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ESTABLISHMENT AND SUCCESSION OF VEGETATION ON DIFFERENT SOIL HORIZONS

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VEGETATION AND SOIL PROFILE

It has long been recognized that different plant species occupy rather distinct soil profiles.(4, 6) Typically, species of the first herb stage inhabit soil profiles where the upper stratum has been removed or where the edaphic conditions of the upper stratum have been altered by biotic influences.(3) In incipient stages of erosion the second herb stage is in evidence. When erosion has not proceeded beyond the norm and the soil profile is mature, climax species usually predominate.

This investigation was initiated for the purpose of studying the behavior of seral activities upon areas where the soil profile had been disturbed in varying degrees. The specific points investigated were: (1) the influence of soil horizons A, B, and C, as delineated by Glinka(3) and others, on the rate of growth of certain annual plants which dominate early successional stages, compared to certain perennial herbs recognized as stable or climax in grassland communities; (2) the comparative plant development in soil horizons A, B, and C; (3) the time of seed maturity in the respective soil horizons of extensive soil series of the state; (4) the water requirements of plants developed in the different soil horizons; and (5) the differences in growth and in water requirements in soils naturally packed as compared with those artificially packed.

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PROCEDURE

The Soils.—Three residual soil series were used, each representing an extensive soil type in California. Two of the series—the Holland and the Aiken—are typical of the Transition Life Zone of the Sierra Nevada Mountains and support a cover of *Pinus ponderosa.* The third series, known as the Olympic, is representative of the Upper Sonoran Life Zone, occupied by woodland in savannah, and was procured in the hills east of Berkeley. Residual soils were used because of the desire to identify the parent material and to be able to determine the depths of the different horizons.

It should be recalled that horizon A is the upper horizon of the soil mass, the surface soil, which typically contains more or less decomposed organic matter and the layer from which various materials have been removed by percolating waters. Horizon B has been referred to as the horizon of deposition, the subsoil, or the layer in which materials have accumulated through percolation. Horizon C is the horizon of comparatively unweathered material, the substratum, underlying horizon B.

The Plants.—Six plant species were used, namely (1) *Stipa pulchra,* a perennial needle grass recognized as typical of climax and subclimax plant associations, found over extensive areas of the state. Its dominance indicates a well developed A horizon[(7)]; (2) *Danthonia californica,* a native perennial bunchgrass found typically in the climax stages of plant succession, hence occurring on lands where soil horizon A is well developed; (3) *Bromus hordeaceus,* and *B. rubens,* annual native grasses of the Mediterranean region but common throughout uncultivated areas of California, and characteristic of low seral communities; (4) *Erodium cicutarium,* an annual herb, believed also to have been introduced from the Mediterranean region; (5) *Triticum vulgare,* a variety known as Sonora wheat. This species was used as a check in each soil horizon studied.

The Phytometers.—The soils and plants were placed in phytometers 16 inches in diameter and 18 inches deep, made from No. 18 galvanized iron. A 6-inch overlap of the rim of the lid extended over the side of the container into a water jacket 7 inches deep, thus forming a water seal between the lip of the lid and the can. Five plants were grown in each phytometer, the lid being perforated for each plant. A capillary tube inserted through a rubber stopper maintained atmospheric pressure and gaseous interchange within the container. Enough soil was removed from the center core of the phytometer to allow for a receptacle 5 inches in diameter and 2½ inches deep, with perforations in the bottom. The receptacle was underlaid with coarse sand, which facilitated uniform distribution of water through the entire soil mass during irrigation. At the end of the experiment it was found that the roots were well distributed in the soil and that the soil moisture content was practically uniform throughout. Several phytometers were equipped with removable bottoms which made possible filling them in the field with naturally packed soil, as described below.

Soil Treatment.—To procure the soils, the phytometers with removable bottoms were sunk into the earth and filled with the soil column. Such phytometers will be referred to as "naturally packed," in opposition to those whose soils were "artificially packed." The soils of the artificially packed phytometers were compacted so that they occupy practically the same volume as in nature. In procuring soils from horizons B and C, the overlying soil was first removed. Since the soils were collected in the autumn and were relatively dry, their moisture content was raised to approximately 10 per cent above the wilting coefficient, the latter being calculated from the moisture equivalents (Shantz and Briggs,[9] pp. 55–57). Special care, as previously indicated, was taken to so work the soil while raising its water content as to procure uniformity of moisture throughout the soil mass of the packed phytometer.[2]

Planting and Recording Growth.—Seed of the species used was collected in the hills east of Berkeley, California. The seed was carefully selected as to size and maturity, and, after germination, seedlings of uniform size were selected and planted in the phytometers. To prevent evaporation from the soil exposed due to the perforations in the lids, a thin layer of a mixture of tallow and beeswax was applied in a melted condition. Except for a short period while the seedlings were becoming established, the phytometers were kept out-of-doors. To prevent excessive heat and possible curtailment of root development the phytometers were packed in moss and held at a temperature much the same as that of the undisturbed soil of the habitat.

