance as determined from Küchler's (1964) map and manual. Significant dominance of shrubs is manifest only in the western shrublands and western shrub and grasslands. Shrubs as subdominants are important to a greater or lesser degree in nearly all vegetative types (table 4). The same general patterns of shrubs rising to dominance are evident in other semiarid and arid climatic regimes on other continents (Le Honérou 2000; McKell 1989; McKell and others 1972; Walter and Box 1976; West 1983; Wilson and Graetz 1979).

We conclude this section with a few comments about some shrub species that characterize the western North American landscapes. Whereas shrubs are widely distributed and are components of many ecosystems and community types, they give landscapes their primary character in areas that they dominate, such as the interior North American West (Francis 2004; McArthur 1984; 1989). McArthur (1989) identified 12

Table 2—Numbers of genera and species including example species and growth forms of selected families (after McArthur 1984 and McArthur and Tausch 1995).

Family[a]	Representative Genera	Number of shrub Genera[b]	Number of species from Western United States (all growth forms)[c]	Number of species (World total, all growth forms)	Growth habits[d]
Anacardiaceae	*Rhus*	1	9	150	S, T
Asteraceae	*Artemisia*				
	Baccharis				
	Brickella				
	Chrysothamnus				
	Happlopappus				
	Tetradymia	18	126	2546	H, S
Caprifoliaceae	*Lonicera*				
	Sambucus				
	Symporicarpos	5	28	317	S
Chenopodiaceae	*Atriplex*	8	29	441	H, S
Ericaceae	*Arctostaphylos*				
	Vaccinium	14	82	1211	S, T
Ephedraceae	*Ephredra*	1	10	40	S
Fabaceae	*Acacia*				
	Dalea				
	Mimosa	19	70	3276	H, S, T
Fagaceae	*Quercus*	3	20	700	S, T
Fouquieriaceae	*Fouquieria*	1	1	9	S, T
Lamiaceae	*Salvia*	5	24	1175	H, S
Polygonaceae	*Eriogonum*	1	20	250	H, S
Rhamnaceae	*Ceanothus*	6	68	295	S
Rosaceae	*Amelanchier*				
	Prunus				
	Rosa				
	Rubus	23	81	760	H, S, T
Scrophulariaceae	*Mimulus*				
	Penstemon	4	22	454	H, S
Zygophyllaceae	*Larrea*	2	2	22	S

[a] Families selected on the basis of at least one species included by a dominant by Küchler 1964.
[b] Number of shrub genera in the United States west of 100° W longitude.
[c] Total number of species in the United States west of 100° W longitude.
[d] Growth habits of congeneric relatives: H = herbs, S = shrubs, T = trees.

Table 3—Most important families with shrub representatives in the United States and its territories (after Francis 2004).[a]

Family	Number of shrub species
Asteraceae	618
Rosaceae	510
Fabaceae	342
Cactaceae	193
Ericaceae	189
Scrophularaceae	182
Rubiaceae	165
Malvaceae	148
Euphorbiaceae	128
Lamiaceae	124
Polygonaceae	123
Companulaceae	112
Boraginaceae	106
Ramnaceae	103

[a] There are 152 additional families with from one to 82 species each.

successful Western North American shrub species complexes (table 5). These species complexes demonstrate the variety of important entities in widespread and dominant shrubs inasmuch as they represent 8 families, a mix of polyploid systems versus diploid only chromosome numbers, a mix of wind and insect pollination, different degrees of dominance in their respective plant communities (table 5). The group is primarily outcrossing. The principal shrubland ecosystems of the western United States are sagebrush, chaparral, mountain brush, coastal sage, blackbrush, salt desert, creosote bush, palo verde-cactus, mesquite, ceniza shrub, shinnery, and sand-sage prairie (Küchler 1964, McArthur and Ott 1996). As an example of these important shrublands, we briefly discuss some of the characteristics of sagebrush, an American West icon (fig. 2). Sagebrush (the subgenus *Tridentatae* of *Artemisia*) occupies vast tracts of land west of the 100th meridian west longitude (McArthur and Sanderson 1999). As such, it gives the land its character, serves as habitat for resident wildlife, and

