Population Dynamics of Green Rabbitbrush in Disturbed Big Sagebrush Communities

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Highlight: *We investigated the dynamics of green rabbitbrush populations in relation to burning, livestock grazing, and chemical shrub-control as a range-improvement practice in big sagebrush communities. Green rabbitbrush plants sprout from roots, and density increases by seedling establishment after a fire. Achene production and seedling establishment are paramount to dominance by rabbitbrush after burning of big sagebrush communities. Rabbitbrush continues to dominate and periodically reestablishes itself for at least 15 years. Reduced populations of rabbitbrush persist in communities where dominant big sagebrush plants are 40 to 50 years old. Partial reduction in big sagebrush or rabbitbrush populations by applications of 2,4-D results in a large increase in seedling establishment of both species. When these communities are not disturbed or when all shrubs are removed, no shrub seedlings are established.*

Our purpose was to investigate the dynamics of populations of green rabbitbrush (*Chrysothamnus viscidiflorus* var. *viscidiflorus*) in seral big sagebrush (*Artemisia tridentata*) communities in western Nevada. Parameters emphasized are dominance and tenure of rabbitbrush in relation to stand reduction and renewal processes of burning, livestock grazing, and shrub control as a range-improvement practice.

An increase in dominance of rabbitbrush, usually attributed to root sprouting, is an almost universal response to disturbance in big sagebrush communities in the central Great Basin. Big sagebrush does not sprout when stands are destroyed in wildfires. Rabbitbrush, which is a subdominant in many big sagebrush communities, sprouts profusely after fires destroy the aerial portion of the plant (McKell and Chilcote, 1957). The natural stand reduction and renewal process of recurrent wildfires therefore leads to destruction of dominant big sagebrush, followed by a successional stage dominated by rabbitbush. These sequential relations have been a part of the ecology of the Great Basin since the climate became more arid as a result of uplifting of the Sierra Nevada and Cascade Mountain ranges (Axelrod, 1950).

Green rabbitbrush, and to a lesser extent big sagebrush, are largely rejected by browsing livestock. The essential-oil content of the herbage of big sagebrush apparently contributes to this rejection because it inhibits or depresses rumen activity (Nagy et al., 1964). Heavy grazing by domestic livestock for many seasons reduces grasses and increases density of brush species.

Grazing of the herbaceous understory of big sagebrush communities by domestic livestock revolutionized plant succession in the Great Basin little more than a century ago (Young et al., 1972). The ecological niche for large herbivores that was filled by domestic livestock had been vacant since the close of the Pleistocene (Martin, 1967).

Two decades ago, technology produced herbicides that offered the possibility of balancing the ecological changes produced by a century of grazing not in equilibrium with the environment (Bovey, 1971).

How has stand reduction and renewal by fire, grazing, and herbicide application influenced succession of rabbitbrush and big sagebrush communities?

Procedure and Area Description

Sampling Methods

The basic sampling design consisted of 10 macroplots, each 100 m^2 in area. These 10 plots were randomly located in each of the 52 stands selected for sampling. The stands were selected to provide examples of the various types of stand reduction and renewal on sites of varying potential. The density, age class, projected herbage cover, and diameter of shrubs rooted in each plot were recorded by species. Herbage cover of perennial grasses and forbs and annuals was estimated for each plot. Age classes of shrubs were established by sectioning stems and counting growth rings (Ferguson, 1964).

In 1970, at maximum herbage production, we clipped to ground level the herbaceous vegetation on 10 plots 1 m^2 in area in each stand. At the same time, we frequency-sampled the herbaceous vegetation with 100 plots 0.1m^2 in area. Frequency samples were arranged within each stand following the methods of Evans and Love (1957).

We excavated and described soil profiles of the major soils represented, using methods described in the Soil Survey

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Manual (Anon., 1960).

We initiated sampling in 1968 and added stands through 1972. The stands treated with herbicides in 1968 were sampled in 1969 and 1972. In 1972, we determined seedling density of rabbitbrush and big sagebrush on 75 plots $10m^2$ in area in relation to percent kill of the original brush stand.