The leaves of each plant were counted and their lengths measured at 14-day intervals, these periods corresponding to the dates when the phytometers were brought up to weight by adding water (Sampson and Weyl,[8] p. 14). The length of stems and of inflorescence of each plant were also recorded. Plants which matured before the termination of the experiment, as a whole, were harvested when the seed ripened. The late maturing species were allowed to grow until

November 1. Harvesting consisted of cutting the plants at the surface of the soil. All plant material was dried in an oven at 80° C for a period of 48 hours and the dry weight of panicle or spike, and stems and leaves recorded.

Physical Factor Measurements.—A class "A" physical factor station was maintained near the experiment. The factors recorded were air and soil temperature, precipitation and evaporation. These measurements were of value chiefly because they showed that conditions were favorable for plant growth during the experimental period.

Experimental Error.—Slight variations in the growth rate of a species were noted within a single phytometer. These variations may be accounted for in part by differences in the soil, but they were probably caused chiefly by the inherent tendency of individual plants to vary. The probable error in each mean measurement for each species in the respective soil horizons was calculated and is presented in table 1.

TABLE 1

THE PROBABLE ERROR OF PLANT MEASUREMENT IN EACH SOIL HORIZON

Plant species	Soil, series and horizon	Leaf length		Weight of dry material	
		Average per plant	Probable error‡†	Average per plant	Probable error‡†
		centimeters	*centimeters*	*grams*	*grams*
Stipa pulchra	Holland A*	3152.6	557.9	9.56	1.92
Stipa pulchra	Holland A	1938.8	133.2	7.40	2.13‡
Stipa pulchra	Holland B	463.0	56.5	1.52	0.32
Stipa pulchra	Holland C	399.8	39.2‡	1.22	0.14‡
Stipa pulchra	Holland C*	140.6	63.5	0.16	0.06
Triticum vulgare	Holland A*	896.2	90.9	20.78	1.60
Triticum vulgare	Holland B*	259.4	43.9	6.90	1.49
Triticum vulgare	Holland C*	56.5	5.9	1.00	0.34
Erodium cicutarium	Aiken A*	247.0**	147.3	6.16	4.75
Erodium cicutarium	Aiken B*	30.3**	10.8	1.06	0.30
Triticum vulgare	Aiken A	262.9	48.1	11.08	3.09
Triticum vulgare	Aiken B	26.9	5.2	0.32	0.16
Triticum vulgare	Aiken B*	154.6	49.5	4.52	1.30
Danthonia californica	Olympic A	2951.4	356.9	6.76	1.68
Danthonia californica	Olympic B*	1206.1	651.3	2.42	1.28
Bromus rubens	Olympic A*	1306.5	326.0	6.76	1 69
Bromus rubens	Olympic B*	496.9	273.5	4.20	2.30‡
Triticum vulgare	Olympic A*	101.1	7.1	2.30	2.03
Triticum vulgare	Olympic B*	70.5	27.3‡	0.84	0.48‡

*Artificially packed soil

**Average stem length per plant.

†Formula used in determining *probable error* is: the summation of all the deviations from the mean, regardless of sign, divided by the number of cases, multiplied by the constant 0.845 (Peter's formula).

‡Probable errors of comparative data conflict.

In cases where the probable errors of comparative data overlap, positive results were procured with other species in the same soil series.

RESULTS AND DISCUSSION

The results are discussed under (1) rate of growth; (2) extent of plant development; (3) time of seed maturity; (4) water requirements; and (5) the effect of naturally and of artificially packed soils.

Rate of Growth.—The rate of growth was procured by noting the total length of leaves (length of stems with *Erodium cicutarium*) to a plant. The results are summarized in table 2.

