

STUDIES OF A NEW HYBRID TAXON IN THE *ARTEMISIA TRIDENTATA* (ASTERACEAE: ANTHEMIDEAE) COMPLEX

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ABSTRACT.—Members of the *Artemisia tridentata* complex (ASTERACEAE: Anthemideae: *Artemisia* subgen. *Tridentatae*) have adapted to changing environmental conditions through geographic migration, introgression, and hybridization. These processes have resulted in morphologic and genetic variation. A presumed hybrid (“Bonneville” big sagebrush) of the complex occurs in the moister ranges of *A. t. ssp. wyomingensis* and can be found growing with shrub species commonly associated with *A. t. ssp. vaseyana*. These populations appear to be preferred habitat for sage-grouse and are more heavily grazed by ungulates than the parental populations. We determined ploidy levels and conducted a detailed morphological analysis to determine if “Bonneville” is a hybrid entity. Sixteen populations (12 in Oneida Co., ID, and 4 in Rich Co., UT) were selected for the study, representing the putative hybrid (Taxon B) and the putative parents—*A. t. ssp. vaseyana* ($2n = 18$), *A. t. ssp. wyomingensis* ($2n = 36$), and *A. t. ssp. tridentata* ($2n = 36$). Each population consisted of 25 randomly selected individuals for a total of 400 samples. Our analysis showed 3 populations with morphological and chemical characteristics indicating introgression of *A. t. ssp. wyomingensis* with populations containing *A. t. ssp. vaseyana*. Based on these results, we designate the Bonneville sagebrush with formal hybrid status of nothotaxon: *Artemisia tridentata ssp. ×bonnevillensis* H. Garrison, L. Shultz, and E.D. McArthur [pro subsp.], $2n = 36$.

RESUMEN.—Los arbustos que forman parte del complejo *Artemisia tridentata* (ASTERACEAE: Anthemideae: *Artemisia* subgénero *Tridentatae*) se han adaptado a las condiciones ambientales cambiantes a través de la migración geográfica, la introgresión y la hibridación, lo cual ha dado como resultado variación morfológica y genética. Un supuesto híbrido (*Artemisia* “Bonneville”) del complejo habita en sitios húmedos de *A. t. ssp. wyomingensis* y se puede encontrar creciendo entre las especies de arbustos que habitualmente se asocian con *A. t. ssp. vaseyana*. Estas poblaciones parecen ser el hábitat preferido del gallo de salvia y donde pastan más los ungulados, en comparación con las poblaciones parentales. Determinamos niveles de ploidía y realizamos un análisis morfológico exhaustivo para determinar si “Bonneville” es una entidad híbrida. Se seleccionaron dieciséis poblaciones para realizar el estudio, que representan el híbrido potencial (Taxón B) y los parentales potenciales: *A. t. ssp. vaseyana* ($2n = 18$), *A. t. ssp. wyomingensis* ($2n = 36$), *A. t. ssp. tridentata* ($2n = 36$): doce en el condado de Oneida, Idaho y cuatro en el condado de Rich, Utah. Cada población consistió de veinticinco individuos seleccionados al azar con un total de cuatrocientas muestras. Nuestro análisis mostró tres poblaciones con características morfológicas y químicas que indican introgresión de *A. t. ssp. wyomingensis* con poblaciones de *A. t. ssp. vaseyana*. Con base en estos estudios, asignamos a la *Artemisia* Bonneville la condición de híbrido formal de un nototaxon, como *Artemisia tridentata ssp. ×bonnevillensis* H. Garrison, L. Shultz, y E.D. McArthur [pro subsp.], $2n = 36$.

The big sagebrush complex, *Artemisia* subgenus *Tridentatae* (ASTERACEAE: Anthemideae), comprises one of the most widespread and economically important shrub groups of the North American continent (Freeman et al. 1991). These shrubs provide critical habitat for wildlife and livestock (McArthur et al. 1981, Shultz et al. 1991) and are a major food source, especially during the winter months (Sheehy and Winward 1981, Welch et al. 1991, Weber et al. 1994, Wambolt 1996). They are also recommended for rangeland rehabilitation (McArthur et al. 1981, Mahalovich and McArthur 2004, Shaw et al. 2005).

Shultz (2009) recognizes 13 species and 20 subspecies within the *Tridentatae* complex that collectively have a wide geographic distribution and altitudinal variation. Garcia et al. (2011a, 2011b) proposed some adjustments based on molecular DNA sequencing studies. This geographically extensive and ecologically important complex dominates vegetation on approximately 69 million ha in the Colorado Plateau and Great Basin (West and Young 2000). With this wide geographic distribution, *Tridentatae* species are subject to varying climates, soils, nutrients, water availability, herbivores, and pathogens. Heterogeneity in the

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physical and biological environment means that plant populations must compensate for a wide variety of environmental conditions. The extensive genetic differentiation within *Tridentatae* is manifest in subspecific differentiation, including ecotypes, varieties, and subspecies that are adapted to specific habitats (Downs 2000, Garcia et al. 2011a, 2011b).

Geographic migration, introgression, and hybridization have all played crucial roles in the differentiation and evolution of these shrubs. Here we focus on hybridization processes as they apply to a recently identified big sagebrush taxon. Hybridization has been implicated in the origin and diversification of *Tridentatae* taxa (McArthur et al. 1988, Winward and McArthur 1995, McArthur and Sanderson 1999b, Shultz 2009).

In the early 1980s, Alma Winward discovered what he considered to be a new taxon of *Artemisia tridentata* that he informally called "Bonneville" big sagebrush, a common name that has been used in subsequent publications (McArthur and Sanderson 1999b, Winward 2004, Garrison 2006, Shultz 2009, 2012, Rivera et al. 2011). These populations were first noticed on lakeshore sediments of Pleistocene Lake Bonneville within the lower elevations of the pinyon-juniper vegetation type to upper sagebrush steppe. Goodrich (2005) also reported a broad hybrid or mixing zone between *A. tridentata* ssp. *wyomingensis* and *A. t.* ssp. *vaseyana* that he discovered through examination of water soluble coumarin compounds from leaves that fluoresce bright blue under longwave ultraviolet light (Stevens and McArthur 1974, McArthur and Sanderson 1999a). Goodrich et al. (1999) sampled 82 populations above, in, and below the pinyon-juniper belt from many locations in Utah. They found that 60% of the *A. t.* ssp. *wyomingensis* populations were below this belt, 75% of the *A. t.* ssp. *vaseyana* populations were above this belt, and 91% of what appeared to be an intermediate between *A. t.* ssp. *wyomingensis* and *A. t.* ssp. *vaseyana* were within this belt. This putative taxon is the subject of our study and it will be designated "Taxon B" for the remainder of the paper.

Taxon B has morphological characteristics of both *A. t.* ssp. *wyomingensis* and *A. t.* ssp. *vaseyana* but occurs in the moister ranges of *A. t.* ssp. *wyomingensis*. McArthur and Sanderson (1999b) and McArthur (2005) suggested

that these populations should be considered *A. t.* ssp. *wyomingensis* introgressed with *A. t.* ssp. *vaseyana*. Taxon B has been found growing with Gambel oak (*Quercus gambelii*), antelope bitterbrush (*Purshia tridentata*), serviceberry (*Amelanchier alnifolia*), and mountain snowberry (*Symphoricarpos oreophilus*). These species are not commonly associated with *A. t.* ssp. *wyomingensis* (Winward 2004). Taxon B is of particular interest because of its high utilization by wild ungulates and birds (Winward 2004), a preference that presumably indicates a chemical differentiation present in the hybrid.

The evolutionary consequences of hybridization include increased intraspecific genetic diversity, origin and transfer of genetic adaptations, origin of new ecotypes or species, and reinforcement or breakdown of reproductive barriers (Arnold 1992, Rieseberg 1997). Hybridization is a widely known feature of the micro- and macroevolutionary patterns of vascular plants. Hybridization is not a universal process in all plant species; it seems to be concentrated in a small number of families and in an even smaller number of genera (Ellstrand et al. 1996). A survey of 5 biosystematic floras revealed that hybridization is suggested at an average frequency of 11% across the families reviewed (Rieseberg 1997). Hybridization can lead to the production of a pool of introgressed genotypes that are more or less fit, genotypes that may expand into a novel habit or produce a "hybrid sink" where preferential selection takes place. Hybrid species can also be formed through processes that involve polyploidy, parthenogenesis, hybridogenesis, or homoploid speciation (Arnold 1992).

Allendorf et al. (2001) define 6 categories of hybridization, which include a natural hybrid taxon; natural introgression; a natural hybrid zone; hybridization without introgression; and 2 types of hybrid swarms, one with widespread introgression and one with complete admixture. A natural hybrid taxon is one that arises through natural genetic admixture. A natural introgression involves an exchange of genes between taxa that does not lead to a new taxon. A natural hybrid zone is a contact area between 2 genetically distinct species that hybridize. Hybridization without introgression occurs when the F₁ generation is sterile. A hybrid swarm is a population of individuals that have varying numbers of generations of

backcrossing with parental types and mating among hybrids. The 2 types include widespread introgression where the parental taxa are still genetically different and complete admixture where the parental taxa are no longer genetically distinct.