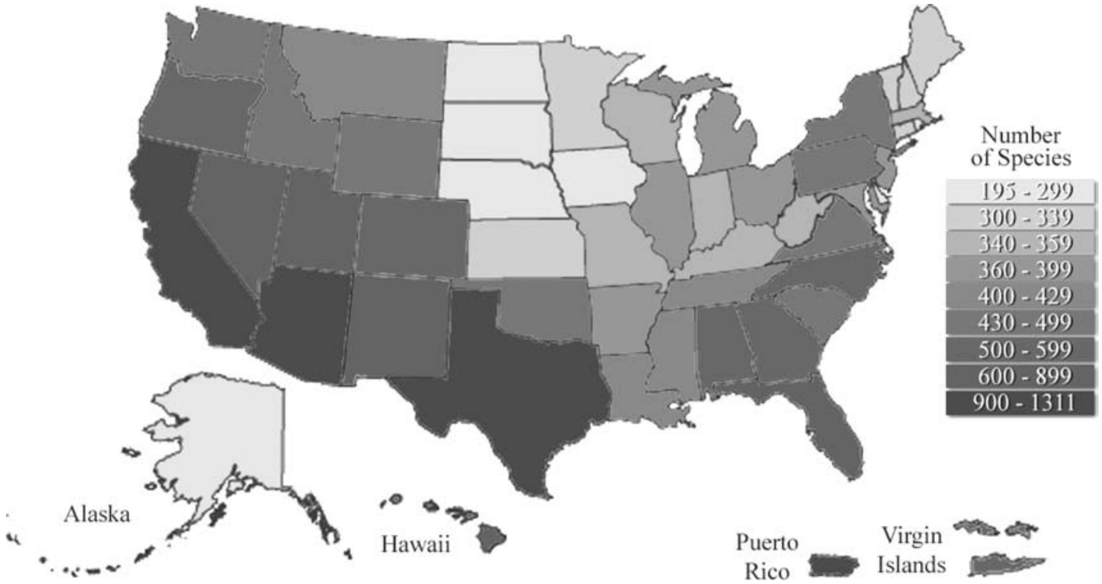

Figure 1. Numbers of shrub species in the States and Territories of the United States (Francis 2004).

contributes to livestock ranges (McArthur and Stevens 2004; Welch in press). Other *Artemisia* species of other subgenera are important landscape dominants in Eurasia (Vallès and McArthur 2001; West 1983). For additional details on western North American dominant shrub species complexes we recommend the first three wildand shrub symposium proceedings—McArthur and Welch (1986), Tiedeman and Johnson (1983), and Tiedemann and others (1984) (table 1); Francis (2004); and chapters on shrub species in Monsen and others (2004a)—McArthur and Monsen (2004), McArthur and Stevens (2004), Monsen and others (2004b), and Shaw and others (2004).

Dynamics

Like all plant species, communities, and ecosystems, shrub species and their attendant plant communities or ecosystems are not static. Evolutionary forces and environmental change have been active over geological time in leading to present day species, communities, and ecosystems. Two recent wildland

Table 4—Dominant and subdominant shrub species occurrence in the principal vegetative types of the conterminous United States (after McArthur 1989).

		Dominant species			Subdominant species			
		All species	Shrubs		All species	Shrubs		All shrubs
Vegetative type	**N**	$\bar{X}$ **+ se**	$\bar{X}$	**%**	$\bar{X}$ **+ se**	$\bar{X}$	**%**	**(** $\bar{X}$ **+ se)**
Western needleleaf forests	24	2.3 + 0.2	0.04	1.7	10.0 + 1.1	3.9	39.0	3.9 + 0.6
Western broadleaf forests	3	1.3 + 0.3	0	0	10.0 + 2.3	3.7	37.0	3.7 + 1.8
Western broadleaf and needleleaf forests	5	5.6 + 0.7	0.2	3.6	16.4 + 3.0	7.6	46.3	7.8 + 2.1
Western shrublands	13	2.7 + 0.6	1.9	70.4	13.6 + 1.9	8.7	63.9	10.6 + 1.7
Western grasslands	8	3.6 + 0.8	0	0	11.6 + 2.0	1.6	13.8	1.6 + 0.6
Western shrubs and grasslands	6	3.2 + 0.4	1.3	40.6	17.0 + 2.5	3.8	22.4	5.2 + 1.0
Central and eastern grasslands	17	2.9 + 0.3	0	0	14.2 + 1.4	1.4	9.8	1.4 + 0.4
Central and eastern grasslands and forests	15	3.4 + 0.5	0	0	17.2 + 2.5	1.7	9.9	1.7 + 0.3
Eastern needleleaf forests	5	2.4 + 0.2	0	0	6.8 + 0.8	2.0	29.4	2.0 + 0.7
Eastern broadleaf forests	8	3.1 + 0.7	0	0	14.9 + 2.1	1.1	7.4	1.1 + 0.7
Eastern broadleaf and needleleaf forests	11	4.0 + 0.5	0.09	2.2	13.4 + 2.3	1.9	14.2	2.0 + 0.4
Total	115	—	—	—	—	—	—	—
$\bar{X}$		3.1 + 0.5	0.3	9.7	13.2 + 1.9	3.4	25.8	3.7 + 0.9

Table 5—Twelve successful Western North American shrub complexes (McArthur 1989)[a].

