PLANT SUCCESSION DUE TO OVERGRAZING IN THE *AGROPYRON* BUNCHGRASS PRAIRIE OF SOUTHEASTERN WASHINGTON

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Introduction

During the period when southeastern Washington was settled by white man the bunchgrass prairies, which covered large areas in this region, were used chiefly for grazing cattle. This industry had scarcely become established when it was demonstrated that the deep loessal soils characteristic of the region were excellent for growing wheat. Starting about 1880 this new type of land use began to replace the earlier, and by about 1910 all areas except those on which cultivation was either impractical or impossible had been brought into cropland. The remaining areas, the so-called "scablands," where the soil is shallow, or stony, or the surface is too frequently interrupted by such outcrops, have remained as grazing lands and probably will be used in this manner in the future. Within the last few decades the livestock industry in this region has undergone a second great change due to the replacement of the cattle by sheep over most of the range lands.

Wherever the soil of the non-agricultural land was deeper than about 1.5 dm. and was not sandy, the original bunchgrass cover was apparently identical with that of the deeper soils. As a result of long continued heavy grazing of these grasslands, the appearance and the forage value of the primeval prairie have been considerably changed. The bunchgrass, a climatic climax, has undergone a retrogression which in many cases has culminated in a biotic climax. The latter is as permanent as the present system of spring-fall sheep grazing.

An excellent opportunity of studying this vegetational retrogression exists today in northeastern Franklin County and adjacent Whitman County. Here, in different areas, exist fragments of the climatic climax in essentially virgin condition, several stages of retrogression, and in some cases the end point in this biotic succession appears to have been attained.

Climate

Precipitation records within the area of study consist of observations from 1899 to 1903 at Hooper, Washington (U. S. D. A. Wea. Bur., '36). During this period the mean annual precipitation was 31.2 cm., which includes a snowfall averaging 26.7 cm. each year. Calculations based on considerably longer records at Lacrosse and Lind, which are just outside the area studied, indicate that the average precipitation at Hooper is approximately 29 cm.

Considerably over half the annual precipitation occurs during the winter. Almost exactly half of the annual sum falls during the four months of November, December, January, and February.

At Lacrosse the average maximum temperature of the hottest month (July) is 31.5° C. with the average minimum of the coldest month (February) — 6° C. The average annual extremes of temperature are 43° C. and — 33° C.

Some evaporation figures for the summer months are available (U. S. D. A. Wea. Bur., '36) for Lind, Washington, which is situated about 43 kilometers northwest of the center of the area of study. These data make possible the calculation of the precipitation/evaporation ratios for the summer months at that station (table I), and such ratios are probably very similar to those in the region where the successional studies were made.

The growing season ends in early summer at which time the soil moisture becomes practically exhausted. During the dry mid-summer and early fall the sheep

TABLE I. *Some average precipitation and evaporation data at Lind, Washington: 1926 through 1930 (U.S.D.A. Wea. Bur., '36)*

Month	Evaporation in cm.	Precipitation in cm.	Prec./Evap. ratio
April	13.60	0.81	.059
May	19.14	1.27	.066
June	21.74	2.03	.093
July	27.75	1.02	.037
August	22.97	1.17	.051
September	13.85	2.46	.178

are taken to the mountains for grazing. In late fall when the rainy season returns, the perennial grasses and forbs and a few annuals such as *Bromus tectorum* put out new leaves and again afford green forage until the colder part of winter. In midwinter, when no other forage is available, the dead shoots of *Agropyron* are grazed, at which time they may be eaten to the ground line.

METHODS

Most studies of plant succession, including the present one, are made by analysing a group of associations which are then arranged in a sequence illustrating the investigator's concept of the stages through which the final stage has gone. Such a procedure is necessary chiefly because of the great expanse of time which would be required to observe the succession from beginning to end on the same plot. This method opens a way for fallacious conclusions, since one of the most fundamental principles of the scientific method can be so easily violated. Obviously, a study of the effects of variation of a single factor become significant only when all other factors remain constant. In any study of the grazing factor, one must have evidence that the original vegetation was essentially identical at all the stations which are analysed, and that the environment, except for the herbivores, was uniform.