Physiography of Study Area

The investigation was located at Medell Flat, about 35 km north of Reno, Nev. Medell Flat is an irregularly shaped depression, bordered on the east by the Dogskin Mountains and on the west by granitic hills, which merge into the Peterson Mountain Range.

Recent tectonic activity of the granitic mountain ranges that surround Medell Flat has provided decomposing quartz diorite for the bulk of the raw material for soil formation in the basin.

The east and northeast sides of Medell Flat are covered with Pleistocene alluvium (McJannet, 1957). These fanglomerate deposits head at about 1,580 m elevation against the bold fault scarp of the Dogskin Mountains.

In contrast to the undifferentiated soils of the fanglomerate, the westside alluvium soils have argillic horizons and sometimes contain highly indurate pans, which limit rooting depth. These soils belong to the order Aridisols and the group Haplargid or Durargid, depending on the presence of pan development (Anon., 1960). Soils with pans tend to be located on the most recent alluvial surfaces. Terraces have less developed soils and fragile pans subtending the solum.

On the basis of records from the closest station (Reno) and 10 years of collecting precipitation records at Medell Flat, we estimate the mean annual precipitation at from 200 to 250 mm.

There is insufficient water on the approximate 8,000-ha area of Medell Flat to support large herbivores. Domestic livestock grazing depends on a system of windmills, underground pipe, and water troughs.

Stand Renewal Processes

Grazing

Medell Flat has been grazed by cattle, sheep, and horses for more than a century. In general, livestock was introduced to western Nevada in the 1860's, with several population cycles regulated by severe winter kills in the 19th centruy (Hazeltine et al., 1961). Kennedy and Doten (1901) described the general area of Medell Flat as a virtual dust bed at the turn of the century. They attributed the destruction of vegetation to early spring grazing of sheep on lambing grounds between salt-desert winter range and summer range in the Sierra Nevada Mountains. Cattle were annually wintered on the flat area with minimum supplemental feeding until 1971. With the establishment of the Grazing Service in 1935, grazing pressure was reduced to chronic attrition rather than acute destruction of the herbaceous vegetation. The attrition refers to selective utilization of the herbaceous vegetation and subsequent increase in shrub density since the dust bed conditions at the turn of the century.

Fire

Almost all of Medell Flat has evidence of being burned during the 20th century. During the three decades that fire suppression has been practiced on public lands in the area, the records of the Bureau of Land Management, U. S. Department of the Interior, Carson City, Nev., indicate that one large fire swept the western part of the basin. This fire started from a lightning strike in July, 1957.

Artificial Vegetation Manipulations

In 1958, 3.4 kg/ha of (2,4-dichlorophenoxy)acetic acid (2,4-D) was aerially applied to two long strips of big sagebrush communities in the southeastern part of Medell Flat. In 1968, about 1,000 ha of big sagebrush dominated communities were treated with 3.4 kg/ha of 2,4-D. In addition, 10 ha were treated with 2.5 kg/ha of 2,4-D plus 0.4 kg/ha of 4-amino-3,5,6-trichloropicolinic acid (picloram). This combination of herbicides is particularly effective on rabbitbrush (Tueller and Evans, 1969).

Table 1. Density and projected herbage cover of woody species and cover of herbaceous species of plant communities growing on recent alluvial fans.

Plant groups and measurements	Stand reduction and renewal process			
	Burned in 1957			
	Grazed	Grazed extreme	Ungrazed for 10 years	Unburned and grazed
Plants/ha (100's)				
Rabbitbrush				
Seedling	1	0	0	0
Young	2	1	0	0
Mature	1	0	0	0
Senescent	2	0	1	2
Big sagebrush				
Seedling	1	1	0	3
Young	0	1	0	1
Mature	0	0	0	29
Senescent	0	0	0	24
Hop sage	0	0	0	1
Projected herbage cover (%)				
Rabbitbrush	10	1	1	1
Big sagebrush	0	1	0	24
Total shrubs	10	2	1	26
Perennial grasses	3	0	18	2
Annuals	15	26	5	18
Number of stands sampled	4	1	1	4

