

# Ecotones: Introduction, Scale, and Big Sagebrush Example

E. Durant McArthur  
Stewart C. Sanderson

---

**Abstract**—Ecotones and other boundary concepts are important in biological processes. The scale of biological boundaries is enormous (from molecular and cellular to landscape and biome). Boundaries offer the opportunity for interaction at these many different scales. Traditionally, ecotones have been considered junction zones between two or more communities where the processes of exchange or competition between neighboring communities or subunits of communities occur. Depending on scale, climate, topography, soil characteristics, species interactions, physiological parameters, and population genetics are important considerations at ecotonal boundaries. Hybridization between compatible taxa often occurs at ecotones. Members of the big sagebrush (*Artemisia tridentata*) species complex (subgenus *Tridentatae* of *Artemisia*) often meet at ecotones affording opportunities for hybridization. Some taxa form hybrid zones at such sites and others do not. Data from sagebrush hybrid zones favor the bounded superiority hybrid zone model. Stable hybrid zones with their array of genetic recombinants afford the opportunity for evolutionary radiation when dynamic climatic processes change habitats and should be considered for management purposes.

---

Ecotones and other boundary concepts are important in biological processes and systems. Many fundamental processes and functions occur at biological boundaries of various scales. Whereas ecotones are generally considered to be tied to plant community boundaries, the scale of biological boundaries is enormous, from molecular and cellular to landscapes and biomes. Boundaries offer the opportunity for interaction between and among cells and cellular components, organs, organisms, populations of organisms, communities, groups of communities or landscapes, and biomes (large landscapes with a characteristic late seral dominant vegetation type, for example, grasslands). The interactions may be in the nature of exchange of organisms through migration or invasion or of exchange of organismic characteristics by hybridization or introgression, or of displacement of organisms and modification of habitats by invasion or competition from other organisms. This paper presents an introduction to the symposium by examining ecotonal concept history, ecotone definition, the general properties of ecotones, and other biological boundaries in smaller and larger scale than traditional community ecotones. Special

attention will be paid to hybridization in sagebrush (subgenus *Tridentatae* of *Artemisia*) and hybrid zones between subspecies of big sagebrush (*A. tridentata*).

## Ecotones

---

### Ecotone Definition

Pioneering American plant ecologist Frederic Clements (1905) defined an ecotone as a “junction zone between two communities, where the processes of exchange or competition between neighboring formations might be readily observed.” Clements (1905) further described ecotones as tension zones where principal species from adjacent communities meet their limits. Eugene Odum, perhaps the pre-eminent American ecologist of the last half-century, described an ecotone as “a transition between two or more diverse communities.... The ecotonal community commonly contains many of the organisms of each of the overlapping communities...and organisms characteristic (or) restricted to the ecotone” (Odum 1971).

A more recent and formal definition is that of the SCOPE/MAB working group (Holland (1988): “zone of transition between adjacent ecological systems, having a set of characteristics uniquely defined by space and time scales and by the strength of the interactions between adjacent ecological systems.” In this definition the term “ecological system” includes such commonly described hierarchical entities such as demes, populations, communities, ecosystems, landscapes, and biomes (Gosz 1991; Holland 1988). In this definition ecotones are interpreted as biological boundaries of various scales. It is important to remember that boundaries are identifiable and meaningful only relative to specific questions and points of reference. An ecotone at one spacial scale may be seen as a collection of patches on a finer scale (Gosz 1991).

### Scale of Ecotones

Gosz (1993) presented ecotonal hierarchies (table 1). In the table, ecotones and their possible constraints are listed from the biome to population levels. Biological boundaries at smaller scales have analogous properties to the classically understood organismic and community ecotones (Wiens and others 1985). The analogy is that boundaries between elements in a community or landscape function at a different scale or level than those in organismal or physical systems. Like cellular membranes, ecotonal boundaries vary in their permeability or resistance to flows. The currency of flow is contrasting, that is, from organisms to genes to chemicals. The variation is a consequence of characteristics of the

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

E. Durant McArthur is Project Leader and Research Geneticist, and Stewart C. Sanderson is Research Geneticist (Professional), Shrub Sciences Laboratory, Rocky Mountain Research Station, Provo, UT 84606.