All stations occurred within an area having a diameter of 32 kilometers and the elevation varied from 292 to 445 meters above sea level. These features insure a relatively uniform climate at all stations.

In every case the topography is quite level.

To demonstrate that the soils at each of the four study areas are well within the range of texture (which is one of the most important aspects of soils in this region) and depth which allow a good development of the bunchgrass association, a comparable series of wilting coefficient determinations was made at each station. The water-holding power of the soil as indicated by the wilting coefficients in table II, is in all cases well within the range which is favorable to this community in our region. Other observations by the writer have shown that this association is apparently normally developed in this region on soils as shallow as 1.5 dm., a soil depth which is well exceeded on all the areas studied.

TABLE II. *Wilting coefficients of soils as determined indirectly from the hygroscopic coefficients (W.C. = H.C./0.68)*

Decimeter horizons	Station 1	Station 2	Station 3	Station 4
1st	7.9%	8.4	7.9	8.2
2nd	9.5	8.9	8.9	9.0
3rd	8.1	10.3	9.2	8.5
4th	8.0	9.2	9.0	7.6
5th	7.0	9.7	8.3	8.5
6th	6.6	—	8.9	8.7

A check on the uniformity of the original cover is the presence of all of the dominant or characteristic plants in the immediate vicinity of all stations. Careful attention to this point indicated that the original vegetation was at least floristically comparable in all cases.

The area of bunchgrass which approximates the virgin ungrazed condition is on a spur projecting into the Palouse River Canyon. When the railroad was built parallel to the canyon, the end of this spur was severed from the remainder of the prairie by a steep-walled cut about 10 m. deep, and thus has remained absolutely free from grazing for twenty-seven years.

Other areas apparently in near-virgin condition are very similar to this stand, hence the assumption of its undisturbed nature seems to be well supported.

The abundance and stature of the *Agropyron* plants was taken to be an indicator of the relative severity of grazing. Actual records of the kinds and numbers of animals and the periods of range use would be difficult if not impossible to ascertain and to evaluate in the areas studied. The decrease of palatable plants and increase of non-palatable ones both point to the validity of my assumptions of the proper sequential arrangement of the stations.

A statistical comparison of these grazed and ungrazed areas of grassland was made by the frequency method. In each of four areas considered (figs. 1, 2, 3, and 4), a station consisting of 100 frequency plots was studied. The plots were 2 × 5

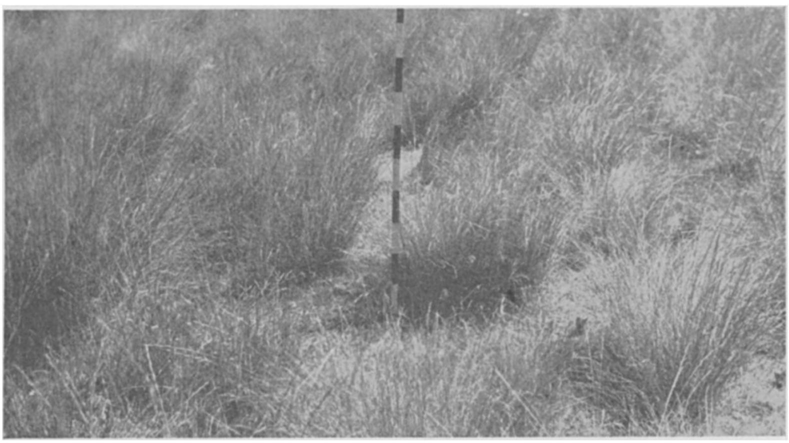

FIG. 1. Station 1. An area which was lightly grazed prior to 1911, and which is apparently typical of the association in virgin condition. The dominant *Agropyron* bunches contribute 85 per cent of the annual forage output in this community, with the smaller interstitial plants of *Bromus* and *Poa* each contributing 5 per cent. The stake is marked off into decimeter units. All four pictures were taken on May 21, 1938.