Five different sagebrush taxa in the *Artemisia* subgenus *Tridentatae* complex are currently thought to have originated as hybrids. These include *Artemisia spiciformis* (Shultz 2009), *A. ×argilosa* (Winward 2004, Shultz 2009), *A. tridentata* ssp. *×xericensis* (Rosentreter and Kelsey 1991, Shultz 2009), *A. t.* ssp. *wyomingensis* (Beetle and Young 1965), and *A. arbuscula* ssp. *×longicaulis* (Winward and McArthur 1995, Shultz 2009). *Artemisia tridentata* ssp. *tridentata* and *A. t.* ssp. *vaseyana* are 2 subspecies that are known to hybridize and produce stable hybrid zones (McArthur and Sanderson 1999b, Miglia et al. 2005, Shultz 2009). Some methods that have been used to make these distinctions include reciprocal transplant gardens (McArthur et al. 1979, 1988, McArthur and Sanderson 1999b), ecological analysis of hybrids (Freeman et al. 1991, Wang 1996, Wang et al. 1997, Miglia 2003, Rivera et al. 2011, Kusbach et al. 2012), community and demographic analyses (Freeman et al. 1999), spatial and temporal patterns of terpene content (Byrd et al. 1999), developmental instability (Freeman et al. 1995), identity of galls (Graham et al. 2001), respiration and water potential (McArthur et al. 1998a), soil properties (Wang et al. 1998), hydrocarbons and elemental uptake (Weber et al. 1994), and niche separation (Wang et al. 1999). Molecular analyses have also been applied to the hybrid zones (McArthur et al. 1998b, 1998c). It has been shown that *A. tridentata* subspecies and their hybrids retain their morphological characters in common garden experiments and reciprocal transplant gardens (Wang et al. 1997), suggesting that they are genetically distinct.

The increasing number of studies performed on the *A. t.* ssp. *tridentata* × *A. t.* ssp. *vaseyana* hybrid zone and other types of hybrid zones shows the importance of understanding hybridization within a species complex. By studying different hybrids within a species, we can gain a better understanding of the genetic variation needed to survive and thrive in different environments.

The *Tridentatae* are common shrubs in western North America and have been prominent

since the late Tertiary or early Quaternary (Axelrod 1950, Freeman et al. 1991), with the earliest occurrence of sagebrush steppe appearing as early as the Miocene (Davis and Ellis 2010). The species are long lived and wind-pollinated, with limited seed dispersal. They flower between midsummer and late fall and can be found parapatrically distributed throughout the region. The present distributional extent was probably established near the end of the last major glaciation (Axelrod 1950, McArthur et al. 1981, Freeman et al. 1991, Shultz 2009). The *Tridentatae* species are apparently built on a reticulate, hybridizing matrix (McArthur et al. 1981, Weber et al. 1994, Shultz 2009). The base chromosome number for these subspecies is $x = 9$, with $2n = 18$ for diploids and $2n = 36$ ($4x$) for tetraploids being common (McArthur et al. 1981).

Morphometrics have been used successfully to identify new taxa arising from hybrid complexes. Freeman et al. (1991) used morphometrics to characterize a well-known hybrid zone between *Artemisia tridentata* ssp. *vaseyana* and *A. t.* ssp. *tridentata* at Salt Creek and Orem, Utah. Their field measurements included height, crown diameter, height to first branch from ground, number of branches >1 cm in diameter that occurred in the first 10 cm of height, and number of inflorescences per shrub. They also collected 2 small branches bearing inflorescences from each individual. These samples were used to measure branch length, inflorescence length, internode length for the first 3 internodes of the inflorescence, leaf length, maximum leaf width, position of maximum leaf width, and distance between the terminal vegetative branch and the closest inflorescence. Freeman et al. (1991) found that at the Salt Creek site, the putative parental taxa differed in 6 of the 13 traits. The putative parents differed in 11 of the 13 traits for the Orem site. *Artemisia tridentata* ssp. *tridentata* is generally larger with greater height, branch length, crown diameter, and stem circumference. *Artemisia tridentata* ssp. *vaseyana* has more branches near the ground that are proportionately broader than those of *A. t.* ssp. *tridentata*.

Freeman et al. (1991) found that the subspecies could be distinguished by morphological measures and that hybrids were intermediate to the parental taxa for the majority of characters. They used multivariate analysis

of variance (MANOVA) to determine whether taxa differed by site in respect to all characters considered simultaneously, and they used univariate ANOVA to compare the means of separate morphological measures. The data were interpreted using the Student–Newman–Keuls multiple range tests. Principal component analysis (PCA) and discriminant function analysis were used to explore morphological variation among the populations. PCA was used on the parental taxa, and discriminant function analysis was used on hybrids and parents.

Winward and McArthur (1995) used inflorescence length, vegetative stalk length, persistent leaf length, persistent leaf width, and persistent leaf length:width ratio to differentiate *A. arbuscula* ssp. *×longicaulis* from its putative parents, *A. t.* ssp. *wyomingensis* and *A. a.* ssp. *arbuscula*. To differentiate between sagebrush taxa in Idaho, Winward and Tisdale (1977) used leaf length, leaf width, leaf length:width ratio, length of vegetative shoots and flower stalks, flower head diameter, number of flowers per head, flower heads per stalk, and average seed weight.

The purpose of this study was to determine the relationship of Taxon B to the putative parents by using multivariate analysis of 19 morphometrics. Taxon B will have additive or intermediate morphology if it is of hybrid origin. Clinal variation is another possible explanation for Taxon B, and such variation can be determined by a gradual change in the morphology from one parental taxon to another. Ploidy levels were determined for each of the populations. Taxon B is either a stabilized hybrid with distinctive morphology representing a new taxon or an introgressed swarm with no morphological discontinuity.

METHODS

Sixteen populations, 4 of each taxon, were selected for this study. Twelve populations occurred on or near the Curlew National Grassland in Oneida and Cassia Counties, Idaho, and 4 occurred on the east side of Bear Lake in Rich County, Utah. Figure 1 indicates the general locations, and Table 1 provides further subspecies information for the 16 *Artemisia tridentata* populations. The study areas were chosen because they were primary sites where Taxon B had previously been identified by Alma Winward.

Study Areas

SOUTHERN IDAHO.—The Curlew National Grassland (CNG) consists of 19,263 ha of land located in Oneida County, Idaho. The CNG is predominately covered with sagebrush and crested wheatgrass and is representative of Basin and Range topography. Over 14,164 ha within the CNG were cultivated and farmed in the early 1900s. With the assistance of different agencies, universities, and private owners, these lands have been intensely managed to promote grassland agriculture and multiple-use, sustained yield of the resources (Beitia and Gunnell 1986). Figure 1 shows the location of the 12 *Artemisia* populations on or near the CNG.

NORTHERN UTAH.—Four *Artemisia* populations were located on the east side of Bear Lake in Rich County, Utah. This was another area where Taxon B had been identified and was being heavily browsed by wild ungulates (A. Winward personal observation). Figure 1 shows the locations of the 4 populations.

Putative Parents of Taxon B

Artemisia tridentata Nuttall ssp. *tridentata* (basin big sagebrush) individuals are mid-sized to tall shrubs. These shrubs have uneven crowns, with long and broad flowering stalks arising from different levels within the crown. The vegetative stalks nearly equal the length of the flowering stalks (Winward 2004, Shultz 2009). Basin big sagebrush is primarily diploid (McArthur et al. 1981, McArthur and Sander-son 1999a). Basin big sagebrush occurs in deep, well-drained, often alluvial soils in drainage and valley bottoms at elevations of 1300–2200 m (Winward 2004, Shultz 2009). It ranges from southern British Columbia to southwestern North Dakota and south to Baja California and northern New Mexico (Goodrich 2005). This taxon is more valuable for its cover and less for its palatability, except during severe winters (McArthur and Stevens 2004, Winward 2004).

