Growth Rate Differences among Big Sagebrush [*Artemisia tridentata*] Accessions and Subspecies

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Abstract

Even-aged plants of 21 big sagebrush *(Artemisia tridentata)* accessions were grown in a uniform garden to test growth parameter variation. Growth parameters measures (height, crown diameter, yield, and annual nonfloral leader growth) were scored after the 1975, 1976, and 1977 growing seasons. Nested analyses of variance and mean comparison tests showed significant ($p<0.05$) accession and subspecies differences in each measure, each year. On a subspecies level, basin big sagebrush *(A.t.* ssp. *tridentata)* exceeded the other two subspecies (mountain big sagebrush = *A.t. vaseyana,* Wyoming big sagebrush = *A.t. wyomingensis)* for each character. In general, the values for the last two subspecies were not significantly different, but mountain big sagebrush tended to have larger values. Using 1975 data for yield and 1976 data for the other growth parameters, basin big sagebrush accessions averaged 147.9 ± 14.7 (se) cm in height, 193.0 ± 12.1 cm in maximum crown spread, 2217 ± 444 g current yield, and 12.7 ± 1.1 cm in annual leader growth. Corresponding values for mountain big sagebrush were 95.8 ± 2.2 cm, 157.3 ± 3.4 cm, 890 ± 77 g, and 8.8 ± 0.6 cm. For Wyoming big sagebrush the values were 77.1 ± 4.1 cm, 129.6 ± 6.4 cm, 545 ± 84 g, and 8.5 ± 1.1 cm. Comparison of three accessions' performances at two uniform gardens and their native sites indicated that growth parameters, while subject to environmental influences, are under genetic control. The fastest growing and largest growing plants of this study were diploid, $2n = 18$, whereas, the slowest growing ones were tetraploid, $2n = 36$. Growth rate characteristics of big sagebrush should be considered for management purposes and in plant improvement programs.

Big sagebrush (*Artemisia tridentata* Nutt.) is among western North America's most widely distributed shrub species and is the most abundant single species (Beetle 1960, McArthur and Plummer 1978, McArthur et al. 1979). With its relatives, it forms the subgenus *Tridentatae*—recently elevated from sectional status (McArthur et al. 1981). The *Tridentatae,* endemic to western North America, form a natural phylogenetic group consisting of several well-defined species as well as a few taxa with fuzzy limits (Ward 1953; Beetle 1960, 1971; McArthur 1979). Big sagebrush itself has been divided into three subspecies and several forms (Beetle and Young 1965, Winward and Tisdale 1977, McArthur et al. 1979).

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Subspecies and lower taxonomic levels including individual accessions or populations are distinct and may require differential management (Winward and Tisdale 1977, McArthur and Plummer 1978, Welch and McArthur 1979a, Nelson and Krebill 1981).

Within the context of populational variability, we see the opportunity for selective use of existing natural material in land rehabilitation efforts (Plummer 1977) and beyond that to the genetic improvement of plant stocks for particular purposes (Welch and McArthur 1979a). This report is the fourth in a series demonstrating accessional and subspecies variability of big sagebrush in uniform garden situations. Earlier, we showed protein (Welch and McArthur 1979b), monoterpenoid (Welch and McArthur 1981), and in vitro digestibility (Welch and Pederson 1981) differences among accessions representing the three subspecies of big sagebrush. Here, we report on growth parameter differences. It has been known for some time that enormous size differences existed in big sagebrush (Pool 1908, Kearney et al. 1914). Beetle (1960, 1962) first ascribed some of these differences to taxonomic or genetic causes. Winward (1970) showed varying amounts of stem diameter correlation with plant age for the big sagebrush subspecies. Other observers have noted, however, that plant size correlates poorly with plant age in big sagebrush (Cottam and Stewart 1940, Ferguson 1964, Roughton 1972, Daubenmire 1975).