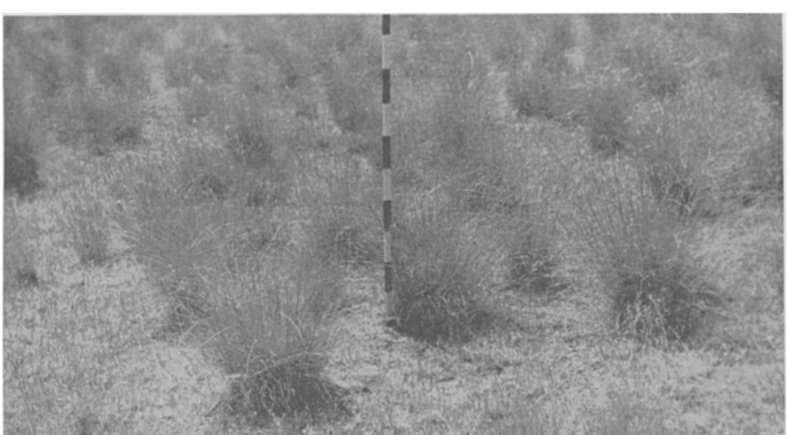

FIG. 2. Station 2. Heavy grazing has eliminated the smallest *Agropyron* bunches and reduced the size of those remaining. The ground is developing a cover of small plants, part of which are annuals and part perennials.

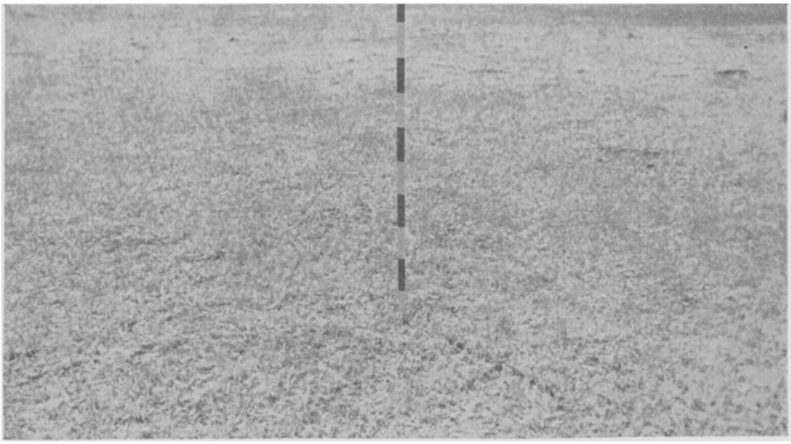

FIG. 3. Station 3. *Agropyron* bunches are eaten back to the ground line so that the short weak shoots which are put forth each year can be distinguished only with close study.

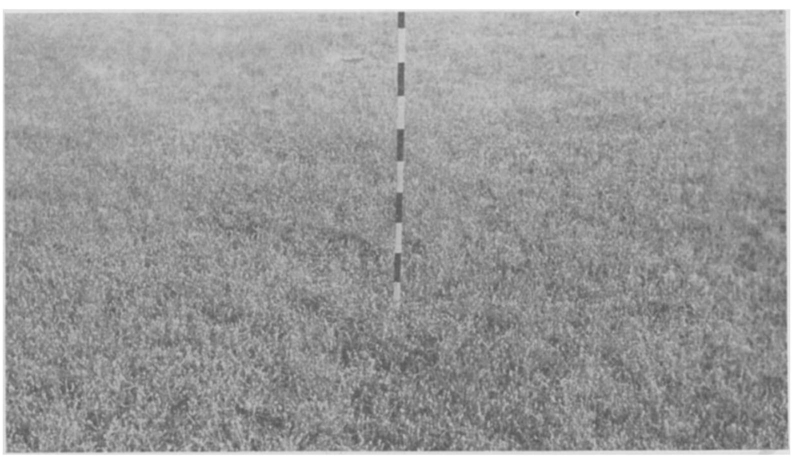

FIG. 4. Station 4. *Agropyron* is completely eliminated here, but the soil is fairly well covered with a community of small unpalatable plants which is dominated by the perennial *Poa secunda* and a group of annual dicots—apparently a biotic climax.

dm. in dimensions, and were arranged in five parallel rows one meter apart. Each plot of the 400 was studied at three critical dates (April 7 or 8, April 30 or May 1, and May 21 or 22) which were so timed on a basis of previous observations that the entire vascular flora (part of which is very ephemeral) could be studied.