Artemisia tridentata ssp. *vaseyana* (Rydb.) Beetle (mountain big sagebrush) individuals are low to mid-sized shrubs. These shrubs have a flat-topped crown with long and narrow flowering stalks arising from near the top, an appearance often described as a “birthday cake with many candles,” and vegetative stalks are less than half the length of flowering stalks (Winward 2004, Shultz 2006). Mountain big

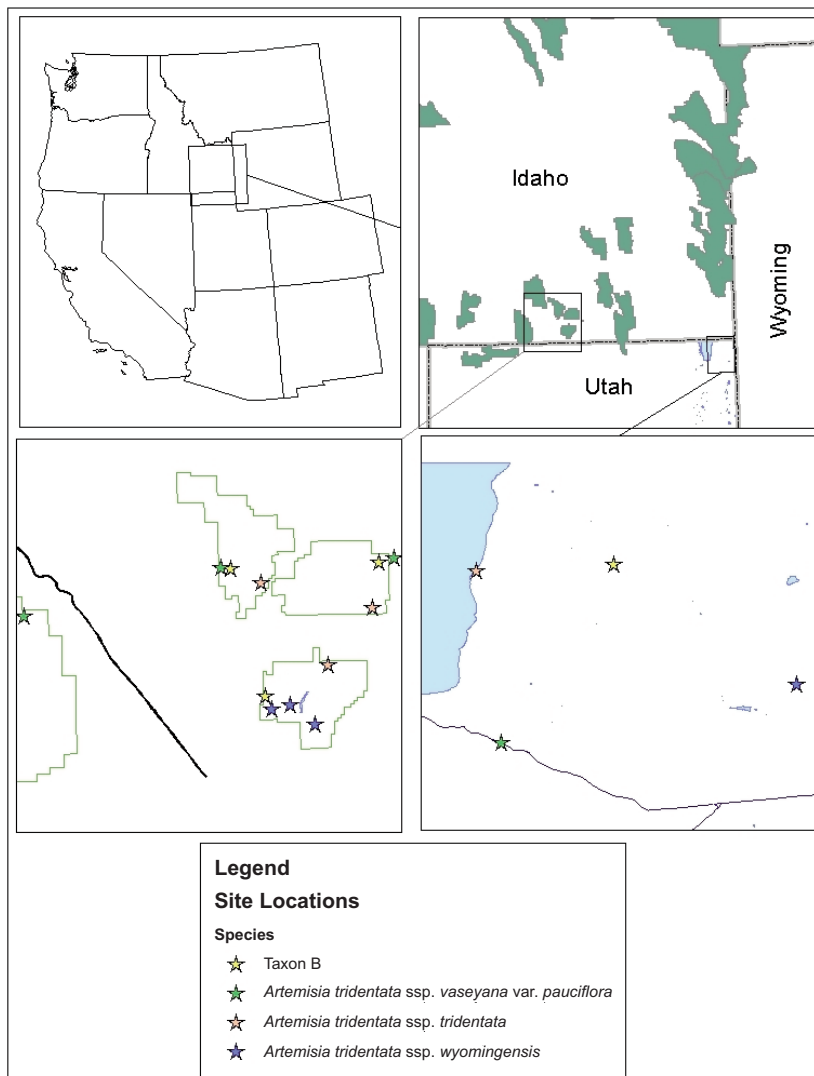


Fig. 1. Mapped locations of *Artemisia* populations showing study areas in Idaho and Utah: Curlew Valley National Grasslands (Idaho–Utah border) and east side of Bear Lake (near Utah–Wyoming border).

sagebrush is primarily diploid (McArthur et al. 1981, McArthur and Sanderson 1999a). This subspecies has been split into 2 varieties by some taxonomists (Goodrich et al. 1985, Winward 2004): *A. t.* var. *pauciflora* and *A. t.* var. *vaseyana*, varying in the number of florets per head. The putative parent of Taxon B would be variety *pauciflora*, which is now included within *A. t.* ssp. *vaseyana* (Shultz 2009). Mountain big sagebrush is typically found in montane meadows between 2000 m and 2800 m, usually in rocky soils (Shultz 2006), but it also occurs on mountain foothills. Mountain

big sagebrush sites are productive, with diverse herbaceous species, and provide habitat and forage for many wildlife species (McArthur and Stevens 2004, Winward 2004).

Artemisia tridentata ssp. *wyomingensis* Beetle & Young (Wyoming big sagebrush) is a low-growing shrub occurring mostly in drier environments. Individuals have an uneven crown and short flowering stalks. The mature shrubs have a “twiggy” appearance due to past inflorescences that persist for many years (Shultz 2006). The flowering stalks occur in clusters mixed throughout the crown, giving

TABLE 1. Location and subspecies information for the *Artemisia tridentata* populations used in the morphometric analysis. Abbreviations: ID = Idaho, UT = Utah, FS = USDA Forest Service, BLM = USDI Bureau of Land Management, CNG = Curlew National Grassland.

<i>Artemisia tridentata</i> subspecies or variety	Population number	Location	Elevation (m)
<i>×bonnevillensis</i>	B1	Oneida County, ID: CNG middle unit, up Sheep Creek Canyon	1609
<i>vaseyana</i>	V1	Oneida County, ID: BLM lands adjacent to CNG, up Sheep Creek Canyon	1756
<i>tridentata</i>	T1	Oneida County, ID: CNG middle unit, just past FS boundary	1512
<i>wyomingensis</i>	W1	Oneida County, ID: CNG south unit, east of Stone Reservoir	1405
<i>×bonnevillensis</i>	B2	Oneida County, ID: CNG north unit, Salyer Springs	1670
<i>vaseyana</i>	V2	Oneida County, ID: CNG north unit, Salyer Springs	1731
<i>tridentata</i>	T2	Oneida County, ID: CNG north unit, just off Meadow Creek Road	1536
<i>wyomingensis</i>	W2	Oneida County, ID: CNG south unit, west of Stone Reservoir	1408
<i>×bonnevillensis</i>	B3	Oneida County, ID: CNG south unit, northwest of Stone Reservoir near FS boundary	1454
<i>vaseyana</i>	V3	Cassia County, ID: North Black Pine Mountain, SNE, up Sweetzer Canyon	1829
<i>tridentata</i>	T3	Oneida County, ID: CNG south unit, south of Holbrook, just south of FS boundary	1451
<i>wyomingensis</i>	W3	Oneida County, ID: CNG south unit, west of reservoir, just past corral	1411
<i>×bonnevillensis</i>	B4	Rich County, UT: east of Bear Lake, up South Eden Canyon	2097
<i>vaseyana</i>	V4	Rich County, UT: east of Bear Lake, off Hwy. 30	2115
<i>tridentata</i>	T4	Rich County, UT: in South Eden campground	1817
<i>wyomingensis</i>	W4	Rich County, UT: north of Sage Junction	1920

mature shrubs an uneven appearance (Winward 2004). Wyoming big sagebrush is uniformly tetraploid (McArthur et al. 1981, McArthur and Sanderson 1999a). It is found on xeric sites from temperate desert basins to high plateaus on rocky to fine-grained soils. Such stands where Wyoming big sagebrush is dominant occur between 800 m and 2200 m elevation (Shultz 2009). They range from eastern Washington to western North Dakota and south to California and northern Arizona and New Mexico (Goodrich 2005). Wildlife utilization of Wyoming big sagebrush is dependent on many factors, ranging from high in some areas to low in others (McArthur and Stevens 2004, Winward 2004).

Ploidy Level Determination

Flow cytometry analysis is a technique proven to determine ploidy levels when samples of known ploidy status are compared to study populations (McArthur and Sanderson 1999a, Koontz and Soltis 2001). Samples were collected from May to early August 2005 and consisted of a 6-inch branch removed from 6

to 10 individuals per population. The branches were placed in labeled plastic sandwich bags and transported on ice to the Rocky Mountain Research Station (RMRS), Shrub Sciences Laboratory, USDA Forest Service, Provo, Utah. Flow cytometry analysis uses the relative amount of DNA to determine ploidy levels and is useful in the *Tridentatae* complex to show whether individuals are diploid or tetraploid (McArthur and Sanderson 1999a, Garcia et al. 2004). The ploidy determinations were made on a Partec Ploidy Analyser PA II Flow Cytometer (Partec GmbH, Munster, Germany).

Morphometrics

Nineteen morphometric characters were measured for 100 individuals (25 individuals in 16 populations, 4 of each taxon):

1. Height (cm)
2. Crown diameter (cm)
3. Crown diameter: height ratio
4. Height to first branch from ground (cm)
5. Stem circumference at 10 cm height (cm)
6. Number of branches >1 cm in diameter that occurred in the first 10 cm of height

7. Branch angle of divergence
8. Inflorescence length (cm)
9. Vegetative branch length (cm)
10. Inflorescence : vegetative branch ratio
11. Flowers per head
12. Flower heads per 10 cm stalk length
13. Fluorescence of leaf material under ultraviolet light

For ephemeral and persistent leaves:

14. Leaf length (cm)
15. Leaf width (cm)
16. Leaf length : width ratio
17. Position of maximum leaf width (cm)
18. Leaf lobe length (cm)
19. Ephemeral leaf length : persistent leaf length ratio

Twenty-five mature individuals from each population were randomly selected for the measurements. Height, crown diameter, height to first branch from ground, number of branches >1 cm in diameter in the first 10 cm height, stem circumference at 10 cm of height, and branch angle of divergence were measured in the field during summer 2005. Twenty-five branches were clipped from the shrubs in June to early August and pressed for measurements of the ephemeral leaves. Fifty branches were clipped from September to October for persistent leaves, inflorescences, and vegetative branches. Ages of the 25 individuals, except for population T4, which was located in a state campground, were determined after all other measurements were taken in 2006. Age was determined by cutting down the individuals and counting the growth rings (Ferguson 1964). Ephemeral and persistent leaves differ in shape and size and are produced at different times of the year (Miller and Shultz 1987). Measurements of leaf length, leaf width, and position of maximum leaf width and leaf lobing were taken from 10 leaves of each type. Measurements were taken of vegetative branch length and inflorescence branch length. Flowers per head were counted from fresh or frozen material.