Materials and Methods

Plant Materials

Accessions representing about 80 natural populations of big sagebrush have been established at the Snow Field Station, Ephraim, Utah. Plants have been collected as young wildings and transplanted as bare-root stock to rows in the Snow Field Station either in the spring (March-June) or in the fall (October-November). Many of these accessions have also been established at the Gordon Creek Wildlife Management area near Helper, Utah, and at other small outplanting sites. The 21 accessions of this study (Table 1) represent the three big sagebrush subspecies; basin big sagebrush (*A.t.* ssp. *tridentata*), mountain big sagebrush (*A.t.* ssp. *vaseyana* (Rydb.) Beetle), and Wyoming big sagebrush (*A.t.* ssp. *wyomingensis* Beetle and Young). The 21 accessions were chosen because they were established about the same time (1970), they represent a fairly broad geographic and elevational range (Table 1), they encompass much of big sagebrush's morphological variability, and they are growing on a homogenous 1.5 ha section of the Snow Field Station. The plants were irrigated only once to aid establishment. Weed control was exercised by manual and mechanical means.

The 21 accessions have chromosome numbers mostly at the characteristic diploid ($2n = 18$) and tetraploid ($2n = 36$) levels of big sagebrush (Ward 1953, McArthur et al. 1981). Two accessions have mixed chromosome numbers, a phenomenon not unknown in the *Tridentatae* (McArthur et al. 1981).

Subspecies determinations were made following the key of

McArthur et al. (1979). Chemical tests (Hanks et al. 1973, Stevens and McArthur 1974) were also used as an aid to taxonomic identification. Representative specimens of each accession are deposited at the Shrub Sciences Laboratory Herbarium (SSLP).

Study Sites

The principal study site was the Snow Field Station. This facility, immediately northeast of Ephraim, Utah, is in Sanpete Valley. It is a former basin big sagebrush site later converted to agricultural uses. About 20 ha are presently assigned to shrub genetics, seed production, adaptation, and related research activities. The soil there is a deep alluvial limestone-derived clay. It is about 2 km west of the base of the monoclinal western front of the Wasatch Plateau. The Snow Field Station has an elevation of about 1700 m. Annual precipitation for the 1959-1979 period was 26.8 cm (data on file at Snow Field Station). Price and Evans (1937) reported 29.7 cm over a longer time period at a nearby site. They also stated that 45% of the precipitation comes in the winter (November 1 to April 30), mostly as snow. Data filed at the Snow Field Station (1959-1979) showed that about 53% of the precipitation came during the winter period.

A secondary study site was the Gordon Creek Wildlife Management Area about 15 km west of Helper, Utah. This site is at about 2130 m in elevation and receives about 28.6 cm precipitation annually (data on file at Great Basin Experimental Area, Ephraim, Utah). It is located in a valley formed by dissection of the eastern edge of the Wasatch Plateau. The site consists of about 2 ha of the much larger Wildlife Management Area. As at the Snow Field Station, the site is on agricultural land that had included big sagebrush in its original vegetation. The soil here is limestone derived as is that at the Snow Field Station, but has a sandier texture. A mule deer (*Odocoileus hemionus* Raf.) herd of more than 200 animals winters at and near the site.

Three natural big sagebrush populations were sampled in a preliminary attempt to access site impacts on growth parameters. These were the Dove Creek and Loa basin big sagebrush and the Colton mountain big sagebrush sites (Table 1). The Dove Creek site is about 2 km west of Dove Creek, Colo., in arroyo breaks in an agricultural area and along adjacent roads and fence rows. Black sagebrush (*A. nova* Nelson) occurs in the rocky outcrops of the arroyo breaks. The Loa site is about 8 km west of Loa, Utah, in a basin big sagebrush community of undulating topography adjacent to the Fremont River Valley. The Colton site is on the Wasatch Plateau in a large mountain big sagebrush community in Utah County, Utah.