RESULTS

In table III the species encountered in all 400 plots are classified into four groups. Group one includes those species which decrease in abundance as the intensity of grazing increases. This decrease in some if not most cases seems directly due to stock eating the aerial shoots. In perennials, such as *Agropyron,* the underground organs become weakened due to undernourishment caused by the repeated removal of photosynthetic tissue, and the decline in vigor of such plants is gradual until the plant succumbs. With an annual which is grazed, such as

Bromus tectorum, the first few years during which the stock feed on the plants so heavily that no seeds are matured spell a rather sudden extinction of these plants from the range. Scattered groups and individuals of *Bromus* seem to escape grazing and smut epidemic each year and these mature a few seeds which are scattered somewhat by the sheep, perpetuating the species in a very thin population.

In this same group there may be other causes for the disappearance of the plants. Some of those species which are not grazed, such as *Lithospermum,* may owe

TABLE III. *Frequency of plants as affected by grazing. Presence in the community, although not frequent enough to have been included in one of the plots, is indicated by +*

Behavior under influence of heavy grazing	Species	Per cent frequency of occurrence: Climatic climax	Early retrogr.	Late retrogr.	Biotic climax	Annual (aa) or perennial (p)
Decreasing in Frequency	*Agropyron spicatum* (Pursh) Scribn. & Smith *	70	53	22	+	p
	Bromus tectorum L.	100	3	31	2	aa
	Gayophytum ramosissimum T. & G.†	58	17	4		aa
	Agoseris heterophylla (Nutt.) Greene	16	9	9	10	p
	Achillea lanulosa Nutt.	6	3	+	+	p
	Calochortus macrocarpus Dougl.	4				p
	Lomatium macrocarpum (Nutt.) C. & R.	3	6			p
	Astragalus spaldingii Gray	2			+	p
	Erodium cicutarium (L.) L'Her.	1	+	+		aa
	Gilia gracilis Hook.	1				aa
	Lagophylla ramosissima Nut.	1				aa
	Festuca idahoensis Elmer	+	+			p
	Lomatium triternatum (Pursh) C. & R.	+	+	1		p
	Sisymbrium longipedicellatum Fourn.	1				aa
	Lithospermum ruderale Dougl.	+				p
Increasing in Frequency	*Plantago purshii* Nutt.	84	100	100	100	aa
	Plagiobothrys tenellus (Nutt.) Gray	12	2	28	100	aa
	Cryptanthe flaccida (Dougl.) Greene		53	56	100	aa
	Pectocarya penicillata (H. & A.) A. DC.				79	aa
	Lepidium densiflorum var. *elongatum* (Rydb.) Thell.				67	aa
	Lappula redowskii (Hornem.) Greene	1			32	aa
	Erigeron concinnus (H. & A.) T. & G.				30	p
	Antennaria dimorpha (Nutt.) T. & G.	+	3	2	8	p
	Agoseris glauca (Pursh) Steud.	1	+	2	6	p
	Stephanomeria paniculata Nutt.				2	aa
Apparently Characteristic of Intermediate Stages	*Lithophragma bulbifera* Rydb.	25	98	100	36	p
	Festuca pacifica Piper	63	100	70	8	aa
	Alchemilla occidentalis Nutt.		79	69		aa
	Sisymbrium altissimum L.		2	61	2	aa
	Lomatium farinosum (Hook.) C. & R.		27	2		p
	Madia exigua (Sm.) Gray	+	32			aa
	Delphinium nelsoni Greene		2	+		p
	Ranunculus glaberrimus Hook.		1	2		p
Frequency Scarcely Affected	*Poa secunda* Presl.	99	100	100	100	p
	Draba verna L.	100	100	100	100	aa
	Brodiaea douglasii Wats.	21		66	23	p
	mosses (all *Bryales*)	99	100	100	100	p

* Includes *A. inerme* (Scribn. & Smith) Ryd. which is considered by the writer as one form of *A. spicatum* (Daubenmire, '39). All have identical ecology in our region.