Chemical Analysis

Fluorescence of water-soluble coumarins was measured from the pressed specimens. The measure of the coumarin content was based on the protocol of McArthur and Sanderson (1999a) by using a scale of 0–5, with 0 being no fluorescence and 5 being a bright bluish white color. Three to 4 leaves per sample were crushed and placed in a beaker with approximately 50 mL of water. The beaker was then placed under longwave UV light and

scored according to the level of fluorescence compared to reference samples from the herbarium of the Shrub Sciences Laboratory of the Rocky Mountain Research Station (SSLP).

The number of heads per 10 cm stalk length was measured by cutting the stalk 10 cm distal to the apex and counting individual flower heads.

Voucher specimens were taken from the group B fall collections and were deposited in the Intermountain Herbarium (UTC).

Statistical Analysis

Univariate and multivariate statistical analyses of morphometric data were performed using SAS statistical packages (SAS 2006). The means and standard deviations were calculated for all morphometrics except position to maximum leaf width, which was a similar measurement to overall leaf length.

Three of the morphological measurements—height, crown diameter, and stem circumference—are age related. These 3 measurements were tested for correlation with age using Pearson's correlation coefficient in a univariate analysis (SAS 2006). Correlations were performed by taxa for each of the measurements. *Artemisia tridentata* ssp. *vaseyana*, *A. t.* ssp. *wyomingensis*, and Taxon B had 100 observations each, and *A. t.* ssp. *tridentata* had 75 observations.

A multivariate cluster analysis using Proc Cluster with the Flexible Method in SAS was performed on the individual observations by using all variables except age and ploidy level. The data were first standardized using Proc Distance with the "dgowor" method (SAS 2006), and the variables height to first branch, vegetative branch length, and heads per 10 cm stalk length were log-transformed. The other clustering algorithms available in Proc Cluster were tried and produced either similar results with less clarity or a single cluster of all the observations. Analyses were performed using a modified data set with 2 outliers from 2 different *A. t.* ssp. *wyomingensis* populations removed. A default β level of -0.25 was used with the Flexible Method, which gives good recovery of the underlying structure of the data (Milligan 1989). An analysis was also performed with the original data set with a β level of -0.5 , a level suggested for better recovery of the data structure when outliers are present (Milligan 1989). Only the results from the

TABLE 2. Ploidy levels for populations as determined with a Partec PA II Ploidy Analyzer. The top row of numbers refers to individual plants from the sampled population. V = *Artemisia tridentata* ssp. *vaseyana*, B = *Artemisia tridentata* ssp. *×bonnevilleensis*, T = *Artemisia tridentata* ssp. *tridentata*, and W = *Artemisia tridentata* ssp. *wyomingensis*.

Population number	Ploidy									
	1	2	3	4	5	6	7	8	9	10
V1	2x	2x	2x	2x	2x	2x				
V2	2x	2x	2x	2x	2x	2x	2x	2x	2x	2x
V3	2x	2x	2x	2x	2x	2x	2x	2x	2x	2x
V4	2x	2x	2x	2x	2x	2x	2x	2x	2x	2x
B1	4x	4x	4x	4x	4x	4x	4x	4x	4x	4x
B2	4x	4x	4x	4x	4x	4x	4x	4x	4x	4x
B3	4x	4x	4x	4x	4x	4x	4x	4x	4x	4x
B4	4x	4x	4x	4x	4x	4x	4x	4x	4x	4x
T1	2x	2x	2x	2x	2x	2x	2x	2x	2x	2x
T2	2x	2x	2x	2x	2x	2x	2x	2x	2x	2x
T3	2x	2x	2x	2x	2x	2x	2x	2x	2x	2x
T4	2x	2x	2x	2x	2x	2x	2x	2x	2x	2x
W1	4x	4x	4x	4x	4x	4x	4x	4x	4x	4x
W2	4x	4x	4x	4x	4x	4x	4x	4x	4x	2x
W3	4x	4x	4x	4x	4x	4x	4x	4x	4x	4x
W4	4x	4x	4x	4x	4x	4x	4x	4x	4x	4x

second analysis are presented here because both analyses distinguished between the parental taxa.

RESULTS

Results of ploidy determinations are given in Table 2. *Artemisia tridentata* ssp. *vaseyana* and *A. t.* ssp. *tridentata* individuals are consistently diploid ($2n = 18$), and *A. t.* ssp. *wyomingensis* individuals are tetraploid ($2n = 36$). Taxon B was found to be tetraploid ($2n = 36$). The tenth individual of the W2 population was reselected for the morphometric study because it was diploid.

Correlations between height, crown diameter, and stem circumference and age are shown in Figures 2–4. Figure 2a and 2b show a weak positive correlation between height and age for *A. t.* ssp. *tridentata* ($0.32, P = 0.005$) and *A. t.* ssp. *vaseyana* ($0.28, P = 0.004$), respectively. Figures 2c and 2d for *A. t.* ssp. *wyomingensis* and Taxon B, respectively, show no significant correlation between height and age ($P = 0.36$ and $P = 0.93$, respectively). Figure 3a, 3b, and 3d show no significant correlation between average crown diameter and age for *A. t.* ssp. *tridentata*, *A. t.* ssp. *vaseyana*, and Taxon B ($P = 0.86, P = 0.70$, and $P = 0.56$, respectively). Figure 3c shows that *A. t.* ssp. *wyomingensis* has a slight positive correlation between average crown diameter and age ($0.23, P = 0.02$). All taxa have a slight positive correlation between stem circumference and age (Fig. 4a–4d:

$0.25, P = 0.03$; $0.55, P \leq 0.0001$; $0.27, P = 0.007$; and $0.45, P = <0.0001$, respectively). The general lack of significant correlation between these 3 variables and age could be an artifact of the sampling design. Samples were taken only from larger, mature shrubs that were more uniform in age.

Figures 5–6 show the results of multivariate analyses with clusters representing the 4 study taxa. In the putative parental taxon analysis, 98 of 100 of *A. t.* ssp. *wyomingensis* individuals are in cluster 1; 94 of the 100 *A. t.* ssp. *vaseyana* individuals are in cluster 2; and 100 of 100 of the *A. t.* ssp. *tridentata* individuals are in cluster 3 (Table 3). Figure 5 is a visual representation of the cluster analysis using the first 2 compound variables from a canonical discriminant analysis (Proc Candisc in SAS, 2006). Cluster 1 represents *A. t.* ssp. *wyomingensis*; cluster 2 represents *A. t.* ssp. *vaseyana*; and cluster 3 represents *A. t.* ssp. *tridentata*. This analysis shows that the parental taxa segregate well using morphometrics.

Table 4 shows that 96 of 100 *A. t.* ssp. *wyomingensis* are in cluster 1; 83 of 100 *A. t.* ssp. *vaseyana* are in cluster 2; and 93 of 100 *A. t.* ssp. *tridentata* are in cluster 3. Thirty-five out of 100 observations for Taxon B are in cluster 4. Table 5 shows the distribution of the observations within the 16 populations and between the 4 clusters. Populations segregate as follows: of the 83 *A. t.* ssp. *vaseyana* observations in cluster 2, 25 are from population

