UNITED STATES DEPARTMENT OF AGRICULTURE

BULLETIN No. 791

Contribution from the Forest Service
HENRY S. GRAVES, Forester

Washington, D. C. PROFESSIONAL PAPER August 27, 1919

PLANT SUCCESSION IN RELATION TO RANGE MANAGEMENT

By

ARTHUR W. SAMPSON, Plant Ecologist

CONTENTS

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ARTHUR W. SAMPSON, *Plant Ecologist.*

CONTENTS.

THE PROBLEM.

The carrying capacity of a large portion of the millions of acres of western range has been materially decreased by too early grazing, overstocking, and other faulty management. Stockmen generally recognize this fact and are doing what they can to overcome these faults in management and to increase the productivity of the range. Where grazing has been subject to regulation for some years and the stock has been handled according to most approved methods the productivity of the range has been appreciably increased.

One of the most serious drawbacks in the past has been the lack of a means of recognizing overgrazing in its early stages. In deciding upon the lands especially in need of improvement, the stockmen and those regulating grazing have essentially relied upon general observations of the abundance and luxuriance of the forage supply and upon the condition of the stock grazed. The depletion of the lands is seldom recognized by these general observations until their carrying capacity has been materially reduced, or until the animals grazed are in poor condition of flesh. So long as the cover is more or less intact, there is little indication that the range is being slowly but certainly depleted; the depletion is not recognized until the more palatable and important forage species are in low vigor, and their growth and reproduction seriously impaired, or perhaps not until a large proportion of the plants actually have been killed. Until there is insufficient feed to support the animals, they will retain their condition of flesh fairly well; but long before there is insufficient feed to satisfy their appetites a large portion of the vegetation is killed. To reestablish the stand after impoverishment has reached such an advanced stage requires many seasons of most skillful management.

Enterprising stockmen and those concerned with the administration of grazing know that the live-stock industry has now reached a point where the intensity of the use of the forage crop must be governed by a finer discrimination than mere observation of the density of the plant cover and the condition of the stock. The margin between what clearly constitutes overgrazing and what is clearly undergrazing must be reduced to a minimum if the lands are to be utilized within from 10 to 20 per cent of their maximum carrying capacity and the herbage cropped on the basis of a sustained yield.

The most rational and reliable way to detect overgrazing is to recognize the replacement of one type of plant cover by another. Certain more or less temporary species almost invariably succeed the more stable weakened or killed plants on lands that are being overgrazed, hence the incoming species are the most reliable indicators of small departures from the normal carrying capacity of the range.[1] It is the object of this bulletin to point out what plants are reliable indicators of overgrazing in the various types and how they may be used as guides in revegetation and the maintenance of the forage crop.

SUCCESSION OR THE DEVELOPMENT OF VEGETATION.

In studying the laws underlying the occupation of lands by vegetation from its earliest stages to the development of the highest type of plant life which the habitat is capable of supporting, a somewhat

[1] Shantz, H. L. (Department of Agriculture Bulletin 201, 1911), Kearney, T. H., Briggs, L. F., Shantz, H. L., McLane, J. W., and Piemeisel, R. L. (Journal of Agricultural Research, 1: 365–417, 1914), and others, have shown that the character of the native vegetation affords a reliable index of the conditions favorable or unfavorable to the production of farm crops, and have incidentally established correlations between the native vegetation and the available moisture and the physical and chemical properties of the soil. Relationships between the native vegetation and the carrying capacity of range lands have been developed through the investigations here reported, application of which appears to be of far-reaching importance in the judicious management of the lands.

regular replacement of one type of plants by another is found. This phenomenon, known as succession, is explained on the basis of certain more or less distinct changes that take place simultaneously in the substratum and may be accounted for in various ways, probably the most influential and universal cause being the addition of humus.[1] The plants themselves, by adding humus to the soil through the decomposition of their tissues, and in this way changing the physical and chemical composition of the soil, prepare the way for a new and higher form of life, hence in a way work out their own destruction. Accordingly, quite different plant types are recognized on soils in different stages of formation. The characteristic types are shown graphically in figure 1.

Beginning with the bare, consolidated rock, the first vegetation consists of such inconspicuous, uneconomic forms of plant life as algæ and crustaceous lichens. These forms mark the initial or pioneer stage of development. Occasionally, amid the somewhat thickened cushion of moss growth or in the crevices of the rocks, an early-maturing annual herb will find its way. This consociation of lichen, moss, and herb is characteristic of what may be termed the "transitional" stage of development; and so far as humus, soil moisture, and wide spacing of the herbaceous plants are concerned, it is not dissimilar to desert conditions. Like annual plants of the desert, the initial herbs must be able to germinate and grow to maturity in the shortest possible period and with the use of a minimum amount of moisture.

At the advent of the first-weed stage, which, typically, is characterized by a semidecomposed soil, poor in organic matter and relatively low in available moisture content, there is a distinct predominance of shallow-rooted, early-maturing annuals. At first widely scattered, the annuals gradually become more numerous, so that finally, as more and more soil is preempted, there is a cover well-nigh completely clothing the soil surface during the period of maximum seasonal development (Pl. I). As soon as this vegetation has reached maturity, or when growth has been arrested by frost or other adverse conditions, the greater portion of the soil surface is at once exposed. It is then that the casual observer notes, possibly for the first time, that a few aggressive, drought-resistant,[2] short-lived perennial grasses and weeds have invaded the habitat. This stage of development affords a small amount of inferior forage if utilized at the proper time.

[1] This statement refers only to the evolutionary development of vegetation. The transformation from a complex to a more simple or earlier vegetational stage will be considered later.

[2] A drought-resistant plant, as here used, implies a species which is a conservative user of water and which can complete its growth cycle under conditions of low available soil moisture content and under trying atmospheric conditions.

The second-weed stage is characterized by a fairly well decomposed soil. The improved condition of the rock as a habitat for plants which results from the formation of soil is obvious. This is particularly evident when we recall that the rate of succession is largely determined by the moisture conditions of the substratum.

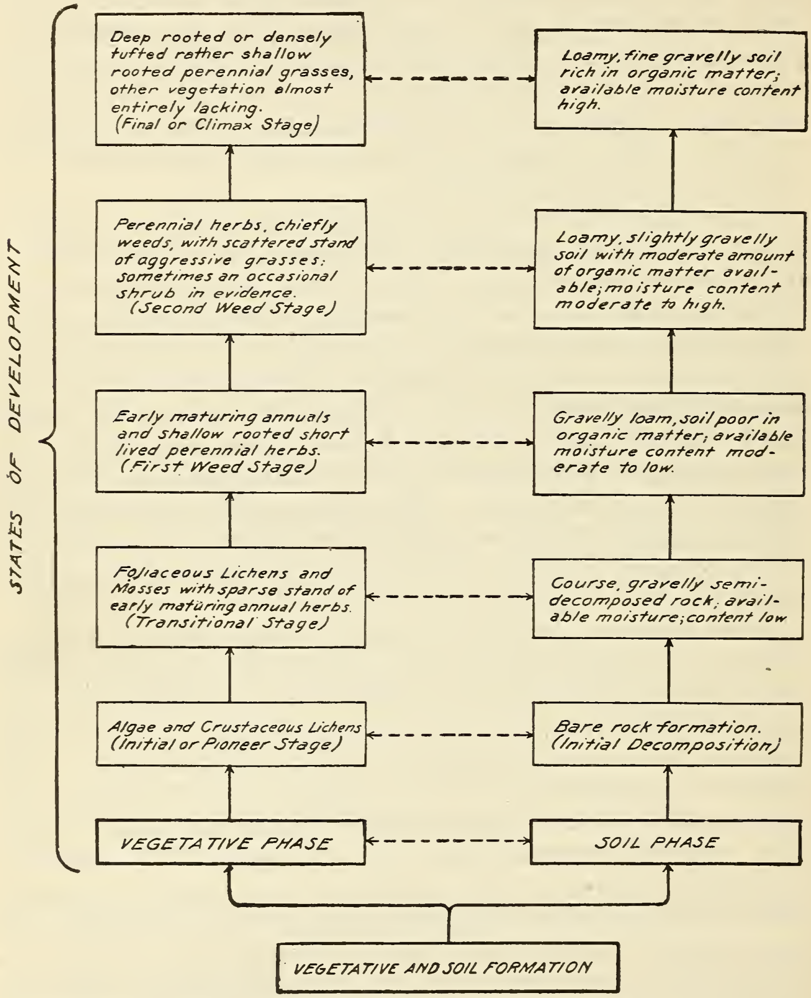

FIG. 1.—Plant succession or the development of vegetation where grass constitutes the climax or subclimax type.

The soil upon which the second-weed stage develops, being moderately well impregnated with organic matter, is fairly moist throughout the growing season. This condition permits the establishment of a stand of perennial herbs of varying density, the weedy, unpalatable species often predominating. These, in addition to an admixture of bunch grasses and often of turf-forming species as well, give character to the landscape, and the interlacing roots and rhizomes bind the soil somewhat firmly, though at this point of development the grasses are not sufficiently abundant to form a sod.

By the time the second-weed stage has had its growth and has thus prepared the way for the next set of plants the soil is sufficiently decomposed and contains sufficient organic matter and soil moisture to make possible the establishment of the climax or the subclimax grass cover.[1]

In the utilization of lands as grazing areas, the invasion by the higher type of vegetation is often prevented, especially where the species high in the development are grazed with greater relish than those lower in the succession. Thus the plants well up in the development of the type may disappear gradually or suddenly, according to the degree of disturbance caused by the adverse factor, until the plant stages lower in the development predominate. If the factor adverse to the progressive development of the vegetation continues to have its play for an indefinite period the vegetation will continue to revert until the first-weed stage reappears, or, indeed, until practically all the soil is carried away and the pioneer stage returns. Such a succession of the plant cover down the scale from the more complex to the primitive type will be referred to in this bulletin as retrogression,[2] retrogressive succession, or degeneration.

The destruction of the entire soil formation and the exposure of consolidated rock occurs only in the worst possible cases. More commonly the productivity of the soil is decreased to a point where it

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[1] Areas well within the woodland type are often occupied by a temporary cover in which grasses constitute the herbaceous climax. Within a woodland formation, however, grasses seldom if ever hold their own permanently against the invasion of timber species as they do on prairie and plain.

[2] The writer's concept and use of the term "succession" differs from that of some ecologists (e. g., Clements, F. E., "Plant Succession, an Analysis of the Development of Vegetation," Carnegie Inst. Wash. Pub. No. 242 : 161–167, 1916) in that both progressives and retrogressive succession are recognized. Coming as it does from the Latin verb "succedo," meaning literally "I go under," the word "succeed" originally had nothing to do with the superiority of one crop over another. Thus, succession is here considered in the sense to "follow," "take the place of," etc., and is applied in a vegetative invasional sense. Accordingly, if the developmental trend of an association or other plant unit is ascending toward the climax, it may be referred to as a positive or progressive succession; if descending from the climax it may be termed a negative or retrogressive succession. Regardless of whether retrogressive succession occurs in the same specific descending series as it has been recorded to occur in the ascending development toward the climax, the use of the term "retrogression" or "retrogressive succession" is a convenient and self-explanatory term, and its use in no way involves a fundamental principle.

For a further discussion of the subject of progressive succession the reader is referred to:

Cowles, Henry C., The Physiographic Ecology of Chicago and Vicinity. Botanical Gaz., vol. 31, No. 2 : 73–108, Feb., 1901.

Moss, C. E., The Fundamental Units of Vegetation. The New Phytologist, vol. 9, Nos. 1 and 2 : 36–37, Feb., 1910.

Hole, R. S., On Some Indian Forest Grasses and Their Ecology. Indian Forest Memoirs, vol. 1, No. 1 : 13–16, 1911.

Sampson, Arthur W., Succession as a Factor in Range Management. Journal of Forestry, vol. 15, No. 5 : 593–96, May, 1917.

can support only vegetation characteristic of the first-weed stage; in still more common instances it may support an admixture of annual and perennial weeds of the first and second vegetational stages.

While changes in the ground cover from a more or less permanent (subclimax) type of high forage value to an unstable or temporary one of low forage value, may be brought about in many ways, overgrazing or other faulty management is usually accountable for the retrogression in the vegetation on range lands as a whole.[1]

The grazing of live stock may either appreciably change the original palatable vegetation, for instance, transforming a pure grass cover to a mixed grass and weed consociation; or it may cause an entirely new plant cover to come in, as is almost invariably the case on denuded grazing lands. The character of the vegetation following denudation is largely determined by the topographic features and the seriousness of the depletion of the soil as a result of erosion or other adverse factors. On level areas, if they are not subject to severe wind or sheet erosion, the climax vegetation is sometimes destroyed without appreciably changing the fertility of the soil or its available water content. Where the fertility of the soil is not appreciably lowered, the higher type of vegetation reappears without the more primitive forerunners, or the intervening successional stages are short-lived and more or less intermixed with the climax species. But on the hillsides or other exposed, readily drained lands, where the upper, fertile layer of soil has been much depleted and its water-holding capacity greatly decreased, and a large proportion of the soluble salts and other plant foods carried with the water down the drainage channels, the plant cover is thrown back to shallow-rooted, early-maturing annual herbs, similar to those characteristic of the first-weed stage (fig. 1 and Pl. I).

The time required for thorough revegetation of lands where retrogressive succession has taken place is approximately in direct proportion to the degree of depletion of the soil, hence to the stage of vegetation which the soil is capable of supporting, so long as the climatic conditions, topographic features, and type of soil remain the same. On range lands the rate of progressive development, or revegetation, may be greatly expedited by cropping the herbage in such a manner as to interfere as little as possible with the life history and growth requirements peculiar to the different successional plant stages. Accordingly, the best results in promoting progressive succession are obtained where the season of grazing is determined on the basis of

[1] Factors such as the formation of a road or trail, the colonization of a prairie dog town, and the like, may greatly change or even destroy the vegetative cover, but the effect of such factors is seldom far-reaching economically as compared with faulty management of live stock.

the life history of the different species, and notably upon the time of seed maturity.

THE PLANT TYPES.

Following the general classification of the successive plant stages, both in the building up and in the deterioration of the range, an intensive study of the succession of the vegetation was carried out on overgrazed protected areas, on overgrazed unprotected areas, and on undergrazed depleted lands, the quadrat method being used.

The investigations were conducted in the vicinity of the Great Basin Experiment Station, located in that part of the Wasatch Mountains embraced by the Manti National Forest in central Utah. The area studied lies between about 9,000 and 11,000 feet in elevation in the spruce-fir type—in the subalpine (Hudsonian) zone—which includes the typical summer range. In flora and climate this region is somewhat intermediate between the extremes of the Northwest and the Southwest. Broadly considered, the species making up the predominating vegetation are similar to those conspicuous on the summer ranges included within the National Forests in northern New Mexico, Utah, western Colorado, and parts of Idaho and Nevada; and the conditions in the high mountain ranges generally are such that the principles involved will apply elsewhere.

Careful grouping of the vegetation up and down the scale of development into divisions which can be readily recognized and used in applying the principles here set forth reveals four major stages of vegetation. These stages embrace all the lands which receive their moisture directly from precipitation, but do not include the relatively small acreage of marsh lands and other similar areas.[1] The plant stages from the subclimax down to the most transitory cover are as follows:

The wheat-grass consociation (subclimax stage).
The porcupine-grass-yellow-brush consociation (mixed grass-and-weed stage).
The foxglove-sweet-sage-yarrow consociation (second or late weed stage).
The ruderal-early-weed consociation (first or early weed stage).

In order fully to appreciate the significance of the changes that take place in the development of the vegetation either toward or away from the subclimax type, as well as the significance of the component consociations in their relation to the management of the range, it is essential to know the ecological peculiarities and economic value of each.

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[1] Justification for the elimination of wet meadows and similar areas is found in the facts that such lands are limited in extent, and the forage which they produce is rather inferior, and is seldom grazed destructively.

THE WHEAT-GRASS CONSOCIATION.

The wheat grasses (*Agropyron*), broadly considered, constitute the climax herbaceous cover. In the vegetative cover as a whole, however, the wheat grasses are the subclimax type, the timber species, of course, constituting the true climax.

In its unhampered development the wheat-grass consociation occupies all well-drained timberless or sparsely timbered areas in the subalpine belt, where the soil is well decomposed and of at least average fertility. Turf-forming wheat grasses—that is, those that reproduce largely by means of rootstocks—usually occupy the drier hillsides and exposed flats; but where slightly more than average moisture prevails during the growing season, the turfed species disappear and the taller and deeper-rooted wheat grasses of the bunched habit of growth become conspicuous.

Owing to the variation in the rate of soil formation and in moisture conditions, intensity of grazing, and other factors, the wheat-grass subclimax is often patchy, and is frequently temporarily replaced by rather distinct consociations of the lower successional stages.

Like most drought-resistant grasses, the wheat grasses thrive best in full sunlight. Accordingly, they are inconspicuous or entirely lacking where the herbaceous type meets the true fir-aspen cover in the lower reaches of the subalpine zone and, of course, in the dense spruce-fir cover of the higher elevations of the subalpine type.

Turfed and bunched wheat grasses are seldom associated, owing chiefly to the difference in the character of their root systems and the difference in the distribution of the moisture content of the soils which they occupy (Pl. II). Small wheat grass (*Agropyron dasystachyum*) is the most common and typical of the turfed species. (Pl. II). Slender wheat grass (*A. tenerum*) and blue bunch wheat grass (*A. spicatum*) are the most conspicuous species of the bunched habit of growth, violet wheat grass (*Agropyron violaceum*) being next in order of abundance. Small wheat grass occurs on the drier hillsides, exposed flats, and on ridges where the soil is in a relatively high state of productivity; while slender wheat grass and blue bunch wheat grass, which are commonly associated, are largely confined to areas rather too moist for the successful development of small wheat grass, but not sufficiently moist for plants appreciably less drought-resistant than the wheat grasses. Thus, the well-drained areas subject to the full play of the high winds peculiar to the elevated summer range are characteristically occupied by turfed species; while habitats which are reasonably well protected from the wind and devoid of barriers which tend to diminish the reception of the normal rainfall are occupied by bunched wheat grasses.

A TYPICAL EARLY-WEED-STAGE COVER OF WHICH DOUGLAS KNOTWEED CONSTITUTES THE DOMINANT FORM OF VEGETATION. RELICTS OF BLUE FOXGLOVE ARE INCLUDED IN THE QUADRAT.

IN THE FOREGROUND A FULLY ESTABLISHED COVER; IN THE BACKGROUND A YOUNG SCATTERED STAND OF SMALL WHEAT GRASS (AGROPYRON DASYSTACHYUM).

The stand is so dense and the soil, below a foot or so in depth, so dry that deep-rooted species, like the bunch wheat grasses, are short-lived and often entirely lacking. Elevation 10,000 feet, Manti National Forest.

The rather strict line of demarcation in the habitat requirements of the two forms may be explained in two ways—(1) by the difference in the distribution of the available moisture of the soil and (2) by the depth to which the roots of the two grass forms extend.

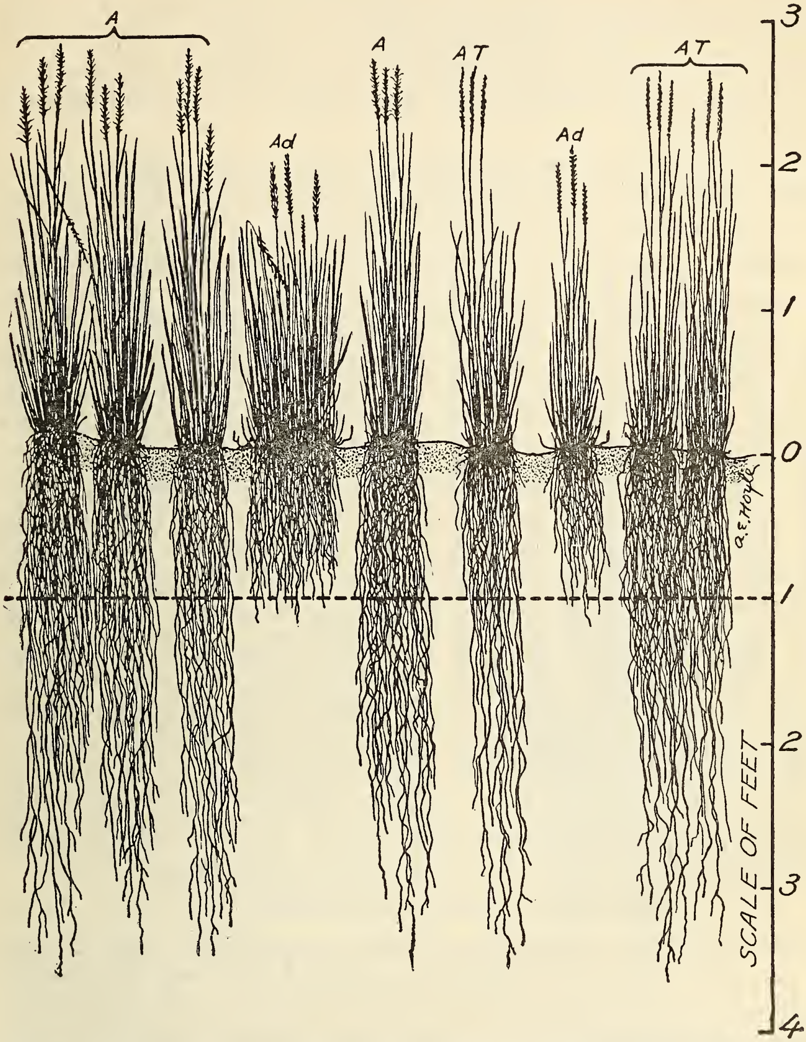


FIG. 2.—Relative height and character of root system of typical wheat grasses of the bunched and of the turfed habit of growth. *A,* Blue bunch wheat grass (*Agropyron spicatum*) : *Ad,* Small wheat grass (*Agropyron dasystachyum*) ; *AT,* Slender wheat grass (*Agropyron tenerum*).

By far the greater portion of the absorbing surface of small wheat grass is confined to the upper 8 inches of soil, the average maximum depth of individual roots not exceeding about 15 inches (fig. 2). Because of the densely matted sod on areas where small wheat grass has become well established the percolation of moisture is exceedingly slow; and, except after prolonged and heavy rainstorms, a surprisingly small proportion of the moisture passes beyond the densely matted soil stratum. Accordingly, the difficulty which other species encounter in gaining a foothold and their practical failure to compete successfully with the grass for the moisture essential to their proper development and perpetuation account chiefly for the characteristically pure stand of small wheat grass where its development is undisturbed.

The roots of the bunched species, slender wheat grass and blue bunch wheat grass (fig. 2), extend approximately 3½ times as deep into the soil as those of the small wheat grass, the average maximum depth being about 40 inches. Hence a large proportion of the root-absorbing surface of the bunch grasses is well below the average maximum depth of that of the turfed species. There is no appreciable difference in the root characteristics of the two bunch grasses under consideration. The distance between the bunches varies from a few inches to several feet, depending upon the moisture and other physical conditions. However, regardless of the distance between the bunches, provided the type is fully developed, there is relatively little difference in the character, density, and luxuriance of the other species which inhabit the intervening space, the normal stand of which is usually sparse.

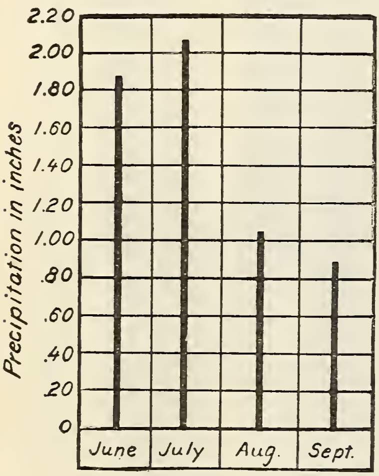


FIG. 3.—Average monthly precipitation in the wheat-grass formation during the growing season, 1914–1917, inclusive.

CONDITIONS OF GROWTH AND REPRODUCTION.

While the wheat grasses thrive under a considerable range of conditions, their optimum development is reached only where the soil is reasonably well decomposed and in a fairly high state of productivity and where sufficient moisture is available to supply vigorous plants during the first half of the growing season.

In the area under observation there is usually ample precipitation early in the spring of the year to saturate the soil (see Table 1 and fig. 3). Occasionally, however, the rainfall in June and in the first half of July is so light that the soil contains insufficient moisture for the promotion of vigorous growth.[1]

[1] Growth in the subalpine zone begins about the last week of June.