**Table 1**—Ecotone hierarchy for biome transition area. The range of constraints and interactions at each level in the ecotone hierarchy is given; x symbolizes interactions between constraints (from Gosz 1993).

Ecotone hierarchy	Probable constraints
Biome ecotone	Climate (weather) x topography
Landscape ecotone (mosaic pattern)	Weather x topography x soil characteristics
Patch ecotone	Soil characteristics x biological vectors x species interactions x microtopography x microclimatology
Population ecotone (plant pattern)	Interspecies interactions x intraspecies interactions x physiological controls x population genetics x microtopography x microclimatology

boundary, for example, its thickness, the degrees to which the separated patches, organisms, cells, and cellular component differ and their responses of different materials, organisms, or abiotic factors to the boundary (Gosz 1991).

We conclude this brief discussion on scale by citing some cellular ecotone examples that demonstrate boundary exchange phenomena:

- Chloroplasts are more homologous to blue-green algae RNA (47 percent) than they are to cytoplasmic RNA from their same cells (~1 percent) (Schwemmler 1989).
- Mitochondrial ribosomes are more similar to bacteria than they are to cytoplasmic ribosomes (Schwemmler 1989).
- The sagebrush (*Artemisia* subgenus *Tridentatae*) chloroplast genome has been captured by sand sage (*Artemisia filifolia* of subgenus *Dracunculus*) (Kornkven 1997).

## Traditional Views of Ecotones

After Clements' (1905) clarion call about ecotones being a junction zone between plant communities, scientists and resource managers began to study ecotones. By the 1930's three spacial scales of ecotones with attendant scientific and management implications had developed (Risser 1995). These were:

- Wildlife biologists awareness of the value of local edges or margins for habitat, cover, and food for many game and nongame species.
- Scientists began studying conspicuous transitional areas at mountain and tundra tree lines including exploring adaptations that enable plants to survive in those locations.
- Scientists were interested in the broad transitional areas between continental-scale biomes, for example, Arctic tundra and boreal forest, North American deciduous forest, and central plains grassland.

Currently, ecotones are studied over broader scales than these traditional areas, but these areas remain topical (Holland and others 1991; Levin 1995; Risser 1995; Unwin and Watson 1997). Risser (1995) in his review of the study of

ecotones suggests that the most important current ecotonal studies are the dynamic impact of ecotones on an active landscape, ecotones significant roles in supporting a high level of biological diversity, ecotones role as a source of high levels of primary and secondary productivity (ecotones frequently intensify or concentrate the flows of water, nutrients, and other materials, as well as the movement of organisms across the landscape), ecotones provision of important components of wildlife habitat, and ecotones acting as sensitive indicators of global change. As an example of shifting ecotonal boundaries, one of Risser's (1995) important areas of current ecotonal study, Walker and others (1996) presented data showing changes in the principal cover types on the Great Basin Experimental Range (see field trip report—McArthur and others, this proceedings) from 1937 to 1991, wherein quaking aspen (*Populus tremuloides*) cover types declined from 40 percent to 22 percent, Gambel oak (*Quercus gambelii*) cover types increased from 16 to 27 percent, and spruce-fir (*Picea* spp.–*Abies* spp.) increased from 13 to 22 percent). We also comment briefly on another of Risser's (1995) important areas of current study, that of the importance of ecotones to biological diversity. Not only do ecotones function as an area of concentration of higher numbers of species through the accommodation of a higher number of species ( $\approx$  species diversity) than the adjacent more traditional communities, but they may also be areas of greater genetic diversity of individual species or serve as bridges of gene flow between species populations (Levin 1995; McArthur 1989). Ecotones in time can be considered not only as species and community migration in response to changing conditions but also on a particular site as succession occurs.

Two conditions favor the formation of traditional community ecotones (Gosz 1992; Risser 1995): (1) Steep gradients in physical environmental variables, for example, topography and climate, that directly affect key ecological processes and the distribution of organisms; (2) Threshold or nonlinear responses to gradual gradients in the physical environment that cause large changes in ecosystem dynamics and the distributions of dominant species. Population ecotones (table 1) are facilitated by the traditional community ecotones because it is often at the traditional community ecotones that interspecific and intraspecific contact occurs so that interactions can occur.