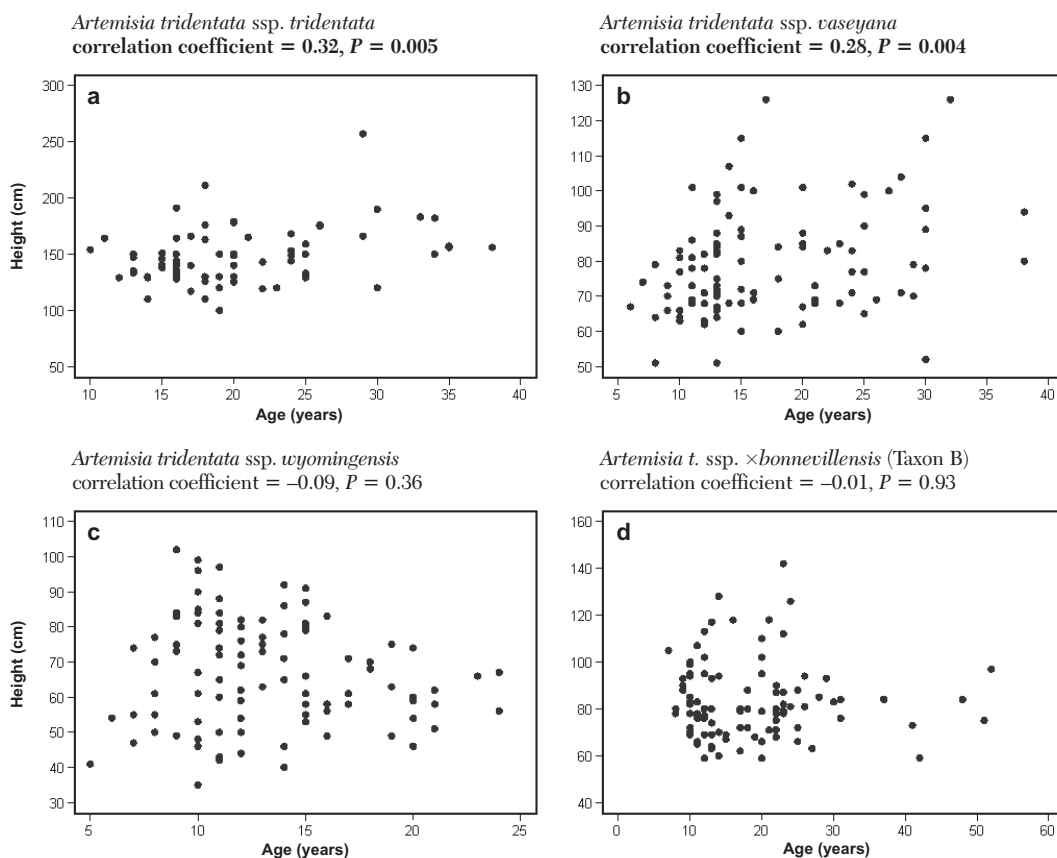


Fig. 2. Correlation between height and age for each taxon: a, *Artemisia tridentata* ssp. *tridentata*; b, *A. t.* ssp. *vaseyana*; c, *A. t.* ssp. *wyomingensis*; d, *A. t.* ssp. \times *bonnevillensis* (Taxon B).

V1, 17 are from population V2, 23 are from population V3, and 18 are from population V4. Of the 96 *A. t.* ssp. *wyomingensis* observations, 23 are from population W1, 24 from population W2, 25 from population W3, and 24 from population W4. Of the 93 *A. t.* ssp. *tridentata* observations, 19 are from population T1, 25 from population T2, 24 from population T3, and 25 from population T4. B1 has 22 of 25 observations in cluster 4, 2 observations in cluster 2, which represents *A. t.* ssp. *vaseyana*, and 1 observation in cluster 3, which represents *A. t.* ssp. *tridentata*. B2, B3, and B4 have the majority (19, 22, and 19, respectively) of their individuals in cluster 1, which represents the *A. t.* ssp. *wyomingensis* taxon. The other individuals are in cluster 4, with 1 from B2 and 1 from B4 in cluster 3, which represents *A. t.* ssp. *tridentata*. V2, V3, and V4 all have observations in cluster 4 (8, 2, and 7, respectively), and T1 has 6, W1 has 2, and W4 has 1.

Figure 6 is a visual interpretation of the cluster results for all 400 observations using the same process outlined for the parental taxa. Clusters 1, 2, and 3, which correspond to the parental taxa, are well defined. Cluster 4, which corresponds to Taxon B, is not well defined and overlaps the other 3 clusters.

Elevation

Figure 7 shows the distribution of populations charted against elevation. *Artemisia t.* ssp. *vaseyana* usually occurs at higher elevations (1731–2115 m) than the other 4 taxa. *Artemisia tridentata* ssp. *wyomingensis* occurs at the lowest elevations (1405–1411 m), except at the Bear Lake site (1920 m). *Artemisia tridentata* ssp. *tridentata* occurs at slightly higher elevations than *A. t.* ssp. *wyomingensis* (1451–1536 m), except at the Bear Lake site (1817 m). Taxon B is just below *A. t.* ssp. *vaseyana* for B1, B2, and B4 (1609, 1670, and 2097 m,

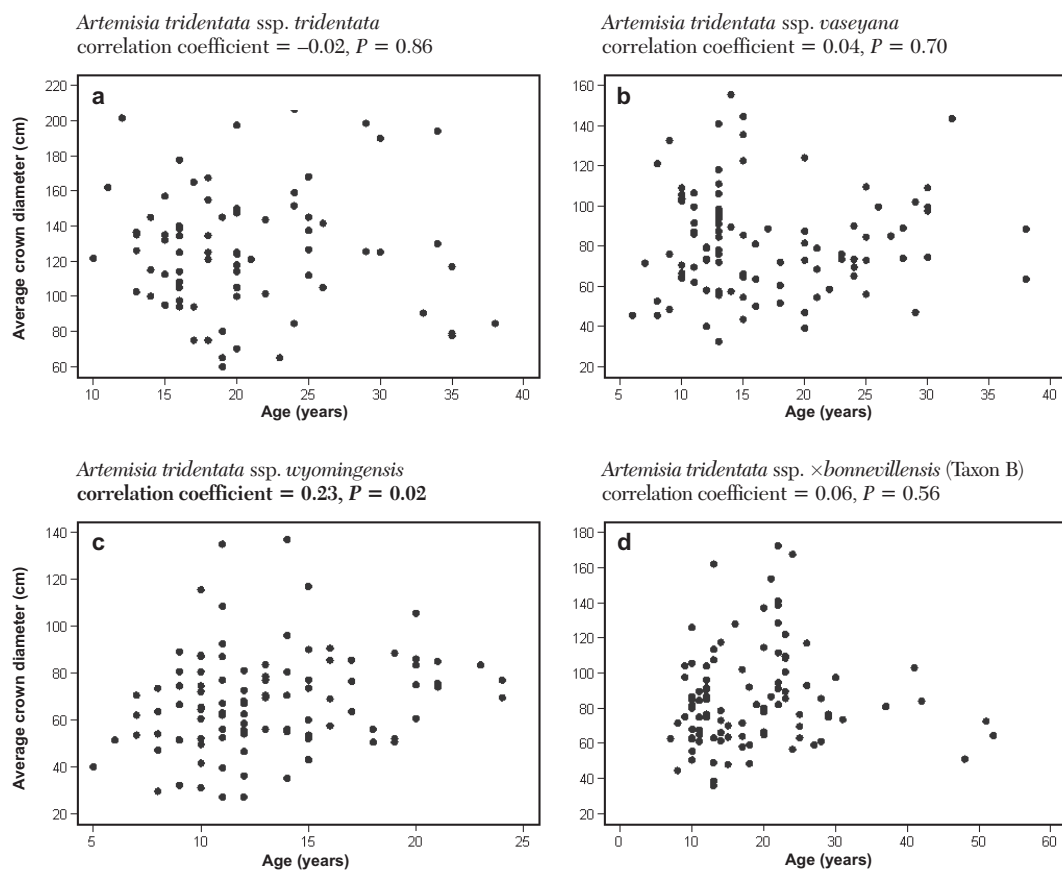


Fig. 3. Correlation between average crown diameter and age for each taxon: a, *Artemisia tridentata* ssp. *tridentata*; b, *A. t.* ssp. *vaseyana*; c, *A. t.* ssp. *wyomingensis*; d, *A. t.* ssp. \times *bonnevillensis* (Taxon B).

respectively), and B3 is only slightly higher in elevation than T3 (1454 m and 1451 m, respectively). All 4 populations on the east side of Bear Lake are higher in elevation than the Curlew National Grassland (CNG) populations. Although the Bear Lake populations are higher in elevation, they are in the rain shadow of the Bear River Range (State of Utah Natural Resources, Division of Water Resources 2002). The rain shadow creates a climate similar to that at the CNG populations, and the populations are therefore comparable.

Summary of Morphometric Measurements

Table 6 compares mean morphometric measurements and standard deviations among taxa and is the basis for following summary.

Artemisia tridentata ssp. *tridentata* are the tallest shrubs (156 cm) with a larger crown diameter (133 cm) and height:crown diameter

ratio (1.3) than other taxa. These shrubs also have larger stem circumference (27 cm), higher first branching from the ground (15 cm), smaller branch angle of divergence (36°), and fewer branches in the first 10 cm of height (2). *Artemisia t.* ssp. *tridentata* has the largest persistent leaf length:width ratio (5.4) and has little to no fluorescence (0).

Artemisia tridentata ssp. *wyomingensis* are the smallest shrubs in height (67 cm) and crown diameter (68 cm). These shrubs have the smallest stem circumference (11 cm), low first branching from the ground (4 cm), and the highest number of branches in the first 10 cm (5). *Artemisia t.* ssp. *wyomingensis* also has the shortest inflorescences (12.6 cm).