Results

The most immediate problem in establishing the tenure of rabbitbrush as a seral stage dominant is to obtain a reliable estimate of age of the shrubs. We obtained a highly significant correlation ($r = 0.889$) between shrub height (x) and the number of annual rings on rabbitbrush stems (y). Using this relation, we calculated the linear regression equation $y = 1.5894 + 0.2109x$. Height as an estimate of age provides a convenient tool for stratifying populations by age classes. Difficulties are encountered with senescent plants. At maturity, rabbitbrush plants virtually cease growth in height, and their stems are largely destroyed by channels of the larvae of *Acamaeodera pulchella* (Strickler, 1956).On an area at Medell Flat, burned 12 years previously, 5.6 percent annual mortality of rabbitbrush was found.[1] This high mortality suggests that many plants in the population had become senescent. A scattered population of rabbitbrush plants in a high-seral big sagebrush stand apparently is less subject to *Acamaedera* infestation than dense low seral populations.

There are four convenient groupings based on vegetative appearance in the height/age classes of rabbitbrush populations: seedlings (5 to 15 cm tall, 1 to 2 years old); young plants (20 to 30 cm tall, 3 to 5 years old); mature plants (35 to 65 cm tall, 6 to 12 years old); and senescent plants (70 to 80 cm tall, 13 plus years old).

[1] Unpublished data, Agr. Res. Serv., U.S. Dep. Agr., Reno, Nev.

Table 2. Frequency (%) and cover (%) of species composing various herbaceous communities found in association with degraded brush stands, and the herbage production (kg/ha) of each community measured by clipping in 1970.[a] These basic plant communities reoccur through the study area in relation to site potential and level of disturbances.

	Herbaceous plant communities									
	Downy brome on burns		Downy brome, shrub canopy & interspace		Downy brome/ squirreltail/ Thurbers and western needlegrass		Desert needlegrass		Downy brome/Great Basin wildrye	
	Frequency	Cover	Frequency	Cover	Frequency	Cover	Frequency	Cover	Frequency	Cover
Annual grass										
Downy brome	70	15	80	9	38	5.2	10	0.5	68	13
Perennial grasses										
Squirreltail	3	0.1	3	0.1	16	0.7	10	0.5	5	0.1
Thurbers needlegrass		T	T	T	5	T	4	T	T	T
Western needlegrass	5	10	2	0.1	6	0.8	14		2	0.1
Desert needlegrass	0	0	0	0	T	T	18	6	0	0
Great Basin wildrye	T	T	0	0	0	0	0	0	0	0.3
Other species	4	0.2	0	0	6	0.2	11	4.4	2	0.1
Alien annual forbs	10	1.0	6	0.4	3	T	0	0	11	0.3
Native annual forbs	T	T	T	0.1	18	0.7	31	2.2	1	0
Perennial forbs	8	1.1	3	0.1	15	0.7	5	0.5	4	0.1
Total herbaceous cover		27.4		9.8		8.3		14.1		14.0
Herbaceous production kg/ha		150 to 300		75 to 100		280		940		430

[a]T indicates less than 1.0% frequency or less than 0.1% cover.

Plant Communities and Stand Reduction by Burning and Renewal Under Grazing

Recent Alluvial Fans

Unburned areas on alluvial fans on the west side of Medell Flat support dense stands of big sagebrush (Table 1). These sites have downy brome- or downy brome/Great Basin wildrye (*Elymus cinereus*)-dominated herbaceous communities (Table 2). The stands are clearly dominated by old big sagebrush plants, and big sagebrush seedlings are establishing in the stands. The oldest stem section of plants in these communities had 52 growth rings and the center of the stem was decayed. Average age for the mature big sagebrush plants was 35 years. Only a few senescent green rabbitbrush plants occur in the stands (Table 1). The green rabbitbrush plants appear to be very old.