TABLE 1.—*Precipitation in the heart of the wheat-grass formation, 10,000 feet elevation, Manti National Forest, 1914–1917, inclusive.*

Year.	June.	July.	Aug.	Sept.
	Inches.	*Inches.*	*Inches.*	*Inches.*
1914	0.35	0.97	1.54	1.23
1915	2.12	1.84	.30	1.67
1916	.18	1.77	1.81	.39
1917	4.78	3.73	.50	.30
Average	1.86	2.08	1.04	.90

The average precipitation for the month as well as for the season varies widely. The greatest variation since 1914 in rainfall in June was 4.6 inches, the maximum being 4.78 inches in 1917, and the minimum 0.18 inch in 1916. In July the variation was 2.76 inches, the maximum being 3.73 inches in 1917 and the minimum 0.97 inch in 1914. Nearly 40 per cent of the 0.18 inch of precipitation recorded in June, 1916, fell during the first half of the month, while nearly 68 per cent of the 0.97 of an inch recorded in July, 1914, fell after July 20. Since only 0.35 of an inch of rain was recorded in June, 1914, the soil was far below the average in water content. Observations indicated that the unquestionable slowing down of growth noted after the first week in July, 1914, was due to an inadequate water supply.

FIG. 4.—Small wheat grass (*Agropyron dasystachyum*).

Owing to the exceptionally low water requirements for the survival of both the bunched and the turfed species of wheat grass, prolonged periods of soil desiccation, covering critical periods of one or more seasons, seem to have little effect on well-established plants other than to decrease temporarily the aerial growth and the reproduction. However, young stands of turfed species usually suffer appreciably less injury from soil desiccation than stands of bunch grass of similar age. This is accounted for by the fact that reproduction in the case of the turfed species is largely by extensive rootstocks which have little or no tendency to shoot out until the plant is permanently established and in vigorous condition (fig. 4). True bunch grasses, on the other hand, reproduce entirely from seed, two to three years being required to establish fully a seedling plant. Thus, while a shoot originating from the rootstock of a turf-forming species is largely nourished through the medium of the deep-rooted parent plant, the establishment of a bunch-grass seedling is dependent upon its own development for moisture and nutriment. Accordingly, turfed wheat grasses gain dominion over the soil in the drier situations where their rate of occupation may from time to time be more or less seriously interrupted through drought, but where the well-established plants are seldom killed. In such habitats the bunch grasses are usually killed out in the seedling stage, or the established plants, in competition for water, are crowded out by the shallow-rooted turfed species. On the other hand, habitats which receive considerable precipitation and are characterized by soils which permit of ready percolation of water are capable of supporting the deep-rooted plants. Such habitats are seldom if ever congenial to the domination, or indeed the conspicuous presence, of the turfed wheat grasses.

SOIL WATER CONTENT.

A comparison of the soil moisture conditions on a typical turfed (small wheat grass) area and on a typical bunch grass (blue bunch wheat grass) area in close proximity to each other may be made by observing the graphs in figure 5.

Section A of the graph, representing the moisture conditions of the soil supporting a typical stand of small wheat grass during the growing season of 1915, shows a rather sharp decline in the moisture content in the three soil strata studied (0–6, 6–12, and 12–24 inch depths) from July 1, which marks the beginning of vigorous spring growth, to September 20, the end of the growing period. On July 1 the highest per cent of moisture was recorded in the 0–6 inch layer of soil, 11.8 per cent of the water content being available for the use of the plant. In the 6–12 inch layer of soil for the same period there was approximately 1 per cent less moisture than in the upper layer, while in the 12–24 inch depth there was 4 per cent less. During the second period, however, there was a sharp decline in the moisture of the surface layer, and during the third period a rather striking increase. In the 6–12 and 12–24 inch depths for the same periods the decline was gradual, which is typical of all subsequent periods at the two lower depths.

The most significant facts brought out in section A, however, are (1) the rather striking fluctuations in the water content in the 0–6 inch layer, and (2) the fact that the water content in the 0–6 inch depth of soil is reduced to a point at which it becomes unavailable

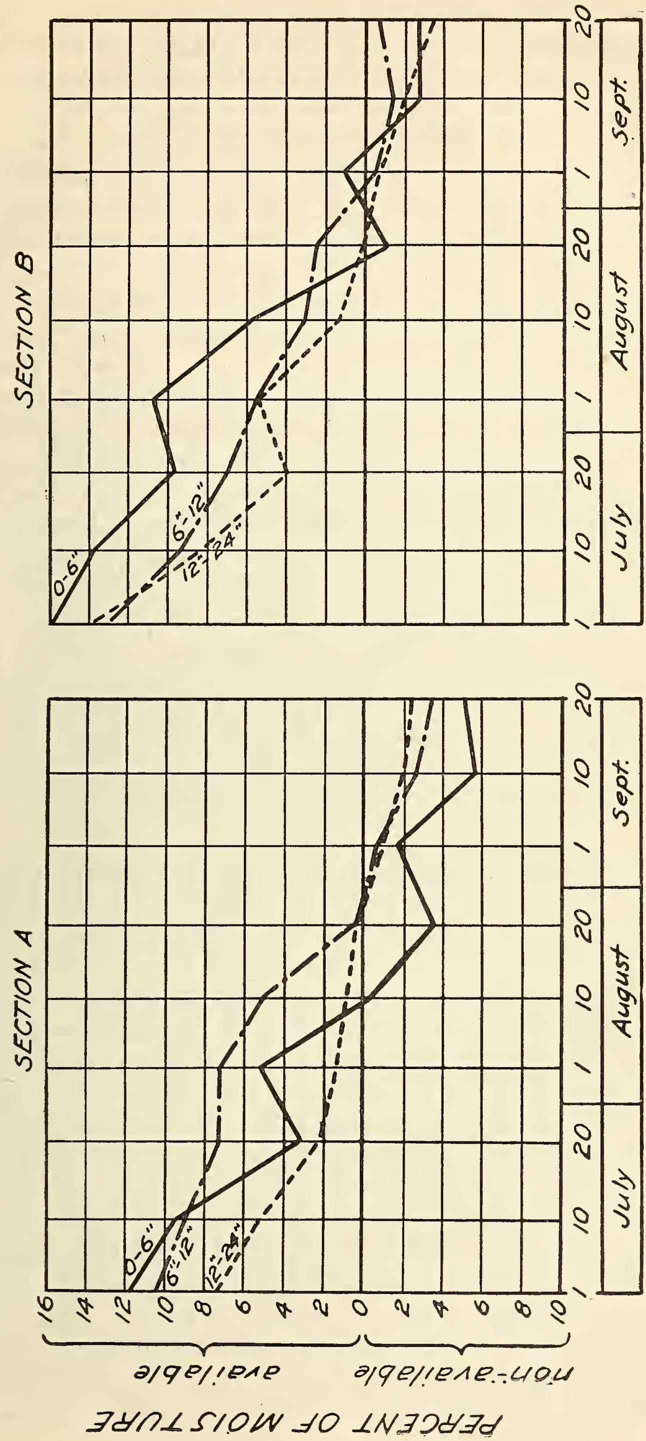


FIG. 5.—(*A*) Average available and nonavailable soil moisture on a typical area fully occupied by small wheat grass (*Agropyron dasystachyum*), 1915. (*B*) Average available and nonavailable moisture on area occupied by a normal stand of blue bunch wheat grass (*Agropyron spicatum*), 1915.

to the plant 10 days earlier than in the two lower depths. During the driest period of the season, usually beginning about August 10 in the 0–6 inch depth, and about August 20 in the deeper layers, the main root system often occupies soil whose moisture content is well below that at which vegetation can absorb moisture. The fluctuations in the water content observed to occur in the superficial soil layer and the practical absence of such fluctuations in the deeper layers, notably the 12–24 inch depth, are chiefly accounted for by the fact that the supply of moisture in the upper stratum, in which the greater portion of the feeding roots are located, is used up by the vegetation at a relatively rapid rate. Since the upper soil layer is especially rich in organic matter, hence is capable of absorbing a very high percentage of water (45–65 per cent) as it percolates through the matlike layer, the rapid desiccation of the superficial soil is all the more significant. Thus it will be seen that the reduction in the water content in the superficial layer to a point below the amount necessary to make it available to the use of the plant was reached as early as August 10, so that any water absorbed by the plant later in the season had to be obtained at a depth greater than 6 inches. The two lower depths of soil, it will be noted, likewise became desiccated after August 20. Therefore at the end of the growing season the 0–6 inch layer of soil was 5 per cent below the point of available moisture, while the 6–12 and 12–24 inch layers were 3.3 and 2.1 per cent below, respectively. In general the growth and seed production are completed in the case of small wheat grass by August 15, when the herbage dries up and remains dormant until the spring.

Section B of figure 5 represents the moisture conditions on a blue bunch grass area during the growing season 1915, the soil samples from which the data were obtained being taken simultaneously with those represented in section A. Comparing first the general position of the respective curves, it will be seen that the water content was greater on the blue bunch grass area than on the turfed wheat grass area in each period, with the exception of September 10 to 20 in the 12–24 inch depth, prior to which growth had been arrested. In contrast with the condition on the turfed area, the moisture content in the 0–6 inch layer on the bunch grass type was appreciably in excess of that at greater depths during the first four periods. In the fifth period the moisture content decreased rapidly in the upper soil layer and dropped below that recorded at the two lower depths; but in the sixth period, as the result of a fairly heavy rainstorm, the moisture content again exceeded that in the lower soil layers. Thus, instead of the 6–12 inch soil depth containing the highest percentage of moisture during the most active period of growth, as in the turfed wheat grass type, the 0–6 inch layer contained the maximum amount.

As in the case of the turfed area, the moisture content on the bunch-grass area became unavailable, except for a few days in the superficial layer between August 20 and September 1.

THE EFFECT OF DISTURBING FACTORS.

The opening up by excessive grazing or otherwise of a well-established stand of small wheat grass, as well as of congeneric turfed species, is congenial to the immediate establishment of a rather scattered growth of other plants, both deep-rooted and shallow-rooted, provided, of course, that seed is available and growth is not seriously hampered. Where the fertility of the soil is not appreciably changed as a result of the destruction of the wheat-grass turf, several shallow-rooted species and a few aggressive deep-rooted plants soon make their appearance. Obviously, the shallow-rooted species, as a result of both aerial and subterranean competition, sooner or later yield to the invasion of the more permanent and luxuriant deep-rooted plants.

Among the deeper-rooted perennials which gain a foothold early in the destruction of the matlike growth of wheat grasses where the fertility of the soil is not appreciably decreased, yellow brush (*Chrysothamnus lanceolatus*) is the most characteristic. Of the perennial grasses, small mountain porcupine grass (*Stipa minor*) is the most characteristic. These two plants are among the first of the deep-rooted perennials to signify the waning of the wheat-grass cover. Where the wheat-grass type is relatively young it often supports an occasional plant of yellow brush which may struggle along for several years in competition for water with the superficial roots of the wheat grass.[1] In due time the yellow brush, approximately 90 per cent of whose root-absorbing surface is below that of the wheat grass, gives away; but when the stand is opened up any remaining straggling yellow-brush specimens quickly regain their luxuriance of growth. (Fig. 6.)

Section A of figure 6 portrays a relatively young stand of small wheat grass where yellow brush was conspicuous prior to the establishment of the wheat grass subclimax. Section B shows the incoming of small wheat grass from seed and the unhampered growth of yellow brush. Should the wheat-grass subclimax (section A) again be destroyed, or the stand sufficiently opened up to favor the percolation of a considerable portion of the rainfall to a depth corresponding to the location of the main feeding roots of the yellow brush, the surviving specimens of the latter would immediately show a remarkable response in growth. An increasing abundance of yel-

[1] While yellow brush is persistent in competition with other species, it is not believed to be a very long-lived species. Numerous stem examinations have shown that it seldom attains an age of much more than 10 years. A single specimen with 12 annual rings was found.

low brush, as well as of other plants, especially deep-rooted species, indicates, therefore, a retrogressive succession in the wheat-grass type.

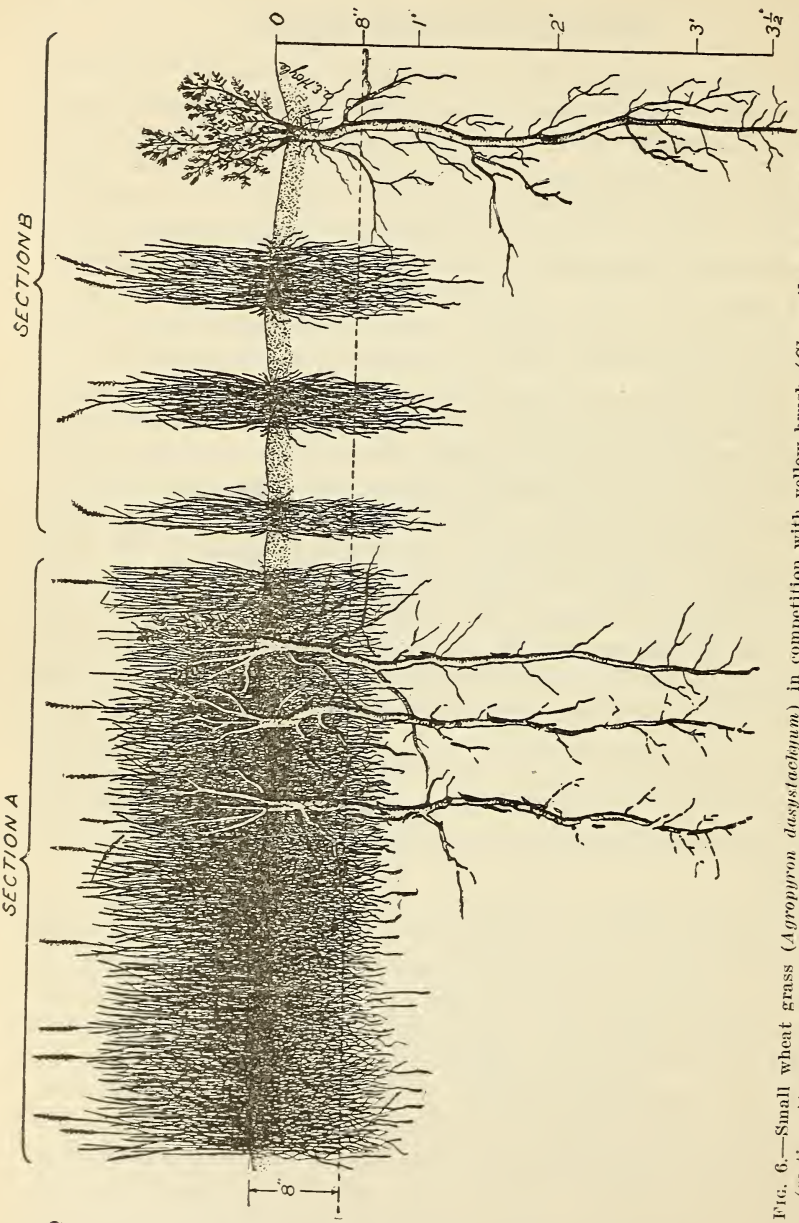


FIG. 6.—Small wheat grass (*Agropyron dasystachyum*) in competition with yellow brush (*Chrysothamnus lanceolatus*), showing (section A) area where yellow brush occupied the soil when grass sod was opened up as a result of overgrazing and where the wheat grass subclimax was subsequently reestablished the yellow brush killed or merely straggling along; (section B) where (1) yellow brush is growing luxuriantly without competition with other plants, and (2) where a greater depth of the root development occurs in the case of specimens of wheat grass as compared with the sodded stand.

Section B of figure 6, in addition to showing that the roots of a healthy specimen of yellow brush may feed at a depth in excess of 3½ feet, emphasizes the interesting fact that small wheat grass develops a somewhat deeper root system when the specimens are isolated than when the plants grow in a well-established sod. This increased development is doubtless accounted for by the fact that the water content of the soil immediately below the deeper roots of the isolated bunched wheat grasses is appreciably higher than in the soil below the deeper roots of the sodded stand. Since all stands of small wheat grass become matted when permitted to develop normally in well-disintegrated soils, it is evident that the increased development in depth of the roots of isolated specimens, as compared with that of the turfed plants, is purely temporary, and probably of little or no economic significance.[1]

In contrast with the turfed wheat-grass type, the conditions that obtain in a normal, fully developed bunch wheat-grass type are such as to permit the presence of other plants of both deep-rooted and shallow-rooted species (fig. 7). The shallow-rooted species, such as mountain squirrel tail (*Hordeum nodosum*), single-flowered helianthella (*Helianthella uniflora*), and others, feed chiefly in the upper foot of soil, but the density of the cover as a whole is never such as to prevent a comparatively rapid percolation of water to a depth of several feet. In general, a large part of the rainfall is absorbed on lands where bunch wheat grass is fully developed, so that serious erosion seldom occurs so long as the natural cover remains unimpaired. Because of the high power of absorption of the soil and the relatively high percentage of available moisture in the lower soil depths, a few deep-rooted species, like wild bean or alpine lupine (*Lupinus alpestris*), yellow brush, and the like, as well as certain surface-feeding plants, like single-flowered helianthella (*Helianthella uniflora*), mountain squirrel tail (*Hordeum nodosum*), and blue foxglove (*Pentstemon procerus*), occupy the space between the grass bunches where the spacing is fairly wide and the intervening soil not fully occupied by grass roots. Therefore, where the bunch wheat grass stand is opened up by grazing or by other adverse factors, a good balance both of deep and of shallow rooted species, chiefly other than grasses, follows, one set of species predominating at one time and another set at another time. Accordingly, a reasonable state of equilibrium in the vegetation occupying the space between the bunch-grass tufts exists only when the maximum density of the bunch-grass stand has been reached and has become stabilized. This stabilization of the rather transitory type of vegetation may be accounted for by the comparative equality in the utilization of the available water content of the soil by the wheat grasses.

[1] Cannon, W. A. (Plant World, vol. 16, No. 12: 323–241, 1913), found that the root development of desert plants varies widely in soils of different texture and depth. These variations were observed to hold regardless of whether the plant was grown under natural conditions, in garden soils, or in artificial cultures.

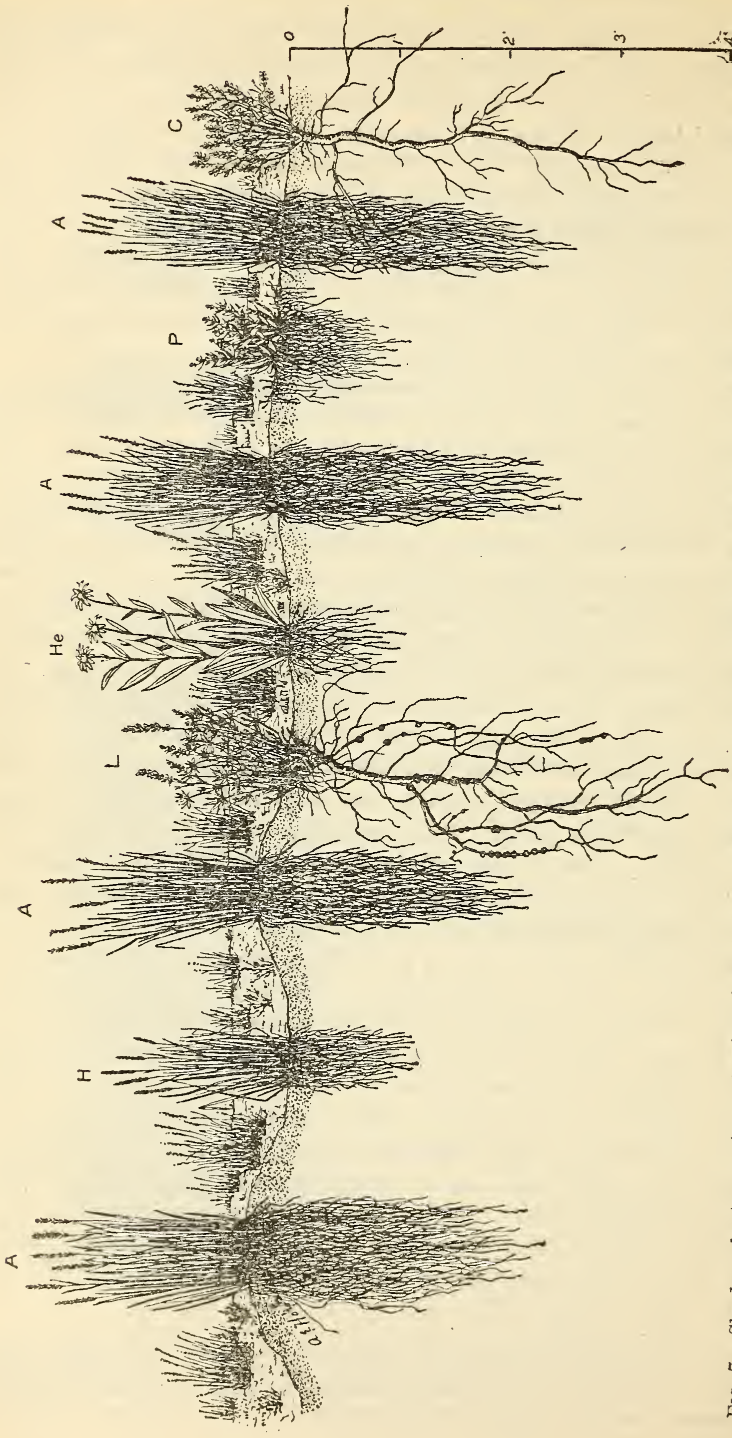


FIG. 7.—Slender wheat-grass type, showing characteristic association of deep and shallow rooted vegetation where the grass stand has been somewhat thinned out as a result of heavy grazing. *A*, Slender wheat grass (*Agropyron tenerum*); *C*, yellow brush (*Chrysothamnus lanceolatus*); *H*, mountain squirrel tail (*Hordeum nodosum*); *He*, single-flowered helianthella (*Helianthella uniflora*); *L*, wild bean (*Lupinus alpestris*); *P*, blue foxglove (*Pentstemon procerus*).

PALATABILITY.

The wheat grasses of the high mountain range afford a large amount of first-class forage for all classes of stock. However, the herbage of the wheat grasses as a whole, especially after the plants have reached maturity, is of only average palatability compared with the finer-leaved genera of grasses, such as the blue grasses (*Poa*) and fescues (*Festuca*) of a lower successional stage. When green and succulent the leafage is cropped rather closely by cattle, sheep, and horses; but as the plants reach full growth the leafage of some of the species becomes somewhat harsh. At that stage cattle and horses devour the herbage less closely than when the plants are young, leaving the rather coarse seed stalks practically untouched. Sheep, on the other hand, crop only a relatively small proportion of the herbage of the maturing or matured plant, but in general eagerly consume the seed heads of the awnless or slightly awned species.

Like the majority of the congeneric species, small wheat grass when green and tender is eaten closely by all classes of stock. As the plant approaches maturity, however, the leafage becomes rough on the upper side, and only cattle and horses graze upon it to an appreciable extent. The palatability of the wheat grasses throughout the season being taken into account, small wheat grass affords the least feed of any under discussion in proportion to the amount of dry matter produced.

Of the bunch wheat grasses, slender wheat grass and violet wheat grass compare favorably as to palatability, both being grazed closely by all classes of stock. Blue bunch wheat grass is only slightly less palatable. All of these species are grazed with unusual eagerness by cattle, sheep, and horses early in the season. Toward the approach of maturity the herbage, especially of blue bunch wheat grass, is consumed much less closely than early in the summer, and the seed stalks of all species are left practically untouched. With the exception of blue bunch wheat grass, the spike of which is conspicuously awned, the seed heads are grazed with avidity and with good results to stock.

FORAGE PRODUCTION.

The largest amount of dry matter, exclusive of the unpalatable flower stalks, is produced by the small wheat-grass type. This type, when permitted to develop normally, usually occupies the entire soil surface. Owing to its relatively low palatability after about August 10, however, small wheat grass affords no more forage, season for season, than good stands of the bunched wheat grasses. Also on account of the lack of forage variety due to the practical exclusion of other plants, the small wheat-grass areas are not so well adapted to the grazing of sheep as are the bunch wheat-grass areas.

Of the bunch wheat grasses, slender wheat grass and blue bunch wheat grass are about equal in the amount of dry matter produced per unit of area, while violet wheat grass, occurring as it usually does in rather scattered stands, seldom produces as much forage as the other two species. Owing to the slightly higher palatability of slender wheat grass as compared with blue bunch wheat grass, the former supports slightly more stock per acre than the latter.

The bunch wheat-grass areas, because of the class of plants which they support, are better suited to the grazing of sheep than are the turfed wheat-grass areas. The latter, on the other hand, are especially well adapted to the grazing of cattle and horses; for to make good gain these animals require less variety than sheep, and they consume, proportionately, a smaller amount of weeds than sheep.

In general the most efficient range for cattle and horses is one upon which the palatable subclimax grass species have been preserved. In the case of sheep the range which will afford the largest percentage of first-class feed and at the same time prove the most efficient from the standpoint of pounds of gain for the season is one upon which the grass stand has been sufficiently opened up to permit of a good admixture of grass, weeds, and even browse. The fact that sheep prefer a greater forage variety than is found on ranges where wheat grasses predominate does not imply that the climax grass type should be grazed destructively with a view of fostering the establishment of a large variety of more or less transitory weed species. As a rule by far the biggest returns will be obtained from the lands by grazing the class of stock upon them which will most fully utilize the forage crop. Sooner or later the original stand of palatable plants may give way to other species, a condition which may fully justify the grazing of both cattle and sheep.