## Hybridization and Hybrid Zones

For the balance of this paper we discuss population ecotones or plant patterns (table 1) using the sagebrush (subgenus *Tridentatae* of *Artemisia*) example.

## Introgression and Hybridization in Sagebrush

Big sagebrush (*Artemisia tridentata*) in particular and sagebrush (subgenus *Tridentatae*) in general have apparently gained their landscape-dominant, broad-niche-filling status through a reticulate, hybridizing, evolutionary pathway (McArthur and others 1981, 1988; Ward 1953; Winward and McArthur 1995). Several extant taxa are thought to be the product of hybridization events, some involving

polyploidization as well (table 2). We believe that ecotonal boundaries created as sagebrush and other plant species moved across the landscape in response to past climatic and geological changes facilitated contact between sagebrush taxa (McArthur and Plummer 1978; McArthur and others 1981; Thompson 1991). Given the opportunity, sagebrush taxa will hybridize. Such opportunities are documented in table 3 where tightly parapatric or sympatric populations of several sagebrush taxa are listed. Hybrids resulting from populations of different taxa in close proximity are probably incidental and not significant in the long run (Beetle 1970). However, some have resulted in new adaptive forms, formally described or otherwise (table 2). We believe that hybrid zones (see next section) form a stable reservoir of adapted plants available to migrate into areas that become available with changing environmental conditions, for example, climate and geology.

### Sagebrush Hybrid Zones

Several papers in this proceedings, that is Graham and others, Freeman and others, Smith and others, Young and Clements, and Goodrich and others, report the results of research in sagebrush hybrid zones or ecotones. Hybrid zone theory is an area of considerable current interest by evolutionary ecologists (Arnold 1997; Harrison 1993). Why is this so? It is because of the dilemma posed by the number and stability of hybrid zones despite the dogma of the biological species concept that hybrids inherently have a reduced fitness in respect to their parents (Arnold 1997; Freeman and others, this proceedings; Graham and others, this proceedings; Harrison 1993; and references cited therein).

**Table 3**—Sympatric and tightly parapatric distributions of sagebrush (subgenus *Tridentatae* of *Artemisia*) taxa (data from McArthur and Sanderson, in press).

<i>A. tridentata</i> ssp. <i>tridentata</i> and <i>A. tridentata</i> ssp. <i>vaseyana</i>
<i>A. tridentata</i> ssp. <i>tridentata</i> and <i>A. tridentata</i> ssp. <i>wyomingensis</i>
<i>A. arbuscula</i> ssp. <i>arbuscula</i> and <i>A. tridentata</i> ssp. <i>wyomingensis</i>
<i>A. tridentata</i> ssp. <i>vaseyana</i> and <i>A. cana</i> ssp. <i>viscidula</i>
<i>A. tridentata</i> ssp. <i>vaseyana</i> and <i>A. tridentata</i> ssp. <i>spiciformis</i>
<i>A. arbuscula</i> ssp. <i>arbuscula</i> and <i>A. tridentata</i> ssp. <i>vaseyana</i>
<i>A. cana</i> ssp. <i>cana</i> and <i>A. tridentata</i> ssp. <i>wyomingensis</i>
<i>A. tridentata</i> ssp. <i>wyomingensis</i> and <i>A. tripartita</i> ssp. <i>tripartita</i>
<i>A. tridentata</i> ssp. <i>wyomingensis</i> and <i>A. nova</i>
<i>A. nova</i> and <i>A. arbuscula</i> ssp. <i>arbuscula</i>

There are three principal hypotheses that address the stability of hybrid zones. Two of these accept the reduced fitness of hybrids: (1) the dynamic equilibrium model is built on the premise that stability is maintained by a counterbalance of gene flow across the hybrid zone offset by reduced hybrid fitness (Barton and Hewitt 1985)—with this model the hybrid zone is independent of the environment and would not necessarily occur at an ecotone; (2) the mosaic hybrid zone model is built on the premise that hybrid zones occur in ecotones that are a mosaic of two habitats with each parental type adapted to different elements of the mosaics and with unfit hybrids not adapted to either mosaic element (Harrison and Rand 1989). The third model, the bounded hybrid superiority model (Moore 1977), is built on the premise that hybrids are of superior fitness but only in the hybrid zone that occupies an ecotone between parental habitats.

