Downy Brome — Intruder in the Plant Succession of Big Sagebrush Communities in the Great Basin

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Highlight: *We investigated succession on six big sagebrush sites of different potential ranging from the edge of the salt desert shrub to seral communities in the pinon/juniper woodland where the brush overstory had been removed by hand cutting. Depending upon the site, herbaceous communities that developed after elimination of overstory cover were composed of either a diversity or a relatively limited number of species of native annual forbs. Alien annual forbs were initial dominants on sites where seed source of these species was available. Dominance by downy brome caused a marked reduction of native annual species.*

Downy brome was seeded for 3 consecutive years in each of six different big sagebrush communities. On the majority of the sites, providing a seed source resulted in establishment and near total dominance by downy brome. The established populations have persisted and continued to dominate the communities. Some sites were outside the seedbed potential of downy brome, and seeding resulted in establishment only once in 3 years. Presence of plant litter and a rough microtopography were key seedbed characteristics permitting downy brome establishment on these sites.

Plant communities within the big sagebrush (*Artemisia tridentata*)[1] bunchgrass vegetation type are extraordinarily subject to invasion by alien annual species (Jardine and Anderson, 1919). Apparently no highly competitive native annual species were evolved to dominate low seral communities created by intensive grazing.

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[1] Scientific names are given the first time the common name of a plant is mentioned. Unfortunately, for many of the native forbs encountered, there are no accepted common names. Therefore, to avoid making up names, we continued to employ scientific names for the species without common names.

The invasion by alien annuals is fairly recent. Downy brome (*Bromus tectorum*) was not known to be present in western Nevada at the turn of the century (Kennedy and Doten, 1901). Today this species characterizes the landscape on millions of acres in the Great Basin (Klemmedson and Smith, 1969).

Wildland managers are continuously faced with the problem of anticipating what the successional response of a plant community will be to management-induced disturbance. Piemeisel (1938 and 1951) developed in a classic series of papers the successional pattern for downy brome on abandoned cropland or excessively grazed and burned big sagebrush rangeland. How do we extend this information? There are a multitude of plant communities, representing a wide range of environmental potential within the sagebrush formation. In addition to their inherent potential, the successional response of these communities is also a function of their seral status when disturbed or subjected to a changed stand renewal process. The interactions of potential, seral stage, and type of stand renewal process make it difficult for the land manager to know what the response will be to a grazing management system, brush spraying, or tillage and reseeding treatment on a given piece of ground.

Our purpose in this investigation was to assess the role of downy brome as an alien in a series of low seral big sagebrush communities and to study how this species responds under different site conditions.

Methods

This investigation was conducted in the Churchill Canyon watershed located about 6.8 km northwest of Yerington, Nev. We selected the area because detailed description of the soils and plant communities of the watershed had been developed and presented by Blackburn et al. (1969). In order to conserve space we will hold site descriptions to a minimum and refer the reader to Blackburn's excellent bulletin.

We selected six big sagebrush plant communities in the watershed, ranging from the edge of the salt desert shrub to seral communities in the pinon (*Pinus monophylla*)/ juniper (*Juniperous osteosperma*) woodland. A representative portion of each community was included in the study initiated in 1968. The projected herbage cover of all shrubs was estimated from 10 plots 10 m^2 in area at each site. Herbaceous vegetation was sampled with 10 lines of 100 step-points each, following the procedures of Evans and Love (1957). Following the sampling, we removed the woody vegetation with a minimum of soil disturbance. An area approximately 25 by 25 m was fenced to exclude livestock and large rodents at each location.

In 1968 to determine the seed reserves in soil, we collected 25 2 by 5-cm samples at each location. The samples were taken from the soil surface and at 2.5-cm intervals beneath the surface to a depth of 7.5 cm. The samples were placed in the greenhouse and seeds germinated. Using the method developed by Young et al. (1969), we obtained an estimate of the number of viable seeds per unit area since this procedure provides an estimate of reproductive potential in seral communities.

During October, 1968, at each site we planted 10,000 downy brome caryopses per m^2 on 3 by 3-m plots. A 3-replicated, randomized block design was used. The caryopses were incorporated into the surface soil by raking. At each site we seeded new plots with the same number of caryopses of downy brome in 1969 and 1970.