SUMMARY OF THE WHEAT-GRASS CONSOCIATION.

Wheat grasses constitute the potential subclimax type in the high mountain summer range of the Wasatch Mountains. That is to say, lands occupied by a maximum cover of wheat grass support the highest and most stable type that the soil is capable of supporting. Accordingly, this type, when in a maximum state of productivity, affords most reliable evidence of the fact that the range has not been overgrazed, at least within a reasonable length of time.

The wheat-grass type is composed of two general growth forms; namely, turf-forming and bunch-forming species. The turfed type is characterized by roots which feed in the upper few inches of soil, which tends to bind the soil firmly. The bunch type is characterized by deeply penetrating roots, and since the space between the bunches varies from a few inches to several feet, the stand is rather open.

Owing to the small amount of precipitation that penetrates beyond the shallow matlike surface of the turfed wheat-grass type, bunch wheat grasses and other deep-rooted species are seldom associated with a fully established stand of the sodded wheat-grass cover. The bunch wheat-grass type, on the other hand, supports a considerable variety of weeds and other plants, both of deep and of shallow rooted characteristics.

Regardless of the growth form of the wheat-grass cover, yellow brush (*Chrysothamnus lanceolatus*) is the most characteristic forerunner of other aggressive perennial plants which gain a foothold as the wheat grasses are killed out by overgrazing or other adverse factors. Small mountain porcupine grass is commonly associated with the yellow brush. As the turfed wheat grass is reestablished, yellow brush and porcupine grass are entirely replaced. In the revegetation of the bunch wheat-grass cover, both yellow brush and porcupine grass are rather persistent, as the moisture conditions remain comparatively favorable to the invading species until the original grass cover is fully reestablished. Eventually, however, most of the yellow brush and porcupine grass plants are crowded out. Thus the invasion and conspicuous establishment of yellow brush and porcupine grass on the wheat-grass type generally indicate clearly that one or more unfavorable factors are at play, which, if permitted to continue, may result in the destruction of the wheat-grass type. On the other hand, the waning of the indicator plants, due to competition with the wheat grass, affords reliable evidence of the reestablishment of the wheat-grass type.

There is relatively little difference in the number of cattle and horses that the turfed and the bunched wheat-grass areas are capable of supporting in good condition. Sheep, on the other hand, make better returns on typical bunch wheat-grass lands than on the turfed areas because of the greater variety of forage which the bunch-grass type usually supports. In spite of this fact, however, no attempt should be made to overgraze either grass cover with the idea of improving the lands for the grazing of sheep. To do so will seriously decrease the forage production of the lands for the grazing of cattle and horses. After a few years of full utilization of the wheat-grass consociation by cattle and horses a large variety of plants usually appears. This natural replacement of the palatable grasses by plants successionally lower in the scale of development will improve the lands for the grazing of sheep and thus bring about a condition which will justify cropping by all classes of stock in proper proportions. Where common use of a wheat-grass range is resorted to, after the cover has partly reverted to the weed stage, the cattle grazed should be reduced in number to the point where the remaining vegetation palatable to this class of stock will be safe from further destruction.

If this is not done, the retrogression of the vegetation to a pure second-weed stage, or, indeed, to the first-weed stage, is inevitable.

THE PORCUPINE-GRASS-YELLOW-BRUSH CONSOCIATION.

As a result of the serious overgrazing in the Wasatch Mountains prior to the inclusion of the lands in the Wasatch Forest in 1905, the wheat-grass consociation was much injured in many localities. Where the fertility of the soil was not appreciably impaired after the destruction of the subclimax grass cover, the wheat grasses soon reestablish themselves; but where appreciable erosion took place or where a considerable proportion of the soluble soil nutrients was leached out, the wheat-grass species failed to reoccupy the lands. On the seriously impoverished soils, only a sparse stand of short-lived plants at first gained a foothold; but on areas where the fertility and the water-holding capacity of the soil were only slightly impaired, grasses, notably small mountain porcupine grass (*Stipa minor*) (fig. 8), and its ever-present associate, yellow brush (*Chrysothamnus lanceolatus*), predominated. Where the soil was more seriously depleted, blue grasses, fescues, brome grasses, and others were invariably associated with porcupine grass and yellow brush.

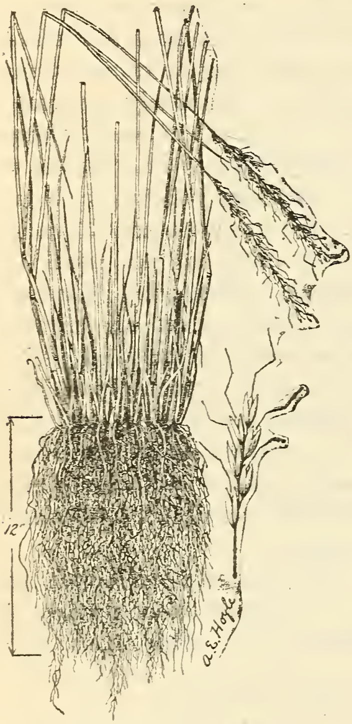


FIG. 8.—The dominant species of the porcupine-grass-yellow-brush consociation.

After the destruction of the wheat-grass consociation by overgrazing, a large proportion of the entire cover was then either of the early or late weed stage; but as a result of correcting the destructive factor of overstocking, the porcupine-grass-yellow-brush type now constitutes the most extensive consociation of relatively high-carrying capacity in the high mountain region.

Small mountain porcupine grass and the local congeneric species grow as bunch grass, and the intervening space is occupied by other grasses and nongrasslike plants. Where the soil has undergone only slight change physically and chemically as compared with its condition when occupied by the wheat-grass cover, the stand of small mountain porcupine grass and yellow brush is full, and the stand of secondary species is relatively sparse. On the other hand, when the soil has been more seriously depleted, these two species merely occupy the chief place, many other species, especially grasses, being associated with them (fig. 9). Much of the acreage which had become so badly depleted in 1905 as to support only a scattered stand of the most drought-resistant and short-lived vegetation, has now been revegetated to the point of supporting a good, and in some instances a maximum, cover of porcupine grass and yellow brush, with the scattered admixture of other species, especially grasses high in the cycle of development. On areas where the vegetation has for one reason or another met with reversals from time to time, porcupine grass and yellow brush are much less conspicuous, though they constitute the predominating species. At this stage in the revegetation only the grasses that are characteristic of early successions are associated with the porcupine grass and yellow brush.

In general, the secondary species of the porcupine-grass-yellow-brush consociation are numerous and of much importance economically.[1] Among the more common grasses may be mentioned Nevada blue grass (*Poa nevadensis*), Malpais blue grass (*P. scabrella*), little blue grass (*P. sandbergii*), spiked fescue (*Festuca confinis*), western fescue (*F. occidentalis*), mountain June grass (*Koeleria cristata*), spiked trisetum (*Trisetum spicatum*), mountain brome grass (*Bromus marginatus*), Porter's brome grass (*B. porteri*), and frequently a scattered stand of wheat grasses, of which Scribner's wheat grass (*Agropyron scribneri*) is somewhat conspicuous. Typical examples of the more important grasses are shown in figure 10. Among the more common herbs other than grasses (aside from the ever-present yellow brush) are yarrow (*Achillea lanulosa*), sweet sage (*Artemisia discolor*), several species of loco, notably *Astragalus decumbens* and *A. tenellus*, single-flowered helianthella (*Helianthella uniflora*) geum (*Geum oregonense*), wild bean (*Lupinus alpestris*), and blue foxglove (*Pentstemon procerus*). Upon closer view one normally finds a very scattered stand of James' chickweed (*Alsine jamesiana*), scarlet gilia (*Gilia pulchella*), gymnolomia (*Gymnolomia multiflora*), pingue or rubberweed (*Hymenoxys floribunda*), and others. In addition there are a number of inconspicuous annuals.

These numerous secondary species (fig. 9) vary widely as to the distribution of their chief feeding roots. All the more important grasses, with the exception of the brome grasses, obtain their moisture supply from practically the same soil stratum as does porcupine grass. The brome grasses, the locos, and wild bean, on the other hand, extend their roots to approximately the same depth as yellow brush. Accordingly, single-flowered helianthella, geum gymnolomia,

[1] See also Pound, Roscoe, and Clements, Frederic F., The Phytography of Nebraska, 381–383, 1900.

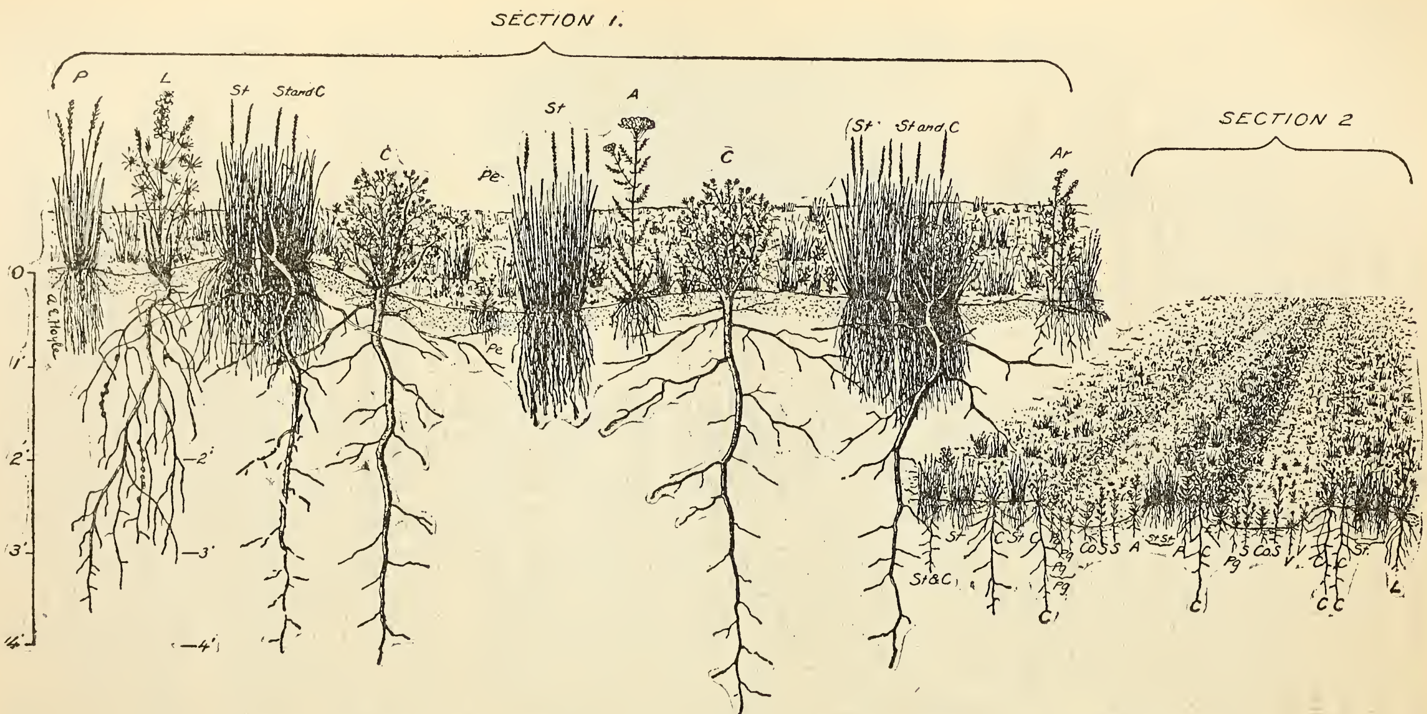
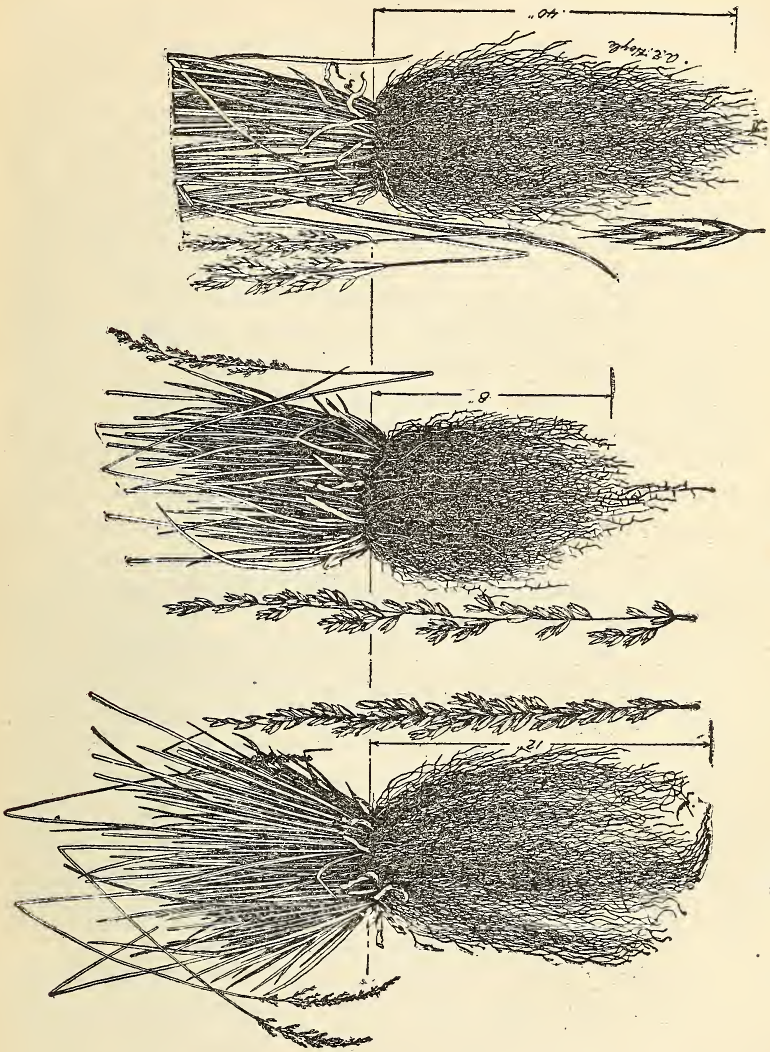


FIG. 9.—Porcupine-grass-yellow-brush consociation—showing (section 1) character of root systems of the dominant species and of the species characteristically associated with porcupine grass and yellow brush, and (section 2) the character of the vegetation on old road through a stand of porcupine grass and yellow brush abandoned for five years (1913–1917). *A*, Yarrow (*Achillea lanulosa*); *Ar*, sweet sage (*Artemisia discolor*); *C*, yellow brush (*Chrysothamnus lanceolatus*); *Co*, slender-leaved collomia (*Collomia linearis*); *E*, erigeron (*Erigeron macranthus*); *L*, wild bean *Lupinus alpestris*); *P*, Nevada blue grass (*Poa nevadensis*); *Pe*, blue foxglove (*Pentstemon procerus*); *Pg*, knotweed (*Polygonum aviculare*); *S*, tansy mustard (*Sophia incisa*); *St*, small mountain porcupine grass (*Stipa minor*); *V*, tongue-leaved violet (*Viola linguaefolia*).

and rubberweed may be classed as intermediate in the elongation of their roots between small mountain porcupine grass on the one hand and yellow brush on the other. Yarrow, sweet sage, and blue foxglove, James' chickweed, scarlet gilia, and the annuals, being less deeply rooted than small mountain porcupine grass, may be classed



Sec. A. Nevada blue grass (*Poa nevadensis*).

Sec. B. Malpias blue grass (*Poa scabrella*).

Sec. C. Mountain brome grass (*Bromus marginatus*).

FIG. 10.—Characteristic grasses of the porcupine-grass-yellow-brush consociation.

as superficial feeders. This wide variation in the extension of the roots is accounted for, of course, by the uniformity in the distribution of the water in the soil from the surface to the extreme depth to which the roots extend. The roots of the numerous species constituting this consociation are so evenly distributed through the soil from the surface to a depth of 3 feet or more that the substratum usually becomes desiccated from a few inches below the surface to the average depth of the longest roots at approximately the same time in the season.

CONDITIONS OF GROWTH AND REPRODUCTION.

Porcupine grass feeds in approximately the same soil stratum (fig. 9) as turfed wheat grass, the average maximum depth of the roots being about one-third that of the bunched wheat grass. Yellow brush, on the other hand, extends its roots to about the same depth as the bunched wheat grasses. Porcupine grass and yellow brush therefore enter into serious competition for water only where the porcupine-grass tufts occur so densely as to prevent ready percolation of water to the lower depth of soil, a condition which occurs somewhat commonly only on the older and fully stocked areas. Generally, the porcupine-grass-yellow-brush consociation is more open, at least below ground, than the bunched wheat-grass lands (compare figs. 7 and 9); hence it is characterized by a more rapid percolation of water through the soil than occurs in the bunched wheat-grass cover. For this reason there is less variation in the distribution of the water from the surface downward on a porcupine-grass-yellow-brush area than on an area supporting a normal stand of bunched wheat grass. The depth to which the precipitation penetrates on the sodded wheat-grass area is extremely shallow as compared with the depth of penetration on a bunched wheat-grass area or on a porcupine-grass-yellow-brush area. Therefore, it is clear that so far as the available soil water supply is concerned, conditions are far more favorable for the establishment of species of variable length and character of root system on the porcupine-grass-yellow-brush type than on the turfed wheat-grass areas. Likewise, owing to the more open stand and the shallow feeding roots of porcupine grass, the soil water content, between 1 and 4 feet in depth, is available to a greater variety of plants other than grasses on this consociation than on a fully developed area of bunched wheat grass, the moisture supply for which must be obtained from the same soil depth as for the support of other deep-rooted plants.

While a relatively large proportion of the precipitation is absorbed on the porcupine-grass-yellow-brush consociation, this cover, as in the case of the wheat-grass type, never occupies soils that remain too moist for the promotion of vigorous growth. During unusually dry years, growth slows down markedly, a condition which results in the temporary disappearance of many of the secondary species. Small mountain porcupine grass and yellow brush, however, are persistent, though yellow brush yields more readily to the effects of soil desiccation than does its grass associate.

SOIL WATER CONTENT.

Specific measurements of the water content of the soil have brought out two interesting facts. First, the water-holding capacity in the upper foot of soil on a well-established stand of porcupine grass and yellow brush is less than on similar areas where the wheat-grass type is equally well established. The average of 15 soil samples obtained in 1915 of soils supporting a turfed cover of wheat grass was 11.2 per cent higher than the average of the same number of soil samples on the porcupine-grass-yellow-brush area previously occupied by turfed wheat grass. Soil samples taken on the same areas in 1916 and 1917, as in the preceding year, gave practically the same relative figures. Likewise, the same number of soil samples, representing the bunched wheat-grass cover showed an average of 4.6 per cent more moisture than that of the porcupine-grass-yellow-brush cover. Second, the average available water content of the soil when saturated was less on the porcupine-grass-yellow-brush areas than on the wheat-grass lands; and, as might be expected, the available water content was exhausted correspondingly earlier in the season. Therefore, on an average, growth is arrested somewhat earlier on fully stocked porcupine-grass-yellow-brush areas than on fully stocked areas of the wheat-grass type.

THE EFFECT OF DISTURBING FACTORS.

The most reliable indication of the presence of conditions adverse to the perpetuation and maintenance of the highest development of the porcupine-grass-yellow-brush consociation, including its less stable cover of secondary species, is the replacement of one or both of the dominant species by other aggressive plants, chiefly nongrasslike species. As shown in figure 9, there is normally present on the porcupine-grass-yellow-brush areas a more or less scattered stand of plants of the second-weed stage, of which yarrow (*Achillea lanulosa*), sweet sage (*Artemisia discolor*), and blue foxglove (*Pentstemon procerus*) are the most typical. These species are almost invariably among the first of the more permanent nongrasslike plants to increase in abundance as the porcupine grass and yellow brush are killed out. Because they reproduce almost entirely by vegetative means from long rootstocks, these nongrasslike plants probably increase more rapidly than any other perennial nongrasslike species. Accordingly, they may be declared the most reliable indicators of the presence of some factor, or combination of factors, adverse to the porcupine-grass and yellow-brush stand with its many desirable associated species. For a time the dead or dying porcupine-grass-yellow-brush cover is replaced by plants of the same species. As the unfavorable conditions continue their play, however, the soil with its decreased moisture supply becomes unfavorable to the maintenance of the original plant cover, and reproduction, both by vegetative means and by seed, is greatly curtailed; but the conditions produced strongly favor the rapid invasion and establishment of the formerly suppressed blue foxglove, sweet sage, and yarrow, and these with certain other plants soon become established. The majority of these invading species feed in approximately the same soil stratum as small mountain porcupine grass—that is, chiefly in the upper foot or so of soil.

The safest indications pointing toward the maintenance or perhaps the progressive or higher development of the depleted and thinned porcupine-grass-yellow-brush consociation, is an increasing density and luxuriance of certain blue grasses and fescues, all of which are shallow-rooted, and a decreasing abundance or entire absence of the brome grasses and other deep-rooted species characteristic of earlier successional stages.[1] This gradual elimination of the deep-rooted species is, of course, accounted for by the fact that the available moisture supply in the lower soil depth decreases in somewhat the same proportion as on the wheat-grass areas. Among the blue grasses characteristically associated with the highest developed stands of the porcupine-grass-yellow-brush type, Nevada blue grass and little blue grass are the most conspicuous. In less abundance, but in approximately the same stage in the succession, occur Buckley's blue grass (*Poa buckleyana*), and Fendler's blue grass (*P. fendleriana*). Malpais blue grass, on the other hand, usually reaches its maximum abundance prior to the highest development of the porcupine-grass-yellow-brush cover. Like many of the perennial nongrasslike species, it has all but disappeared when the porcupine-grass and yellow-brush stand has attained its maximum density.[2]

When the porcupine-grass-yellow-brush consociation has prepared the way for the invasion and establishment of the wheat-grass type, porcupine grass is usually more abundant than yellow brush, and competition of a more or less serious character occurs between the porcupine-grass and the yellow-brush plants. As the bunches of porcupine grass increase in number and size, the rate and depth of the percolation of rainfall into the soil greatly decrease. This re-

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[1] In general the brome grasses are relatively low in the cycle of succession. They usually precede the blue grasses, fescues, and porcupine grasses. Likewise, the blue grasses and fescues usually precede the porcupine grasses, though this varies somewhat with the species. Because of the exceptionally strong seed habits of porcupine grass and the fact that the seeds are self-planted, and a good stand of seedlings is therefore assured under favorable conditions of soil and moisture, a somewhat general belief prevails that porcupine grass may precede the brome grasses, the blue grasses, the fescues, and certain other grasses in the succession. Detailed quadrat data have proved this belief erroneous.

[2] The approach toward the highest development of the porcupine-grass-yellow-brush type can usually be recognized by the presence of at least a scattered cover of wheat grasses, of which violet wheat grass is usually the first to appear.

tention of the water supply in the upper layer of the soil in seasons of less than normal rainfall often causes somewhat serious desiccation in the lower soil layer, upon which yellow brush is largely dependent for water, and results in the death of many of these plants. Obviously, however, the desiccation of the lower soil layer is most serious immediately beneath the dense bunches of porcupine grass. As a result of the seed of porcupine grass finding ready lodgment and conditions especially favorable for germination immediately beneath the expanded branches of yellow brush, dense tufts of porcupine grass, as shown in figure 9, often develop around the yellow-brush plants. The established yellow-brush plant is killed in a season or two or possibly straggles along for a few seasons. Where the competition is not too severe some of the branches of the yellow brush die and most of the branchlets on the remaining branches are killed, thus greatly reducing the leaf surface as well as the loss of water from transpiration. This reduction in the leaf surface often permits yellow brush to hold its place with the porcupine grass for a considerable time. Naturally under such conditions yellow brush produces few flowers and practically no viable seed, so that physiologically its behavior is much the same as a plant that has been seriously weakened as a result of too frequent cropping.

PALATABILITY.

With its large variety of palatable plants and its relatively small percentage of waste range, the porcupine-grass-yellow-brush consociation probably furnishes as ideal a vegetative cover for all classes of grazing animals as the lands are capable of producing. Small mountain porcupine grass, of which the foliage is finer leaved and less harsh than that of the wheat grasses, is grazed with relish by all classes of stock throughout the foraging season. While vigorous growth ceases in most habitats during the first half of August, the herbage remains more or less green until well into September. When cured, the leafage of small mountain porcupine grass, like that of many other fine-leaved grasses, is cropped with relish by cattle and horses. Sheep take a fair proportion of the herbage after the plant has reached maturity, but the writer has never observed this class of stock to graze porcupine grass as closely as cattle and horses unless forced to subsist upon it.