**Table 2**—Described and undescribed hybrid taxa or populations in sagebrush (subgenus *Tridentatae* of *Artemisia*).

Taxon or population	Putative parents	References
<i>A. arbuscula</i> ssp. <i>longicaulis</i>	<i>A. arbuscula</i> ssp. <i>arbuscula</i> x <i>A. tridentata</i> ssp. <i>wyomingensis</i>	Winward and McArthur 1995; McArthur and Sanderson, in press
<i>A. argillosa</i>	<i>A. cana</i> ssp. <i>viscidula</i> x <i>A. longiloba</i>	Beetle 1959
<i>A. tridentata</i> ssp. <i>spiciformis</i>	<i>A. tridentata</i> ssp. <i>vaseyana</i> x <i>A. cana</i> ssp. <i>viscidula</i>	Beetle 1959; Goodrich and others 1985; McArthur and Goodrich 1986; Gunawardena 1994
<i>A. tridentata</i> ssp. <i>xericensis</i>	<i>A. tridentata</i> ssp. <i>tridentata</i> x <i>A. tridentata</i> ssp. <i>vaseyana</i>	Winward 1970; Rosentretter and Kelsey 1991; McArthur and Sanderson, in press
<i>A. tridentata</i> ssp. <i>wyomingensis</i>	<i>A. tridentata</i> ssp. <i>tridentata</i> x <i>A. tridentata</i> ssp. <i>vaseyana</i> with perhaps some involvement with <i>A. nova</i> as well	Beetle and Young 1965; Winward 1975; McArthur 1983; McArthur and others 1998b,c
“Introgressed Wyoming big sagebrush”	<i>A. tridentata</i> ssp. <i>wyomingensis</i> x <i>A. tridentata</i> ssp. <i>vaseyana</i>	Winward, personal communication; McArthur and Sanderson, in press; discussion, this paper
“Dubois sagebrush”	<i>A. tripartita</i> x <i>A. tridentata</i> ssp. <i>wyomingensis</i>	Winward, personal communication; discussion, this paper
“Gosiute sagebrush”	<i>A. tridentata</i> ssp. <i>wyomingensis</i> x <i>A. longiloba</i>	Winward, personal communication; discussion, this paper
“Big sagebrush hybrid zone”	<i>A. tridentata</i> ssp. <i>tridentata</i> x <i>A. tridentata</i> ssp. <i>vaseyana</i>	Hybrid zone papers in table 4, those footnoted <sup>a</sup>

A series of studies in natural hybrid zones and in gardens comprised of parental and natural and synthesized hybrids have led us and our colleagues (principally Carl Freeman, John Graham, and Han Wang) to support the validity of the bounded superiority hybrid zone model for the sagebrush system (table 4). These studies have involved plant morphology, growth rates, plant chemistry, selection gradients and fitness, developmental instability, insect relationships, soils, mineral uptake, plant community dynamics, and respiration and water potential. Whereas each study may not clearly distinguish among the validity of the three principal hybrid zone models, taken in toto, the studies strongly support the bounded hybrid superiority model.

## Consequences of Sagebrush Hybridization and Hybrid Zones

We believe that there are important evolutionary and management considerations for fit hybrids in a stable hybrid zone. Such zones may be narrow as in the case of the Salt Creek Hybrid Zone (see Field Trip report—McArthur and others, this proceedings, and the narrow hybrid zone papers of table 4) but also broad. Our colleague, Alma Winward (personal communication, August 1998, and on other occasions), has suggested that at least three sagebrush forms, which have not been formally described, may be stabilized hybrids (see table 2 for summary of described and non-described hybrid taxa or populations). The first is a plant that has intermediate characteristics between mountain (*Artemisia tridentata* ssp. *vaseyana*) and Wyoming (*A. t.* ssp. *wyomingensis*) big sagebrush. It is widespread in a broad ecotone, generally just below or within the pinyon-juniper (*Pinus edulis-Juniperus osteosperma*) belt, in Utah and neighboring States (see Goodrich and others, this proceedings for many locations) above typical Wyoming big sagebrush habitat and below typical mountain big sagebrush habitat. This plant is most like Wyoming big sagebrush but occurs in more mesic habitats than typical Wyoming big