Big sagebrush communities growing on a portion of the recent alluvial fans were burned in 1957. The burned sites are currently dominated by a green rabbitbrush overstory and a downy brome understory (Tables 1 and 2). The burned area has been heavily grazed since the fire. Where a portion of this site was protected from grazing by an exclosure constructed in 1952, a squirreltail (*Sitanion hystrix*)/downy brome/western needlegrass (*Stipa occidentalis*)/Thurbers needlegrass (*S. thurberiana*)[2] plant community is found with very few green rabbitbrush plants (Table 1). In contrast to the protected area, there is an area at Medell Flat where cattle are wintered annually with limited supplemental feeding. The concentration of livestock suppressed green rabbitbrush and perennial grass establishment and favored a downy brome community, which includes alien weeds that are noxious to grazing.

Alluvial Terraces

Closely related to the recent alluvial fans, both in physical position and soil development, the alluvial terraces have more diverse plant communities before and after burning (Table 3). Unburned communities are dominated by big sagebrush, but they also contain a relative abundance of green rabbitbrush, horsebrush (*Tetradymia canescens*), and desert peach (*Prunus andersonii*). The oldest big sagebrush plants had more than 50 growth rings. The number of growth rings of mature big sagebrush stems is much more variable here than in the alluvial

Table 3. Density and projected herbage cover of woody species and cover of herbaceous species of plant communities growing on alluvial terraces.

	Stand reduction and renewal process		
	Burned 1957 and subsequently heavily grazed		Unburned and always heavily grazed
Plant groups and measurements	Horsebrush Sites	Rabbitbrush Sites	
Plants/ha (100's)			
Rabbitbrush			
Seedling	16	18	1
Young plants	7	9	3
Mature plants	2	1	0
Senescent	3	4	6
Big sagebrush			
Seedling	1	1	4
Young plants	1	0	2
Mature plants			6
Senescent			11
Other species			
Horsebrush	26	1	4
Hop sage	0	0	1
Spiney phlox	1	2	1
Desert peach			1
Projected herbage cover (%)			
Rabbitbrush	11	14	2
Big sagebrush	1	1	16
Total shrubs	23	16	24
Perennial grasses	8	5	2
Annuals	15	8	5
Number of stands	4	3	3

[2] Four species of *Stipa*—*S. thurberiana, S. occidentalis, S. speciosa,* and *S. comata*—occur in the same communities at Medell Flat. It is difficult to separate the first three species when they are closely grazed throughout the year and not allowed to flower.

Table 4. Density per hectare and projected herbage cover (%) of woody species and cover of herbaceous species of plant communities growing on fanglomerate in relation to herbicide, burning, and grazing treatments.

Plant groups and measurements	Burned, currently moderately grazed		Unburned, currently grazed[1]			2,4-D in 1968, grazed[1]			2,4-D plus picloram in 1968, no grazing	2,4-D in 1958, heavy grazing
	Less than 10[2]	More than 10[2]	Heavy	Moderate	Light	Heavy	Moderate	Light		
Plants/ha (100's)										
Rabbitbrush										
Seedlings	14	1	2	2	1	0	0	0	0	0
Young plants	8	2	0	2	0	0	0	0	0	1
Mature plants	3	1	0	2	0	0	0	0	0	15
Senescent plants	1	4	1	1	1	0	1	0	0	8
Big sagebrush										
Seedlings	4	1	0	4	10	0	0	0	1	4
Young plants	1	0	3	6	4	0	0	0	0	1
Mature plants	0	2	2	8	8	0	0	0	0	1
Senescent plants	0	1	45	12	18	1	1	0	0	0
Other shrubs										
Spiney phlox	1	1	1	2	0	0	1	0	0	0
Green ephedra	2	3	0	1	2	1	1	2	2	2
Horsebrush	1	1	0	2	0	0	0	0	0	0
Desert peach	8	9	0	8	1	1	1	2	0	1
Projected herbage cover (%)										
Rabbitbrush	3	6	1	9	2	0	1	0	0	11
Big sagebrush	1	2	14	3	18	1	1	0	1	3
Total shrub	15	22	16	20	22	2	5	3	3	17
Perennial grasses	5	5	2	6	8	2	2	8	12	3
Annuals	10	2	1	5	2	10	12	6	2	12
Number of stands sampled	2	3	3	4	2	3	4	2	1	8

[1] Gradient uphill and away from water.
[2] Years since burned.

fan communities.