The seed heads of porcupine grass, unlike those of the wheat grasses and many other grass species, are not particularly sought for by stock, especially when the plant is approaching maturity or after the seeds have ripened. In the first place, the seeds are rather small and do not attract stock. In the second place, the basal portion of the seed is sharp-pointed while the apex elongates into a rather prominent awn, which, when the plant approaches maturity, becomes rather stiff and is objectionable to stock. This lack of palatability of the seed heads, however, in no way impairs the value of the herbage. The fact, however, that the seeds after they become well formed are consumed to only a very limited extent by stock, accounts in part for the unusual aggressiveness[1] of porcupine grass.

The palatability and forage value of the yellow brush dominant is comparatively low, so that where this species occurs in such abundance as appreciably to decrease the stand of other palatable plants the carrying capacity of the lands is considerably lower. While sheep and cattle browse the leafage and flower clusters to some extent, yellow brush can not be classed as a plant of sufficient forage value to be seriously considered in the management of the range with a view of increasing its abundance and luxuriance of growth.[2]

A large proportion of the secondary perennial species characteristic of the porcupine-grass-yellow-brush consociation, particularly the grasses, are probably first in importance among our valuable forage species. Practically all of the blue grasses, the fescues, the bromes, spiked trisetum, and mountain June grass, which occur in varying abundance throughout this consociation, are inferior to none as forage, cattle, sheep, and horses grazing them with relish at all times in the season. Likewise, some of the more conspicuous nongrasslike perennials, like yarrow, are good forage plants, though as a rule the nongrasslike species are grazed much more closely and with greater relish by sheep than by cattle and horses.[3] It is quite evident, therefore, that the porcupine-grass-yellow-brush lands generally are well suited to the common use of stock, that is, the joint grazing of cattle, horses, and sheep. In this respect, then, the porcupine-grass-yellow-brush consociation differs from that of the wheatgrass type, which in its highest development is best suited for the grazing of cattle and horses.

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[1] The seeds of porcupine grass are usually high in viability and reproduction is greatly fostered by the self-burial device of the seed, the alternate twisting and untwisting of the awn coupled with the sharp-pointed appendage at the base of the seed. For a discussion on this point see Journal Agri. Research, vol. 3, No. 2 : 118–119, 1913, and U. S. Department of Agriculture Bulletin No. 545 : 9–10, 1914.

[2] Sheep browse yellow brush with more relish than cattle. Because the foliage remains green late in the autumn after the herbage of most plants has dried up, sheep browse yellow brush more closely in the autumn than at any other time in the season. Even so, however, this plant furnishes only a small amount of rather inferior feed.

[3] Cattle and horses prefer grass to nongrasslike plants, such as weeds and browse. Sheep, on the other hand, prefer the weed and browse type, and consume a relatively small proportion of grass. Exception to this statement has been recorded when the grass is unusually palatable and the nongrasslike species are of an inferior kind. Therefore, where the vegetation consists of about the same amount of palatable weeds as of grass, the proportion of four sheep to one cow unit usually results in the most economic utilization of the forage crop. On a pure or practically pure grass range, on the other hand, cattle alone, or cattle and horses, usually afford the most economical utilization of the forage. On a strictly weed range the best utilization may be expected from the grazing of sheep only.

FORAGE PRODUCTION.

Calling forth, as it does, a conspicuous amount of blue grasses, some fescues, a scattered stand of wheat grasses, and other less important grasses, and at the same time permitting a number of the nongrasslike plants to persist, the porcupine-grass-yellow-brush consociation ranks high as forage. Expressed in terms of dry matter of palatable herbage per unit of surface, the porcupine-grass-yellow-brush consociation reaches its maximum production where the two dominant species are little more than holding their own in competition with the grasses higher in the scale of succession development; that is, where the highest possible development of the porcupine-grass-yellow-brush cover has been reached. Per unit of area, the uppermost development of this consociation, with its typically conspicuous admixture of highly palatable blue grasses, fescues, and other grasses, interspersed with numerous nongrasslike species, furnishes not only more feed but better herbage than any other forage combination that may occur in its lower developmental stages.

While the study has shown that a decrease in the stand of weedy species follows the progressive development of the consociation, it is seldom necessary to decrease the number of sheep that are grazed on the lands. Owing to the character of the feed, cattle rather than sheep should be increased in number to consume the additional grass forage, but the bulk of the nongrasslike herbage must be consumed by sheep. Except on a turfed grass range, a fair proportion of weeds, most of which are palatable to sheep but not to cattle and horses, is always present. Full utilization season after season of the grass herbage by cattle and horses tends to hold in check any striking increment in the grass cover, so that appreciable revegetation may be effected only where special methods of management are applied. Indeed, close utilization of the grass cover from season to season, as already indicated, has a tendency to decrease the grass stand and increase the stand of nongrasslike plants in much the same proportion, thus improving the conditions for the grazing of sheep.

SUMMARY OF THE PORCUPINE-GRASS-YELLOW-BRUSH CONSOCIATION.

The cover of small mountain porcupine grass and yellow brush, next to the wheat-grass consociation, constitutes the highest and most stable forage type. Accordingly where conditions become unfavorable to the maintenance of the wheat-grass cover, but not so adverse as drastically to change the fertility and available water content of the soil, porcupine grass and yellow brush soon gain dominion over the soil. Owing to the practical absence of turf-forming species within the porcupine-grass-yellow-brush consociation, precipitation penetrates deeply into the soil, hence both deep and shallow rooted plants make up the ground cover in somewhat equal proportions. The highest development of the porcupine-grass-yellow-brush cover is indicated by a scattered stand of wheat grasses, a rather conspicuous presence of blue grasses (*Poa*), and a somewhat smaller amount of fescue grasses. The lower development of the type in question is characteristically indicated by the conspicuous presence of brome grass, and not uncommonly of fescue grasses, with the addition of several perennial nongrasslike plants, among which blue foxglove, sweet sage, and yarrow are the most common.

So long as porcupine grass and yellow brush, including the typical associated species, hold their place in competition with plants of lower successional stages, or yield to the invasion of plants higher in the cycle of succession, like the wheat grasses, it is perfectly clear that the range is not being misused. If, on the other hand, the porcupine-grass-yellow-brush consociation is being replaced by brome grasses, fescues, and more especially by blue foxglove, sweet sage, yarrow, and other plants of the second weed stage, there is indisputable evidence of the deterioration of the range.

In view of the large variety of palatable plants associated with the porcupine-grass-yellow-brush cover, the highest possible development of this type is probably the most desirable of any for the grazing of all classes of stock. Since the forage crop is composed both of weeds and grasses, with the latter distinctly predominating on the better developed types, the highest grazing efficiency is obtained through "common use," that is, through the combined grazing of cattle, horses, and sheep.

THE FOXGLOVE-SWEET-SAGE-YARROW CONSOCIATION.

Detailed quadrat data and extensive observations have shown that when conditions unfavorable to growth are sufficiently prolonged gradually to destroy the porcupine-grass-yellow-brush cover, but not such as seriously to change the condition of the soil, shallow-rooted perennial weeds of the second weed stage, notably blue foxglove (*Pentstemon procerus*), sweet sage (*Artemisia discolor*), and yarrow (*Achillea lanulosa*) are the natural successors. On the other hand, where the porcupine-grass-yellow-brush cover is suddenly destroyed and considerable portions of the upper soil layer carried away, as often takes place where live stock are injudiciously handled, the immediate successional cover consists chiefly of annual plants characteristic of the first or early weed stage, with or without an admixture of perennial species.

In the gradual elimination of the porcupine-grass-yellow-brush cover perennial weed species usually gain a foothold shortly after the ground is exposed or when the roots of the grass and brush cover no longer bind the soil firmly. The usual increase in the available soil water resulting from the lowered absorption and transpiration power of the former cover greatly favors the germination, growth, and reproduction of the perennial weeds. Generally, however, where the cover has been below normal in density for a number of years, the humus content, and, indeed, the water-holding power of the soil is lower than on the more densely covered lands, so that germination and invasion of the species which immediately precede the porcupine-grass-yellow-brush consociation is less vigorous than where the grass-brush stand has just been destroyed.

In the degree of invasional aggressiveness, little difference has been observed among the three dominants; all have fairly strong seed habits. Once the plants are well established, however, yarrow easily leads in the rate of spread, the blue foxglove being the least aggressive, and the sweet sage rather intermediate between the two. This behavior is significant in view of the fact that the rootstocks of the species concerned are practically equal in length.

As to the longevity of the dominant species few data are available. Owing to the relatively high palatability of the yarrow, however, this species is usually the first to give way under excessive grazing.

Because of the slight difference in moisture requirements, the three species are often closely associated, but they seldom occur in equal density. When fully developed the plants form a matlike growth more or less pure in stand. The most luxuriant and permanent stand of blue foxglove is found on protected, moderately moist habitats, while yarrow and sweet sage occur in rather close association in somewhat drier situations.

Regardless of the density of the cover of the foxglove-sweet-sage-yarrow consociation, a scattered stand representing a large number of secondary species occurs in association with the dominants. Among the grasses occasional specimens of large mountain brome grass (*Bromus marginatus*), nodding brome grass (*B. porteri*), Scribner's wheat grass (*Agropyron scribneri*), onion grass (*Melica bulbosa*), and showy onion grass (*M. spectabilis*) are characteristic. Of the more conspicuous nongrasslike plants, the most typical are aster (*Aster frondeus*), horsemint or giant hyssop (*Agastache urticifolia*), mountain dandelion (*Crepis acuminata*), geranium (*Geranium viscosissimum*), sneezeweed (*Helenium hoopesii*), rubberweed (*Hymenoxys floribunda*), Sampson's mertensia (*Mertensia sampsonii*), cinquefoil (*Potentilla filipes*), false cymopterus (*Pseudocymopterus tidestromii*), and butterweed (*Senecio columbiana*).[1]

The root systems of blue foxglove, sweet sage, and yarrow are largely superficial in character, so that the water supply is derived

[1] Congeneric species of the plants here named occur in varying abundance.

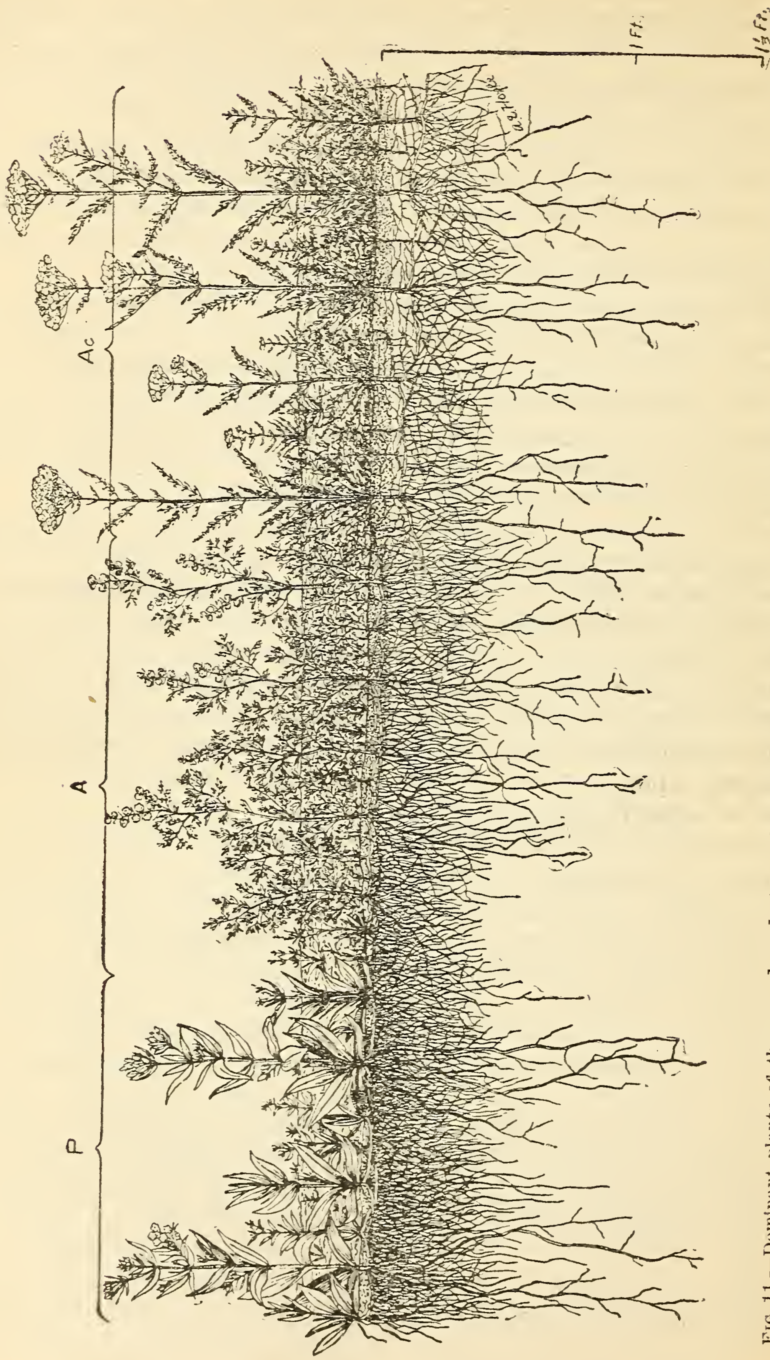


FIG. 11.—Dominant plants of the second-weed stage, showing habits of growth. *P*, Blue foxglove (*Pentstemon procerus*); *A*, sweet sage (*Artemisia discolor*); *Ac*, yarrow (*Achillea lanulosa*).

chiefly from the first foot of soil (fig. 11). The surface soil is somewhat matted but seldom bound so firmly as entirely to prevent the presence of other species. Where the second-weed stage is well established little serious erosion takes place.

CONDITIONS OF GROWTH AND PRODUCTION.

The foxglove-sweet-sage-yarrow consociation thrives wherever conditions are favorable to the growth of porcupine grass and yellow brush, and even where the soil is not so good. As in the porcupine-grass-yellow-brush consociation, however, the best development of the dominant species of the second-weed stage is found where the soil is fairly well decomposed, mellow, and reasonably moist. In general, the waterholding power of the soil is lower where the perennial weed species predominate than where plant types higher in the succession prevail. This difference in the water-holding capacity of the soil is also associated with differences in soil fertility, and to some extent at least with its physical texture, as Table 2, showing the relative chemical properties of typical soil samples, would imply. The soil representing the porcupine-grass-yellow-brush cover is richer than the soil characteristic of the second-weed stage in all chemical constituents here considered, and the difference in the total organic matter of 81 per cent in favor of the porcupine-grass-yellow-brush soil is particularly significant. Aside from the fact that this high percentage of organic matter implies the presence of correspondingly large amounts of available nitrates and other plant foods, it has a direct bearing upon the water-holding capacity and the power of water retention of the soil. The average difference in the available water content of the soil samples was 4.6 per cent in favor of the porcupine-grass-yellow-brush area. Obviously, blue foxglove, sweet sage, yarrow, and the associated species will thrive on the moister and richer soils; but owing to more highly developed root systems, greater longevity, and other life-history characteristics of the plants of the higher developmental stages, the second-weed-stage species are sooner or later forced to yield their places to the more permanent species. However, plants of the foxglove-sweet-sage-yarrow consociation, particularly the dominant species, are comparatively resistant to drought, and maintain themselves well under adverse climatic conditions.

TABLE 2.—*Average chemical properties of typical soil samples taken from the surface to a depth of 6 inches of an area supporting a cover of foxglove, sweet sage, and yarrow, and of similar samples representing soil supporting a cover of porcupine grass and yellow brush.*

Samples.	Total lime (CaO).	Carbon dioxide (CO_2).	Calcium carbonates ($CaCO_3$).	Organic carbon.	Total nitrogen.	Nitrates (parts per million of dry soil).	Total organic matter.
	Per cent.	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*		*Per cent.*
Foxglove, sweet-sage, and yarrow cover	1.03	0.08	0.18	1.52	0.17	11	3.03
Porcupine-grass and yellow-brush cover	1.13	0.10	0.38	3.20	0.35	17	5.60

The blue foxglove, sweet sage, and yarrow reproduce mainly by means of rhizomes or rootstocks; and like most high mountain plants which give rise to new individuals by vegetative means, their seed habits are only moderately strong. Germination tests conducted from 1914 to 1916, inclusive, gave the following average percentages:

Blue foxglove	11.8
Sweet sage	14.2
Yarrow	9.3

In addition to the low viability of the well-filled seeds, a rather small seed crop is produced, a large proportion of the flowers either not being fertilized or failing to develop after fertilization. However, where the soil is exposed and conditions favor germination and growth, seedlings of varying density and vigor are in evidence. Three years are required for the developmental cycle of most species—that is, from the time of germination of the seed until the resulting plant produces viable seed and gives rise to new individuals. Some species send up one or more flower stalks late in the second year following germination, but, as a rule, no fertile seeds are produced until in the third year of growth. By the end of the third season, the rootstocks are well formed, so that reproduction both by vegetative means and by seed usually takes place more or less simultaneously.

THE EFFECT OF DISTURBING FACTORS.

Like the vegetation composing the types already discussed, the foxglove-sweet-sage-yarrow cover readily replaces itself where the edaphic conditions are not appreciably changed as a result of the cover being eliminated or thinned out. Where the physical or chemical conditions of the soil are rendered less favorable to growth than formerly, however, several species lower in the succession promptly gain dominion over the soil. Among the first and most reliable species to announce the waning or retrogression of the foxglove-sweet-sage-yarrow cover are certain inconspicuous, rather short-lived perennials which usually occur very sparsely in association with the dominants of the second-weed stage. By far the most aggressive and reliable indicators of degeneration are low pea vine (*Lathyrus leucanthus*), evening primrose (*Lavauxia flava*), false cymopterus (*Pseudocymopterus tidestromii*), Mexican dock (*Rumex mexicanus*), false Solomon's seal (*Vagnera stellata*), and tongue-leaved violet (*Viola linguæfolia*). These rather temporary second-weed-stage species obtain the greater part of their moisture supply below the first foot of soil (figs. 12, 13, and 14.) Except in the case of low pea vine and false Solomon's seal, their root systems are on the taproot order, most of the species having well-developed laterals, many being several inches long. With the exception of low pea vine and false Solomon's seal, which reproduce profusely by rhizomes, new individuals arise only from seed. Considering the elevation and the conditions of growth, the four species whose regeneration depends entirely upon seed have strong seed habits. Low pea vine and false Solomon's seal, on the other hand, produce only a small amount of seed per plant, but the viability of the seed is nevertheless relatively high, as Table 3 shows.

TABLE 3.—*Viability of seed crop of short-lived perennial weeds produced in 1914–1916, inclusive.*[1]

Plant.	Viability of seed.		
	Average.	Maximum.	Minimum.
	Per cent.	*Per cent.*	*Per cent.*
Tongue-leaved violet	52.7	78.4	20.5
Evening primrose	33.1	35.4	26.4
Low pea vine	29.4	36.8	17.3
False cymopterus	19.9	28.7	11.2
Mexican dock	16.3	28.1	6.3

[1] Seed was collected from a number of specimens of each species grown in different soils and in different exposures so that, presumably, the figures given are representative for the seasons in question.

In view of the fact that tongue-leaved violet is the most aggressive invader immediately subsequent to the destruction of the foxglove-sweet-sage-yarrow cover, it is interesting to note that the viability of the seed of this species is superior to that of its associates. While it may be true that enough more viable seeds are produced by the competing plants to equal, or indeed exceed, the total number of viable seeds of tongue-leaved violet, it is not improbable that under field conditions, the seeds of the violet, with their higher germination strength, may outnumber those of high germination power in the species having an appreciably lower percentage of viability.

Next to tongue-leaved violet, evening primrose is the most aggressive and abundant. This species is followed in aggressiveness by

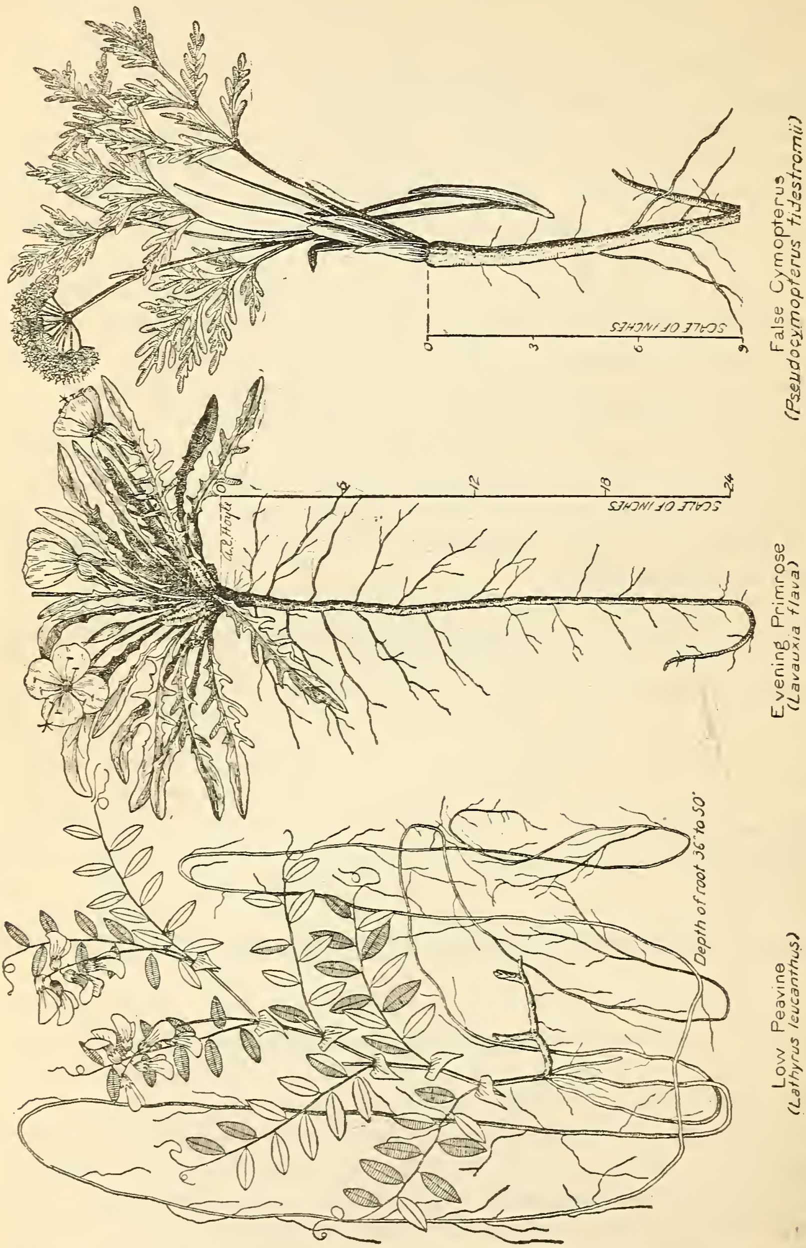


FIG. 12.—Plants characteristic of the early second-weed stage.

Mexican dock, the increase in which is held in check to an appreciable extent, however, by the fact that it is relished more by stock than the associated species. Low pea vine, because of its profusion of long rootstocks (fig. 12), and the rapid rate at which new shoots arise vegetatively, forms the densest cover of any of these rather temporary species.

The further exposure and depletion of the soil usually brings forth a conspicuous admixture of a number of other short-lived perennial species, some of which may predominate for a time. The most characteristic of these are mountain rock cress (*Arabis drummondii*),

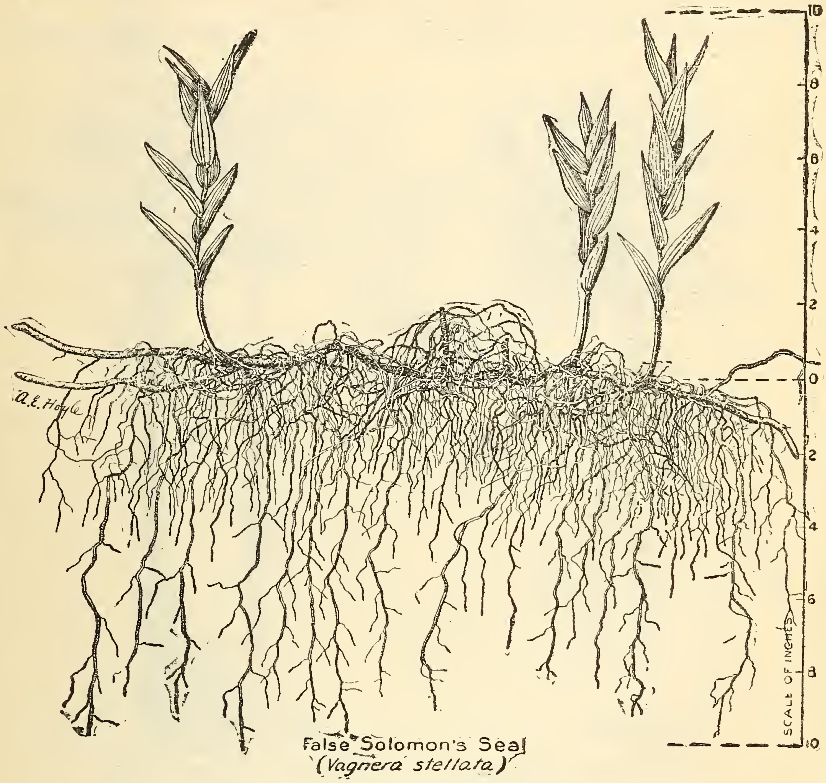


FIG. 13.—Plants characteristic of the early second-weed stage.

low larkspur (*Delphinium menziesii*), scarlet gilia, (*Gilia pulchella*), peppergrass (*Lepidium ramosissimum*), bladder pod (*Lesquerella utahensis*), plantain (*Plantago tweedyi*), and butterweed (*Senecio columbianus* and *S. crassulus*). Very few grasses are associated with this cover. Like their immediately superior associates successionally considered, the roots of most of these species are specialized, or of the tap order, with more or less conspicuous lateral feeders. Generally the roots are rather shallow, the moisture supply being procured chiefly from the upper foot of soil (figs. 15 and 16).