Data Collection and Analyses

Accessions at the Snow Field Station were sampled for height, crown, and annual plant yield in 1975 and for height, crown, and annual leader growth in 1977 and 1978. Five plants from each accession were sampled. Plants were required to be healthy, but otherwise were taken at random. Height (cm) was measured to the highest vegetative point on the plant. Maximum crown (cm) was measured across each plant's largest crown diameter. Current annual forage yield (g of leaves and twigs) was estimated using the ocular method of Pechanec and Pickford (1937). Annual leader growth (cm) was determined by measuring the length of 10 twigs distally from the current year's bud scar. Five of the twigs or leaders were randomly picked from branches with an axis more horizontal than vertical and five more from branches with more vertical axes. The 1975 data were taken in summer (August). The 1977 and 1978 data collections were taken in late winter (March). Even though big sagebrush is evergreen and photosynthesizes year round (Pearson 1975), its vegetative growth occurs in the late spring and early summer, diminishing sharply in summer (mid-July) (DePuit and Caldwell 1973; Caldwell 1979). Our summer (1975) and winter (1977, 1978) data collections, therefore, were taken after the effective growing seasons of 1975, 1976, and 1977. Data collection at the Gordon Creek Wildlife Management Area and the three natural sites was performed in the same manner as at the Snow Field Station.

At Gordon Creek, sample plants were randomly picked from accessional rows. Plants at the native sites, however, were selected by arbitrarily picking a transect direction and then sampling every fifth, healthy, mature plant. Plants were deemed mature if they (1) had produced flower stalks and (2) were >45 cm in height. In natural big sagebrush populations, seedlings are produced regularly, but not every year. New individuals are established, however, only when the plant community opens up—sporadically through individual deaths or as a modal class after a catastrophic disturbance, such as fire or chaining (Harniss and Murray 1973, Daubenmire 1975).

Data analyses were performed through nested analysis of variance technique (Snedecor and Cochran 1967). When warranted by the analysis of variance results, accession and subspecies means were tested for significance. Tukey's *post hoc* mean comparison

Table 1. Big sagebrush accessions studied.

Subspecies	Accession collection site	Culture number	Elevation (m)	$2n$ Chromosome[1] number
Tridentata	Loa, Wayne County, Utah	*U*-44	2140	18
	Dove Creek, Dolores County, Colorado	*U*-74	2070	18
	Wingate Mesa, San Juan County, Utah	*U*-75	2060	36
	Clear Creek Canyon, Sevier County, Utah	*U*-76	1720	18
	Dog Valley, Juab County, Utah	*U*-79	1700	18
	Brush Creek, Uintah County, Utah	*U*-82	1830	36
	Evanston, Uinta County, Wyoming	*U*-105	2050	18
Vaseyana	Benmore, Tooele County, Utah	*U*-9	1900	18
	Alton, Kane County, Utah	*U*-11	2100	18
	Indian Peaks, Beaver County, Utah	*U*-13	2140	18
	Colton, Utah County, Utah	*U*-14	2260	36
	Sardine Canyon, Cache County, Utah	*U*-15	1800	18
	Salina Canyon, Sevier County, Utah	*U*-19	2350	18, 36
	Pinto, Washington County, Utah	*U*-23	1850	36
	Clear Creek Canyon, Sevier County, Utah	*U*-24	2130	18
	Durkee Springs, Piute County, Utah	*U*-31	2270	18
	Petty Bishop's Log, Sanpete County, Utah	*U*-72	2380	18
Wyomingensis	Trough Springs, Humboldt County, Nevada	*U*-1	1400	36, 54
	Milford, Beaver County, Utah	*U*-17	1540	36
	Evanston, Uinta County, Wyoming	*U*-37	2130	36
	Kaibab, Coconino County, Arizona	*U*-80	2340	36

[1]From McArthur et al. 1981.

Table 2. Nested analyses of variance for growth parameters of big sagebrush at the Snow Field Station (1976 growing season).