One distinct successional plant community on the terraces that has been burned is dominated by green rabbitbrush, while on the remainder of the area horsebrush and rabbitbrush share dominance. There are no consistent differences in soils or topography between these two types of seral communities (Table 3).

Prickly phlox (*Leptodactylon pungens*), a semiwoody shrub, increases in density on the burned areas. The most prevalent understory community is downy brome, which gradually intergrades into downy brome/squirreltail/western needlegrass/Thurbers needlegrass with greater distance from stockwater (Table 2).

The herbaceous cover and frequency of alien annuals are higher in downy brome communities than in adjacent unburned big sagebrush communities with downy brome growing under the shrubs (Table 2). The cover and frequency of native annuals decrease after burning and the invasion of alien weeds. In degraded big sagebrush communities, native annual forbs occur on the margins of nests of harvester ants (*Pogonomyrmex occidentalis*). The ants persist in the burned areas and apparently harvest the seeds of the alien weeds. Persistent colonies of prickly skeletonweed (*Lygodesmia spinosa*) have developed in areas of rodent disturbance in the burns.

Fanglomerate

Casual observation reveals few differences between degraded big sagebrush stands on the fanglomerate and those growing on the alluvial terraces. On burned areas, a much higher density of creeping-rooted shrubs clearly identifies the fanglomerate areas (Table 4). The significance of the presence of these additional root sprouting shrubs to the dynamics of rabbitbrush is that they occupy space available for rabbitbrush dominance on sites with more developed soils. The creeping stemmed or clonal root sprouters have a much longer tenure than rabbitbrush. Desert peach forms dense thickets that exclude other woody species. Individual stems of desert peach apparently are short-lived, with a maximum of 6 to 8 growth rings. The dead stems persist, and new sprouts from underground burls add to the thickets. The clumps of stems are joined by underground runners. Each thicket may represent a large clone. Green rabbitbrush is not found in the desert peach thickets.

The second characteristic root-sprouting shrub of the fanglomerate is green ephedra (*Ephedra viridis*). Green ephedra plants may consist of a clump of stems or a single trunk 10 to 30 cm in diameter and 2 m high. Large stems have 60 to 100 growth rings, while the maximum number for big sagebrush stems in the same stand is 50.

The heaviest-grazed parts of the fanglomerate have a preponderance of senescent big sagebrush plants (Table 4). Farther up the slope, where grazing pressure is reduced by distance from stockwater, big sagebrush stands are younger and contain more of the root sprouting fire-associated species.

In stands burned less than 10 years ago, density of rabbitbrush plants is far greater than in stands not recently burned (Table 4). Increase in density of rabbitbrush must be from establishment of seedlings. Root sprouting apparently furnishes a source of achenes for seedling establishment by providing young vigorous plants, because the surrounding unburned stands contain only senescent green rabbitbrush plants that produce few achenes.

Perennial grasses increase higher on the fanglomerate slopes and away from the stockwater. There is a gradual transition from communities dominated exclusively by downy brome to ones dominated by squirreltail, downy brome, western needlegrass, and Thurbers needlegrass.

The increase in dominance of green rabbitbrush after disturbance is remarkably constant in the variety of plant communities and topoedaphic situations sampled at Medell Flat.