Artemisia tridentata ssp. *vaseyana* has the largest branch angle of divergence (55°). These shrubs have the longest leaves (1.7 cm), the longest inflorescences (27.1 cm), and the

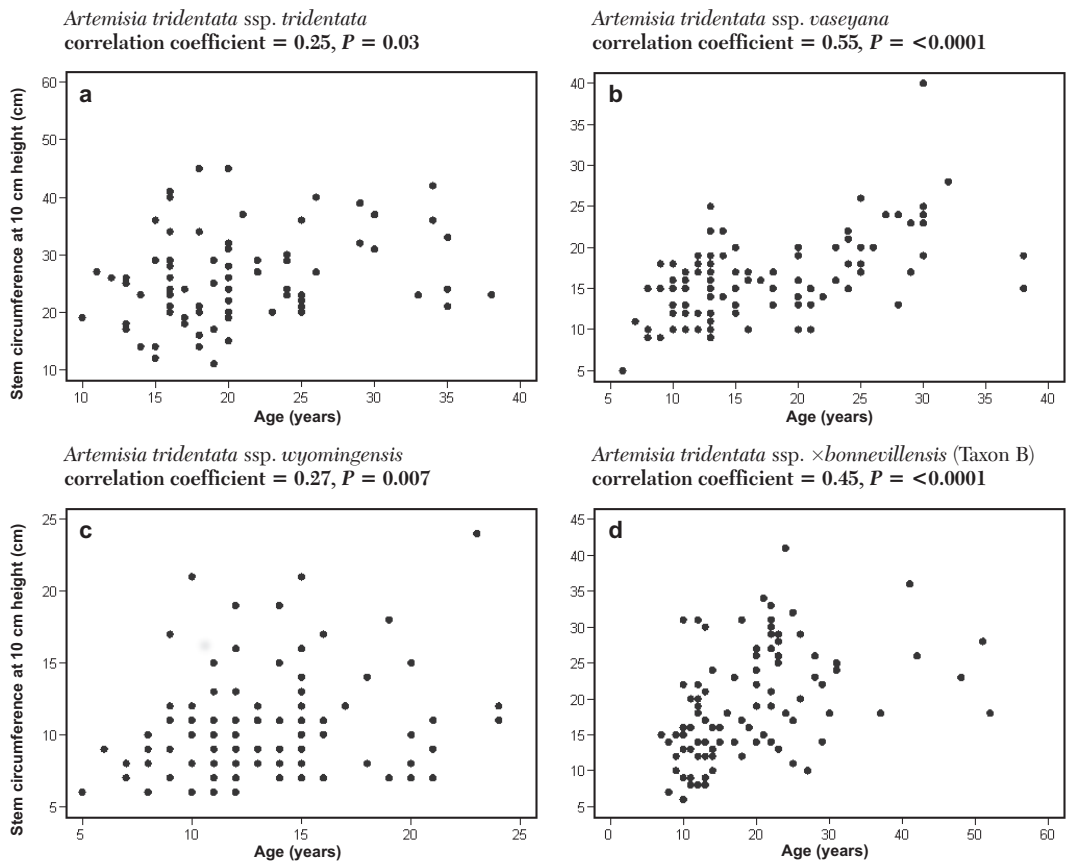


Fig. 4. Correlation between stem circumference and age for each taxon: a, *Artemisia tridentata* ssp. *tridentata*; b, *A. t.* ssp. *vaseyana*; c, *A. t.* ssp. *wyomingensis*; d, *A. t.* ssp. \times *bonnevilleensis* (Taxon B).

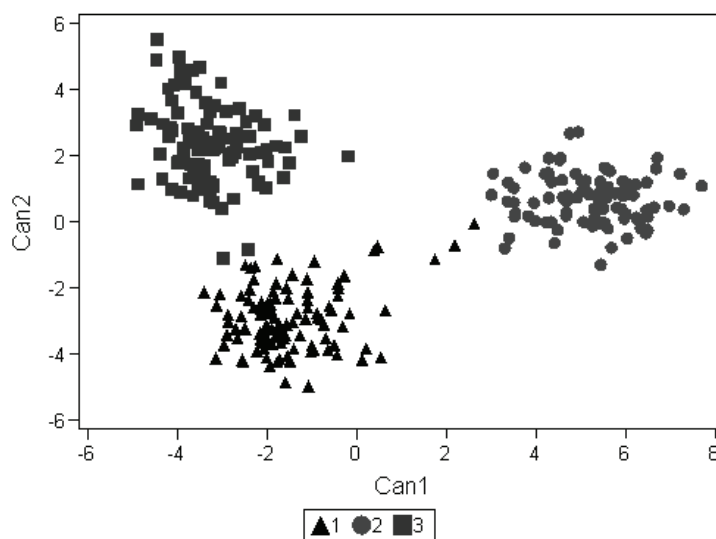


Fig. 5. Cluster analysis for parental taxa. Triangle represents *A. t.* ssp. *wyomingensis* (cluster 1), circle represents *A. t.* ssp. *vaseyana* (cluster 2), and square represents *A. t.* ssp. *tridentata* (cluster 3).

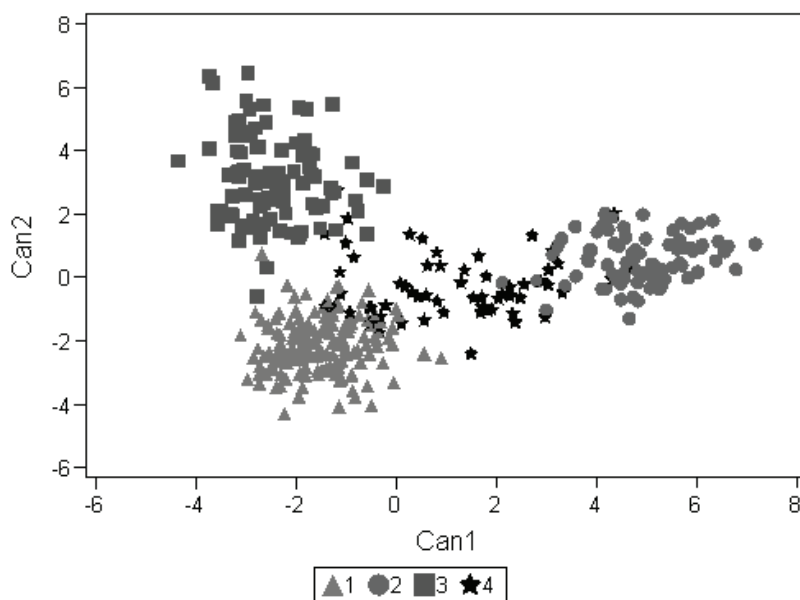


Fig. 6. Cluster analysis for parental taxa plus putative hybrid "B." Triangle represents *A. t. ssp. wyomingensis*, circle represents *A. t. ssp. vaseyana*, square represents *A. t. ssp. tridentata*, and star represents Taxon B (*Artemisia tridentata* ssp. *×bonnevillensis*).

TABLE 3. Frequency of observations in each cluster by putative parental taxon.

Taxon	Cluster			Total
	1	2	3	
<i>Artemisia tridentata</i> ssp. <i>tridentata</i>	0	0	100	100
<i>Artemisia tridentata</i> ssp. <i>vaseyana</i>	6	94	0	100
<i>Artemisia tridentata</i> ssp. <i>wyomingensis</i>	98	0	2	100
TOTAL	104	94	102	300

TABLE 4. Frequency of observations in each cluster by taxon.

Taxon	Cluster				Total
	1	2	3	4	
<i>Artemisia tridentata</i> ssp. <i>tridentata</i>	1	0	93	6	100
<i>Artemisia tridentata</i> ssp. <i>vaseyana</i>	0	83	0	17	100
<i>Artemisia tridentata</i> ssp. <i>wyomingensis</i>	96	0	1	3	100
<i>Artemisia tridentata</i> ssp. <i>×bonnevillensis</i> (Taxon B)	60	2	3	35	100
TOTAL	157	85	97	61	400

TABLE 5. Frequency of observations in each cluster by population. B = *Artemisia tridentata* ssp. *×bonnevillensis* (Taxon B), V = *A. t. ssp. vaseyana*, T = *A. t. ssp. tridentata*, and W = *A. t. ssp. wyomingensis*. Numbers following the letters indicate the population number.

Population number	Cluster				Total
	1	2	3	4	
B1	0	2	1	22	25
B2	19	0	1	5	25
B3	22	0	0	3	25
B4	19	0	1	5	25
V1	0	25	0	0	25
V2	0	17	0	8	25
V3	0	23	0	2	25
V4	0	18	0	7	25
T1	0	0	19	6	25
T2	0	0	25	0	25
T3	1	0	24	0	25
T4	0	0	25	0	25
W1	23	0	0	2	25
W2	24	0	1	0	25
W3	25	0	0	0	25
W4	24	0	0	1	25
TOTAL	157	85	97	61	400

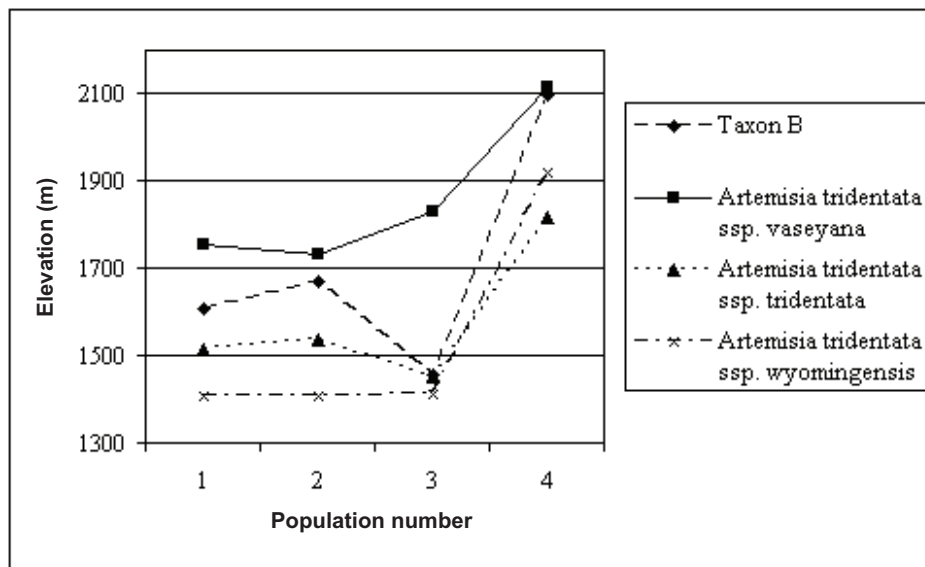


Fig. 7. Distribution of taxa by elevational ranges.