	Annual leader growth				Crown				Height			
Source	D.F.	S.S.	M.S.	F[1]	D.F.	S.S.	M.S.	F[1]	D.F.	S.S.	M.S.	F[1]
Subspecies	2	5,156	2,578	5.5*	2	58,321	29,160	10.2**	2	82,070	41,035	15.2**
Accessions	18	8,513	473	15.8**	18	51,635	2,869	2.9**	18	48,453	2,692	12.2**
Plants	84	2,498	30	1.8**	84	82,966	988	—	84	18,523	221	—
Branches	945	16,894	18	—	—	—	—	—	—	—	—	—
Total	1,049	33,061			104	192,922			104	149,046		

[1]Level of significance for F values is indicated by * $p<0.05$ and ** $p<0.01$.

test was used for accessional comparisons. In making subspecies comparisons with different sample sizes (Table 1), however, a Scheffé's test was deemed more appropriate (Steele and Torrie 1960, Hays 1963). Growth rate indexes were constructed so that 200 cm in height = 33.3 units, 250 cm crown = 33.3 units and, alternatively, 3000 g yield (1975) or 15 cm annual leader growth (1976, 1977) = 33.3 units. Gaged by this index, plants with large growth parameters would approach or exceed 100 units.

Results

Accessional Differences at the Snow Field Station

For all 3 years of the study, accessions showed highly significant ($p<0.01$) differences among the growth parameters: height, crown, annual leader growth, and yield. The data for 1976 are illustrated in Table 2. Mean heights (Table 3) ranged from 69.2 to 221.2 cm. For crowns, the range was from 111.4 to 249.2 cm. Annual leader-growth means varied from 5.6 to 15.4 cm. Current annual-yield means ranged from 350 to 3680 g. Many of these mean differences were highly significant ($p<0.01$) (Table 3).

The growth rate indices (Table 4) reflect consistent growth parameter differences among accessions from year to year. In general, the 3-year patterns are about the same. It must be remembered the index was calculated differently from 1975 than for the other 2 years. Some of the movement in the table is, perhaps, attributable to different individual bushes being sampled the various years. Another cause may be a differential accessional response to the 2-year (1976–1977) drought (Richardson et al. 1977, McArthur and Freeman 1981). We believe the last cause, through self pruning and lower annual production, to be a primary cause for the generation of lower indices for all but one accession for 1977 as compared to 1976. Four accessions are missing for the 1977 analysis (Table 4) due to excessive mortality and poor health.

Intersite Comparison of Accessions

Our preliminary comparisons of the growth parameters of three accessions at two uniform gardens and the natural sites of each accession showed accessional and site consistency (Table 5). In each case, the plants at the Snow Field Station performed best, often significantly better ($p<0.01$). Plant performance at the native sites and the Gordon Creek Wildlife Management Area followed generally in that order. Only two out of eight mean comparisons were significantly different for the latter sites (Gordon Creek versus native). At each site, the accessional order of growth parameter performance was Dove Creek >Loa >Colton.

There are, however, several complicating factors. The different age structure of the native site plants must be borne in mind for comparisons. Furthermore, the Gordon Creek site has an additional complication in that the shrubs there are browsed by wintering mule deer and browsed differentially (Hanks et al. 1973, Scholl et al. 1977, Welch et al. 1981). Because of man's activities and the snow depth, browsing rarely occurs at the other sites. The data, nevertheless, are interpretable on the basis of genetic differences. The plants perform differently on different sites, but maintain coherent patterns.

Subspecies Comparison

Subspecies effects were responsible for a significant portion of the variation in all growth parameter values (Table 2). Subspecies effects are especially strong on height, crown, and yield ($p<0.01$) as

Table 3. Growth characteristics of big sagebrush accessions at the Snow Field Station.