Each year (1969 through 1971) at the end of the growing season for annuals, we sampled the density per 0.1 m^2 of annuals on the previously seeded plots. In 1971, we also determined caryopses production of downy brome.

For environmental measurements precipitation gauge was installed at each experimental location. The entire watershed is instrumented with accumulating and recording rain gauges (Blackburn et al., 1969). At each location we installed stacks of gypsum soil moisture blocks at 7.5, 15, 30, 45, and 60 cm depths.

Results

Vegetation Before Clearing

Experimental site 1 is located on a terrace at the bottom of the watershed. Mean annual precipitation was 165 mm for the period 1963 to 1971. The soil of this site approaches a gray desert soil in characteristics. The overstory was dominated by big sagebrush with some gray ephedra (*Ephedra nevadensis*) and green rabbitbrush (*Chrysothamnus viscidiflorus*) (Table 1). The shrubs formed a very open overstory with slightly more than 10% ground cover.

Table 1. Projected herbage cover (%) of woody species at each site before plots were cleared in 1968.[1]

	Experimental sites					
Species	1	2	3	4	5	6
Big sagebrush	8	6	12	12	4	78
Gray ephedra	2	T	T			
Green rabbitbrush	1		2	2		
Horsebrush	T		T			T
Hop sage	T					
Shadscale	T					
Bitterbrush				1	2	
Desert peach				T	5	
Current						T
Snowberry						T
Singleleaf pinon				T	18	2
Utah juniper					2	
Green ephedra					T	T

[1] T indicates species present at less than 1% cover.

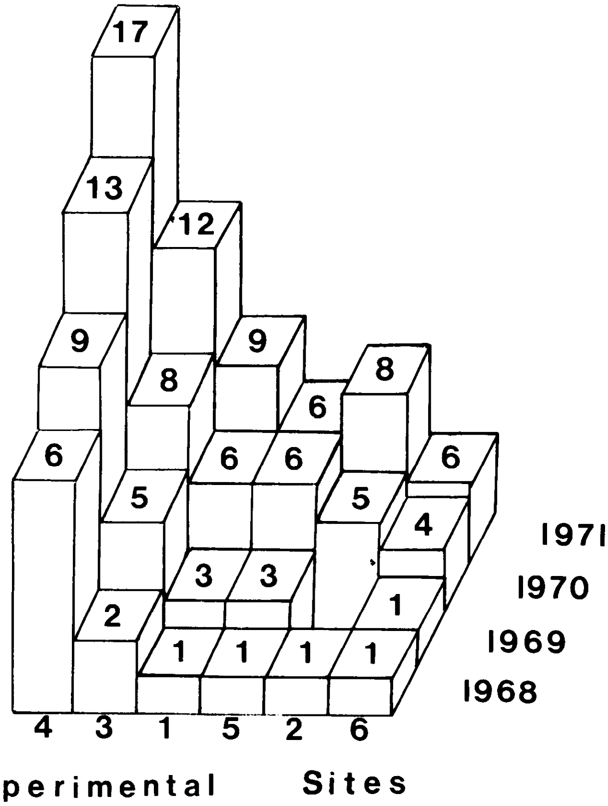

Fig. 1. *Percent ground cover of herbaceous vegetation on control plots from 1968 through 1971 at six sites.*

At site 1, the herbaceous ground cover was only 1% (Fig. 1). The understory was dominated by the native annual forbs (*Eriogonum baileyi* and *Nama densum*) (Fig. 2). There were occasional plants of the alien grass downy brome (*Bromus tectorum*); the native perennial grass, Indian ricegrass (*Oryzopsis hymenoides*); and the native perennial forb, apricot mallow (*Sphaeralcea ambigua*). This area has been used for a lambing ground by domestic sheep for at least 100 years.

The second experimental site was located on a broad alluvial fan at a slightly higher elevation with slightly greater precipitation (1963 to 1971 mean was 190 mm) and a more developed soil. This soil was largely derived from decomposed granite and has a very smooth-sandy surface.