TABLE 6. Comparison of morphometrics between taxa.

Morphometric trait	<i>Artemisia tridentata</i> ssp. <i>×bonnevillensis</i> (Taxon B)		<i>Artemisia tridentata</i> ssp. <i>vaseyana</i>		<i>Artemisia tridentata</i> ssp. <i>tridentata</i>		<i>Artemisia tridentata</i> ssp. <i>wyomingensis</i>	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Height (cm)	83	16	80	15	156	31	67	15
Crown diameter (cm)	85	28	82	26	133	38	68	21
Height : crown diameter ratio	1.0	0.3	1.1	0.3	1.3	0.4	1.0	0.3
Height to first branch from ground (cm)	8	8	6	6	15	16	4	2
Stem circumference at 10 cm height (cm)	19	8	16	5	27	9	11	4
Number of branches >1 cm in diameter in the first 10 cm of height	3	2	4	3	2	2	5	2
Branch angle of divergence (°)	46	9	55	10	36	11	47	12
Ephemeral leaf length (cm)	2.3	0.4	3.1	0.4	2.8	0.4	2.1	0.4
Ephemeral leaf width (cm)	0.4	0.1	0.5	0.1	0.4	0.1	0.3	0.1
Ephemeral leaf length : width ratio	5.9	1.1	5.9	1.0	6.9	1.5	6.8	1.6
Ephemeral leaf lobing (cm)	0.3	0.1	0.3	0.1	0.2	0.1	0.3	0.1
Persistent leaf length (cm)	1.1	0.2	1.7	0.2	1.4	0.2	0.9	0.1
Persistent leaf width (cm)	0.3	0.1	0.4	0.1	0.3	0.1	0.3	0.1
Persistent leaf length : width ratio	3.5	0.8	4.4	0.9	5.4	1.0	3.2	0.6
Persistent leaf lobing (cm)	0.1	0.0	0.1	0.0	0.1	0.0	0.1	0.0
Ephemeral leaf length : persistent leaf length ratio	2.2	0.4	1.8	0.3	2.0	0.3	2.2	0.4
Inflorescence length (cm)	14.3	4.5	27.1	6.1	15.8	5.1	12.6	2.8
Vegetative branch length (cm)	7.5	1.9	8.0	1.9	9.0	2.9	7.0	1.6
Inflorescence : vegetative branch ratio	1.9	0.4	3.5	0.6	1.8	0.3	1.8	0.4
Flower heads per 10 cm stalk length	125	98	237	115	287	200	79	54
Flowers per head	4	1	4	1	4	1	5	1
Florescence	2	1	4	1	0	1	1	1
Age (years)	19	9	17	7	21	6	13	4

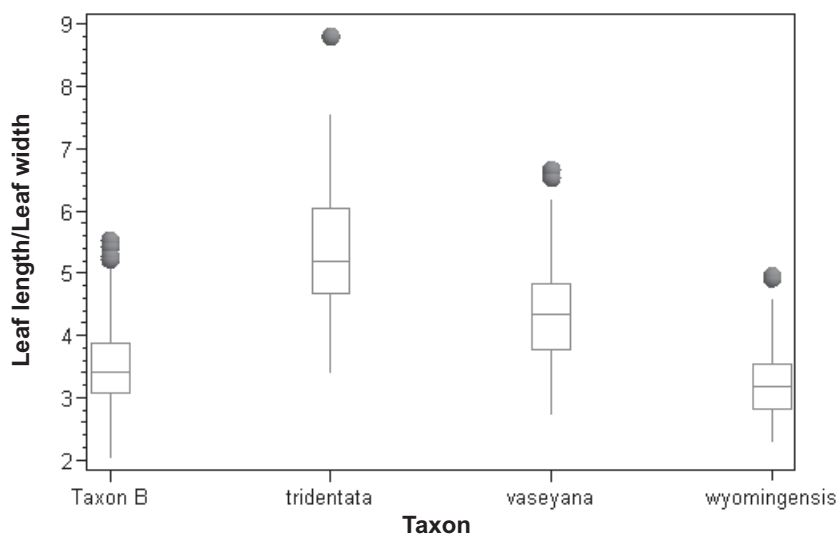


Fig. 8. Leaf length/leaf width ratio of persistent leaves by taxa. The box length represents the interquartile range (the distance between the 25th and the 75th percentiles), the horizontal line in the box interior represents the median, the vertical lines issuing from the box extend to the minimum and maximum values of the analysis variable, and the dots represent outliers.

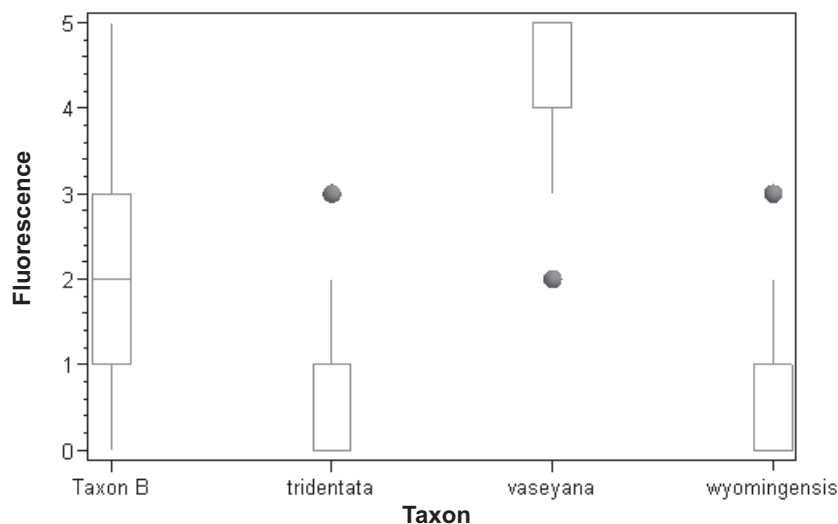


Fig. 9. Fluorescence by taxa. The box length represents the interquartile range (the distance between the 25th and the 75th percentiles), the horizontal line in the box interior represents the median, the vertical lines issuing from the box extend to the minimum and maximum values of the analysis variable, and the dots represent outliers.

highest inflorescence:vegetative branch ratio (3.5). *Artemisia t. ssp. vaseyana* also has the highest fluorescence (4).

“Bonneville” sagebrush (Taxon B) is similar to *A. t. ssp. vaseyana* in height (83 cm compared to 80 cm) and crown diameter (85 cm

compared to 82 cm). Taxon B is similar to *A. t. ssp. wyomingensis* in persistent leaf length:width ratio (3.5 compared to 3.2) and is similar in inflorescence:vegetative branch ratio to both *A. t. ssp. wyomingensis* and *A. t. ssp. tridentata* (1.9 compared to 1.8 and 1.8, respectively).

Taxon B is intermediate in fluorescence (2) between *A. t. ssp. wyomingensis* (1) and *A. t. ssp. vaseyana* (4).

Of the 4 Taxon B populations, only one (B1) is distinct from all 3 of the putative parental taxa. B1 is located on the middle unit of the CNG and is characterized by larger shrubs that appear to represent a hybrid between *A. t. ssp. tridentata* and *A. t. ssp. vaseyana*. These shrubs are tall, with a large stem circumference like *A. t. ssp. tridentata*. However, the leaves fluoresce as bright as most leaves from *A. t. ssp. vaseyana* populations. This population is tetraploid, a condition that could be a result of allopolyploidy. Hybridization between these 2 subspecies is well documented, and the name designated is *A. t. ssp. xericensis* Winward (Shultz 2009).

Population B2 is located on the north unit and according to the cluster analysis has many similarities with *A. t. ssp. wyomingensis*. B2 shrubs were shorter, with many branches within the first 10 cm of height. They were also similar to *A. t. ssp. vaseyana* in that the inflorescences were longer and clustered near the top of the shrub, and they had an average fluorescence of 3. This population was also found in a moister, more productive site with more forbs than are normally found with *A. t. ssp. wyomingensis*. Population B3 is located on the south unit and also clustered out with *A. t. ssp. wyomingensis*. These shrubs were very similar to *A. t. ssp. wyomingensis* in appearance and habitat. This population may have had some influence from *A. nova*, because the inflorescences were characterized by glabrous bracts, which is normally a trait of *A. nova* (Shultz 2009). B3 appears to be at a slightly higher elevational range than the other *A. t. ssp. wyomingensis* populations.