Accession	ssp[1]	Height (cm)	Crown[2] (cm)	Height/crown	Annual leader growth[2] (cm)	Annual yield[2] (g)
Dove Creek	t	221.2 a[3]	249.2 a[3]	0.89	15.1 a[3]	3,680 a[3]
Clear Creek	t	162.2 b	233.0 ab	.70	14.5 ab	3,020 ab
Loa	t	156.8 b	200.2 abc	.78	15.4 a	3,510 a
Evanston	t	140.0 bc	170.6 abcd	.82	14.0 abc	1,530 c
Dog Valley	t	138.4 bcd	193.2 abc	.72	12.1 abcd	1,760 bc
Wingate Mesa	t	116.4 cde	175.6 abcd	.66	10.2 abcde	1,340 c
Benmore	v	106.6 cdef	167.4 abcd	.64	7.6 de	750 c
Pinto	v	104.0 cdef	152.8 bcd	.68	9.3 abcde	1,080 c
Alton	v	101.6 cdef	158.8 bcd	.64	7.7 cde	680 c
Brush Creek	t	100.2 def	138.6 cd	.73	7.7 cde	680 c
Clear Creek	v	98.2 ef	173.6 abcd	.57	11.6 abcde	1,140 c
Sardine Pass	v	95.6 ef	148.0 cd	.65	7.4 de	800 c
Petty Bishop's Log	v	94.2 ef	153.0 bcd	.62	8.2 bcde	1,310 c
Colton	v	92.6 ef	150.6 cd	.62	5.6 e	610 c
Durkee Springs	v	89.6 ef	171.6 abcd	.52	10.9 abcde	625 c
Milford	w	88.6 ef	140.0 cd	.63	8.7 bcde	550 c
Indian Peak	v	88.4 ef	141.2 cd	.63	9.3 abcde	850 c
Salina Canyon	v	86.8 ef	156.0 bcd	.56	9.9 abcde	1,060 c
Kaibab	w	75.8 f	140.4 cd	.54	6.9 de	520 c
Evanston	w	74.6 f	126.2 cd	.59	11.4 abcde	760 c
Trough Springs	w	69.2 f	111.4 d	.62	6.9 de	350 c

[1]Subspecies: t=*tridentata*, v=*vaseyana*, w=*wyomingensis*
[2]Height, crown, and annual leader growth for 1976 growing season; annual yield for 1975 growing season.
[3]Means in each column followed by the same letter are not significantly different ($p<0.01$) by Tukey's test.

Table 4. Growth rate indices[1] of big sagebrush accessions at the Snow Field Station.

Accession	ssp[2]	1975	1976	1977
Dove Creek	t	111.8	103.7	99.8
Clear Creek	t	90.2	90.3	91.0
Loa	t	91.7	87.0	—
Evanston	t	63.1	77.2	74.3
Dog Valley	t	67.8	75.7	69.1
Wingate Mesa	t	58.7	65.5	65.4
Clear Creek	v	52.5	65.3	—
Pinto Canyon	v	50.1	58.3	57.4
Durkee Springs	v	39.1	62.0	57.9
Salina Canyon	v	47.1	57.3	—
Indian Peak	v	48.6	54.1	52.1
Petty Bishop's Log	v	51.8	54.3	45.1
Alton	v	44.1	55.2	45.6
Evanston	w	41.3	54.6	—
Benmore	v	46.5	57.0	38.7
Brush Creek	t	42.6	52.3	40.2
Sardine Pass	v	42.5	52.1	45.3
Milford	w	35.9	52.8	45.0
Colton	v	41.8	48.0	34.8
Kaibab	w	37.5	46.7	34.9
Trough Springs	w	30.3	41.7	30.6

[1]Based equally on height, crown, and annual biomass production. See section on Data Collection and Analyses (Materials and Methods) for details.
Subspecies: t = *tridentata*, v = *vaseyana*, w = *wyomingensis*.

opposed to annual leader growth ($p<0.05$). In every case, for all 3 years, basin big sagebrush growth performance parameters exceed significantly those of mountain and Wyoming big sagebrush (Table 6). The last-mentioned two subspecies, on the other hand, do not significantly differ except in one out of nine comparisons. In eight of these nine comparisons, however, mountain big sagebrush means exceed those of Wyoming big sagebrush. The ninth case, annual leader growth for 1976, has equal means (Table 6).