The overstory of this site consisted of a sparse stand of senescent big sagebrush (Table 1). The understory of site 2 was also very sparse (Fig. 1). Except for an occasional plant of the native perennial grass, squirreltail (*Sitanion hystrix*), the understory was dominated by the native annual forbs *Navarretia Breweri, Franseria acanthicarpa,* and *Nama* sp. (Fig. 2).

The third experimental site was also located on a broad alluvial fan with a well-developed soil. Precipitation averaged 210 mm (1963 to 1971) at this site. The overstory was dominated by a vigorous stand of mixed age classes of big sagebrush (Table 1). The understory of site 3 had slightly greater ground cover than the first two locations (Fig. 1). The native annual forbs *Navarretia* and *Nama* dominated the understory (Fig. 2), but the alien annual forbs Russian thistle (*Salsola kali* var. *tenuifolia*) and tumble mustard (*Sisymbrium altissimum*) were present. There was some downy brome under the shrub canopies. A remnant stand of the perennial grasses squirreltail and Thurbers needlegrass (*Stipa thurberiana*) was

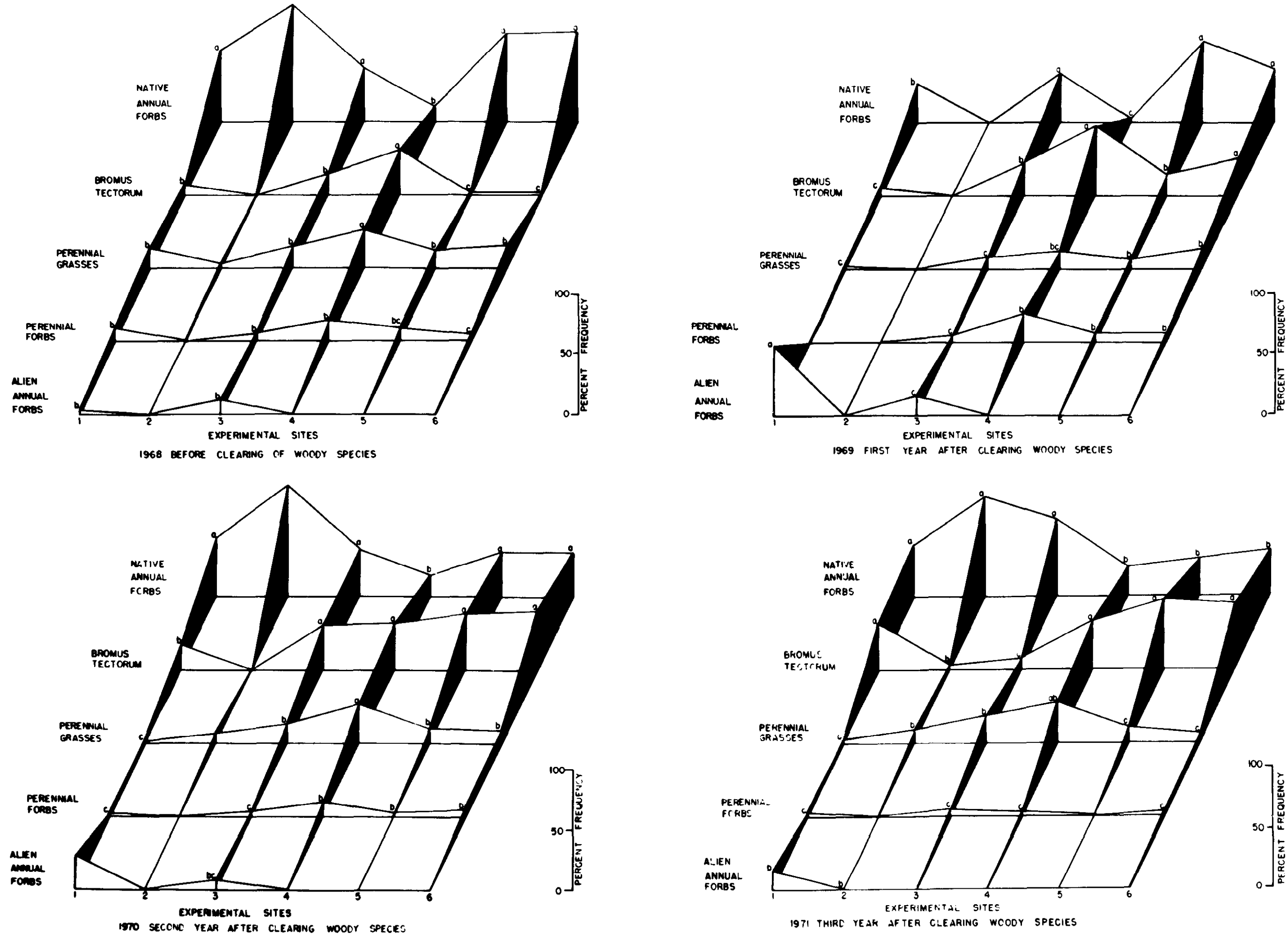

Fig. 2. *Frequency of herbaceous species in 1968 through 1971 at six sites. Means followed by the same letter are not significantly different at the 0.05 level of probability as determined by Duncan's multiple range test. All comparisons are made within sites.*

also present under the shrubs. Between the shrubs, the shortlived perennial native forb skeleton weed (*Lygodesmia spinosa*) was found.

Experimental site 4 was located near the top of an alluvial fan at the base of the eastern side of the Pine Nut Mountain escarpment. The soil, precipitation (1963 to 1971 average was 310 mm), and elevation (1770 m) of this site are fairly typical of the higher potential of big sagebrush sites in western Nevada. The overstory was dominated by an even-age-stand of mature big sagebrush (Table 1). A few heavily browsed plants of bitterbrush (*Purshia tridentata*) were present in the overstory. The site was located 300 m below the edge of the pinon/juniper woodland, but several pinon seedlings were present on the plot area.

The fourth site had the greatest understory cover (Fig. 1). This understory was dominated by downy brome and the perennial grasses squirreltail and Thurbers needlegrass (Fig. 2).