TABLE 2

RATE OF GROWTH IN HORIZONS A, B, AND C OF THE HOLLAND SOIL

Date	Stipa pulchra					Triticum vulgare				
	Leaf length per plant			A=100 per cent		Leaf length per plant			A=100 per cent	
	A	B	C	B, per cent of A	C, per cent of A	A*	B*	C*	B, per cent of A	C, per cent of A
	centimeters	*centimeters*	*centimeters*			*centimeters*	*centimeters*	*centimeters*		
April 5	88.9	13.6	11.5	15.29	12.93	....	....	....	....	....
April 19	246.7	19.4	9.8†	7.87	3.97	....	....	....	....	....
May 3	596.8	34.4	23.5	5.76	3.94	....	....	....	....	....
May 17	949.3	69.6	44.8	7.33	4.72	20.3	9.3	7.7	45.82	37.94
May 31	1119.9	120.9	69.2	10.80	6.18	109.6	25.6	13.7	23.37	12.50
June 14	1447.0	248.1	187.1	17.14	12.92	645.7	142.5	28.7	22.08	4.45
June 28	1809.2	330.0	280.7	18.24	15.50	828.7	250.5	37.7	30.20	4.55
July 12	1938.8	463.8	399.8	23.88	20.63	885.0	259.8	48.1	29.36	5.42
July 26	....	585.0	556.9	....	....	877.5	260.5	54.2	29.70	6.18
Aug. 23	....	875.4	875.6	....	....	887.3	250.5	58.4	28.24	6.58
Sept. 20	....	1220.1	1155.2	....	....	896.2	259.4	56.5	28.95	6.69

*Artificially packed soils. †Decreased length due to broken leaves.

In all instances growth was more rapid in horizon A than in horizon B regardless of the soil type or species used. Moreover, growth in horizon B was greater and more rapid than in horizon C, although the contrast in these horizons was less than in the two uppermost.

In the Holland soil the growth of *Stipa pulchra*, a climax species, and of *Triticum vulgare* (fig. 1), is outstanding. In horizon B growth of *Stipa pulchra* at maturity was 23.88 per cent of that in horizon A, whereas in horizon C the total growth was 20.63 per cent of that in horizon A for the corresponding period. In horizon B the growth of *Triticum vulgare* was 28.95 per cent of that in horizon A at the time the plants reached maturity, whereas in horizon C the total leaf length was only 6.69 per cent of that produced in horizon A.

The difference in growth of *Stipa pulchra* in horizons B and C at the time of maturity of the plants grown in horizon A was only 3 per cent of the growth produced in horizon A. With *Triticum vulgare* the difference in growth in the lower horizons was appreciably more, being 22 per cent of the growth in horizon A. These differences are probably not surprising, for extensive observations have indicated that climax species are more exacting in their growth requirements than are ruderal species.

In the Aiken soil the rate of growth of *Erodium cicutarium* in horizon B was 12.27 per cent of that in horizon A at the time of simultaneous harvesting. With *Triticum vulgare* the plants grown in horizon B were 10.24 per cent of those produced in horizon A when the plants of the latter horizon had matured.

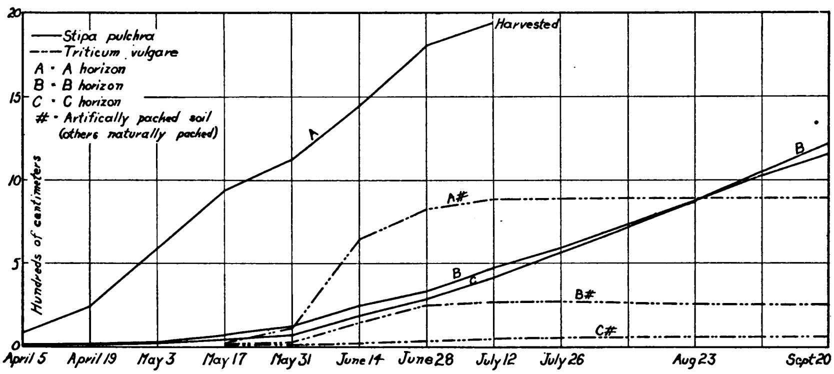

Fig. 1. Growth curves of *Stipa pulchra* and *Triticum vulgare* in soil of the Holland series.

In the Olympic soil there was less contrast in the growth rate in the different horizons. With *Danthonia californica,* for instance, the growth in horizon B was 40.85 per cent of that in horizon A when the plants in the latter horizon had matured. With *Bromus rubens* the growth rate in horizon B was 29.70 per cent of that of horizon A; with *Triticum vulgare* the growth in horizon B was 87.15 per cent of that in horizon A.