Discussion

We have demonstrated accessional and subspecies differences in big sagebrush parameters (Tables 2, 3, 4, 5, 6). These differences augment earlier findings on differences (reviewed by McArthur and Plummer 1978 and Welch and McArthur 1979a) in protein levels, phenolics and terpenoids, seed germination, phenology, palatability, and digestibility.

Height and Crown

These two measures are correlated quite highly (r^2 for data in Table 3 is 0.86). In the uniform garden situation, however, basin big sagebrush has a different height/crown (h/c) ratio than the other two subspecies. It has an h/c ratio of 0.75 ± 0.03 (se), whereas mountain big sagebrush's h/c is 0.61 ± 0.02 and Wyoming big sagebrush's h/c is 0.60 ± 0.02 (Table 3). This difference is a reflection of a more upright growth form for basin big sagebrush (Beetle and young 1965, Winward and Tisdale 1977, McArthur et al. 1979).

Our values for height and crown (Table 3) are larger than those observed in many natural situations. Apparently, the Snow Field Station is a favorable site for good growth parameter expression for big sagebrush (Table 5). These values are subject to environmental influence as Kearney et al. (1914) long ago realized. There is, however, a genetic or taxonomic component as well, as our data (Tables 3, 5) show. The subspecies occur together in ecotonal areas (Hanks et al. 1973; McArthur et al. 1979) and maintain their stature differences just as they do in uniform gardens. Whereas our values are large, they do not approach those of some large basin big sagebrush specimens occurring in nature. Pase (1956) reported a plant 475 cm tall near Kanab, Utah, which he suspected was about 13 years old. Beetle (1962) reports finding a specimen that was not quite as tall, but had a stem circumference of 165 cm. Van Epps et al. (1982) reported individual biomass production up to 15.9 kg/plant for big sagebrush growing in favorable locations. Basin big sagebrush is consistently the largest of the subspecies (Table 6; Beetle 1962). Within basin big sagebrush ecotypes and accessions differences exist (Table 3). Hanks et al. (1973) recognized the exceptionally large forms as a specific ecotype which they called the "fence-row" type because it reaches its maximum size potential along fence rows and in other protected areas. Hanks et al. (1973) reported that this ecotype produced a characteristic phenolic chromatograph.

We find it interesting that our biggest forms—those with growth indexes (Table 3) above 60—are diploids (Table 1). The smallest of our basin big sagebrush accessions (Brush Creek and Wingate Mesa) are tetraploids. These two accessions may have an additional genome which codes for smaller size. The four smallest accessions and six of the eight smallest accessions are tetraploid or hexaploid (Tables 1, 4). The smallest subspecies, Wyoming big sagebrush, is tetraploid with occasional hexaploid plants (McArthur et al. 1981). The apparent correlation of the *gigas* forms with diploidy is contrary to the usual norm in herbaceous plants, but similar to the situation in the woody saltbushes (*Atriplex* sp.) of western North America (Stutz et al. 1975, Stutz 1978, Stutz personal communication).