Stand Renewal with Herbicides

Rabbitbrush release

Spraying big sagebrush communities with 2,4-D in 1958 induced dominance by rabbitbrush (Table 4). There were 8 times more rabbitbrush plants in the area treated with herbicide than in adjacent nonsprayed stands. There are three probable reasons for this conversion: 1) rabbitbrush is more resistant to phenoxy herbicides than sagebrush (Hyder et al., 1962); 2) judging from adjacent stands, there were insufficient perennial grasses in the understory to preempt the environmental potential released by killing the sagebrush; and 3) the area was not protected from grazing to give the perennial grasses a chance to use the released potential. The understory of this area is dominated by a downy brome community (Table 2).

Failure of 2,4-D to kill the rabbitbrush does not account for a greater density of this species than in the adjacent unsprayed stands because the post-spray density is so much higher than in unburned or nonsprayed communities (Table 4). The surviving rabbitbrush plants must have responded dynamically to the released environmental potential by producing many high-quality achenes. Investigations of the reproductive phenology of green rabbitbrush at Medell Flat have shown that vigorous stands of young plants produce 20 million achenes/ha annually.[1]

Variable Control of Shrubs

Highly variable reductions in shrub density, from 0 to 100% in different parts of the sprayed area, resulted from the 1968 spraying (Table 4). In areas where green rabbitbrush and big sagebrush were killed, annuals have dominated. This is especially true of the lower and intermediate slopes that were previously moderately to heavily grazed. On the upper parts of the fans where grazing had been light, remnant stands of perennial grasses were released after the brush was killed.

Green ephedra and desert peach were not killed by 2,4-D (3.36 kg/ha) applied in 1968. Where big sagebrush and green rabbitbrush were completely controlled, there was a dramatic conversion to shrubs resistant to the phenoxy herbicide.

Dynamic Shrub-Seedling Establishment

Where a partial reduction in shrub canopy was obtained by application of 2,4-D in 1968, a dynamic response in terms of seedling establishment of brush was apparent by 1972. Very few green rabbitbrush or big sagebrush seedlings became established where either none or all of the shrub population was killed by the herbicide application (Fig. 1). A slight reduction in shrub density, however, produced a tremendous increase in seedling establishment. Shrubs left by the herbicide treatment showed vigorous vegetative growth and abundant inflorescences. Both green rabbitbrush and big sagebrush can dynamically respond to increased environmental potential. In contrast to wildfires, where big sagebrush is totally destroyed and the rabbitbrush root-sprouts, partial stand reductions with herbicides leave a source of achenes of both species. A vital consideration for management is how a more abundant stand of perennial grasses in the understory would dampen and moderate seedling establishment of the partially-controlled shrubs.

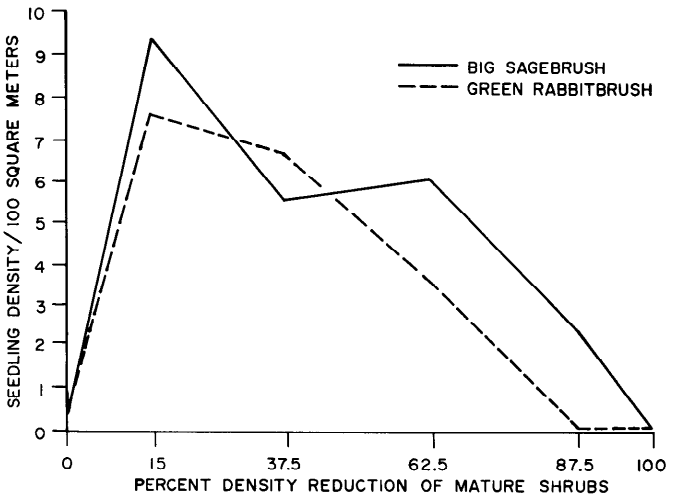

Fig. 1. *Relation between reduction of green rabbitbrush and big sagebrush densities and shrub seedling establishment.*

Spiney skeletonweed and prickly phlox increased in density by seedling establishment in areas where shrub canopy was eliminated. The increase of these native species occurred only in areas where downy brome did not increase and remnant perennial grasses were not abundant.