sagebrush and shares its habitats with some other shrub species that are not usual for Wyoming big sagebrush, for example, bitterbrush (*Purshia tridentata*), Gambel oak (*Quercus gambelii*), and Martin ceanothus (*Ceanothus martinii*). Its stands also have a richer forb and grass understory than do typical Wyoming big sagebrush stands. It is tetraploid like Wyoming big sagebrush but shares some distinctive chemical characteristics with Wyoming big sagebrush (the bitter methacrolein smell) and mountain big sagebrush (some of the water soluble, ultraviolet light visible coumarins). We suspect that it is best treated, until more definitive studies are conducted, as Wyoming big sagebrush that has been introgressed by tetraploid mountain big sagebrush or by unreduced pollen from diploid mountain big sagebrush (McArthur and Sanderson, in press).

The second plant may also best be considered as a variant of Wyoming big sagebrush until definitive studies are performed. It occurs in the area of ancient Tertiary Lake Gosiute in the Upper Green River drainage of Sublette County, WY. Dr. Winward believes that it may be a stabilized hybrid between Wyoming big sagebrush and alkali sagebrush (*A. longiloba*). It has a tendency to layer, a trait absent in typical Wyoming big sagebrush but present in alkali sagebrush; otherwise it is much like Wyoming big sagebrush (Winward, personal communication, February 1996 and August 1998). Large stands of typical Wyoming big sagebrush, typical alkali sagebrush, and the undescribed plant occur in the area. This suggests that an adapted, stabilized hybrid may have developed at a ecotone in the distant past. Its history may be somewhat analogous to Lahontan low sagebrush (*A. arbuscula* ssp. *longicaulis*). Winward and McArthur (1995) formally described this taxon and suggested that it is a stabilized hybrid between low sagebrush (*A. arbuscula* ssp. *arbuscula*) and Wyoming big sagebrush. It occurs in the area of Pleistocene Lake Lahontan. It shares traits inherent in both low sagebrush and Wyoming big sagebrush. Lahontan low sagebrush is a hexaploid. Neighboring populations of low sagebrush are diploid, and Wyoming big sagebrush are tetraploid (McArthur and Sanderson, in press).

The third undescribed plant occurs in the upper Snake River Plain centered near Dubois, ID. Like the previous examples, it involves Wyoming big sagebrush. In this case the new plant is quite similar to three-tip sagebrush (*A. tripartita*) but also has some similarities to Wyoming big sagebrush (Winward, personal communication, August 1998). The undescribed plant incorporates the drought tolerance of Wyoming big sagebrush and has less dramatic leaf indentations than does typical three-tip sagebrush. In the general area of its occurrence, both putative parental taxa are tetraploid (McArthur and others 1998b; McArthur and Sanderson, in press). Until the definitive taxonomic work is performed, we suggest that this plant be referred to as three-tip sagebrush.

We believe that stable hybrid zones serve as a reservoir of fit hybrid plants that are available for exploitation of new habitats. In the past, we believe, this has led to differentiation and new taxa formation. It is a dynamic process; incipient new forms are available for niches as they develop. The tools of molecular genetics allow for the testing of the hypotheses that we have suggested. We believe the results of such research would be interesting.

**Table 4**—Publications on sagebrush hybrid zones or parental and hybrid plants grown in common gardens.

---

Noller and McArthur 1986
McArthur and others 1988
Freeman and others 1991 <sup>a</sup>
Weber and others 1994
Freeman and others 1995 <sup>a</sup>
Graham and others 1995 <sup>a</sup>
Messina and others 1996
Wang and others 1997 <sup>a</sup>
McArthur and others 1998a <sup>a</sup>
McArthur and others 1998b
Wang and others 1998 <sup>a</sup>
Byrd and others 1999 <sup>a</sup>
Freeman and others in 1999 <sup>a</sup>
Wang and others, in press <sup>a</sup>
Graham and others, in review <sup>a</sup>
Freeman and others, this proceedings <sup>a</sup>
Graham and others, this proceedings
Smith and others, this proceedings

---

<sup>a</sup>These papers are part of the series "Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae)."