† This species and *Epilobium paniculatum* Nutt. cannot be distinguished by vegetative structures, and since very few of the plants flower, both species have been lumped under the name of the one which seems to be the most abundant.

their extinction to trampling. Still others may have a more remote cause for decadence, namely, the removal of protection afforded by the larger and more palatable plants. That this can be a potent factor is well shown by the great reduction in stature of *Poa* in the biotic climax (or even in the spaces between the *Agropyron* bunches in the climatic climax) as compared to specimens close up under *Agropyron* bunches. Those in the latter situation are from 50 to 100 per cent taller, apparently due to the protection from insolation and desiccating winds which the tall plants afford.

It is significant from the standpoint of range management that 90 per cent by dry weight, of the total annual output of shoots in the *Agropyron* bunchgrass association is produced by two members of this group of species (*Agropyron* 85 per cent and *Bromus* 5 per cent). The amount of this forage available in the biotic climax is negligible.

A second group contains those species which seem to be favored by grazing. These plants for the most part are not palatable (except for the basal leaves of *Lepidium* and *Agoseris* and small amounts of the young shoots of *Cryptanthe*), are not seriously injured by trampling, and their shoots can withstand exposure to the full force of drying winds and intense insolation. Apparently these species are kept out of the climatic climax by the competition afforded by the dominants of that community. This competitive influence of other plants seems more detrimental to these species than the influence of the animals.

Most of the plants in this group are small annuals, and members of the Boraginaceae are conspicuous among them. Some may be avoided because they are woolly (*Plantago*), others because they are hispid (*Lappula*) or otherwise distasteful to stock. Certain of them may escape only because their foliage appears at the same time as that of a more desirable species. In the case of *Festuca pacifica* the foliage is extremely scanty and the stems wiry. Obviously these plants make up most of the biotic climax.

A third group of species is made up of plants which appear to be immediately benefited by the removal of the competitive influence of the climatic climax dominants, but which are not very well adapted to the biotic and aerial factors which accompany the final stages of range deterioration. The conditions which favored group two also favor this group during the early stages of overgrazing, but some or all of the factors which operate against group one finally come into play so that these plants are ultimately eliminated. Most of these species are primarily seral, being practically without representation in either climax.

The fourth and last category is an assemblage of hardy unpalatable plants whose abundance seems scarcely increased or reduced by the radical changes in biotic and aerial factors which are brought about by intense grazing. All were present in the climatic climax, have persisted throughout the period of deterioration, and are important members of the biotic climax.

One plant in this last group, *Poa secunda,* deserves special mention. This bluegrass forms about 5 per cent of the total shoots (by dry weight) produced annually by the vegetation under climatic climax conditions. The forage value of this species over most of its range is rated as fair, and the average height is about 3 dm. (U. S. D. A. For. Ser., '37). As the protective influence of the larger plants in our region is removed, the stature of *Poa* decreases until the plant is considerably below this average, and the leaves become so fine and wiry that they are scarcely ever eaten by any class of livestock. Undoubtedly the nature of this plant's response to the removal of the larger and more palatable *Agropyron* is the key factor in its persistence into the biotic climax. The climate of this region, with its extremely dry summers, probably emphasizes this phenomenon.

From the foregoing it is evident that

plant succession leads from the climatic climax of *Agropyron-Poa-Bromus* to a biotic climax dominated by *Poa* and small annual dicots among which members of the Boraginaceae are conspicuous. This process is not marked into recognizable stages. Animal influence results in bare areas only where trampling is excessive, such as around a corral or bedding ground.