The fifth experimental site was located in a nearly mature pinon/juniper woodland (Table 1). The shrubby vegetation was composed of senescent big sagebrush, bitterbrush, and green ephedra (*Ephedra viridis*) growing between the trees where the arborescent crowns had not closed. Mean annual precipitation for 1963 to 1971 at this site was 350 mm.

The understory at the fifth site was extremely sparse (Fig. 1). The dominant species were the native annuals *Eriogonum* and *Navarretia* (Fig. 2). Soils at this site were relatively rock free and derived from decomposing granite of a sandy texture.

The sixth experimental site is located high on the mountain escarpment at 2130 m elevation. The area was an island of brush that had burned in the pinon/juniper woodland. As indicated by the ages of the shrubs, the areas was burned about 25 years previous to 1968. The brush overstory was very dense with a virtually closed canopy (Table 1). Big sagebrush dominated the overstory, but several shrubs characteristic of the mountain-brush type (Blackburn et al., 1969) were also present. Pinon and juniper saplings were beginning to emerge from the 1.5 to 2 m high brush canopy.

Under the brush canopy the herbaceous understory was very sparse (Fig. 1). Alien annual forbs dominated, with wild tobacco (*Nicotiana attenuata*) being the most important species (Fig. 2). There were occasional clumps of squirreltail and the native short-lived-perennial forb prickly poppy (*Argemone munita*).

Seed Reserves in the Soil

Seedlings grown in the greenhouse from soil samples collected at each site gave some indication of the reproductive potential available at each site the first year after removing the shrubs (Table 2). We did not find any perennial forb or grass seedlings. The herbaceous perennials have been overgrazed for

Table 2. Seedlings (per 0.1 m²) obtained from soil samples taken at each site before plots were cleared in 1968.

Species	Experimental site 1	2	3	4	5	6
Native annual forbs	18	4	24	30	2	2
Alien annual forbs	28	0	6	0	0	0
Downy brome	4	0	34	186	0	0
Big sagebrush	40	34	38	56	44	86
Other shrubs	2	0	0	3	2	0
Native perennial grasses or forbs	0	0	0	0	0	0

such a long period, little or no seeds or caryopses are produced, and we could determine no reserve in the soil. The lack of a seed reserve of perennial grasses, may be characteristic of degraded stand of big sagebrush (Young et al., 1969). All sites produced some annual forb seedlings.