## Acknowledgments

We thank our colleague Alma Winward for sharing his insights on sagebrush hybridizations. Some of our discussion was made possible by his "fill-in" unscheduled presentation on sagebrush hybrid variants at the symposium and other stimulating discussions on this subject. We also appreciate the opportunity that we have had for ongoing research and discussions with our colleagues Carl Freeman, John Graham, Bruce Smith, Han Wang, and others on the big sagebrush hybrid zone. We thank Clyde Blauer, Sherel Goodrich, and Alma Winward for constructive comments on an earlier version of this manuscript.

## References

- Arnold, M. L. 1997. Natural hybridization and evolution. New York, NY: Oxford University Press. 215 p.
- Barton, N. H.; Hewitt, G. M. 1985. Analysis of hybrid zones. Annual Review of Systematics and Ecology. 16: 113-148.
- Beetle, A. A. 1959. New names within the section *Tridentatae* of *Artemisia*. Rhodora. 61: 82-85.
- Beetle, A. A. 1970. An ecological contribution to the taxonomy of *Artemisia*. Madroño. 20: 385-386.
- Beetle, A. A.; Young, A. 1965. A third subspecies in the *Artemisia tridentata* complex. Rhodora. 67: 405-406.
- Byrd, D. W.; McArthur, E. D.; Wang, H.; Graham, J. H.; Freeman, D. C. 1999. Narrow hybrid zone between two subspecies of big sagebrush, *Artemisia tridentata* (Asteraceae). VIII. spatial and temporal pattern of terpenes. Biochemical Systematics and Ecology. 27: 11-25.
- Clements, F. E. 1905. Research methods in ecology. Lincoln, NB: University Publishing Company. 334 p.
- Freeman, D. C.; Graham, J. H.; Byrd, D. W.; McArthur, E. D.; Turner, W. A. 1995. Narrow hybrid zone between two subspecies of big sagebrush, *Artemisia tridentata* (Asteraceae): III. developmental instability. American Journal of Botany. 82: 1144-1152.
- Freeman, D. C.; Miglia, K. J.; McArthur, E. D.; Graham, J. H.; Wang, H. This proceedings. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). X. performance in reciprocal transplant gardens.
- Freeman, D. C.; Turner, W. A.; McArthur, E. D.; Graham, J. H. 1991. The characterization of a narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*). American Journal of Botany. 78: 805-815.
- Freeman, D. C.; Wang, H.; Sanderson, S. C.; McArthur, E. D. 1999. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae): VII. community and demographic analyses. Evolutionary Ecology Research. 1: 487-502.
- Goodrich, S.; McArthur, E. D.; Winward, A. H. 1985. A new combination and a new variety in *Artemisia tridentata*. Great Basin Naturalist. 45: 100-104.
- Goodrich, S.; McArthur, E. D.; Winward, A. H. This proceedings. Sagebrush ecotones and mean annual precipitation.
- Gosz, J. R. 1991. Fundamental ecological characteristics of landscape boundaries. In: Holland, M. M.; Risser, P. G.; Naiman, R. J., eds. Ecotones, role of landscape boundaries in the management and restoration of changing environments. New York, NY: Chapman and Hall: 8-30.
- Gosz, J. R. 1992. Ecological functions in biome transition zones: translating local responses to broad-scale dynamics. In: Hansen, A. J.; di Castri, F., eds. Landscape boundaries: consequences for biotic diversity and landscape flows, ecological studies 92. New York, NY: Springer Verlag: 55-75.
- Gosz, J. R. 1993. Ecotone hierarchies. Ecological Applications. 3: 369-376.
- Graham, J. H.; Freeman, D. C.; McArthur, E. D. 1995. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae): II. selection gradients and hybrid fitness. American Journal of Botany 82: 709-716.
- Graham, J. H.; Freeman, D. C.; McArthur, E. D. [In review]. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae): XI. insect-plant interactions.
- Graham, J. H.; Freeman, D. C.; Wang, H.; McArthur, E. D. This proceedings. Ecological analysis of the big sagebrush hybrid zone.