Shrub complex	Polyploidy	Breeding system	Dominance characteristics
Manzinata—*Artostaphylos* spp. (Ericaceae)	yes	Outcrossing, insect	Many dominant species in communities
Sagebrushes—subgenus *Tridentatae* of *Artemisia* (Asteraceae)	yes	Outcrossing (limited self), wind	Dominant by itself with occasional subordinate co-dominants
Saltbushes—*Atriplex* spp. (Chenopodiaceae)	yes	Outcrossing, wind	Usually dominant by self or with other congeners and chenopods[b]
Buckbrushes—*Ceanothus* spp. (Rhamnaceae)	no	Outcrossing (limited self in some species), insect	Many dominant species in communities
Mountain mahoganies—*Cercocarpos* spp. (Rosaceae)	no	Outcrossing (limited amount of self), wind	Few dominant species aside from *Cercocarpus*
Rabbitbrushes—*Chrysothamnus* spp. (Asteraceae)[c]	no	Self (limited outcrossing), insect	Usually a sub or co-dominant
Blackbrush—*Coleogyne* (Rosaceae)	no	Outcrossing, wind[d]	Usually dominant by self
Cliffrose and bitterbrush—*Purshia* spp.[e] (Rosaceae)	no	Outcrossing, insect	Usually a sub or co-dominant
Mormon tea or joint fir—*Ephreda* spp. (Ephredaceae)	no	Outcrossing, wind	Usually a co-dominant
Bursage—*Ambrosia* (Asteraceae)	yes	Outcrossing, wind	Usually a co-dominant
Creosote bush—*Larrea* (Zygophyllaceae)	yes	Outcrossing, insect	Usually a co-dominant
Oakbrush—*Quercus* spp. (Fagaceae)	no	Outcrossing, wind	Usually a co-dominant

[a] Documenting references in McArthur (1989) except as noted in additional footnotes.
[b] Including greasewood (*Sarcobatus* spp.) which has been recently segregated into its own family (Sanderson and others 1999).
[c] Taxonomy in the rabbitbrushes is under scrunity; some or all are alternately treated as *Ericameria* (Anderson 1995).
[d] Confirmed by Pendleton and Pendleton (1998).
[e] The former independent generic standing of cliffrose (*Cowania*) has been submerged into *Purshia* (Hendrickson 1986; Reichenbacher 1994)

Figure 2. Wyoming big sagebrush, Sweetwater County, Wyoming (photo by E. Durant McArthur).

shrub symposia addressed these issues: McArthur and Fairbanks (2001), Shrubland Ecosystem Genetics and Biodiversity and Barrow and others (1996), Shrubland Ecosystem Dynamics in a Changing Environment. Johnson (this proceeding) addressed these issues for the Southern High Plains. These changes in shrub communities (in other words, community structure and species evolution) are on distinct time scales. Both time scales are ordinarily very long in terms of the human lifespan perspective. Species evolution is ordinarily the longer of the two phenomena. Betancourt (1996) and Tausch and others (1993) reviewed climatic influences that have lead to current vegetation communities. Since settlement of the American West by Euro-Americans, especially in recent decades, shrubland vegetation communities have changed rapidly. Consensus is that these changes have been driven not only by global warming, but also by management activities, especially livestock grazing, and by a change in the frequency of wildfires mediated by the higher fine fuel loads of exotic annual grasses such as cheatgrass. Two contrasting examples of changed communities are the fragmentation of sagebrush communities in the Intermountain West as a result of agricultural conversions, brush control projects, and increased fire frequency (Knick 1999; Welch 2005; Whisenant 1990) and the expansion of woody shrubs (principally mesquite—*Prosopis* spp., tarbush—*Flourensia cernua*, and creosote bush—*Larrea tridentata*) into warm desert grasslands in the Southwest as a result of overgrazing and climate change (Havstad and Schlesinger 1996; Herbel 1979). The likelihood is that changes will continue, even accelerate, with climate change, industrial activities, and intensive land management (Neilson and Drapek 1998). The challenges for land managers and ecologists is to understand the fluidity of the system and to be proactive and sensitive to the needs of healthy, productive landscapes.

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The Authors

[1] Program Manager and Research Geneticist, USDA Forest Service, Rocky Mountain Research Station, Shrub Sciences Laboratory, Provo, UT. dmcarthur@fs.fed.us

[2] Research Botanist, USDA Forest Service, Rocky Mountain Research Station, Shrub Sciences Laboratory, Provo, UT.