Site 4 had a tremendous reserve of viable downy brome caryopses in the soil; lesser amounts were found in the soil from sites 1 and 3. No downy brome seedlings were obtained from sites 2, 5, and 6. All sites had a large reserve of achenes of big sagebrush.

Succession After Clearing

Herbaceous vegetation

First Year after Clearing. On the control treatments, where succession was allowed to proceed without further treatment after the shrubs were removed, there was unique successional vegetation development for each site (Fig. 2).

At site 1 there was a dominating expression of Russian thistle (Fig. 2). Samples taken the year before indicated a large seed reserve of Russian thistle and other alien annual forbs in the soil (Table 2).

The control and all treatment plots at site 2 were devoid of vegetation in 1969 (Fig. 2). The litter halos, which marked the shrub canopies after clearing, had disappeared and the entire plot was smooth, bare soil.

Native annual forbs, especially *Navarretia*, dominated the first year's vegetation at site 3 (Fig. 2). There was an increase in downy brome and in total ground cover (Fig. 1).

Downy brome was clearly the dominant species at site 4 in 1969 (Fig. 2). *Eriogonum*, *Nama*, and *Navarretia* were native annual forbs that dominated site 5 in 1969. There were no alien forbs on this site.

The herbaceous vegetation of site 6 was dominated by *Nicotiana*, but there was an increase in the frequency of downy brome (Fig. 2). The total ground cover (Fig. 1) was extremely low; therefore, changes in relative frequency since clearing should be judged in terms of continued 99% bare ground.

Second Year after Clearing, The second year (1970) after clearing the woody species, total ground cover continued to increase at site 1 (Fig. 1). There was a reduction in Russian thistle and the frequency of downy brome increased, but dominance of the herbaceous vegetation returned to native annual forbs, especially *Eriogonum* (Fig. 2). The second year, control plots at site 2 were again vegetated predominantly with *Eriogonum* and *Nama*. There was no establishment of alien annuals. On experimental site 3, downy brome increased to share dominance with the native forbs. There was a continuing increase in perennial grasses. Perennial grasses had increased in frequency by 1970 until they shared dominance with downy brome on site 4. Total ground cover remained low (Figs. 1 and 2) on sites 5 and 6; however, downy brome increased in frequency.

Third year after clearing. There was a continued decline in alien forbs on site 1 in 1971 (Fig. 2). Downy brome increased in frequency until it shared dominance with native annual forbs. There was a diversity of native forbs at this location (Table 4).

The native annual forbs continued to dominate site 2. Some downy brome had become established, and there was an

Table 3. Frequency (%) and constancy (%) of herbaceous species on control plots at six locations in 1971, 3 years after clearing of shrubs.

Species	Experimental locations 1	2	3	4	5	6	Constancy
Native annual forbs							
Erigonum Baileyi var. *divaricatum*	14	40	18	18	25	4	100
Lepidium flavum	3						16
Navarretia Breweri	6	7	36	3			66
Mentzelia Lindleyi	8				3		33
Nicotiana attenuata						33	16
Chaenactis Douglasii var. *rubricauls*			5				16
Nama densum	8	28	4	3	3		83
Franseria acanthicarpa		7					16
Linanthus Bigelovii	3						16
Alien annual forbs							
Russian thistle	11			4			33
Tumble mustard	3						16
Tansy mustard	2						16
Alien annual grass							
Downy brome	38	7	10	40	57	53	100
Perennial grasses							
Indian rice grass	2	3	4				50
Squirreltail		8	9	21	12	7	83
Thurbers needlegrass			9	12			33
Perennial forbs							
Apricot mallow	2						16
Skeleton weed			5	3			33
Prickly poppy						3	16