Useful characteristics for distinguishing between the 4 taxa include persistent leaf length: leaf width ratio (Fig. 8). *Artemisia t. ssp. tridentata* has an average persistent leaf length: leaf width ratio of 5.18 (range 4.67–6.04), compared to 4.33 (3.77–4.83) for *A. t. ssp. vaseyana*, 3.18 (2.81–3.54) for *A. t. ssp. wyomingensis*, and 3.41 (3.06–3.88) for Taxon B.

Fluorescence of water-soluble coumarins in the leaf material also was a useful characteristic (Fig. 9). *Artemisia t. ssp. tridentata* and *A. t. ssp. wyomingensis* typically have little to no fluorescence (median 0, range 0–1; median 1, range 0–1, respectively). *Artemisia t. ssp. vase-*

yana typically has a very bright blue fluorescence (median 5, range 4–5). Taxon B has a medium fluorescence (median 2, range 1–3). The intermediate fluorescence of Taxon B is a key characteristic of the involvement of *A. t. ssp. vaseyana* in the hybridization. A cross between a high-coumarin-producing plant (*A. t. ssp. vaseyana*) and a low-coumarin-producing plant (*A. t. ssp. tridentata* or *A. t. ssp. wyomingensis*) would produce the intermediate coumarin (i.e., fluorescence) levels between 2 and 4.

Populations B2–4 of Taxon B, hereafter called “Bonneville sagebrush,” best fit a hybrid swarm according to the definition in Allendorf et al. (2001). A hybrid swarm is a population of individuals that have varying numbers of generations of backcrossing with parental types and mating among hybrids. The most likely type of hybrid swarm is with widespread introgression, where the parental taxa are still genetically distinct. This is different from the type where complete admixture occurs and the parental taxa are no longer genetically distinct. Other studies of *A. t. ssp. vaseyana* and *A. t. ssp. tridentata* show that these subspecies hybridize regularly and form stable hybrid zones (McArthur et al. 1988, McArthur and Sanderson 1999b, Miglia et al. 2005). These stabilized hybrid zones are common in areas where there is interaction between the parental taxa (A. Winward personal observation).

KEY TO THE *ARTEMISIA TRIDENTATA* SUBSPECIES IN THIS STUDY

- 1a. Even-crowned shrubs, flower stalks arise from upper crown and extend above foliage; leaf extract fluoresces bright blue. *A. t. ssp. vaseyana*
- 1b. Uneven-crowned shrubs, flower stalks arise throughout crown 2
- 2a. Persistent leaves narrowly wedge shaped; >4 times longer than wide; leaf extract does not fluoresce or fluoresces very faintly *A. t. ssp. tridentata*
- 2b. Persistent leaves broadly wedge shaped; <4 times longer than wide 3
- 3a. Flower stalks mostly clustered in upper half of crown, leaf extract fluoresces medium blue *A. t. ssp. xbonnevillensis*
- 3b. Flower stalks arise throughout the shrub; leaf extract does not fluoresce or fluoresces very faintly. *A. t. ssp. wyomingensis*

NOTHOTAXON DESCRIPTION

Based on the results of our studies, we designate Taxon B as a hybrid taxon involving *Artemisia tridentata* ssp. *wyomingensis* and *A. t.* ssp. *vaseyana* and propose the nothotaxon *Artemisia tridentata* subsp. \times *bonnevillensis* H. Garrison, L. Shultz, and E.D. McArthur [pro subsp.].

TYPE.—USA, Utah, Rich Co.: east side of Bear Lake, Eden Road, Lat. 41.9333° N, Long. 111.1921° W, elevation 2097 m; voucher for population B4. 1 Aug 2005. *H. Garrison 17* (holotype UTC; isotypes BRY, NY, and others). Chromosome number: $2n = 36$ [based on fluorescence examination].

ADDITIONAL SPECIMENS EXAMINED.—Idaho, Oneida Co.: Curlew National Grasslands, Lat. 42.2269° N, Long. 112.7908° W, elevation 5509 ft., with *Purshia tridentata*, *Poa bulbosa*, *Astragalus* sp., 2 June 2004; *L. Shultz*, *A. Winward*, *D. Tart*, *H. McClure* (*Garrison*) 19649 (UTC). Idaho, Oneida Co.: Curlew National Grassland, middle unit, Sheep Creek Canyon, Lat. 42.2308° N, Long. 112.5752° W, elevation 1609 m, 26 July 2005; *H. Garrison 5* (UTC). Idaho, Oneida Co.: Curlew National Grassland, north unit, Salyer Springs, Lat. 42.2283° N, Long. 112.8051° W, elevation 1670 m, voucher for population B2, 28 June 2005; *H. Garrison 9* (UTC). Idaho, Oneida Co.: Curlew National Grassland, south unit, W of Stone Reservoir, Lat. 42.0872° N, Long. 112.7439° W, elevation 1454 m, 22 June 2005, *H. Garrison 13* (UTC).

DESCRIPTION.—Shrub of medium height, usually <1 m (average 0.8 m), crown irregular in shape; leaves shallowly trilobed, 0.9–1.1 cm long \times 0.2–0.3 cm wide (length-to-width ratio averages 4.3); inflorescence length 12–15 cm; flowers 3 or 4 per head. Crushed leaves soaked in water or alcohol fluoresce light blue under ultraviolet radiation (using a black light). Differs from *A. t.* ssp. *wyomingensis* primarily by its longer inflorescence branches and light blue fluorescence (as opposed to none for Wyoming sagebrush). Differs from *A. t.* ssp. *vaseyana* by its irregular crown, shorter leaves, and lighter fluorescence (as opposed to bright blue for mountain sagebrush).

ADDITIONAL COMMENTS.—Results from the morphometric analysis suggest that Bonneville sagebrush is most closely related to *A. t.* ssp. *wyomingensis*, with introgression from *A. t.* ssp. *vaseyana*. This relationship could explain

the elevated fluorescence levels, clustered inflorescences near the top of the shrub, and height and crown diameter similar to *A. t.* ssp. *vaseyana* and the persistent leaf length:width ratio and inflorescence:vegetative branch ratio similar to *A. t.* ssp. *wyomingensis*. These intermediate effects may indicate that Taxon B is an intermediate ecotype as part of a cline grading from *A. t.* ssp. *wyomingensis* to *A. t.* ssp. *vaseyana*. Studies of the hybrid zone of *A. t.* ssp. *vaseyana* and *A. t.* ssp. *tridentata* show a gradation in morphology from one taxon to another (McArthur and Sanderson 1999b, Miglia et al. 2005). More research, including molecular genetics and chemical analyses, is needed to determine if other characters may yield more information on whether Bonneville sagebrush results from sporadic hybridization events or many generations of introgression.

Ecologically, Bonneville sagebrush occupies a zone that can be predicted and modeled based on biophysical parameters of temperature, moisture, and elevation (Rivera et al. 2011). In addition to its apparent importance as wildlife habitat, Bonneville sagebrush occurs on more productive and floristically rich sites than typical *A. t.* ssp. *wyomingensis* populations (Winward 2004, Garrison 2006). This trend is repeated in all the hybrid zones in this study. B1 (tentatively called the “xeric sagebrush”) was associated with *A. tripartita*, *Purshia tridentata*, and *Rosa woodsii*. B2 was associated with *A. tripartita* and *Purshia tridentata*. B4 was associated with *Purshia tridentata* and *Symphoricarpus oreophilus*. These are shrubs that are not commonly associated with *A. t.* ssp. *wyomingensis* (Winward 2004).

We believe Bonneville sagebrush is best classified as a stabilized hybrid involving *A. t.* ssp. *wyomingensis* and *A. t.* ssp. *vaseyana*, as shown in populations B2 and B4. Population B3 may represent an introgression involving *A. t.* ssp. *wyomingensis*, *A. nova*, and *A. t.* ssp. *vaseyana*, based on the glabrous bracts on the inflorescences. B1 is considered unique from the putative parents based on morphometrics. This population also needs further study to determine if it is similar to the well studied *A. t.* ssp. *vaseyana* \times *A. t.* ssp. *tridentata* hybrid that it resembles morphometrically, and if so, *A. t.* ssp. \times *xericensis* (“xeric sagebrush”) is the appropriate name.

Bonneville sagebrush clearly occupies a distinct environmental niche. It occurs consistently

and frequently at an elevational range below *A. t. ssp. vaseyana* and above *A. t. ssp. wyomingensis*, and it occupies moister areas than does *A. t. ssp. wyomingensis* (Garrison 2006). A recent species ordination study confirms this pattern over a wide geographic area in northern Utah (Rivera et al. 2011). This study supports the hypothesis that hybridization plays an important and continuing role in the evolution of sagebrush (McArthur and Sanderson 1999b). We believe this study demonstrates the stabilizing role created by the tension between adaptation and hybridization in the evolution of distinct taxa. The genetic heterogeneity provided by introgressed populations provides raw material for the evolution of populations uniquely adapted to changing environmental conditions, a process that is amplified by climatic extremes.

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