No systematic attempt has been made to determine the viability of the seed crop of these secondary weed species, but various laboratory tests and field observations indicate that the germination strength of the seed is high. This lower successional stage of vegetation, like the second-weed consociation generally, is early maturing, earlier, in fact, by 10 days or so than the wheat-grass cover, so that as a rule plants mature their seeds and the herbage dries up well in advance of the occurence of killing frosts. The herbage of most of the species, however, cures poorly. On some lands these species are so closely associated with low pea vine, evening primrose, false cymop-

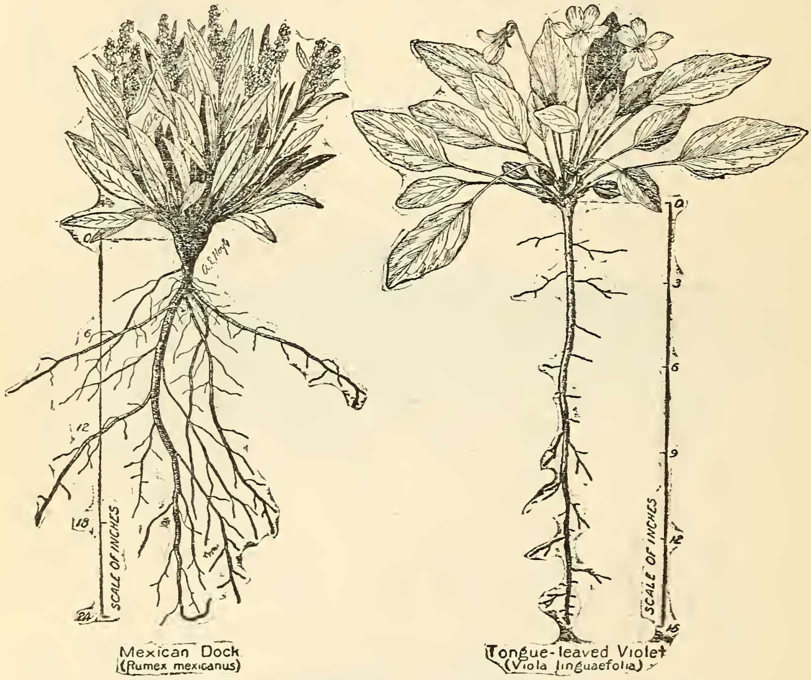


FIG. 14.—Plants characteristic of the early second-weed stage.

terus, Mexican dock, and tongue-leaved violet that it is difficult to recognize where one set supersedes the other. Generally, however, the line of demarcation is fairly distinct. As a rule the latter group is associated with a larger percentage of annual plants than the former, though this varies somewhat with the density of the cover of perennial plants, moisture conditions, and numerous other factors. In the absence of a nurse cover, such as shrubby plants or other robust and conspicuously branched perennials, it is evident that a site supporting the lower successional cover of the second-weed stage is at best severe and less favorable to germination and establishment than are sites supporting a higher type of vegetation.

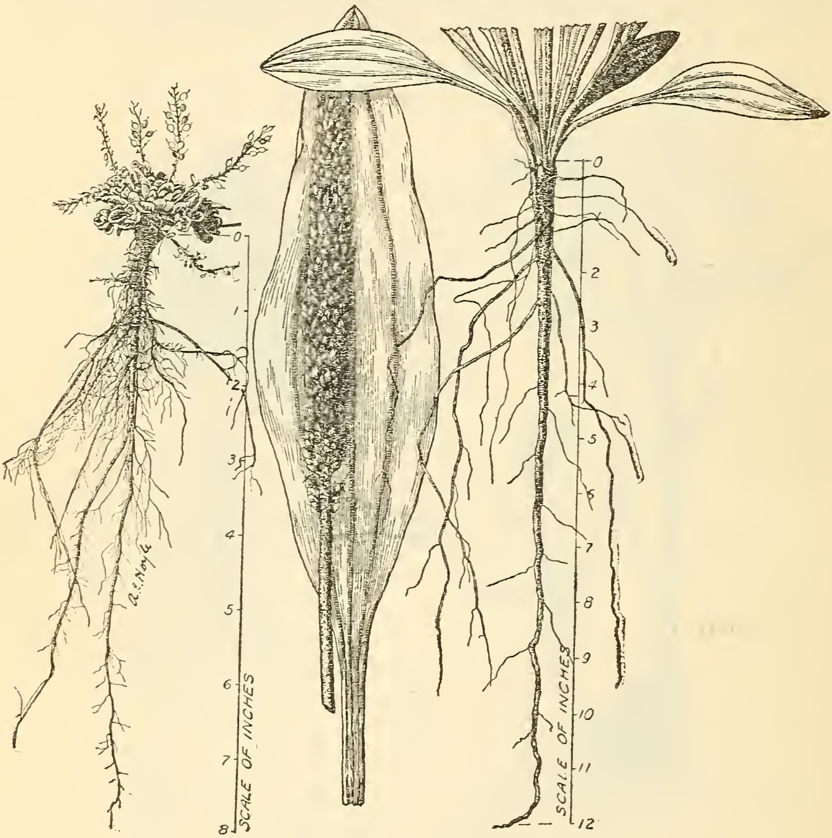
PALATABILITY.

The profusion of weedy or nongrasslike plants and the scattered occurrence of grasses make the foxglove-sweet-sage-yarrow consociation best suited for the grazing of sheep. In general, only the grasses and a very few of the nongrasslike species of the vegetation characteristic of the second stage are eagerly grazed by cattle and horses. These constitute only a very small proportion of the plant

Fig. 15.—Plants characteristic of the early second-weed stage.

cover. While, as already stated, sheep crop a grass range less closely than cattle and horses, sheep nevertheless eat the herbage of grasses where such feed constitutes only a relatively small part of the total forage crop. Most of the nongrasslike plants are grazed more or less closely by sheep. Therefore, the highest possible utilization of the second-weed-stage type is obtained by the grazing of sheep, provided, of course, the animals are properly handled.

The relative palatability and forage value of the different species making up the second-weed-stage consociation are summarized in Table 4. Palatability is here classed as high, medium, low, negative, and objectionable; abundance as dense, moderately dense, scattered, and very scattered. Of the 27 species listed, 17, or 63 per cent, are either highly or moderately palatable to sheep; while only 9, or 33



Bladder pod (*Lesquerella utahensis*). Plantain (*Plantago tweedyi*).

FIG. 16.—Plants characteristic ofthe early second-weed stage.

per cent, and 5, or 18 per cent, are either highly or moderately palatable to cattle and horses, respectively. Those of low forage value number 8, or 30 per cent, in the case of sheep, none being listed as negative in forage value; in the case of cattle 16, or 59 per cent, are low or negative in palatability; and in the case of horses 20, or 74 per cent, are listed in the same category. The species of greatest abundance are much more palatable to sheep than to cattle and horses. Accordingly, it is evident that, so far as the forage is concerned, much higher utilization will be obtained by cropping the second-weed-stage cover by sheep than by cattle and horses.

TABLE 4.—*Comparative palatability and forage value of the plants characteristic of the second weed stage.*

Plant.	Palatability.			Abundance.[1]
	Sheep.	Cattle.	Horses.	
Aster	Medium	Low	Negative	Moderately dense.
Bladder pod	Low	Negative	do	Scattered.
Blue foxglove	Medium	Low	do	Dense.
Butterweed	High	Medium	Low	Scattered.
Cinquefoil	Medium	Low	Negative	Do.
Evening primrose	do	do	do	Do.
False cymopterus	Low	Negative	do	Do.
Geranium	Medium	Low	Low	Moderately dense.
Horsemint	Low	do	Negative	Scattered.
Large mountain brome grass	High	High	High	Moderately dense.
Low pea vine	Medium	Low	Low	Do.
Mexican dock	do	do	Negative	Very scattered.
Mountain dandelion	High	Medium	Low	Scattered.
Mountain rock cress	Low	Negative	Negative	Very scattered.
Nodding brome grass	High	High	High	Scattered.
Onion grass	Low	Medium	Medium	Do.
Peppergrass	do	Negative	Negative	Very scattered.
Plantain	Medium	Low	do	Do.
Rubberweed	Objectionable	Objectionable	Objectionable	Scattered.
Sampson's mertensia	High	High	Low	Do.
Scarlet gilia	Medium	Low	Negative	Do.
Scribner's wheat grass	Low	Medium	Medium	Do.
Showy onion grass	do	do	do	Do.
Sneezeweed	Objectionable	Objectionable	Objectionable	Do.
Sweet sage	Medium	Low	Negative	Dense.
Tongue-leaved violet	do	do	do	Scattered.
Yarrow	High	Medium	Low	Dense.

[1] Abundance as here used takes into account the size of the plant and its herbage production as well as the density in which it occurs.

FORAGE PRODUCTION.

As compared with the porcupine-grass-yellow-brush consociation, the carrying capacity, acre for acre, is notably less on the foxglove-sweet-sage-yarrow type, regardless of the class of stock grazed. Even if used by sheep, the more superior second-weed-stage type will probably support only 50 per cent as many year after year without injury to the range, as will an equally desirable cover of the porcupine grass and yellow brush. In the absence of a sufficient stand of grasses and other desirable late-maturing plants the herbage of the second-weed stage is highly succulent; and while palatable and conducive to the production of large gains in the case of sheep it does not produce fat which is as solid or as permanent as that which characterizes the condition of the animal when it eats a fair balance of grasses and of other late-maturing plants. Cattle and horses little more than maintain their weight on a range distinctly in the second-weed stage. The acreage required per cow is proportionately much greater on a range in the second-weed stage than on a porcupine-grass-yellow-brush cover or on a wheat-grass area. Relatively little of the palatable feed is grazed either by sheep or cattle after the plants reach maturity or after killing frosts have occurred.

SUMMARY OF THE FOXGLOVE-SWEET-SAGE-YARROW CONSOCIATION.

The foxglove-sweet-sage-yarrow cover, less specifically known as the second or late weed stage, is the initial type in the retrogressive succession of the porcupine-grass-yellow-brush consociation. The more characteristic plants of this weed stage generally are comparatively aggressive where the conditions of growth are reasonably favorable. A rather large number of species are associated with the foxglove-sweet-sage-yarrow type species, though they seldom occur as dominants. By far the greater number of the secondary plants are nongrasslike. A few grasses are present, however, among which large mountain brome grass is by far the most important.

The type species and several of the secondary plants reproduce both vegetatively and by seed. In several species vegetative reproduction is so active as to produce a loose matlike ground surface. Most of the plants are shallow-rooted. When the soil conditions become unfavorable for the maintenance of the foxglove-sweet-sage-yarrow cover an aggressive succession of shallow-rooted, relatively short-lived perennial plants in association with a number of annual species usually takes place. In instances of severe soil depletion annual species invariably predominate.

Low pea vine, evening primrose, false cymopterus, Mexican dock, and tongue-leaved violet are the most reliable and characteristic initial indicators of the destruction of the more stable second-weed-stage cover. If the disturbing factor continues to operate, these rather short-lived perennials are sooner or later superseded by annual plants.

Much less dry matter and notably less palatable feed are produced on the late-weed-stage type than on the wheat-grass or on the porcupine-grass-yellow-brush consociations. The profusion of weed or nongrasslike plants and the small amount of grass forage produced makes the second-weed-stage cover better suited for the grazing of sheep than for cattle and horses. Owing to the fact that sheep graze nongrasslike plants with considerably greater avidity than cattle and horses, the foxglove-sweet-sage-yarrow consociation can be fully utilized by the grazing of sheep alone. Sheep, however, will not show as much progress on the second-weed-stage consociation as on the porcupine-grass-yellow-brush consociation. The gains may be fairly large but the fat is not of a solid character. Cattle and horses do poorly on the late weed type. As a rule, they little more than maintain their weight.

THE RUDERAL-EARLY-WEED CONSOCIATION.

Soils which were formerly rich but which have been so seriously impaired that their fertility is similar to that of relatively new soils recently invaded by herbaceous plants, support virtually the same type of vegetation as do the new soils.[1] The cover consists essentially of ruderal or annual plants, mostly weeds. This colonization of the early-weed stage continues until enough organic matter has accumulated in the soil to favor the invasion and establishment of the second or late weed stage.

The density of the cover varies greatly according to the character of the soil, the seed crop available for germination, and the growth condition of the current season; the cover may be quite dense one year and relatively sparse the next. When one good growing season follows another the cover is particularly dense and the individual plants are large; also the pioneer species of the second or late weed stage usually begin to appear. A succession of dry years, on the other hand, brings forth a sparse stand of the first, or early weed stage, the plants of which are small; also the pioneer species of the second weed stage are usually absent.

The most typical and abundant species of the first-weed stage are goosefoot or lamb's-quarters (*Chenopodium album*), slender-leaved collomia (*Collomia linearis*), tarweed (*Madia glomerata*), Tolmie's orthocarpus (*Orthocarpus tolmiei*), Douglas knotweed (*Polygonum douglasii*), and tansy mustard (*Sophia incisa*) (figs. 17 and 18). Less abundant, but usually associated with the above species are androsace (*Androsace diffusa*), gilia (*Gilia micrantha*), peppergrass (*Lepidium ramosissimum*), monolepis (*Monolepis nuttalliana*), and knotweed (*Polygonum aviculare*).

In general the first-weed-stage cover reaches maturity earlier than any other. Because of the shallow roots and the lack of conspicuous laterals, this cover is of little value in checking erosion or otherwise preserving the watershed. The root systems are essentially of the specialized or tap character, and are confined almost entirely to the upper foot of soil—indeed the roots of the majority of the species do not penetrate deeper than about 8 inches. Therefore, where the topography, soil, climatic conditions, and other factors favor torrential runoff, the ruderal-weed stage is of the least value of any in protecting the watershed from erosion.

CONDITIONS OF GROWTH AND REPRODUCTION.

No group of perennial plants has as strong seed habits and is subject to as few failures in seed production as the first-weed-stage species. While no systematic study has been made to ascertain the size and viability of the seed crop, observations and repeated germination tests indicate that the normal seed crop is unusually large and fertile. Germination tests of well-developed seed of Douglas knotweed and

[1] Soils heavily packed, which often takes place when stock (especially sheep) trample denuded or sparsely vegetated areas excessively, also commonly support only ruderal or annual plants.

tansy mustard, for example, have averaged more than 70 per cent, considerably exceeding the highest average seed-test records of perennial species. Generally, the seed of the more aggressive annuals are plump and well filled with reserve food. Another distinct advantage observed in the case of the seed of the ruderal weed species

Goosefoot or lamb's-quarters (*Chenopodium album*).

Slender-leaved collomia (*Collomia linearis*).

FIG. 17.—Plants characteristic of the first or early weed stage.

is their ability to germinate under conditions of temperature adverse to most plants. Seed of Douglas knotweed, tansy mustard, and tarweed, for instance, have been observed to sprout when the maximum diurnal temperature has not exceeded 50° Fahrenheit, the mean temperature being 42°, and when the nocturnal temperature has dropped from 2° to 4° below freezing. Few perennial plants, even though restricted in their distribution to the subalpine zone, are capable of germination at such low temperatures. Being entirely dependent upon seed for their perpetuation, obviously only those annuals persist or are conspicuous which are capable of germinating and becoming established at the earliest advent of spring.

Tolmie's orthocarpus (*Orthocarpus tolmiei*). Douglas knotweed (*Polygonum douglasii*). Tansy mustard (*Sophia incisa*).

FIG. 18.—Plants characteristic of the first or early weed stage.

Since the ruderal-early-weed stage represents the lowest or most primitive herbaceous cover possible, it will be instructive to compare briefly the conditions of growth of this type with those of the highest herbaceous successional cover, the wheat-grass consociation. For the purpose of ready comparison the average, maximum, minimum, and optimum depths of the roots of the most characteristic ruderal-weed species and of the chief wheat grasses are tabulated in Table 5. While the depth of penetration of the roots of wheat grasses as a whole is appreciably greater than in the ruderal weed species, small wheat grass obtains its water supply from much the same soil stratum as the ruderal-weed species. Blue bunch wheat grass and slender wheat grass, on the other hand, absorb nearly all of the water they need from soil far below the deepest penetration of roots of the annual plants.

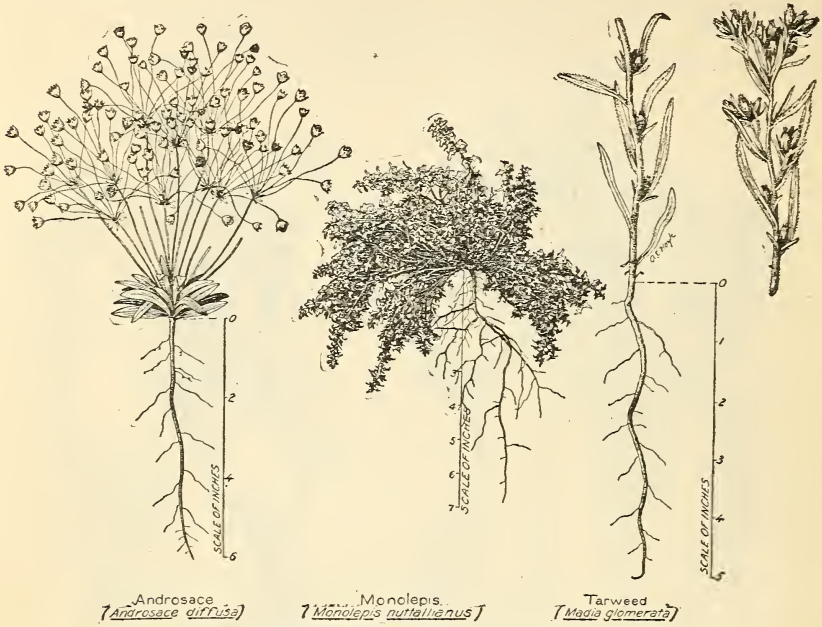


FIG. 19.—Plants characteristic of the first-weed stage.

TABLE 5.—*Comparative depth of roots of typical ruderal-weed species and of the chief wheatgrasses.*

Plant.	Depth of roots in inches.		
	Maximum.	Minimum.	Optimum.
Ruderal-weed species:			
Goosefoot	7	3	5.5
Slender-leaved collomia	9	3.5	6
Tarweed	10	4	7
Tolmie's orthocarpus	8	3	5
Knotweed	11	4	7
Douglas knotweed	10	4	7
Tansy mustard	9	3	6
Average	9.1	3.5	6.2
Wheat grasses:			
Small wheat grass	15	6	8
Blue bunch wheat grass	40	26	32
Slender wheat grass	40	26	32
Average	31.7	19.3	24

The rate of percolation of water is much greater on the ruderal-weed lands than on the small wheat-grass areas. This is due not only to the dense matlike growth of the roots characteristic of the small wheat-grass cover, but also to the comparatively high proportion of humus, and hence water-holding power, of the wheat-grass soil.

Data showing the more important chemical constituents and humus content of representative soils supporting short wheat grass and of soil supporting ruderal weeds are given in Table 6. Except in the amount of potash, the percentage of the chemical constituents important as plant food is higher in the soils representing the small wheat-grass lands than in the soils characteristic of the ruderal-weed cover. The most striking difference is found in the total nitrogen

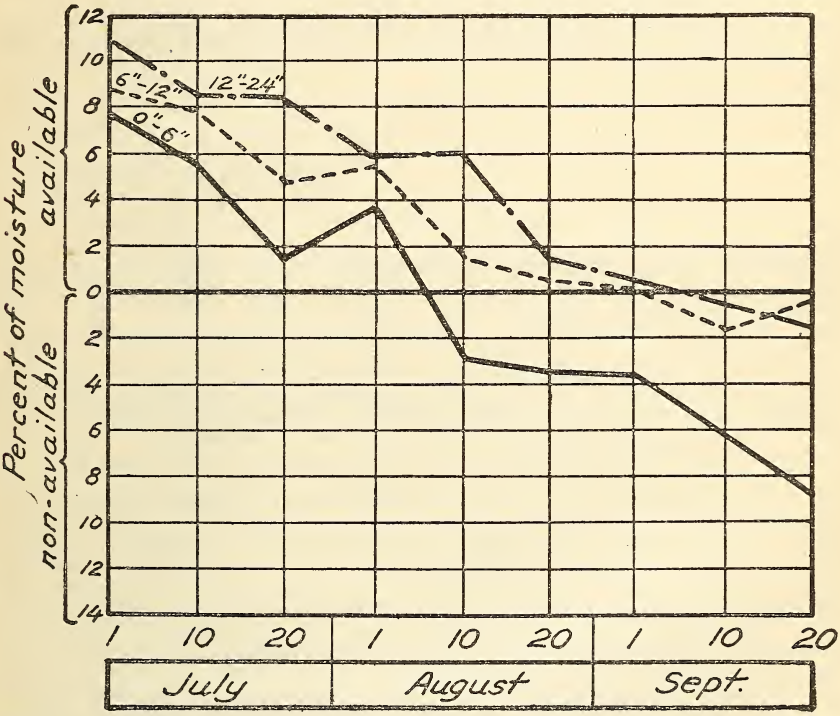


FIG. 20.—Available and nonavailable soil moisture on an overgrazed area supporting a sparse stand of ruderal vegetation, 1915.

content. Also there is a wide difference in the humus content as determined by incineration.

TABLE 6.—*Chemical properties of soil supporting small wheat grass and soil supporting the ruderal-weed consociation.*

Soil.	Lime (CaO).	Potash (K_2O).	Phosphoric acid (P_2O_5).	Total nitrogen.	Loss by ignition (humus).
	Per cent.	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*
Small wheat grass	1.49	1.30	0.38	0.488	14.65
Ruderal weed	1.26	1.53	.22	.158	6.64

The wide difference in the humus content accounts chiefly for the higher water-holding power and available plant water in the wheat-grass soil, which, when it was saturated, were greater by 10.4 per cent than in the soil which supported the ruderal-weed vegetation. In order to determine what effect this difference in fertility and available water might have on the growth and water requirements of vegetation, experiments were made on three batteries each of the selected soils.[1] The vegetative development and the total water requirements of the plants grown in the wheat-grass soil and in the ruderal-weed soil are shown in Table 7.

TABLE 7.—*Summary of vegetative growth and water requirements of peas and wheat developed in soils characteristic of the wheat-grass type and of the ruderal-weed cover.*

Plant.	Peas.		Wheat.	
	Ruderal-weed soil.	Wheat-grass soil.	Ruderal-weed soil.	Wheat-grass soil.
Number of leaves	42	112	22	47
Leaf length ... mm.	791	2,634	4,474	10,080
Dry weight ... grams.	0.79	6.55	5.52	12.09
Water used per plant ... do.	667	3,051	2,516	3,829
Water requirement per unit dry matter ... do.	841	467	472	343

Both wheat and peas show a striking contrast in the vegetative growth and in the water requirements in the two soil types. The

[1] The batteries were so arranged that no water escaped from the soil except by transpiration from the plants grown.