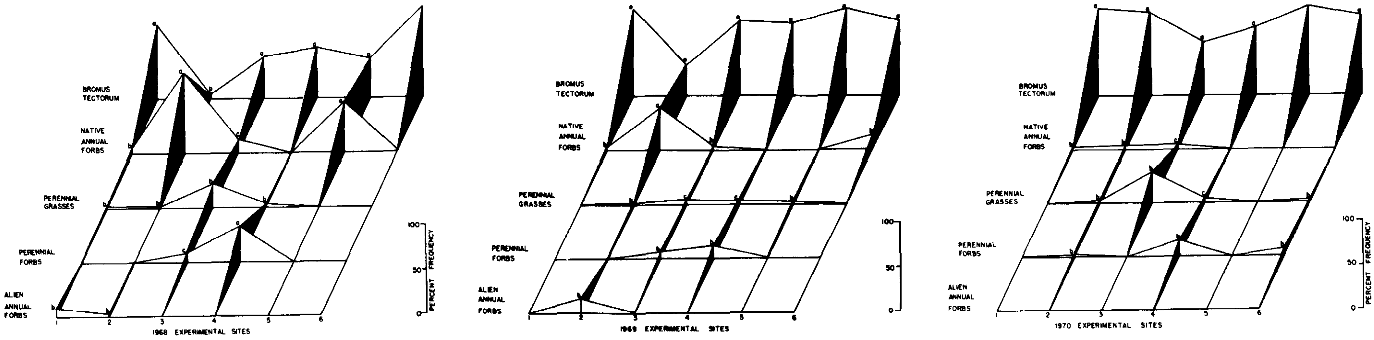

Fig. 3. *Frequency of herbaceous species in 1971 on plots seeded with 10,000 downy brome caryopses per m² in 1968, 1969, and 1970 at six sites. Means followed by the same letter are not significantly different at the 0.05 level of probability as determined by Duncan's multiple range test. All comparisons are made within sites.*

increase in perennial grasses.

There was a surprising decrease in downy brome on site 3 in 1971 even though precipitation was normal. Perennial grasses continued to increase and may be related to the decrease in downy brome.

The composition of the herbaceous community on site 4 was quite similar both in 1970 and 1971. Initial succession had apparently become relatively stable and longer time periods will be required to observe a significant change.

The dramatic increase in downy brome continued at site 5. Total herbaceous cover also increased (Fig. 1). A similar trend was observed at site 6; however, total ground cover remained quite low at this site.

Seeding Downy Brome

Seeding of downy brome at each site eliminated the variable of the availability of caryopses of this species in the development of succession.

An excellent stand of downy brome was established by seeding at site 1 on all three years. The population of downy brome established through seeding persisted annually with a dramatic decrease of native annual species (Figs. 2 and 3).

Table 4. Density (1000's), herbage yield (g), and caryopses production (1000's) of downy brome in 1971 on plots seeded in 1968, 1969, or 1970 with 10,000 caryopses/m².

Site	Year seeded	Per m² Density	Herbage yield	Caryopses production
1	1970	1.2	31.0	12.6
	1969	0.2	7.0	4.1
	1968	0.2	8.0	3.0
2	1970	0.2	18.0	5.2
	1969	0.02	2.0	0.5
	1968	0.01	1.1	0.2
3	1970	1.3	48.0	4.0
	1969	1.7	32.0	5.0
	1968	0.5	21.0	1.7
4	1970	5.2	56.0	22.0
	1969	4.7	63.0	28.0
	1968	4.6	64.0	20.0
5	1970	0.3	14.0	13.0
	1969	0.2	11.0	9.8
	1968	0.08	6.0	1.0
6	1970	8.4	65.0	28.0
	1969	9.6	81.0	27.0
	1968	7.8	75.0	31.0

Each year about 10% of the seeded caryopses became established plants and reproduced (Table 4). The naturally reestablished populations, the second and third year after initial seeding, had a population density of about 2% of the original seeding rate. Apparently more plants can be established by seeding at this site than can be established naturally, even though the caryopses produced from the initial seeding always exceeded the number seeded. This probably resulted from covering the seeded caryopses with soil by light raking.

At Site 2, none of the downy brome caryopses seeded in October, 1968, established in 1969. In 1971, there were 10 downy brome plants per m² on these plots (Table 4). Only an occasional plant established on the plots seeded in 1969. The plots seeded in 1970 contained 200 downy brome plants per m² and drastically reduced the stand of native annual forbs (Fig. 3). The 1970 plants produced more caryopses per plant than populations of 10 plants per m² (1968 plots) on the same site where the latter population was competing with native annuals.