Since *Agropyron* and *Bromus* together form 90 per cent of the climatic climax vegetation and nearly 100 per cent of the valuable forage, any plan of range management which maintains the vegetation in a condition most nearly approximating the virgin state would be most desirable. Although no extensive study has yet been attempted to determine the most appropriate grazing system in this region, some observations by the writer are significant in this connection.

Several clipping experiments were made in eastern Franklin County. When *Agropyron* was clipped to the ground at the height of its growing season in late spring, most of the clipped plants succumbed, and the next year the few survivors produced only small tufts of foliage with no inflorescences. On the other hand, grazing the *Agropyron* bunches to the ground during the summer and fall appears to have only slight detrimental influence upon the plants. The writer has observed a fence-corner relic of this association in Whitman County, which has remained in fair condition despite the fact that livestock which are turned into the field after the wheat is harvested often graze the *Agropyron* to the ground during this period of vegetational aestivation (figs. 5 and 6). These observations indicate that a desirable grazing system would emphasize fall or winter utilization of cured shoots and minimize spring use of the range.

In another experiment, single bunches of *Agropyron* were released from the competition afforded by surrounding plants by keeping the latter clipped to the ground. The experimental plants showed no great response the subsequent season, but by the third year the increase in size and vigor was very apparent, so that it may be concluded that competition checks the stature of even the most dominant plants in the association.

Within the areas where *Agropyron* was practically eliminated by clipping, some of the annuals, chiefly *Bromus, Erodium, Lagophylla, Plagiobothrys* and *Sisymbrium longipedicellatum* showed increase

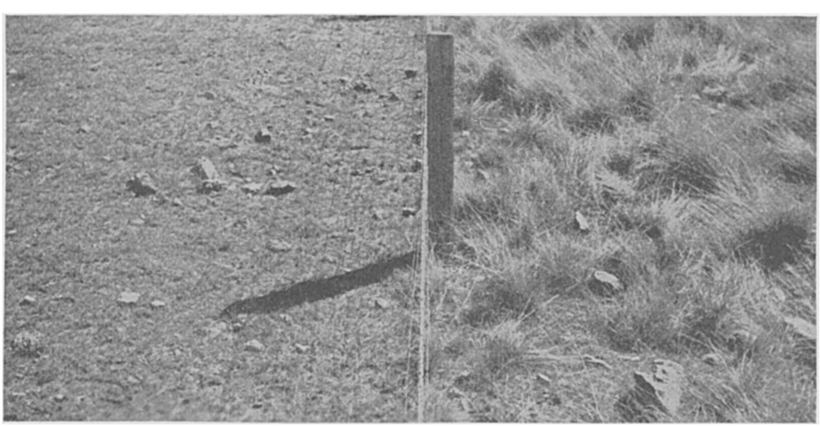

FIG. 5. Whitman County, Washington, April 7. *Agropyron* in the pasture to the left of the fence was grazed to the ground during the preceding autumn. Near-virgin prairie to the right of fence. The soil here is about a meter deep; the stones on the surface were thrown there incidental to the excavation of a deep road cut to the right of the photograph.

FIG. 6. Photograph of the same area shown in figure 5, taken on May 21 after the *Agropyron* within the pasture had attained nearly the size of the ungrazed plants to the right of the fence. The bunches outside the fence are denser and lighter in color due to the presence of old bleached shoots. *Sisymbrium altissimum* is conspicuous within the pasture.

in size the first year, and increase in numbers on subsequent years. *Lappula* has a strong tendency to invade these clipped areas.

These clipping experiments show that there is considerable competition among the dominant plants (*Agropyron* bunches) as well as between them and the subordinate annuals. When *Agropyron* is weakened or destroyed by injury during its period of active growth, the lessening of competition allows the annual flora to expand so that the ground surface remains well covered. Although valueless as forage, these plants of the biotic climax have distinct value as soil binders in as much as they are fairly efficient in retarding erosion of the topsoil.

Discussion

The above studies, together with other observations by the writer, bring out the fact that the ecologic responses of several plants in Washington are different from their responses to grazing in other parts of the western United States, as indicated by the literature. Four plants deserve special mention in this connection: *Salsola kali* L., *Bromus tectorum, Agropyron spicatum,* and *Artemisia tridentata*. Nutt.