After being carefully sifted, the soils were moistened so as to contain approximately 30 per cent of water. The soil was thoroughly mixed, so that the moisture content was uniform throughout, and was firmly packed in heavy galvanized-iron potometers, 17 inches high and 14 inches in diameter. Potometers of this size, having as they do a capacity of about 90 pounds of air-dry soil, provided a soil mass of ample space for development and spread of the roots of the plants selected to be grown in the potometers. The potometers were fitted with lids of the same material as the cans, and five equally spaced holes three-fourths inch in diameter were punched in each for the plants. In the center of the cover a hole 1½ inches in diameter was provided, which was used in watering and which was fitted with a cork stopper and capillary tube for the circulation of air. Before the lid was put on sufficient soil was removed from the surface center of the can for the placing of a granite receptacle 4 inches in height and 5 inches in diameter, perforated centrally in the bottom and underlaid with 1½ inches of gravel. This greatly facilitated the addition of water. After the lids were placed the space between the rim and can was closed by securely sealing with strips of surgeon's adhesive tape, which, when dry was coated with shellac. In order to have as little variation as possible in the individual plants, pedigreed strains of Canadian field peas (*Pisum arvense*) and cultivated wheat (*Triticum durum*), known as Kubanka 1440, were used. In order further to insure uniformity in the plants the seeds were sprouted between moist blotters and the most vigorous sprouts transferred to water cultures from which uniformly sized plants were subsequently selected for planting. In planting, a small amount of soil was removed through the perforations made in the lid, the roots of the sprouts were inserted, and the soil was firmly pressed about the roots. A combination of melted beeswax and tallow was used to seal over the soil exposed by the perforations made in the lid of the potometer through which the plants were inserted. The methods used in sealing and in watering were essentially the same as those devised by Briggs, L. J., and Shantz, H. L., "Water Requirements of Plants," U. S. Department of Agriculture, Bureau of Plant Industry Bulletin 284: 8–14. 1913.

vegetative development was appreciably greater in the wheat-grass soil both in the number of leaves produced and in the total leaf length. The difference in the development of the plant as a whole is best expressed by the dry weight produced. In peas the proportion of dry weight was as 1 to 8.2 in favor of the wheat-grass soil; in wheat the proportion was as 1 to 2.2 in favor of the same soil type. The water requirement for the production of a given unit of dry weight, on the other hand, was much greater in the ruderal-weed soil than in the wheat-grass soil, the proportion being approximately 2 to 1 in peas and 2 to 1.4 in wheat.

The higher water requirement of plants grown in the less fertile soil is particularly significant in view of the fact that impoverished soils absorb and retain very much less water than do the more fertile soils. This fact, coupled with the low fertility of the soil, chiefly accounts for the presence of the temporary weed cover on badly-impoverished, as well as newly-formed soils.

SOIL WATER CONTENT.

The soil moisture conditions on a first-weed-stage area during the season of 1915 are summarized in figure 20. Considering the general trend of the curves representing the available water content from 0 to 6 inches, 6 to 12 inches, and 12 to 24 inches in depth by 10-day periods throughout the growing season, it will be observed that there is a rather sharp decline in the water content of the soil from July 1 to September 20. Except in the last period (September 10 to 20) the highest amount of available plant water was found in the 12 to 24 inch layer. The 0 to 6 inch soil layer, on the other hand, contained the lowest water content throughout the entire period. When saturated the upper 6 inches of soil, except where severe washing has occurred, usually contains several per cent more moisture than the soils of greater depth. The reduction in the water content of the upper soil layer is, of course, chiefly attributable to transpiration [1] and to a slight extent to direct evaporation from the soil.[2]

The most important physiological fact brought out in the graph is the period at which the soil water content becomes unavailable to the vegetation. In the case of the all-important upper 6 inches of soil, from which the first-weed-stage plants procure by far the greater part of their moisture supply, the water becomes unavailable to the vegetation between August 1 and August 10. In the 6 to 12

[1] Germination and growth in the case of this cover in 1915 began on June 23.

[2] Loss of water by direct evaporation from the soil is slight as compared with that lost by transpiration from the vegetation. For a discussion on this subject see Burr, W. W., "Storage and Use of Soil Moisture." Research Bulletin, No. 5, Agricultural Experiment Station of Nebraska: 61: 1914. Also Romistrov, V. G., "The Nature of Drought According to the Evidence of the Odessa Experimental Field." M. L. and A. Department of Agriculture, Odessa: 17: 1913.

inch and the 12 to 24 inch soil layers there was available water until about September 10. Because of the desiccation of the upper soil layer during the first few days in August at least 90 per cent of the vegetation ceased to function. While the rate of growth and the period of maturity vary according to the character of the season, the ruderal-weed cover generally requires only about six weeks in which to complete growth and mature its seed crop.

THE EFFECT OF DISTURBING FACTORS.

The edaphic conditions of few of the deeper and older mountain soils are so adverse as entirely to exclude the first-weed-stage plants. But the density of the cover of the type in question is controlled largely by the proportion of available moisture contained in the soil during the germination period. Likewise the luxuriance of the stand is determined chiefly by the available moisture content during the growing season.

Thorough colonization of the ruderal-weed species for three or more years, in the absence of the play of factors adverse to the unhampered development of the vegetation, generally calls into evidence an admixture of the more aggressive, short-lived species of the second-weed stage, hence marks the initial passing of the ruderal-weed cover. On the other hand, the removal of a large proportion of the soluble plant foods, and indeed of portions of the soil itself, is followed by a distinct retrogression of the first-weed-stage vegetation. Where the destruction of the soil is continued to the extent that the "holdfast" of the ruderal-weed type is destroyed, the pioneer stage of plant life—the algæ and lichens—again appears over the exposed rocks.

PALATABILITY.

With the exception of a very few plants, the ruderal-weed consociation affords little feed for stock. A large number of the plants are cropped by sheep at least to a limited extent, but they afford only a small amount of forage. Cattle graze only a few species, and horses consume practically none. The most palatable plant to sheep and cattle is tansy mustard, the flowers, leafage, and the more tender parts of the stem being devoured with unusual relish until the plant reaches maturity; after that, like nearly all of the first-weed-stage species, it is not grazed noticeably at all. Tansy mustard, however, occurs so scatteringly over the type as a whole that it is of little value as a forage plant. Douglas knotweed, the most abundant of the ruderal-weed species, is grazed to a considerable extent by sheep before the seed is disseminated, apparently with good results to the animals. It probably furnishes more feed than all the rest of the annual species combined. Cattle also graze Douglas knotweed, though with less relish than sheep. Several of the more conspicuous plants, like tarweed, gilia, etc., are practically disregarded by stock.

FORAGE PRODUCTION.

The amount of forage produced on lands in the first or early weed stage is far less than that on lands supporting any of the higher stages of plant growth. Like the second or late weed cover, the ruderal-weed cover is best suited for the grazing of sheep, but the carrying capacity is exceedingly low and the forage distinctly inferior. Aside from the fact that little of the herbage produced is grazed after about the first week in August, anything approaching complete utilization of the forage crop is apt to stimulate erosion of a most destructive character. Hence range lands in the ruderal-weed stage must be managed in the most expert way; anything approaching maximum utilization is hardly to be considered if the more permanent and desirable cover is ultimately to gain dominion over the soil.

SUMMARY OF THE RUDERAL-EARLY-WEED CONSOCIATION.

On lands where the soil has been so seriously impaired as no longer to afford a congenial habitat for the growth of perennial species, the cover consists essentially of annual plants. This first or early weed stage of which goosefoot or lamb's-quarters, slender-leaved collomia tarweed, Tolmie's orthocarpus, Douglas knotweed, and tansy mustard are typical examples, completes its growth in about 6 weeks after the sprouting of the seed. As the plants are entirely dependent upon seed for their perpetuation, their seed habits are exceptionally strong, the viability of the seed from year to year averaging considerably higher than that of the perennial plants. In spite of strong seed habits, however, there is a wider variation from year to year in the density of the stand of the early-weed stage than in any other type. This is chiefly due to the fact that there is not always ample moisture for plant life in the superficial soil layer in which the feeding roots of this consociation are located. While often variable in density, the ruderal-weed type nevertheless persists until enough organic matter has been accumulated in the soil to favor the establishment of plants of the second-weed stage.

Little forage is produced by the first-weed type. While a considerable number of species are grazed by sheep (few are eaten by cattle and practically none by horses), only a small amount of dry matter is produced. Douglas knotweed, the most abundant species, is cropped with moderate relish both by sheep and cattle and probably furnishes as much feed as all the other annuals combined. However, the ruderal-weed cover is grazed only when the herbage is succulent and tender. In view of the early maturity of the vegetation and the fact that the first-weed-stage cover affords poor protection of the watershed, it is essential that stock permitted on this type be handled in accordance with the most approved methods. If serious erosion is to be prevented, the lands should be grazed very lightly or not at all until plants of the second-weed stage have gained a foothold.

THE EFFECT OF GRAZING ON PLANT SUCCESSION.

The grazing of live stock may, under certain conditions, either retard or promote the development of a plant cover and cause either retrogression or progressive succession.

DESTRUCTIVE GRAZING AND ITS RELATION TO EROSION.[1]

The highest grazing efficiency consists in getting the greatest possible use out of the range from year to year. Any system of grazing, therefore, which decreases the carrying capacity of the lands so that the forage production is decreased from season to season may be classed as destructive. If such a method is continued, the ground cover will be partly or wholly destroyed, a condition which is almost invariably associated with erosion.

While it is probably true that the extent of surface run-off and erosion is largely determined by climate, topography, and soil, the combined influence of these factors on the high mountain grazing lands of the West is not such as to cause serious soil depletion except where the vegetative cover has been badly impaired. A typical case of overgrazing, indicating the relation of the vegetative cover to erosion, is shown in figure 21.[2] The more important facts brought out in figure 21 may be summarized as follows:

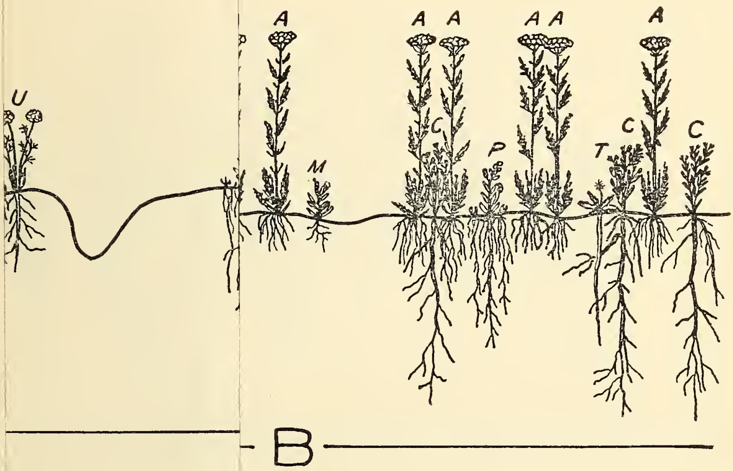
1. Where the original cover remained intact, as in section B to the extreme left in the figure, practically no erosion occurred. Partial destruction of the vegetation (section B to extreme right) was accompanied by moderate erosion, while serious destruction of the cover (section A) was associated with erosion of a most serious character.

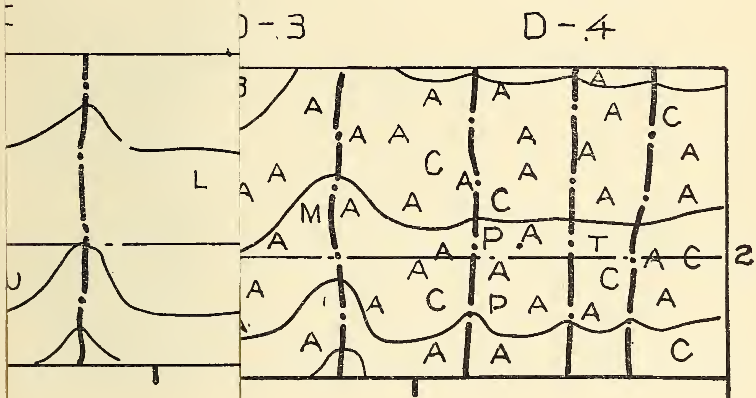
2. The colonization on the moderately depleted areas (section B to extreme right) consists essentially of typical second-weed-stage plants, while on the very sparsely colonized blocks (section A) the vegetation is composed either of the first-weed-stage plants or of

[1] For further information as to the relation of grazing to erosion, see Sampson, Arthur W., and Weyl, Leon H., "Range Preservation and Its Relation to Erosion Control on Western Grazing Lands," U. S. Dept. of Agr. Bul. No. 675, 1918.

[2] The area represented lies at an elevation of about 10,000 feet, has a western exposure, and an average slope of approximately 11 per cent. Until 1905, when the lands came under governmental control, the range had been subject to heavy overgrazing by all classes of stock. Since 1905, the area has been subject to moderate grazing by cattle and sheep. As a result, considerable revegetation has taken place where the original cover remained more or less intact, and where little or no erosion occurred. The badly eroded areas, however, have improved relatively little in carrying capacity during the past 10 or 12 years (1905–1917) of moderate grazing, and now they furnish only a small amount of inferior forage.

ROSS-SECTION





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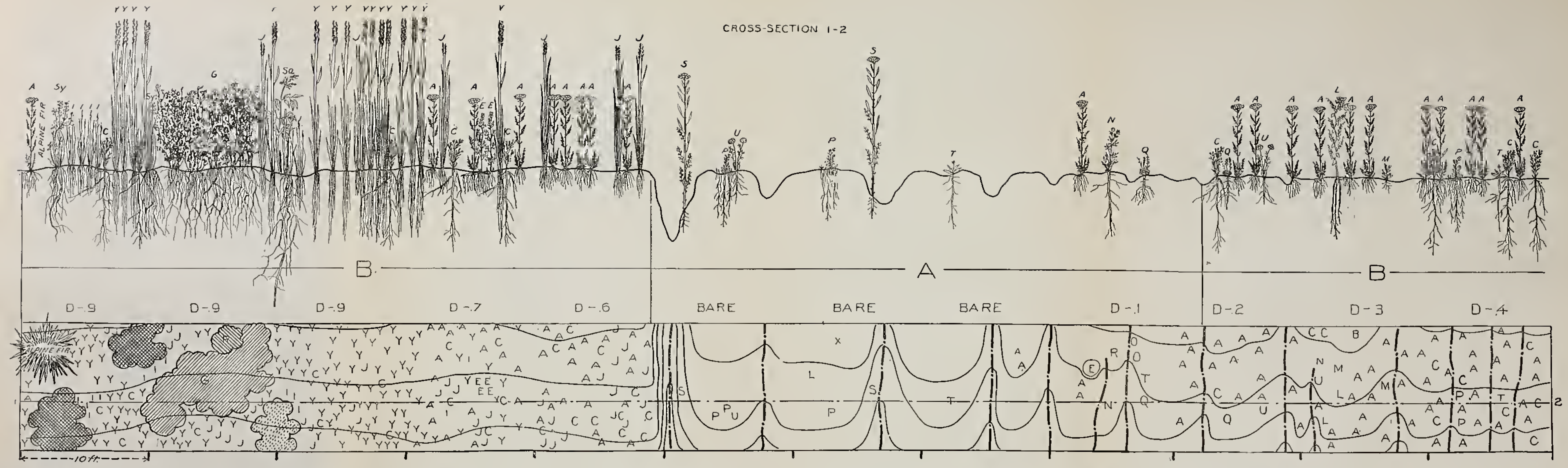

A—Where original cover was destroyed by grazing.

A—Yarrow (*Achillea lanulosa*).
B—Erigeron (*Erigeron macranthus*).
C—Yellow brush (*Chrysothamnus lanceolatus*).
E—Sweet sage (*Artemisia discolor*).
G—False gooseberry (*Ribes montigenum*).
I—Spiked trisetum (*Trisetum spicatum*).
J—Small mountain porcupine grass (*Stipa minor*).
L—Low pea vine (*Lathyrus leucanthus*).
La—Evening primrose (*Lavauxia flava*).
M—Slender-leaved collomia (*Collomia linearis*).
N—Slender cinquefoil (*Potentilla filipes*).
P—Blue foxglove (*Pentstemon procerus*).

B—Where original cover remained more or less intact.

Q—Bladder pod (*Lesquerella utahensis*).
R—Mexican dock (*Rumex mexicanus*).
Ri—Currant (*Ribes inebrians*).
S—Tansy mustard (*Sophia incisa*).
So—Mountain elder (*Sambucus microbotrys*).
Sy—Snowberry (*Symphoricarpos oreophilus*).
T—Dandelion (*Leontodon taraxacum*).
U—False cymopterus (*Pseudocymopterus tidestromii*).
X—Knotweed (*Polygonum aviculare*).
Y—Slender wheat grass (*Agropyron tenerum*).

D—Density. Contour interval 1 foot.

FIG. 21.—Character and density of vegetation.

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species that appear very early in the succession of the second-weed stage. The blocks upon which the cover was only slightly impaired are occupied essentially by the subclimax wheat grasses.

3. The root system of the vegetation as a whole, as shown in the cross-section view of figure 21, is the sparsest and most superficial on the seriously eroded blocks, intermediate both as to depth and density on the moderately eroded areas, and deepest and most abundant on the least eroded and most highly vegetated blocks.

Chemical analyses of the soil have clearly shown that the fertility is roughly in proportion to the extent of the soil depletion, the least soil eroded being the most fertile. In these tests the samples of noneroded soil contained an average of approximately four times more organic carbon, three times more total nitrogen, and four times more total organic matter than did the eroded samples. Likewise the water-holding power in the soil samples from the noneroded blocks, when saturated, was greater by 9 per cent than in the samples from the eroded blocks.

From these facts it is evident that any system of grazing which results in the destruction of the ground cover and at the same time permits erosion to gain headway, not only immediately decreases the carrying capacity of the lands but prevents the establishment of the more permanent cover for an indefinite period—in some instances possibly for 50 years or more.[1] The translocation of the upper few inches of the surface layer of soil, with its comparatively rich impregnation of organic matter, causes the usual reversion of the vegetation to a lower successional stage, not uncommonly the first-weed stage. Under such conditions the former dominance of the subclimax species will not again appear until the original fertility of the soil has been reestablished, which is possible only after the application of many years of judicious range management. The continuance of grazing without regard for the growth requirements of the vegetation causes further soil depletion.

FORAGE PRODUCTION ON DRIVEWAYS AND BED GROUNDS.

The use year after year of established driveways and bed grounds for stock furnishes noteworthy instances of retrogressive succession. While it is true that the majority of the driveways on the National Forests were most seriously depleted before the lands came directly under the control of the Government, and that since that time many have improved somewhat in productivity, generally they support only a sparse cover of inferior transitory vegetation. Established bed grounds are usually depleted in proportion to the length of time

[1] Shantz, H. L., "Plant Succession on Abandoned Roads in Eastern Colorado," Journal of Ecology, Vol. V, No. 1: 19, 44, 1917.

they have been used. Not uncommonly they represent the most serious destruction of the plant cover that can occur on the range.

In order to determine what plant species characteristically colonize heavily on long-used driveways and bed grounds, taking into account the rate at which such areas may revegetate under different methods of management, a number of small sample plots were carefully selected for special study. Some of the selected plots have been protected from live stock by fencing; others received no protection and were subject to normal seasonal grazing.

STOCK DRIVEWAYS.

A generalized sketch of the vegetation and other features on a portion of the driveway selected for special study is shown in figure 22.[1]

While a few grasses have gained a foothold on this driveway, the ground cover is quite open and composed chiefly of a mixed stand of weeds, characteristic of the first and the second weed stage. Listed in the order of their abundance, it will be noted that Douglas knotweed, slender-leaved collomia, and tansy mustard constitute the dominant early-weed species on this portion of the driveway, as indeed they do on the driveway as a whole; tongue-leaved violet, dandelion, and low larkspur constitute the predominating late-weed-stage plants. Other typical species of the late-weed stage are chickweed, evening primrose, low pea vine, meadow rue, and plantain. The more persistent species, blue foxglove and sweet sage, have gained a foothold, but apparently conditions do not yet favor rapid colonization of these plants. In 1917 the vegetative blocks representing the unprotected driveway had a density of stand of about 0.15.[2] The protected area when fenced in 1915 was identical as to species and density with that of the outside range, but in 1917 supported a cover of approximately 0.2. This slight increment in the stand over that on the adjacent unprotected range is composed of annual and perennial weed species in equal proportions.

Much the same vegetative development occurs on another protected plot, a bisect detail of which is shown in Figure 23.[3] Of the

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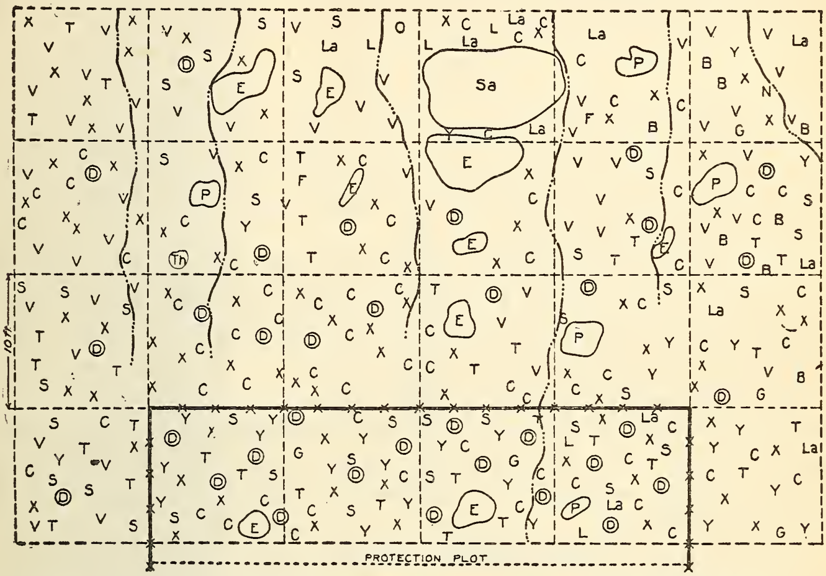
[1] The area here sketched had been so severely overgrazed at the time the lands were included within the National Forest in 1905 that practically every vestige of the herbaceous perennial vegetation had been destroyed. During the past 12 years the area has been grazed in moderation, during the main growing season, by cattle, sheep, and horses. In listing the plants it was the aim to record the species that occurred in each vegetational unit but not every individual. The relative density of the respective blocks, however, is shown.

[2] Density measurement is on the basis of ten-tenths for full cover.

[3] It is noteworthy that of the eight species that occur in the bisect all are typical either of the first or of the second weed stage, a fact which strongly substantiates the conclusion that their increase in abundance on a range in a higher stage of development would announce the waning of the higher type.

perennial plants on both of these protected plots, low larkspur has increased proportionately much more rapidly than any other; on the outside range the colonization of the low larkspur has been only moderately rapid and in proportion to that of other perennial plants.

This difference in aggressiveness of larkspur is accounted for by the fact that the unprotected range is grazed by sheep prior to seed maturity.[1] As larkspur is fairly palatable to sheep, only a small pro-



B—Large mountain brome grass (*Bromus marginatus*).
C—Slender-leaved collomia (*Collomia linearis*).
D—Low larkspur (*Delphinium menziesii*).
E—Sweet sage (*Artemisia discolor*).
F—Spiked fescue (*Festuca confines*).
L—Low pea vine (*Lathyrus leucanthus*).
La—Evening primrose (*Lavauxia flava*).
N—Chickweed (*Alsine jamesiana*).
—×—×— Fence.
P—Blue foxglove (*Pentstemon procerus*).
S—Tansy mustard (*Sophia incisa*).
Sa—Mountain elder (*Sambucus microbotrys*).
T—Dandelion (*Leontodon taraxacum*).
Th—Meadow rue (*Thalictrum fendleri*).
V—Tongue-leaved violet (*Viola linguaefolia*).
X—Douglas knotweed (*Polygonum douglasii*).
Y—Plantain (*Plantago tweedyi*).
—— . . —— Dry gully.

FIG. 22.—Character of vegetation on a formerly depleted stock driveway in process of recuperation.

portion of the seed crop is matured on the open range, whereas maximum seed production is secured on the protected area. Being small, comparatively heavy, and without special contrivances favoring distribution by wind or attachment, the seeds drop near the parent plant, where they give rise to new individuals.

Like certain other species previously discussed, low larkspur holds a more or less conspicuous place in the development of the vegetation

[1] Most larkspurs are grazed with moderate relish by sheep, and, so far as known, without serious results.

from the time of the waning of the early-weed stage to the passing of the late-weed stage; therefore, on the higher ecological types, an increase in the abundance of larkspur may be declared a reliable indicator of overgrazing.

Generally low larkspur is most conspicuous early in the development of the second-weed stage. Accordingly, on cattle range the heaviest losses from poisoning by low larkspur are apt to occur where the lands have been depleted so seriously that the vegetation is in the second-weed stage or in the first and second mixed-weed stage.

BED GROUNDS.

Although some variation is found in the vegetation of different bed grounds and adjacent lands of the region, depending chiefly on the character of the soil and the topographic features, the predominating species are generally the same where the extent of the depletion of the soil is the same.