Annual Leader Growth Rates and Annual Yield

These measures were to assess, at least in part, the annual production of big sagebrush. Production estimates show several orders of mean-value differences among the accessions (Table 3). The contrast is more striking for the yield data because as the size of the bush goes up the number of discrete units of production (twigs) increase in more of an exponential than linear manner. Twig length also increases with the size of the bush (Table 3). Our values for both estimators were highest for basin big sagebrush (Tables 3, 5, 6). Mean values for annual leader growth at the Snow Field Station varied from 5.6 to 15.4 cm for the 1976 growing season. For 1977, the values were generally less, but the range was larger (4.2 to 15.6 cm). Unpublished results of McKell and Van Epps illustrate the large influence of weather on annual big sagebrush leader lengths. Average annual leader lengths ranged from a low of 2.5 cm (1977) to a high of 9.2 cm (1979) over the 5-year study near Bonanza, Utah. (Data on file, Institute for Land Rehabilitation, Utah State University, Logan, Utah.) Our values here for annual leader growth are systematically less than those we reported

Table 5. Growth characteristics of three big sagebrush accessions at their natural sites and in two uniform gardens.

	Accession								
	Dove Creek			Loa			Colton		
Location	Ht[1]	Cr[1]	Alg[1]	Ht	Cr	Alg	Ht	Cr	Alg
Snow Field Station	221.2 a[2]	249.2 a	15.6 a	156.8 a	200.2 a	15.4 a	92.6 a	150.6 a	5.6 a
Natural Site	144.0 b	197.8 a	7.3 b	105.6 b	142.8 b	5.0 b	71.2 a	151.6 a	3.7 a
Gordon Creek Wildlife Management Area	123.0 b	166.8 a	12.7 a	80.8 b	130.4 b	6.4 b	46.6 b	94.2 b	—[3]

[1]Abbreviations: Ht = height, Cr = crown diameter, Alg = annual leader growth. All measurements in centimeters.
[2]Means in each column followed by the same letter are not significantly different ($p<0.01$) by Tukey's test.
[3]Alg of Colton accession at Gordon Creek Wildlife Management Area was not collected because of heavy deer browsing.

Table 6. Comparison of big sagebrush growth parameters by subspecies.

Subspecies	Height 1975	Height 1976	Height 1977	Crown 1975	Crown 1976	Crown 1977	Yield 1975	Annual leader growth 1976	Annual leader growth 1977
tridentata	148.8 a[1]	147.9 a	134.8 a	193.0 a	194.4 a	186.1 a	2217 a	12.8 a	11.7 a
vaseyana	96.3 b	95.8 b	69.3 b	153.7 b	157.3 b	128.3 b	890 b	8.1 b	8.2 b
wyomingensis	77.3 b	77.1 b	61.8 b	129.6 b	129.5 b	109.3 b	545 b	8.1 b	5.4 c

[1]Means in each column followed by the same letter are not significantly different ($p<0.01$) by Schieffe's test.

earlier (McArthur et al. 1978, Welch and McArthur 1979a) because we used only the leaders from branches with vertical axes then. In this study, we used the vertical axis branches plus an equal number of branches with more horizontal axes. Our values for annual leader growth are compatible with the values given by Diettert (1938) (6.0 to 15.2 cm) and Winward and Tisdale (1977) (4.7 to 11.2 cm). Winward and Tisdale reported, as we do, that basin big sagebrush has higher values than do the other subspecies.

Production of new biomass slows down under unfavorable (dry or cold) growing conditions (DePuit and Caldwell 1973). If circumstances get too bad, the plants die or die back (Ferguson 1964). Plants at the Snow Field Station were still producing substantial amounts of new biomass, however, even after a 2-year drought (Table 6; Richardson et al. 1977).

Implication of Growth Rate Differences

Accessional and subspecies growth rate differences are real. They lead to different morphological forms. Growth rate parameters support the division of big sagebrush into subspecies. In fact, they help in subspecies identification (Beetle and Young 1965, Winward and Tisdale 1977, McArthur et al. 1979). A simple chemical test (Stevens and McArthur 1974), however, is a useful adjunct to morphological growth characters for field identification because of uneven ages and microsite-induced variation (West et al. 1978).

In our plans for improvement of big sagebrush, growth rate parameters play an important role (Welch and McArthur 1979a). Whatever genetic gains in forage quality can be made would be augmented by making more of the product available on a per bush or per unit area basis.

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