The comparative growth of *Triticum vulgare* in horizons A, B, and C of the three soil series used is shown in table 3 and figure 2. The growth acceleration in horizon A of the Holland soil is outstanding although an appreciable difference in growth is exhibited between horizons B and C of this soil. Likewise in the Aiken soil, growth in horizon A was much greater than that in horizon B. On the other hand, the growth rate in horizon A of the Aiken soil was nearly the same as in horizon B of the Holland soil. In horizon C of the Holland soil the growth rate was slightly greater than in horizon B of the Aiken series. In the Olympic soil the growth rate in horizons A and B shows less contrast.

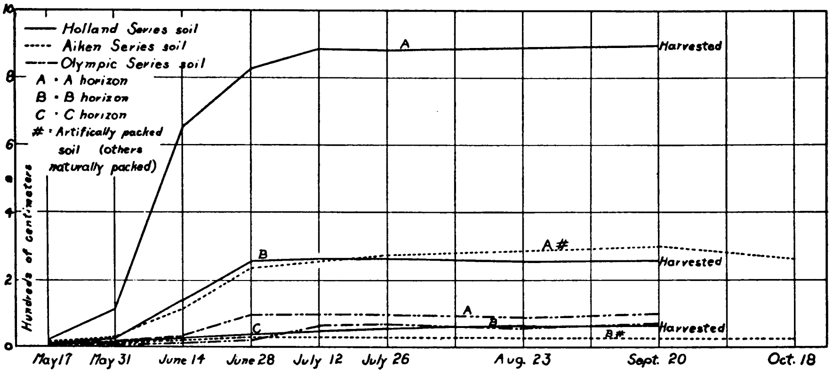

Fig. 2.—Growth curves of *Triticum vulgare* in the Holland, Aiken, and Olympic soils.

TABLE 3

COMPARATIVE RATE OF GROWTH OF *Triticum vulgare* IN THE HOLLAND, AIKEN, AND OLYMPIC SOILS

Date	Holland soil					Aiken soil			Olympic soil		
	Leaf length per plant			A=100 per cent		Leaf length per plant		A=100 per cent	Leaf length per plant		A=100 per cent
	A*	B*	C*	B, per cent of A	C, per cent of A	A	B	B, per cent of A	A*	B*	B, per cent of A
	centi-meters	*centi-meters*	*centi-meters*	*per cent*	*per cent*	*centi-meters*	*centi-meters*	*per cent*	*centi-meters*	*centi-meters*	*per cent*
May 17	20.3	9.3	7.7	45.82	37.99	15.7	8.3	52.86	9.9	9.4	94.94
May 31	109.6	25.6	13.7	23.37	12.50	31.2	16.4	52.55	20.5	18.2	88.80
June 14	645.7	142.5	28.7	22 08	4.45	114.9	23.1	20.10	36.7	21.5	58.59
June 28	828.7	250.5	37.7	30.20	4.55	233.9	28.0	11.97	95.2	44.9	47.20
July 12	885.0	259.8	48.1	29.36	5.42	248.4	28.4	11.42	98.6	66.6	67.58
July 26	877.5	260.5	54.2	29.70	6.18	271.5	30.3	11.16	93.7**	67.7	72.22
Aug. 23	887.3	250.5	58.4	28.24	6.58	285.9	27.5	9.62	84.9**	55.6	65.50
Sept. 20	896.2	259.4	56.5	28.95	6.27	301.0	25.4	8.44	80.9**	70.5	87.15
....	....	....	....	....	....	262.9**	26.9	10.24	....	....	....

*Artificially packed soils. **Decreased length due to broken leaves.

In comparing growth rates in the different soil horizons it should be noted that the percentage of plant material produced varied with the age of the plants. Vegetative production in horizons B and C, when expressed in percentages of that produced in horizon A, was comparatively high when the plants were young, due presumably to reserve food in the seed and to the nitrate nitrogen in the soil, not replaceable owing to the low nitrification in horizons B and C. As this food supply was exhaused the growth rate in the lower horizons declined sharply.

The results of growth here recorded were in agreement with experimental evidence reported by Sampson and Weyl[8] (pp. 18–22) in their studies of growth of peas, brome grass, and wheat in eroded and non-eroded soils, as summarized in table 4.

TABLE 4

SUMMARY OF VEGETATIVE GROWTH IN ERODED AND IN NON-ERODED SOILS OF THE SAME SOIL SERIES

Plant	Leaf length,* millimeters		Horizon A = 100 per cent
	Horizon A, non-eroded soil	Horizon B, eroded soil	B, per cent of A
Peas	2,634	791	30.03
Brome grass	5,218	2,902	55.61
Wheat	10,080	4,474	44.38

*With peas the stem length is given instead of leaf length.