- Gunawardena, G. U. 1994. Synthesis and chemistry of 4-hydroxy-2-cyclopentenones. Salt Lake City, UT: University of Utah. 185 p. Dissertation.
- Harrison, R. G., ed. 1993. Hybrid zones and the evolutionary process. New York, NY: Oxford University Press. 364 p.
- Harrison, R. G.; Rand, D. M. 1989. Mosaic hybrid zones and the nature of species boundaries. In: Otte, D.; Endler, J., eds. Speciation and its consequences. Sunderland, MA: Sinauer Associates: 111-133.
- Holland, M. M. 1988. SCOPE/MAB technical consultations on landscape boundaries report of a SCOPE/MAB workshop on ecotones. Biology International, Special Issue. 17: 47-106.
- Holland, M. M.; Risser, P. G.; Naiman, R. J., eds. 1991. Ecotones, the role of landscape boundaries in the management and restoration of changing environments. New York, NY: Chapman and Hall. 142 p.
- Kornkven, A. B. 1997. Molecular systematics of *Artemisia* sect. *Tridentatae* (Asteraceae). Norman, OK: University of Oklahoma. 114 p. Dissertation.
- Levin, D. A. 1995. Plant outliers: an ecogenetic perspective. American Naturalist. 145: 109-118.
- McArthur, E. D. 1983. Taxonomy, origin, and distribution of big sagebrush (*Artemisia tridentata*) and allies (subgenus *Tridentatae*). In: Johnson K. L., ed. Utah Ecology Workshop I; 1981 September 9-10; Ephraim, UT. Logan, UT: Utah State University College of Natural Resources: 3-13.
- McArthur, E. D. 1989. Breeding systems in shrubs. In: McKell, C. M., ed. The biology and utilization of shrubs. San Diego, CA: Academic Press, Inc.: 341-361.
- McArthur, E. D.; Freeman, D. C.; Graham, J. H.; Wang, H.; Sanderson, S. C.; Monaco, T. A.; Smith, B. N. 1998a. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae): VI. respiration and water potential. Canadian Journal of Botany. 76: 567-674.
- McArthur, E. D.; Goodrich, S. 1986. *Artemisia tridentata* ssp. *spiciformis*: distribution and taxonomic placement. In: McArthur E. D.; Welch, B. L., comps. Proceedings of symposium on the biology of *Artemisia* and *Chrysothamnus*; 1984 July 9-13; Provo, UT. Gen. Tech. Rep. INT-200. Ogden, UT: U. S. Department of Agriculture, Forest Service, Intermountain Research Station: 55-57.
- McArthur, E. D.; Monsen, S. B.; Stevens, R. This proceedings. Field trip report.
- McArthur, E. D.; Mudge, J.; Van Buren, R.; Andersen, W. R.; Sanderson, S. C.; Babel, D. G. 1998b. Randomly amplified polymorphic DNA analysis (RAPD) of *Artemisia* subgenus *Tridentatae* species and hybrids. Great Basin Naturalist. 58: 12-27.
- McArthur, E. D.; Plummer, A. P. 1978. Biogeography and management of native Western shrubs: a case study, section *Tridentatae* of *Artemisia*. Great Basin Naturalist Memoirs. 2: 229-243.
- McArthur, E. D.; Pope, C. L.; Freeman, D. C. 1981. Chromosome studies of subgenus *Tridentatae* of *Artemisia*: evidence for autopolyploidy. American Journal of Botany. 68: 589-605.
- McArthur, E. D.; Sanderson, S. C. [In press]. Cytogeography and chromosome evolution of subgenus *Tridentatae* of *Artemisia* (Asteraceae). American Journal of Botany.
- McArthur, E. D.; Van Buren, R.; Sanderson, S. C.; Harper, K. T. 1998c. Taxonomy of *Sphaeromeria*, *Artemisia*, and *Tanacetum* (Compositae, Anthemideae) based on randomly amplified polymorphic DNA (RAPD). Great Basin Naturalist. 58: 1-11.
- McArthur, E. D.; Welch, B. L.; Sanderson, S. C. 1988. Natural and artificial hybridization between big sagebrush (*Artemisia tridentata*) subspecies. Journal of Heredity. 79: 268-276.
- Messina, F. J.; Richards, J. H.; McArthur, E. D. 1996. Variable responses of insects to hybrid versus parental sagebrush in a common garden. Oecologia. 107: 513-521.
- Moore, W. S. 1977. An evaluation of narrow hybrid zones in vertebrates. Quarterly Review of Biology. 52: 263-277.