On long-used bed grounds, where the adjacent cover is more or less intact, various distinct vegetative stages may commonly be distinguished, radiating from the bed ground proper. This is exemplified in the bed ground shown in figure 24.[1]

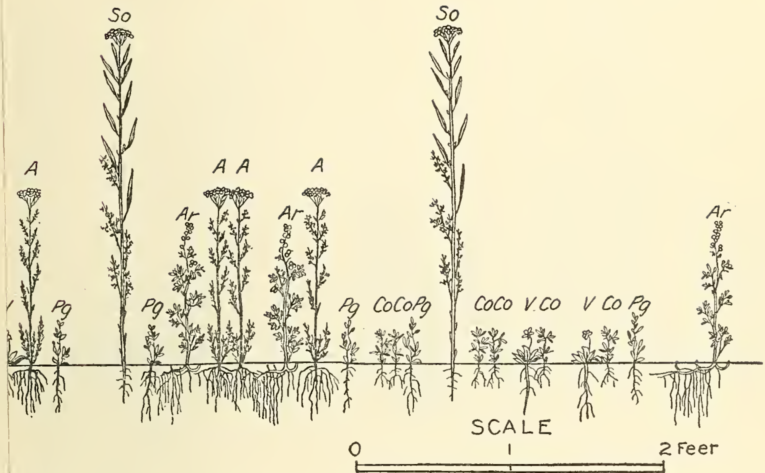
The main part of the bed ground (zone 1) is practically circular and covers 22 acres. Owing to the heavy use made of the bed ground each year, not a vestige of the original wheat-grass vegetation remains; indeed, even the most aggressive annual plants are for the most part lacking.

Adjacent to the bed ground proper is an irregular zone of about 85 acres. Here the colonization is composed solely of plants of the first or early weed stage. The plants are widely scattered (the density being estimated at 0.05 on a basis of ten-tenths representing full cover) and are distinctly lacking in luxuriance of growth. The species predominating in 1917, named in the order of abundance, were Douglas knotweed, Tolmie's orthocarpus, tansy mustard, tarweed, goosefoot, and androsace. Much less conspicuous were the following species: knotweed (*Polygonum aviculare*), monolepis, peppergrass, and slender-leaved collomia.[2] As already indicated, this type of cover afforded practically no grazing for any class of stock.

Zone 3 comprises approximately 215 acres, and consists of a weed cover of the early and late stages, with the early-stage species distinctly predominating. An occasional grass specimen is also seen. Here the density of the cover is estimated at 0.15, or three times that of the pure early-weed stage adjacent to the bed ground. The pre-

[1] The bed ground here represented has been used annually for several successive years by a band of about 1,400 ewes and their lambs. As a rule, the forage cropped in conjunction with the use of this camp has been grazed during the main growing season.

[2] Slender-leaved collomia is often among the first to colonize abandoned bed grounds and sometimes is a predominating species.



So, Tansy mustard (*Sophia incisa*).
V, Tongle-leaved violet (*Viola linguaefolia*).

on in 1917.

A, Yarrow (*Achillea lanulosa*).
Ar, Sweet sage (*Artemisia discolor*).

Co, Slender-leaved collomia (*Collomia linearis*).
D, Low larkspur (*Delphinium menziesii*).

Pg, Knotweed (*Polygonum aviculare*).
Pt, Plantain (*Plantago tweedyi*).

So, Tansy mustard (*Sophia incisa*).
V, Tongue-leaved violet (*Viola linguaefolia*).

FIG. 23.—Sheep driveway used annually until 1915, when protection plot was established showing character of vegetation in 1917.

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dominating plants of the early-weed stage were practically identical with those reported in zone 2. Of the late-weed stage species the following were conspicuous: tongue-leaved violet, evening primrose, low pea vine, Mexican dock, butterweed, plantain, sneezeweed, and false cymopterus. These species, it will be recalled, have been listed as characteristic forerunners of the more permanent species of the late-

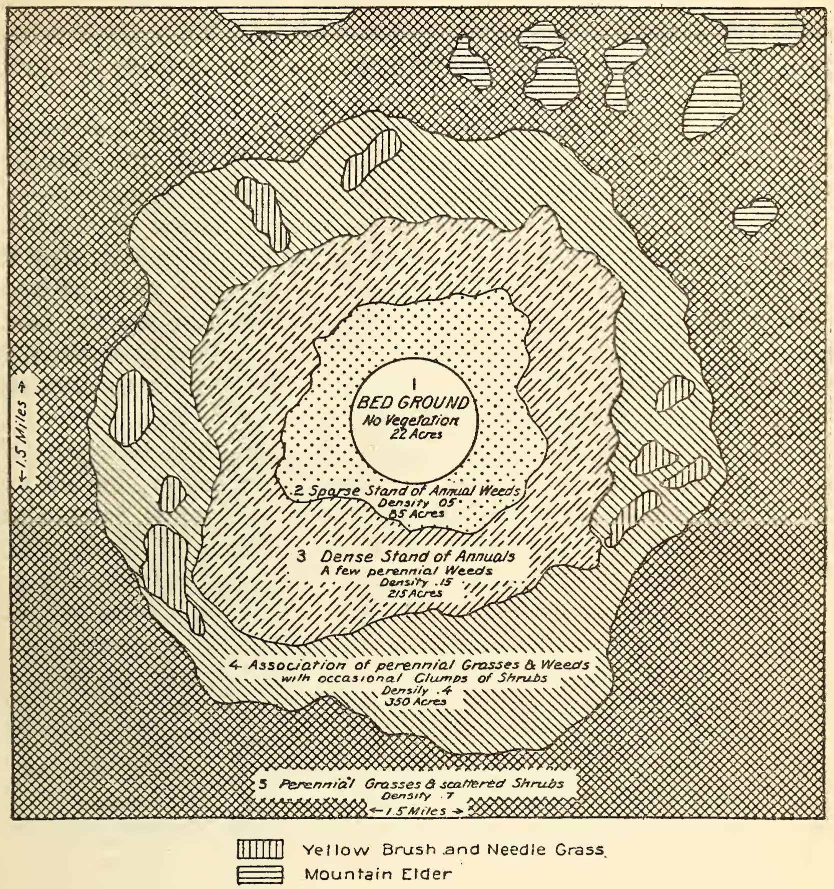


FIG. 24.—Bed ground used for several successive years, showing zones of vegetation and range depletion.

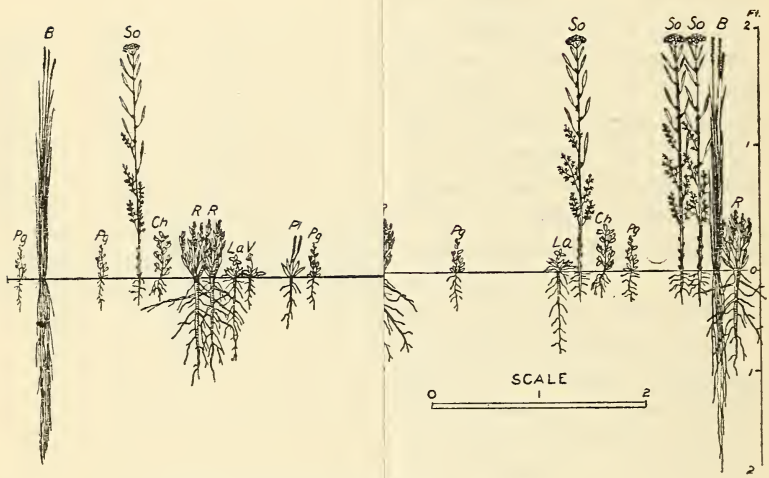
weed stage, a fact which is strongly substantiated in this instance. While they are distinctly second-weed stage species, they may be classed as transitional successionally between the early-weed stage and the second-weed stage when the latter is characterized by turfed plants, such as blue foxglove, sweet sage, and yarrow. Only a small portion of the herbage in this belt is relished by sheep. The feed is low in quality and unless cropped early in the season has practically no forage value.

The fourth zone, a mixed cover of perennial grasses and weeds, comprises an area of approximately 350 acres. The density of this stand is 0.4. The cover as a whole is dominated by plants of the second-weed stage, notably sweet sage and yarrow, though here and there the fescues and the brome grasses have gained dominion over the soil. A few well-defined areas of from a few to many acres are dominated by small mountain porcupine grass and yellow brush. When the density of the cover is considered, this belt affords fairly good feed for sheep; it can not be cropped advantageously by cattle and horses.

The fifth type, composed essentially of a grass cover and an occasional clump of mountain elder, has a density of 0.7. Slender wheat grass and blue bunch wheat grass are the predominating species, while small mountain porcupine grass, several species of the blue grasses, and a few specimens of fescue and of brome grasses occur in varying abundance. In adition, there is a scattered stand of late-weed-stage species, of which sweet sage and yarrow are the most abundant. This type affords good feed for all classes of stock; and the highest grazing efficiency on it may be expected from common use; that is, the grazing both of cattle and sheep.

From the viewpoint of forage production alone, the data pertaining to the use year after year of this established bed ground show:[1] (1) There is practically a total sacrifice of 107 acres, composing zones 1 and 2, which formerly supported at least a 0.7 cover of the choicest of feed—an area large enough to support about 65 sheep, or 16 cows, per summer season of 100 days; (2) there is a belt of 215 acres which, assuming that half of the present vegetation is palatable to stock, may now carry 16 sheep or 4 cows, but formerly would have taken care of 130 sheep, or about 32 cows; (3) there is a zone of 350 acres which, assuming that three-fourths of the cover is palatable, may now carry 105 sheep or 26 cows, but formerly would have supported approximately 210 sheep or 52 cows. In other words, if the range had been used under the bedding-out system, and the lands maintained properly, the data indicate that no less than 280 more sheep, or 70 more cattle, could now be taken care of on this part of the allotment alone. Assuming that there are other similar destructively used bed grounds on the allotment, it is evident that its present car-

[1] In calculating the carrying capacity of the vegetative belts, it is assumed that the entire area originally had a cover similar in density to that of the contiguous perennial grass range at the present time. The writer believes this assumption to be conservative, if not too low, in view of the fact that the soil is deep throughout. Sheep would not completely utilize the former wheat-grass cover with its small amount of weed forage. Cattle, on the other hand, would use little of the weeds. For this reason a deduction of about 14 per cent is made for wastage in utilization of the original cover to be consistent with the deductions for low palatability in the present cover. Since the former wheat-grass cover was undoubtedly much denser prior to the establishment of the bed ground than the present wheat-grass cover on certain portions, no deductions are made for waste of forage in calculating the former carrying capacity of the area.



B, Large mountain brome g*intago tweedyi*).
Ch, Lamb's-quarter (*Cheno*rd (*Sophia incisa*).
H, Mountain squirrel tail (violet (*Viola linguaefolia*).

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rying capacity is far below normal because of the use of established bed grounds.

Contrary to the consensus of opinion among stockmen and others, the reduction in the forage crop on bed grounds can not be classed as temporary. The belief prevails that the large amount of fertilizer contained in the soil on the main part of a bed ground, and on the lands adjacent thereto, will favor the most rapid and thorough revegetation. Experimentation does not substantiate this opinion.

In the plot shown in figure 25[1] after 5 years of protection against grazing, only a sparse stand of vegetation had gained a foothold, the cover being composed chiefly of species of the early-weed stage which are distinctly transitory, notably Douglas knotweed, goosefoot or lamb's-quarters, and tansy mustard, in addition to a few species which have been shown to be forerunners of the more permanent second-stage cover. In addition, the average height of the different species, as well as the depth of their root systems, was considerably less than over the range generally. This delayed colonization is accounted for by the physical rather than by the chemical condition of the soil. To be sure, the abnormally large amount of available nitrogen and other salts in the soil on bed grounds has a tendency to promote the height growth of the plant somewhat at the expense of seed production; but since a large amount of seed is deposited annually on the bed ground, it is not probable that the organic deposits in the soil have any appreciable effect on the rate of the invasion or the extent of the establishment of the vegetation. It is well known, on the other hand, that the soil on bed grounds is packed exceedingly hard. So firmly packed is the surface on long-used bed grounds that nearly all the superficial seed either fails to germinate or the seedling dies as soon as the food stored in the seed is exhausted. As a rule, the radicle of the germinating seed fails to extend itself into the soil to a depth great enough to reach adequate available moisture. Containing, as the local soil does, a large percentage of clay, the trampling, especially in wet weather, tends to produce the single-grain soil structure, which is most unfavorable to establishment and growth of vegetation.

SUCCESSION ON MODERATELY DEPLETED RANGE GRAZED ANNUALLY PRIOR TO SEED MATURITY COMPARED WITH SUCCESSION ON SIMILAR RANGE PROTECTED YEARLONG.

In certain stages of premature grazing or overstocking, the more hardy and persistent perennial plants may become so weakened that all reproduction is temporarily arrested. Long before this condi-

[1] The plot of which figure 25 is typical was fenced against grazing in 1912, prior to which it had been heavily used as a bed ground for several successive years. The bisect here shown traverses the plot and represents a strip 3 inches wide and 16 feet long.

B, Large mountain brome grass (*Bromus marginatus*).
Ch, Lamb's-quarter (*Chenopodium album*).
H, Mountain squirrel tail (*Hordeum nodosum*).
La, Evening primrose (*Lavauxia flava*).
Pg, Douglas knotweed (*Polygonum douglasii*).
R, Mexican dock (*Rumex mexicanus*).
Pl, Plantain (*Plantago tweedyi*).
So, Tansy mustard (*Sophia incisa*).
V, Tongue-leaved violet (*Viola linguaefolia*).

FIG. 25.—Old denuded bed ground abandoned in 1912, showing character of vegetation in 1917.

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tion has manifested itself, however, the less hardy palatable plants have been killed. In such serious instances of physiological weakness, the aerial development of the remaining vegetation is often well-nigh lacking; yet the buds at the crowns of the plants, as well as a considerable portion of the root systems, may survive. So long as the factor disturbing the physiological balance of the vegetation persists, most of the buds at the plant's crown remain dormant, only an occasional aerial shoot being produced to elaborate food and nourish the plant. Where a considerable portion of the vegetation is alive, yearlong protection, or grazing after seed maturity, will greatly promote revegetation. In figure 26 is indicated the effect of protecting yearlong a moderately depleted range. The unprotected area represented has been grazed moderately by sheep and cattle before seed maturity each year during the period of the test, and corresponds to the grazing practice in vogue prior to the experiment. When the protected areas shown in the figure were fenced in 1913, the vegetation appeared identical with that outside in character, density, and vigor.[1] The difference in 1917 in these particulars is summarized in Table 7.

TABLE 7.—*Comparative height and density of vegetation on plot protected from grazing for five successive years and on unprotected adjacent range grazed annually by sheep, usually well in advance of seed maturity.*[1]

Plant.	Density per square foot.			Relative height (physiological index).		
	On protected plot.	On open range.	Per cent difference.	On protected plot.	On open range.	Per cent difference.
Yarrow (*Archillea lanulosa*)	45.6	28.2	38	1.47	0.85	42
Slender wheat grass (*Agropyron tenerum*)	1.6	1.4	12	3.06	1.20	61
Androsace (*Androsace diffusa*)	....	.7	....	....	....	....
Sweet sage (*Artemisia discolor*)	3.2	....	100	1.20	....	....
Aster (*Aster frondeus*)	45.6	16.9	63	1.90	1.03	46
Tall larkspur (*Delphinium barbeyi*)	.8	1.4	[2] 75	5.20	4.40	15
Low pea vine (*Lathyrus leucanthus*)	3.2	2.1	34	1.70	1.20	29
Evening primrose (*Lavauxia flava*)	....	5.6	....	....	....	....
Douglas knotweed (*Polygonum douglasii*)	....	12.7	....	....	1.20	....
Plantain (*Plantago tweedyi*)	.8	1.4	[2] 75	....	....	....
Tansy mustard (*Sophia incisa*)	4.8	4.9	[2] 2	2.82	2.13	24
Small mountain porcupine grass (*Stipa minor*)	12.0	4.2	65	2.56	1.18	54
Dandelion (*Leontodon taraxacum*)	7.2	3.5	51	....	....	....
Meadow rue (*Thalictrum fendleri*)	4.0	0.8	80	2.92	2.92	0
Spiked trisetum (*Trisetum spicatum*)	2.4	2.8	[2] 17	1.95	0.96	51
Tongue-leaved violet (*Viola linguaefolia*)	4.0	1.4	65	....	....	....

[1] The figures here given were compiled from a bisect 16 feet long and 1 inch wide and outside of the protection plot. Owing to the unwieldiness of such a sketch, only half of its length is shown in figure 26.
[2] Indicates more individuals per square foot on the unprotected range than on the protected range.

In the density of the vegetation per square foot, the difference in the percentage figures for the highly palatable perennial plants is

[1] Comparative average height growth of the different species on the fenced and unfenced areas is here used as an index of physiological vigor, of which it is believed to be a reliable criterion.

distinctly in favor of the protected plot. Thus, for instance, yarrow shows a difference of 38 per cent in favor of the protected plot; slender wheat grass, 12 per cent; sweet sage, 100 per cent; small mountain porcupine grass, 63 per cent; and dandelion, 51 per cent. In four species the greatest density occurs on the unprotected area. In the case of at least one plant, tall larkspur, the result is apparently accidental, as the plants concerned are old and thoroughly established, so that it is not probable that they have invaded the area since the establishment of the plot. Two of the species, plantain and tansy mustard, rapidly colonize the more exposed soils, so that their greater rate of increment on the outside range, as compared with that on the better vegetated protected area, is not alogether surprising.

The contrast in the relative height growth of the different species is strikingly in favor of the protected area, the percentages being greater in all but one instance. The exception is meadow rue, a plant which locally is grazed practically not at all, hence is as vigorous physiologically on the unprotected area as on the protected plot. Careful analysis of the data as to relative height shows that the percentage difference is roughly in proportion to the palatability of the plant, as would be expected. According to observations, the difference in height growth corresponds in general to the difference in seed production, the larger seed crop being produced on the protected area. This physiological response, as a result of complete rest of a cover weakened by injudicious grazing, is identical with the vigorous response of a similarly weakened vegetation when the deferred and rotation system of grazing is applied.[1] In either treatment practically complete physiological recovery results in about three years.

[1] Where a good deal of the original forage cover has been destroyed and the remaining plants weakened from overstocking or too early grazing, the deferred and rotation grazing system, if strictly applied, will soon result in revegetation.

In applying the deferred system of grazing, such portion of the range as is consistent with the welfare of the range as a whole is reserved for cropping until after the maturity of the seed of the main forage species. Upon the maturity of the seed, the range is grazed closely, but not destructively, by the stock allotted to the lands. The following year, owing to the large proportion of seedlings destroyed, especially on areas grazed early in the season, the forage is not to be cropped until another season's seed has been produced. If, after the production of two seed crops of the choice native forage species, an ample number of seedling plants have been established, a second area in need of seeding is selected, and the tract upon which grazing was previously deferred is then grazed before seed maturity. This same plan is continued season after season, alternating the deferred grazing first on the one area and then on another, until the entire range has rejuvenated. After the vegetative cover has been established, however, the deferred grazing is alternated or rotated from one portion of the range to another in order to permit the formation and distribution of an occasional seed crop by means of which the old plants may be replaced. In this way the range is brought back and maintained in its maximum state of productivity without the loss of a season's forage crop during the period required for revegetation. For full discussion of this subject see: Sampson, Arthur W., "Natural Revegetation of Range Lands Based upon Growth Requirements and Life History of the Vegetation." Jour. Agri. Research, vol. 3, No. 2, 1914. Sampson, Arthur W., "Range Improvement by Deferred and Rotation Grazing." U. S. Dept. of Agr. Bul. No. 34, 1913.

Owing to the stock working the seed into the ground as the mature herbage is grazed, better reproduction from seed is procured on the area upon which the grazing is deferred than on that protected from grazing yearlong. The vegetative reproduction, on the other hand, is the same in the case of either treatment.

Obviously, the increase in density that occurred on the protected area here shown can not be termed true succession. A large number of running rootstocks of such plants as yarrow, sweet sage, low pea vine, and the like, as well as the weakened inconspicuous tufts of the grasses, existed before the stock was excluded, and the shoots began to appear as soon as sufficient food had been elaborated to stimulate the buds to growth. Therefore, the practice of protecting the lands from stock throughout the year will result in quite as rapid revegetation by vegetative means as will deferred grazing. Reproduction from seed, especially in large-seeded species, however, is much more vigorous on areas where the grazing is deferred until the seed crop has ripened. Hence deferred grazing has all of the advantages of total protection and none of the disadvantages, such, for example, as low or negative reproduction from seed, and waste of forage during the period required for revegetation.

JUDICIOUS GRAZING.

In any well-planned method of grazing designed to handle the lands as permanent grazing areas, two objects must be kept in mind. One is the cropping of the herbage at a time in the season when growth and reproduction will be interfered with as little as possible. The other is the utilization of the forage crop when it is most needed and when the herbage is palatable and nutritious.

At first thought it would appear that the requirements of the vegetation and the requirements of the stock are rather antagonistic, but if proper precautions are taken, this need not be the case. Few plants, even when grazed closely, are appreciably weakened by being grazed early in the season,[1] let us say once in 3 or 4 years. Repeated close early grazing, on the other hand, soon destroys the cover. Through the application of the deferred-and-rotation grazing system, which provides for the cropping of a portion of the range early in the season only every third or fourth year, the vegetation will retain its vitality almost as well as when not utilized at all, provided, of course, that the number of stock carried is correctly estimated. Hence judicious grazing on a well-vegetated area disturbs the cover only to a slight extent.

[1] Early grazing may be defined as cropping of the herbage between the time that the flower stalk is "in the boot" or sheath, that is, on the verge of appearing, and the time of completion of the fertilization of the flowers, approximately between 2 and 4 weeks after growth has begun.

SUMMARY OF THE EFFECT OF GRAZING ON PLANT SUCCESSION ON THE RANGE.

Grazing may cause either progressive or retrogressive succession, depending chiefly upon the closeness with which the herbage is grazed annually and the time when it is cropped. If the forage crop is grazed closely before seed maturity each year, the general trend of the succesion will be retrogressive; if, on the other hand, the crop is maintained in a high state of vigor at all times and then grazed after seed maturity every third or fourth year or so, the succession will be progressive, or, if there is virtually a full ground cover, a maximum density will be maintained. Premature and too close grazing not only favor retrogressive succession and ultimately the destruction of the vegetative cover, but also tend to impair the fertility of the soil through the devastating effect of erosion. The seriousness of the depletion of the soil, provided the lands are judiciously managed, will determine chiefly the time required for thorough revegetation. Therefore, the longer retrogressive succession is permitted to operate the longer will be the time required for the reestablishment of the forage cover. The final outcome of vegetative degeneration and erosion is the translocation of the entire soil formation and the exposure of the underlying rocks. As a rule, however, only the rich surface layer of soil is removed, a condition which favors the immediate establishment of a cover of the first-weed-stage plants.

The continued hard use of established live-stock driveways and bed grounds favors the destruction of the more stable type of vegetation and the establishment of plants of the early and late weed stages. These species afford highly reliable indicators of overgrazing and thus show clearly what lands are being depleted or soon will be in an inferior state of productivity provided the disturbing factor is not corrected. Obviously, therefore, the use of established driveways and bed grounds, especially the latter, tends greatly to decrease the carrying capacity of the lands.

Owing to the hard packing of the soil, these much trampled areas revegetate slowly. The succession on bed grounds, for instance, is similar to that on depleted lands, the revegetation beginning with the early-weed stage and progressing through the intermediate covers to the subclimax.

In the way of revegetation, it is evident that yearlong protection of bed grounds and other depleted lands from live stock tends to hasten vegetative or asexual reproduction no more than when the grazing is deferred until after seed maturity. Deferred grazing, on the other hand, has the additional distinct advantage over yearlong protection of permitting the forage crop to be grazed during the restocking period, and of procuring a maximum stand of seedling plants as a result of the animals planting the seed as they graze. Accordingly, progressive succession is especially active where the deferred-and-rotation grazing system is strictly applied.

GENERAL SUMMARY.

1. The carrying capacity of a large portion of the millions of acres of western ranges has been materially decreased as a result of too early grazing, overstocking, and other faulty management. One of the most serious handicaps has been lack of means of recognizing overgrazing in its early or incipient stages, which has carried with it inability to correct the factor causing the damage before the carrying capacity of the range was more or less seriously depleted.

2. In deciding upon the lands especially in need of improvement in the past, stockmen and forest officers regulating grazing have relied chiefly upon the general abundance and luxuriance of the forage supply and upon the condition of the stock grazed. By these general observations, however, it is not possible to recognize overgrazing before a large proportion of the plants have been killed.

3. The most rational and reliable way of recognizing the incipient destruction of the forage supply is to note the replacement of one type of plant cover by another, a phenomenon which is usually much in evidence on lands used for the grazing of live stock.

4. In tracing the succession of plant life from the consolidated rock to a well-disintegrated, fertile soil several fairly distinct cover stages are recognized. These stages may be grouped as follows: (1) The algæ-lichen type, the pioneer stage; (2) the lichen-moss type with its sparse stand of annual herbs, the transition stage; (3) the ruderal-weed type or cover of annual plants with a scattered stand of short-lived perennials, the first-weed stage; (4) perennial herbs, chiefly weeds, the second-weed stage; and (5) the long-lived perennial grasses, known as the subclimax, or under some conditions, the climax type.

5. In order to observe the principles of succession in the building up as well as in the deterioration of the range, special studies were initiated on the high summer range of the Wasatch Mountains in central Utah. After a careful survey of the vegetation, four major consociations were recognized, namely, the wheat-grass, the porcupine-grass-yellow-brush, the foxglove-sweet-sage-yarrow, and the ruderal-early-weed.