Downy brome became established at site 3 each year. Population densities were fairly low, but there were considerable perennial grasses and forbs in the plots (Fig. 3 and Table 4). Although there was a relatively dense stand of downy brome on the control plots at site 4, the seeding of additional downy brome caryopses resulted in the elimination of native annuals.

Plants failed to become established from the first year of seeding at site 5. In the second and third years, only 2 to 3% of the seeded caryopses became established. This density of downy brome was sufficient to eliminate native annuals in 1971.

Dense stands of downy brome were established and persisted at site 6 on all 3 years. Caryopses produced in 1971 nearly tripled the original seeding rate on all three age stands at this location.

At locations 4 and 6, sufficient herbage was produced to create and maintain a layer of litter on the soil surface. Besides providing a favorable microenvironment for germination (Evans and Young, 1970), the litter contains a reserve of viable caryopses, a major portion of which may have acquired a dormancy thus assuring a reproductive reserve for at least 2 years (Young et al., 1969).

Shrub Reestablishment

Despite the diverse and vigorous populations of annual species that developed after the initial clearing of the shrubs,

Table 5. Density of shrub seedlings or root sprouts per 100 m^2 at six sites in 1971.

Species	Experimental sites					
	1	2	3	4	5	6
Big sagebrush	2.0	3.5	6.5	11.5	12.5	13.0
Green rabbitbrush			0.3			
Horsebrush				0.3[1]	0.5	
Gray ephedra		0.3[1]	0.3[1]			
Green ephedra				0.3[1]		
Current						0.3[1]
Snowberry						0.3
Desert peach		0.3[1]		0.3	0.3	0.5[1]

[1] These are probably root sprouts.

seedlings of woody species became established on all sites (Table 5).

Big sagebrush seedlings were the most abundant of the reestablishing shrubs. Samples taken before clearing had indicated a reserve of viable big sagebrush achenes in the soil (Table 3). The farther up the watershed the sites were located, with resulting greater precipitation and soil development, the greater the density of big sagebrush reestablishment. Root sprouting shrubs reoccupied sites as rapidly as populations of annuals. Desert peach and *Ribes* populations at site 6 provided 20% projected growth cover 3 years after they were cut to the soil surface.

The relatively dense downy brome populations at location 4 did not inhibit big sagebrush establishment. Downy brome populations consistently closed stands to the establishment of perennial grass seedlings (Evans et al., 1967).

Site Quality in Relation to Seedbed Quality

Sites 2 and 6 in this investigation were unfavorable to the establishment of annuals. Both sites have soils derived from decomposed granite. The smooth, rock-free surface of these sites offers a minimum of microtopography for seedbeds. Harper et al. (1965) equate potential population size and composition of annual plants with the quality of microtopography creating safe sites for germination in the seedbed. Evans and Young (1972) have demonstrated that less than 1% of downy brome caryopses seeded on a bare soil surface will establish, while 150% of the seeded rate will establish with favorable microtopography. This illustrates both the microsite requirements and dispersal mobility of downy brome caryopses.

In 1969, the first growing season after clearing, when plots at sites 2 and 6 were largely bare of vegetation, readings from gypsum blocks indicated that the entire soil profile had available moisture. Sites 1, 3, and 4 were favored with a stony soil surface to provide a variety of microtopography which permitted establishment of downy brome.

Discussion

Within the range of variability in big sagebrush communities with which we dealt, there were sites where downy brome had difficulty in becoming established both because of the potential of the seedbed and the lack of a seed source. However, in these studies we did not encounter an assemblage of native annual plant species capable of preventing the assumption of dominance by downy brome. The lack of native annual grasses in these communities provides a void which downy brome is apparently highly adapted to occupy.

When land managers have to make decisions concerning the potential of a site for downy brome invasion and dominance, they must adjust the normal concept of site potential. Site potential is usually equated with quality-oriented factors such as elevation, aspect, soil development, and precipitation. Additional factors that affect downy brome establishment include the successional history of the site and its influence on the development of a seed source. The annual habit places a premium on seedbed characteristics that favor or limit germination and establishment. Plant litter and microtopography are key characteristics for predicting downy brome dominance.

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