- Noller, G. L.; McArthur, E. D. 1986. Establishment and initial results from a sagebrush (*Artemisia tridentata*) mass selection garden. In: McArthur E. D.; Welch, B. L., comps. Proceedings of symposium on the biology of *Artemisia* and *Chrysothamnus*; 1984 July 9-13; Provo, UT. Gen. Tech. Rep. INT-200. Ogden, UT: U. S. Department of Agriculture, Forest Service, Intermountain Research Station: 104-107.
- Odum, E. P. 1971. Fundamentals of ecology, 3<sup>rd</sup> edition. Philadelphia, PA: W. B. Saunders Company. 574 p.
- Risser, P. G. 1995. The status of the science examining ecotones. *BioScience*. 45: 318-325.
- Rosentreter, R.; Kelsey, R. G. 1991. Xeric big sagebrush, a new subspecies in the *Artemisia tridentata* complex. *Journal of Range Management*. 44: 330-335.
- Schwemmler, W. 1989. Symbiogenesis, a macro-mechanism of evolution. Berlin, Germany: Water de Gruyter. 226 p.
- Smith, B. N.; Eldredge, S.; Moulton, D. L.; Monaco, T. A.; Jones, A. R.; Hansen, L. D.; McArthur, E. D.; Freeman, D. C. This proceedings. Differences in temperature dependence of respiration distinguish subspecies and hybrid populations of big sagebrush: nature vs. nurture.
- Thompson, R. S. 1991. Pliocene environments and climates in the Western United States. *Quaternary Science Review*. 10: 115-132.
- Unwin, M.; Watson, L. E. 1997. The role of ecotypes in the speciation process: a molecular re-examination of the Clausen, Keck, and Heisey studies on *Achillea*. *American Journal of Botany*. 84(6) supplement: 238 (abstract 694).
- Walker, S. C.; Mann, D. K.; McArthur, E. D. 1996. Plant community changes over 54 years within the Great Basin Experimental Range, Manti-La Sal National Forest. In: Barrow, J. R.; McArthur E. D.; Sosebee, R. E.; Tausch, R. J., comps. Proceedings: shrubland ecosystem dynamics in a changing environment; 1995 May 23-25; Las Cruces, NM. Gen. Tech. Rep. INT-GTR-338. Ogden, UT: U. S. Department of Agriculture, Forest Service, Intermountain Research Station: 66-68.
- Wang, H.; Byrd, D. W.; Howard, J. L.; McArthur, E. D.; Graham, J. H.; Freeman, D. C. 1998. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae): V. soil properties. *International Journal of Plant Science*. 159: 139-147.
- Wang, H.; McArthur, E. D.; Freeman, D. C. [In press]. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae): IX. elemental uptake and niche separation. *American Journal of Botany*.
- Wang, H.; McArthur, E. D.; Sanderson, S. C.; Graham, J. H.; Freeman, D. C. 1997. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae): IV. reciprocal transplant experiments. *Evolution*. 51: 95-102.
- Ward, G. H. 1953. *Artemisia*, section *Serphidium*, in North America: a cytotaxonomic study. *Contributions from the Dudley Herbarium*. 4: 155-205.
- Weber, D. J.; Gang, D. R.; Hall, S. C.; Smith, B. N.; McArthur, E. D. 1994. Inheritance of hydrocarbons in subspecific big sagebrush (*Artemisia tridentata*) hybrids. *Biochemical Systematics and Ecology*. 22: 689-697.
- Wiens, J. A.; Crawford, C. S.; Gosz, J. R. 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. *Oikos*. 45: 421-427.
- Winward, A. H. 1970. Taxonomic and ecological relationships of the big sagebrush complex in Idaho. Moscow, ID: University of Idaho. 80 p. Dissertation.
- Winward, A. H. 1975. Evolutionary development of *Artemisia tridentata* taxa. In: H. C. Stutz, ed. Proceedings, symposium and workshop, wildland shrubs; 1975 November 6; Provo, UT. Provo, UT: Brigham Young University: 163.
- Winward, A. H.; McArthur, E. D. 1995. Lahontan sagebrush (*Artemisia arbuscula* ssp. *longicaulis*): a new taxon. *Great Basin Naturalist*. 55: 151-157.
- Young, J. A.; Clements, C. D. This proceedings. Ecotones between *Artemisia nova* and *A. tridentata* communities in the Buckskin Mountains of western Nevada.