In the recent summary of range conditions in the western United States (U. S. D. A. For. Serv., '36), some general references are made to the behavior of these plants in regions where *Agropyron spicatum* is dominant. These references seem to be based on researches in the regions to the south and east of Washington since no previous study of grazing succession in this state has appeared. It will be evident from the following discussion that in Washington, which includes only a small part of the total *Agropyron* rangeland, conditions apparently exist which are not typical for the range as a whole.

Salsola, this source states, is widely distributed in some parts of the bunchgrass range. In our particular region it is closely confined to road right-of-ways, and seems wholly incapable of invading virgin or grazed pastures in this prairie type.

Bromus tectorum, this account also remarks, "is now dominating large areas formerly occupied by bunchgrass." This is true in Washington, but the statement needs qualification here. *Bromus* does not dominate ranges which are being heavily grazed during the spring season. When, after heavy grazing, herbivore pressure is reduced, *Bromus* quickly dominates the area, the other species of the climax entering much later. Patches where the density of this plant is very high occur throughout all grazed areas in this region. These may possibly be explained by a lack of uniformity in spring grazing, coupled with the readiness with which the species will enter grazed lands. If on two or more successive years, a given area escaped grazing during the short vernal season when *Bromus* is highly palatable, this grass would undoubtedly dominate the area. These island-like patches of *Bromus* increase in abundance with distance from watering places, a fact which is in harmony with this explanation of their existence. That the *Bromus* colonies are not the simple and direct result of overgrazing is indicated by the extensive gaps between the colonies, which gaps are heavily used by the sheep.

Smut infections are not responsible for the interstitital areas because the *Bromus* islands show strong conformity with fences wherever these result in unequal grazing intensity in adjacent pastures.

There also seem to be other factors (perhaps cultivation, fire, etc.) which promote dense stands of this grass, but it is not to be considered here as a species directly favored by overgrazing, for it is highly palatable and is practically eliminated by uniformly heavy spring grazing.

Again, it is stated that in some regions the *Artemisia tridentata* association may enter and dominate an area which before grazing contained little if any of this shrub. This cannot be said for Washington, however, for the writer has seen no evidence of this phenomenon although he has looked for it for three seasons. Communities of *Artemisia tridentata* are common in the region where the present study was made, but these are to be found only on sandy soils of stream terraces and never show the slightest tendency to invade the surrounding finer-textured uplands from which most or all of the bunchgrass has been grazed.

Agropyron and *Artemisia* seem to be complementary rather than competitive in central Washington, whereas in southern Idaho the competition between the same species is keen. In parts of the latter region overgrazing tends to result in a pure stand of the shrub, while complete protection from grazing allows the grass to become at least equally as important as the shrub in the climatic climax (Craddock and Forsling, '38).

Any peculiarities which may exist in the behavior of plants in southwestern Washington may possibly be attributed to several peculiarities of the climate in this region. In contrast to regions farther south and east, the climate in this north arm of the Columbia Plateau is characterized by considerably greater cloudiness (Kincer, '22, p. 44) and less insolation (Kincer, '28, p. 33), with a consequence that the average relative humidity at 2 P.M. is higher at all seasons (Kincer, '22, p. 45).

Although the total precipitation is not significantly different between the two portions of the Plateau (Kincer, '22, p. 30), the higher moisture content of the air results in a higher precipitation/evaporation ratio for the frostless season in Washington than in southern Idaho (Livingston and Shreve, '21, p. 342).

Winter temperatures seem also to be influenced by the humid air which blankets this northern region. Judging from the number of days with the minimum temperature below freezing (Kincer, '28, p. 9), the winter temperatures are less severe in Washington than in Oregon and southern Idaho.

These climatic data indicate that sufficient differences in climate may exist to account for different ecologic responses of *Agropyron, Artemisia,* and other associated plants, in Washington and in regions farther south.

Acknowledgments

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