THE WHEAT-GRASS CONSOCIATION.

6. The wheat-grass consociation is the subclimax or highest forage type successionally. The turfed wheat-grass cover binds the soil so firmly as largely to prevent the invasion and establishment of other

plants. The bunched wheat-grass areas, on the other hand, are seldom pure in stand, and plants other than grasses usually occupy the soil space between the tufts. The nongrasses occur in varying density, depending chiefly upon the available soil water content.

7. The root-absorbing surface of the densely turfed wheat grasses is relatively superficial, the greater proportion of the roots being confined to the upper 8 inches of soil. The roots of the bunched species typically extend to a depth of 3 feet or more, hence their moisture supply is largely gathered well below the depth at which the turfed species obtain theirs.

8. Precipitation percolates so slowly through the matlike surface of the turfed wheat-grass area that only a small portion of the rainfall, especially that which comes during the growing season, penetrates beyond the lower depths of the sod. Accordingly, other plants, especially deep-rooted species, fail to become established in competition with the turfed wheat grasses.

9. Precipitation percolates deeply on the rather exposed soils of the bunch-grass areas, and as a consequence both deep-rooted and shallow-rooted species, chiefly other than grasses, are commonly found on bunch wheat-grass areas.

11. When a stand of bunch wheat grass is opened up there is an some similar factor but not so as seriously to decrease the fertility of the soil, the precipitation naturally percolates to a much greater depth than where the turf remains intact. There follows an invasion of certain deep-rooted species, the most typical and persistent of which is yellow brush (*Chrysothamnus lanceolatus*). As the wheat-grass cover closes in about the yellow-brush plants, however, regardless of their luxuriance of growth and root development, they are killed. This is due to the desiccation of the soil below the shallow roots of the grass.

11. When a stand of bunch wheat-grass is opened up there is an increase in the density of other plant species. This secondary cover is rather transitory both as to species and density.

12. In terms of the amount of dry matter produced per unit of surface, the turfed wheat-grass areas rank first, but owing to small wheat grass (*Agropyron dasystachyum*), the most conspicuous turfed species, maturing somewhat earlier than the bunch grasses and at the same time becoming less palatable when mature than the bunch grasses, the turfed wheat-grass areas afford little, if any, more forage than do the bunched wheat-grass areas.

13. The wheat-grass type is the most permanent of any and withstands heavy grazing better than any other. Since the turfed wheat grasses typically form a pure stand, this type of vegetation is better suited for cattle and horses than for sheep. The virgin bunch-grass lands, with their "combination" or mixed forage cover, while

probably more fully utilized by cattle and horses than by sheep, are better suited for the grazing of sheep than the turfed wheat-grass areas. The grazing both of cattle and sheep on the bunch-grass lands, as well as on the opened-up stands of the turfed areas, insures the maximum economic use of the entire forage crop.

THE PORCUPINE-GRASS-YELLOW-BRUSH CONSOCIATION.

14. The small-mountain-porcupine-grass and yellow-brush cover is the second highest and the most stable forage type. Accordingly, porcupine grass and yellow brush are among the first perennial plants to occupy wheat-grass areas where unfavorable conditions have killed out the wheat-grass cover but where the soil has not been depleted so much as to favor the establishment of a pure or predominating weed type.

15. Because of the exposure of a considerable portion of the soil surface, precipitation readily percolates into the soil, reaching to or beyond a depth corresponding to the lower extension of the deep-rooted species. Accordingly, an admixture of shallow-rooted and deep-rooted species is characteristic of this consociation. The water-holding capacity of the soil, particularly the upper foot or so, is less in this than in the wheat-grass cover.

16. In the higher development of the porcupine-grass and yellow-brush cover a scattered stand of wheat grasses, and usually a conspicuous presence of blue grasses, and not uncommonly of fescues, is characteristic, though these plants are never dominant. In the lower or earlier development, the brome grasses, and not uncommonly the fescues, in association with numerous nongrasslike perennials, are conspicuous. The higher development is further characterized by fewer weed or nongrasslike species than the lower development.

17. Small mountain porcupine grass, like the majority of the blue grasses and fescues, obtains its moisture supply chiefly from the first foot of soil. Yellow brush and other deep-rooted species, such as loco and wild bean, extend their roots about three or four times as deep. Many plants are present whose root systems are intermediate in length, so that the available water supply from the surface to a depth of 3 feet or more is rather uniformly exhausted as the season advances.

18. The most reliable indication of the presence of conditions adverse to the perpetuation and maintenance of the porcupine-grass-yellow-brush cover, including the typical associated species, is the replacement of one or both of the dominants by aggressive nongrasslike plants. Where the depletion of the soil is gradual and not too severe, blue foxglove, sweet sage, and yarrow are the first to gain dominion over the soil, the increase in these species being associated with an increase in brome grass, and in some cases in fescues.

19. A reliable indication pointing toward the maintenance, or the progressive development of this cover, is an increasing density and luxuriance of growth of certain blue grasses, and in some instances fescues, and a decreasing stand of the brome grasses, and under certain conditions of yellow brush and other deep-rooted species.

20. With its large variety of palatable grasses and other plants this consociation is probably second to none in forage value, all classes of stock considered.

21. In general the highest possible development of this consociation affords the most nutritious forage cover, and will probably support more stock than will any other stage of plant development. It is a mixed grass-and-weed type, with the grasses distinctly predominating, and the highest grazing efficiency is obtained through "combination" or "common-use" grazing, that is, the grazing of cattle, sheep, and horses.

THE FOXGLOVE-SWEET-SAGE-YARROW CONSOCIATION.

22. Where conditions on the porcupine-grass-yellow-brush cover are such as slightly to decrease the fertility and water-holding power of the soil, blue foxglove, sweet sage, and yarrow, the most characteristic species of the second-weed stage, are among the first plants to establish themselves. Where the fertility and water absorptive capacity of the soil are seriously impaired, porcupine-grass-yellow-brush cover is succeeded by annual plants characteristic of the early or first weed stage.

23. Generally the invasional activity of the succeeding late-weed-stage plants is most vigorous shortly after the destruction of the grass-brush cover.

24. A large number of species, including some grasses, are associated with blue foxglove, sweet sage, and yarrow, but they seldom, if ever, occur as dominants. Like the dominant plants, the secondary species are moderately deeply rooted, the water supply being drawn very largely from the upper 2 feet of soil.

25. Blue foxglove, sweet sage, and yarrow reproduce both by seed and by vegetative means, the latter method being so active that the cover characteristically forms a somewhat loose, matlike surface. The seed habits are only moderately strong, yet invasion is fairly active under favorable conditions of germination and growth. Seedling plants as a rule do not produce either fertile seeds, or many shoots from the rootstocks, until the third year of growth.

26. Low pea vine, evening primrose, false cymopterus, Mexican dock, and tongue-leaved violet are the most reliable indicators of the waning of the more permanent and typical second-weed-stage cover. With the exception of pea vine the regeneration of these species is

entirely dependent upon seed. The seed crop is relatively high in viability. However, if the factor detrimental to progressive development of the vegetation is not corrected, these relatively short-lived perennials will sooner or later be superseded by plants of the first-weed stage.

27. The profusion of weedy or nongrasslike plants and the limited occurrence of grasses render the second-weed stage much better suited for sheep than for cattle and horses.

28. The carrying capacity of the second-weed-stage type, acre for acre, is very much less, regardless of the class of stock grazed, than of the porcupine-grass-yellow-brush cover. In addition, a less solid fat is produced.

29. Sheep make rapid gains on the second-weed-stage type early in the season when the herbage is succulent and tender. Cattle and horses, on the other hand, little more than maintain their weight even though the lands are lightly stocked. The vegetation matures early, after which the leafage is largely unpalatable to stock, and the herbage of many species is largely lost through the destructive effect of frost. Therefore the lands are of little value for grazing unless cropped early in the season.

THE RUDERAL-EARLY-WEED CONSOCIATION.

30. On lands whose soils have been so seriously impaired that available water is similar in amount to that held by relatively newly formed soils recently invaded by herbaceous plants, the vegetation consists essentially of annual species characteristic of the first or early weed stage.

31. The most typical and abundant species of the first-weed stage are goosefoot or lamb's-quarters, slender-leaved collomia, tarweed, Tolmie's orthocarpus, Douglas knotweed, and tansy mustard. Numerous less abundant species are associated with these.

32. The seed habits of ruderal-weed plants are strong, the viability of the seed crop averaging considerably higher than that of the perennial species.

33. Because of the entire dependence of the plants on seed for their regeneration and the fact that the conditions of the season are not always favorable to seed production or germination, there is wider variation in the density of the stand of the first-weed-stage cover from year to year than in that of any other consociation.

34. Owing to the low fertility of the soil characteristic of the first-weed stage it contains less available moisture than soil of the higher ecological types. This tends to hold the development of the vegetation in check. At the same time plants grown on inferior soils of this kind require appreciably more water for the production of a

.chillea lanulosa
eatgrass (Agrop
(Androsace dif
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ter frondeus)
ur (Delphinium
.athyrus leucant
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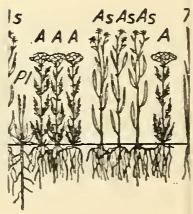

itive cover on range

given unit of dry matter than those grown on more fertile soils. This accounts for the colonization of the badly depleted soil by shallow-rooted, early-maturing, annual vegetation, and the practical exclusion of the deeper-rooted, later-maturing, perennial species.

35. The further depletion of the soil tends to decrease the density of the stand and the luxuriance of growth of the individual specimens. If the depletion is continued until the underlying rocks are exposed, the pioneer stage of plant life—algæ and lichens—again comes into evidence.

36. A considerable number of the ruderal-weed plants are palatable to sheep, a few are grazed by cattle, and a very few by horses. Douglas knotweed, the most abundant species, is fairly palatable to sheep, and probably furnishes as much forage as, if not more than all the rest of the annuals put together. The carrying capacity of the ruderal-weed consociation is exceedingly low, and affords grazing only when the herbage is green and succulent.

37. Because of the early-maturing qualities of the vegetation and the fact that the first-weed-stage cover affords poor protection of the watershed, only the very lightest grazing should be permitted on this type. The safest plan is to exclude stock until the cover has increased appreciably.

THE EFFECT OF GRAZING ON RANGE PLANT SUCCESSION.

38. Grazing may cause either progressive or retrogressive succession, depending chiefly upon the closeness with which the herbage is grazed annually and the time of grazing. Grazing year after year before seed maturity causes retrogressive succession, while grazing every 3 or 4 years or so after seed maturity promotes progressive succession.

39. Overgrazing year after year results not only in the destruction of the ground cover, after which erosion is apt to occur, but robs the soil of its fertility and producing capacity.

40. The rate and character of the colonization of an eroded or otherwise depleted area is normally determined by the degree of soil devastation. The longer retrogressive succession continues, therefore, the more serious is the depletion of the soil and the longer is the time required to reestablish a good ground cover. The ultimate result of continued serious erosion is the exposure of the underlying rock formation.

41. The continued use of stock driveways and bed grounds results practically in complete destruction of the subclimax plant cover, thus favoring the establishment of plants of lower successional stages. The species constituting the cover from time to time afford reliable indicators of overgrazing and inferior states of soil productivity.

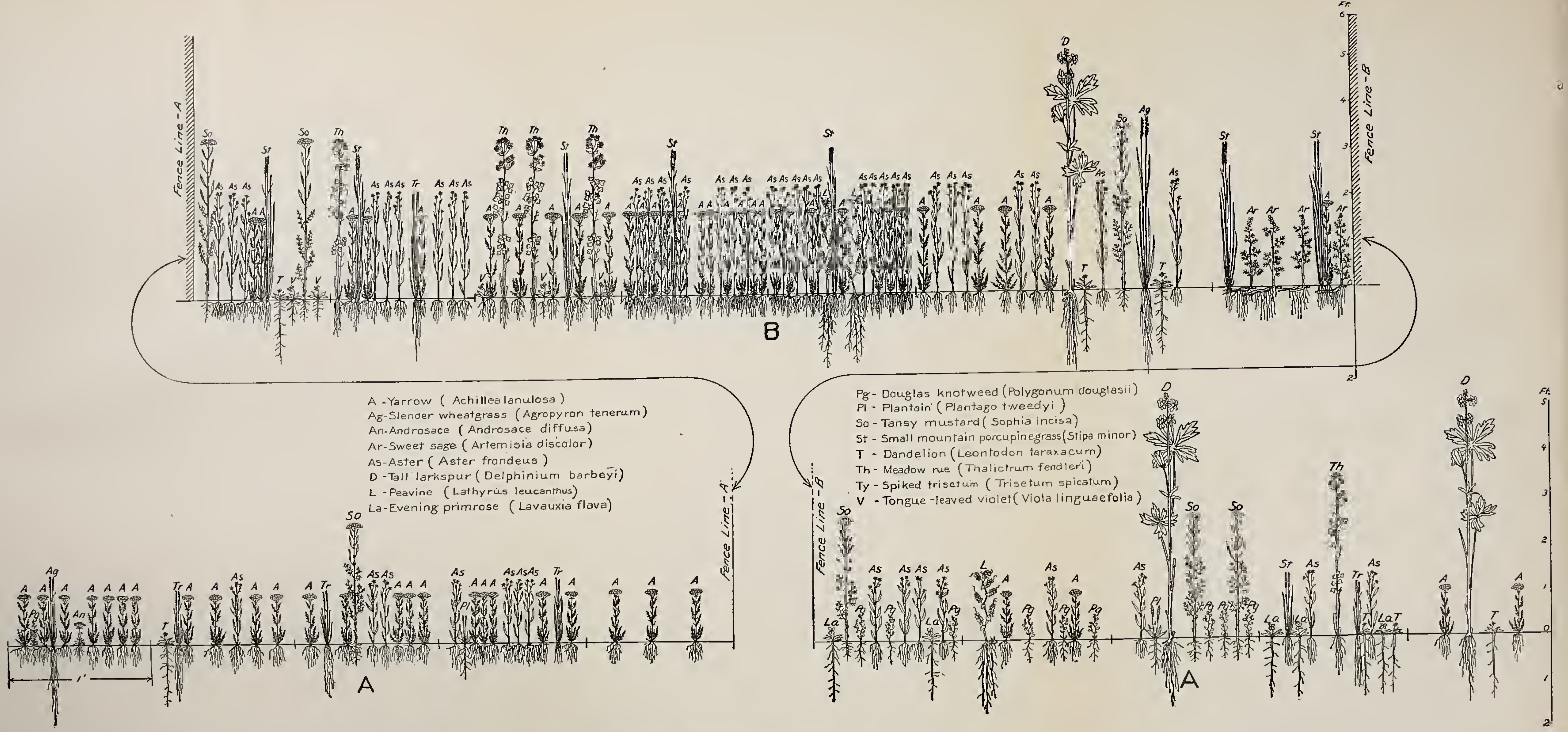

Fig. 26.—Comparative vegetative cover on range (A) grazed annually by sheep prior to seed maturity, and on plot (B) protected from grazing for five successive years, 1913–1917.

42. The use of established driveways and bed grounds, especially the latter, tends materially to decrease the carrying capacity of the lands. Owing to the packing of the soil by the animals, these areas revegetate slowly, the colonization usually starting with species of the early-weed stage.

43. Yearlong protection of driveways and bed grounds, as well as of other sparsely vegetated lands, tends to promote a sexual reproduction no more than deferring the grazing until after seed maturity. Deferred grazing has all the advantages of yearlong protection and none of the disadvantages, such, for example, as low or negative reproduction from seed and waste of forage during the period required for revegetation.

44. Judicious grazing tends to maintain a normal cover of vegetation, while on lands where the stand is sparse, there is a tendency toward the promotion of an upward succession leading to the ultimate establishment of the subclimax species. Progressive succession is particularly active where the deferred and rotation grazing system is strictly applied.

COMPARATIVE FORAGE VALUE.

45. The grazing value of the vegetative covers is essentially determined by the stage of the succession. Locally, and indeed generally, the carrying capacity and forage value are the highest where the cover represents a stage in close proximity to the herbaceous climax and lowest in the type most remote from the climax.

46. The most dry matter per unit of surface is produced in the wheat-grass cover, but the amount is only slightly greater than in the mixed grass-and-weed cover of which porcupine grass and yellow brush are characteristic. By far the least dry matter is found on the ruderal-weed cover, while the amount produced on the second-weed-stage type averages considerably less than on the mixed grass-and-weed type. All classes of stock considered, the porcupine-grass-yellow-brush cover produces more palatable dry matter than any other. For horses and cattle alone, more palatable dry matter is produced on the wheat-grass consociation. Accordingly, virgin stands of wheat grass afford the highest grazing efficiency and will give the biggest returns when cropped by cattle or by cattle and horses; the mixed grass-and-weed type when utilized by cattle, horses, and sheep; and the weed type, if composed either of plants of the first or of the second weed stage, when utilized by sheep alone. Except in practically a pure-weed type or a pure-grass type, the common use of the lands by the various grazing animals is generally justified. As a rule, when the most stable grass type is cropped by cattle and horses alone, it is soon sufficiently opened up to permit the establishment of at least a moderate proportion of weed plants, most of which

are highly palatable to sheep but which may be grazed little or not at all by cattle and horses. Likewise a weed cover grazed exclusively by sheep will sooner or later change to the grass stage.

INDICATORS AND THEIR USE.

The data in this bulletin justify the conclusion that the character of the native vegetation can be used as a reliable indicator of the condition of the range and of the effect of a given method of grazing on the plant cover.

The plant indicators signifying the waning of the wheat-grass cover are essentially porcupine grass and yellow brush; the retrogression of the porcupine-grass-yellow-brush cover is indicated by species of the second-weed stage of which blue foxglove, sweet sage, and yarrow are the most characteristic; the giving way of the second-weed-stage cover, here recognized by blue foxglove, sweet sage, and yarrow, is indicated by the appearance of low pea vine, evening primrose, false cymopterus, Mexican dock, and tongue-leaved violet, in addition to several species of first-weed-stage plants of which goosefoot, slender-leaved collomia, tarweed, Tolmie's orthocarpus, and Douglas knotweed are typical; and the recession or destruction of the first or early weed stage is marked, first, by the thinning out and decrease in the luxuriance of growth of the annual species, and, ultimately, by the erosion of the soil to the extent of exposing the underlying rock and destroying the holdfast for herbaceous vegetation, thus favoring the reappearance of lichens and algæ of the initial or pioneer stage.

APPLICATION OF PLANT SUCCESSION TO RANGE MANAGEMENT.

The species that are increasing appreciably on the range invariably reveal one of two stories. If the invading plants are lower in the succession than the predominating vegetation, the range is being utilized unwisely in one or more respects. If the incoming vegetation is somewhat higher successionally than the type as a whole, improvement under the management in vogue is sure to follow. Where the negative indicators are crowding out the more permanent and desirable species, remedial measures should be adopted with a minimum loss of time.

Since, as pointed out, range depletion is due chiefly to too early cropping or to overgrazing, the application of the deferred-and-rotation grazing system, coupled with a correct estimate of the carrying capacity of the range, may be relied upon fully to revegetate the lands where enough plants of desirable species are found for seed production. Areas in the first-weed stage, in the absence of desirable forage plants, should not be included in the general plan of deferred grazing. Ranges that have been so destructively used as to support chiefly annual vegetation, can not be grazed without further deterioration. Such areas should be entirely closed to stock until the cover is clearly composed of plants of the second-weed stage. Strict application of the deferred grazing system should be applied on areas in the second-weed stage and the practice should be continued until the porcupine-grass-yellow-brush consociation has attained its maximum productivity. After that the deferred grazing plan should be rotated so that each part of the allotment is grazed after seed maturity at least once every 4 or 5 years. In general, there is little or no justification for handling the lands so as to maintain a more or less pure wheat-grass cover. If a good forage crop is to be maintained, however, the practice of using established bed grounds, of too close herding, the excessive use of dogs, and other practices which tend to destroy the vegetation must be avoided as far as possible.

In using the plant indicators as a guide to determine whether or not the range is in need of a change in the management it is well to adopt some definite means of ascertaining the changes that are taking place in the plant cover. While carefully selected plots, the vegetation of which is accurately mapped, are desirable, a careful systematic ocular estimate of the composition and density of the vegetation will suffice in practice. This can be made in various ways. A reliable method, however, is to select carefully some four or five typical areas over the allotment and lay out a plot, let us say, of 2 square rods on each area. After securely staking and tying in the plot to insure its relocation in future, list the chief indicator species as well as the most important forage plants, either the local or Latin name being used, and estimate closely the comparative density of each. Greater accuracy both in listing and in estimating comparative density is secured by running a cord around the corner stakes of the plot and across the plot where the vegetation is dense or forms a rank growth. The value of this work is greatly enhanced by collecting and preparing for the herbarium the main indicator and forage species found on the selected area, and by procuring good photographs showing the character and density of the vegetation additional features of high value may be shown.[1]

The plants here listed as indicators of range conditions are not necessarily the same as those of other regions in the West. As a rule the same genera will be represented, but in many instances the species will be different. As pointed out, reliable indicators of the more serious stages of overgrazing of any region may be determined by study-

[1] In photographing plots it should be the aim to locate, by means of permanently established stakes, the exact place and angle where the original view is procured. Subsequent photographs may then be taken showing the progressive development of the vegetation over the same surface.

ing the plants that characteristically occur on and about bed grounds, on trails, and on other badly depleted areas.

The following list gives the most typical primary and secondary species of the respective covers.

Wheat-grass cover (subclimax type):
- Primary species—
  - Small wheat grass (*Agropyron dasystachyum.*)
  - Blue bunch wheat grass (*Agropyron spicatum*).
  - Slender wheat grass (*Agropyron tenerum*).
- Secondary species—
  - Violet wheat grass (*Agropyron violaceum*).

Porcupine-grass-yellow-brush cover (mixed grass-and-weed type):
- Primary species—
  - Small mountain porcupine grass (*Stipa minor*).
  - Yellow brush (*Chrysothamnus lanceolatus*).
- Secondary species—
  - Blue foxglove (*Pentstemon procerus*).
  - Geum (*Geum oregonense*).
  - June grass (*Koeleria cristata*).
  - Large mountain brome grass (*Bromus marginatus*).
  - Little blue grass (*Poa sandbergii*).
  - Low loco (*Astragalus decumbens*).
  - Nevada blue grass (*Poa nevadensis*).
  - Porter's brome grass (*Bromus porteri*).
  - Single-flowered helianthella (*Helianthella uniflora*).
  - Spiked fescue (*Festuca confinis*).
  - Spiked trisetum (*Trisetum spicatum*).
  - Sweet sage (*Artemisia discolor*).
  - Western fescue (*Festuca occidentalis*).
  - Wild bean (*Lupinus alpestris*).
  - Yarrow (*Achillea lanulosa*).

Foxglove-sweet-sage-yarrow cover (second-weed stage):
- Primary species—
  - Blue foxglove (*Pentstemon procerus*).
  - Sweet sage (*Artemisia discolor*).
  - Yarrow (*Achillea lanulosa*).
- Secondary species—
  - Aster (*Aster frondeus*).
  - Butterweed (*Senecio columbiana*).
  - Cinquefoil (*Potentilla filipes*).
  - Evening primrose (*Lavauxia flava*).
  - False cymopterus (*Pseudocymopterus tidestromii*).
  - False Solomon's seal (*Vagnera stellata*).
  - Geranium (*Geranium viscossissimum*).
  - Horsemint (*Agastache urticifolia*).
  - Large mountain brome grass (*Bromus marginatus*).
  - Low larkspur (*Delphinium menziesii*).
  - Low pea vine (*Lathyrus leucanthus*).
  - Mexican dock (*Rumex mexicanus*).
  - Mountain dandelion (*Crepis acuminata*).
  - Porter's brome grass (*Bromus porteri*).
  - Onion grass (*Melica bulbosa*).

Rubberweed (*Hymenoxys floribunda*).
Sampson's mertensia (*Mertensia sampsonii*).
Scribner's wheat grass (*Agropyron scribneri*).
Snowy onion grass (*Melica spectabilis*).
Sneezeweed (*Helenium hoopesii*).
Tongue-leaved violet (*Viola linguaefolia*).

Ruderal-early-weed cover (first-weed stage):

Primary species—

Douglas knotweed (*Polygonum douglasii*).
Goosefoot or lamb's-quarters (*Chenopodium album*).
Slender-leaved collomia (*Collomia linearis*).
Tarweed (*Madia glomerata*).
Tansy mustard (*Sophia incisa*).
Tolmie's orthocarpus (*Orthocarpus tolmiei*).

Secondary species—

Androsace (*Androsace diffusa*).
Gilia (*Gilia micrantha*).
Knotweed (*Polygonum aviculare*).
Monolepis (*Monolepis nuttalliana*).
Peppergrass (*Lepidium ramosissimum*).

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