Complete Control of Rabbitbrush

Application of a mixture of 2,4-D and picloram eliminated all rabbitbrush and big sagebrush plants, leaving an overstory of large, widely spaced green ephedra shrubs (Table 4). The understory is a desert needlegrass (*Stipa speciosa*) community (Table 2). This area produced 670, 940, 1,150, 1,320 kg/ha of herbage in 1969 through 1972, respectively. The herbage production may seem relatively low, but this production is attained on a site with a maximum of 250 mm of precipitation and on soils without argillic horizons.

Requirements for Perennial-Grass Understory to Limit Green Rabbitbrush Dynamics

The site treated with the mixture of 2,4-D and picloram is the only successful conversion from brush to perennial-grass dominance at Medell Flat. The perennial-grass density (2.5 plants/m^2) that existed in the area before application of the herbicide should provide an indication of the minimum density required to use environmental potential released by brush removal and therefore to prevent seedling establishment of brush species. Using the 2.5 plants/m^2 density as a minimum figure, 75% of the stands we sampled at Medell Flat do not have sufficient remnant perennial grasses to warrant spraying herbicides as a stand renewal process (Fig. 2). Economic evaluation would be required to determine if the remaining 25% could be improved through the use of herbicides. The dampening by perennial grasses of large increases in density of green rabbitbrush is a key factor in the population dynamics of this species.

Discussion

Dominance of green rabbitbrush in successional communities on sites where big sagebrush stands were destroyed by fire or through the use of herbicides is contingent on root-

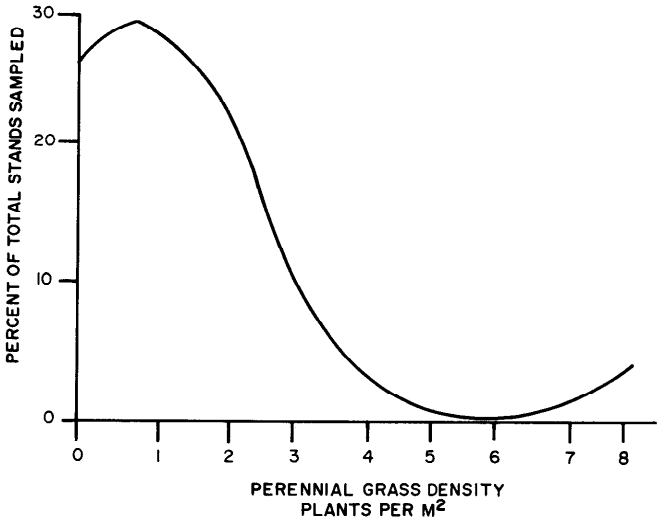

Fig. 2. *Mean density of perennial grasses of stands sampled in relation to minimum density required to occupy site.*

sprouting of green rabbitbrush plants, which provides a source of achenes and an increase in seedbed potential for seedling establishment. The major point of this investigation is that the dominant successional role of rabbitbrush is not simply a product of vegetative sprouting, but is the result of dynamic achene production and seedling establishment. A delay is required after disturbance for achene production and then a season for peak seedling establishment, as evidenced by a dominant age class in seral stands. The delay period is the time for action by land managers if a stable perennial-grass-dominated community is desired. Seedling establishment does not cease after the peak year, but most of the available environmental potential is used by plants from the initial flush of establishment.

Manipulation of these plant communities by land managers is a study of seedbed potentials. Even big sagebrush has dynamic seedling establishment following a partial reduction of stand density. This has importance to land managers who wish to reduce, but not eliminate, the density of sagebrush. In degraded communities that we investigated, partial stand reduction greatly increased seedling establishment of big sagebrush and green rabbitbrush.

An adequate perennial-grass understory is a dampening influence on extreme seedling establishment by shrubs or annual weeds. If the remnant perennial grasses are not present, the land manager must manipulate both the shrub layer and the herbaceous vegetation in terms of competition reduction and seedbed preparation. This involves vertical integration of herbicide treatments for herbaceous fallow and shrub control or the development of a single herbicide that solves both weed control problems.

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