The vegetative growth and water requirement of peas of the eroded and non-eroded soil showed a remarkable contrast in the vegetative growth and other activities. The number of leaves was as 1 to 2.7; the leaf length, 1 to 3.3; and the total dry weight produced was as 1 to 8.3—all in favor of the non-eroded soil. And because of the much larger size of the plants in the non-eroded soil, the water used was as 2.7 to 1 compared with that of the eroded soil. In the water requirement per unit of dry matter, on the other hand, the ratio was reversed, being 1.8 to 1 on the eroded and non-eroded soils, respectively. There were a great many more leaves, greater stem and leaf length, and more dry matter produced on the non-eroded than on the eroded soil. There was also a notably smaller amount of water available for plant growth in the eroded soil.

Extent of Plant Development.—Measurements of plant development were recorded on the basis of the dry weight of the panicle or spike (of grasses) and the total dry weight of the plant as a whole, in the different soil horizons. The results are summarized in table 5.

In horizon B of the Holland soil the panicles of *Stipa pulchra* weighed but 5.47 per cent of those produced by similar plants in horizon A. In horizon C this species never reached the flowering stage (fig. 3). Expressed in terms of total dry weight of a plant, the growth of *Stipa* in horizons B and C was 20.54 and 16.49 per cent, respectively, of the growth in horizon A. Likewise the dry weights of spikes of *Triticum vulgare* in horizons B and C of this soil series were 35.23 and 5.29 per cent, respectively, compared to the weight of spikes in horizon A. On the basis of total dry weight of a plant these percentages were 33.20 and 4.81, respectively. It should be noted that wheat was the only plant to produce seed in horizon C (fig. 4).

TABLE 5

EXTENT OF PLANT DEVELOPMENT IN SOIL HORIZONS A, B, AND C IN THE THREE SOIL SERIES

Species	Soil	Dry weight per plant, grams			Difference between horizons			
					A = 100 per cent			
					Heads		Total weight per plant	
	Series and horizon	Heads	Stems and leaves	Total	B, per cent of A	C, per cent of A	B, per cent of A	C, per cent of A
Stipa pulchra	Holland A	1.3	6.1	7.4				
Stipa pulchra	Holland B	0.1	1.5	1.5	5.5		20.5	
Stipa pulchra	Holland C	0.0	1.2	1.2		0.0		16.49
Triticum vulgare	Holland A*	10.9	9.8	20.8				
Triticum vulgare	Holland B*	3.9	3.0	6.9	35.2		33.2	
Triticum vulgare	Holland C*	0.6	0.4	1.0		5.3		4.81
Erodium cicutarium	Aiken A*	2.2	3.9	6.2				
Erodium cicutarium	Aiken B*	0.4	0.6	1.1	19.4		17.2	
Triticum vulgare	Aiken A	6.0	5.1	11.1				
Triticum vulgare	Aiken B	0.2	0.2	0.3	2.7		2.9	
Danthonia californica	Olympic A	0.4	6.3	6.8				
Danthonia californica	Olympic B*	0.0	2.4	2.4	0.0		35.8	
Bromus rubens	Olympic A*	3.8	2.9	6.8				
Bromus rubens	Olympic B*	2.9	1.3	4.2	76.4		62.1	
Triticum vulgare	Olympic A*	1.4	0.9	2.3				
Triticum vulgare	Olympic B*	0.5	0.4	0.8	33.8		36.5	

*Artificially packed soils.

In the Aiken soil where horizons A and B were used, the dry weight of the floral and fruiting parts of *Erodium cicutarium* in horizon B was 19.37 per cent of the yield in horizon A. Expressed in total dry weight of a plant, horizon B produced 17.21 per cent of horizon A. The dry weight of spikes of *Triticum vulgare* grown in horizon B of this soil was 2.66 per cent of the yield of horizon A. Similarly the total dry weight of plants grown in horizon B was 2.88 per cent of that of plants grown in horizon A.

In the Olympic soil *Danthonia californica* failed to produce seed in horizon B at the time that the plants in horizon A had reached seed maturity (fig. 5). The dry material produced in horizon B was 35.80 per cent of that in horizon A. On the other hand, the dry weight of the inflorescence of *Bromus rubens* grown in this soil was 76.44 per cent in horizon B as compared to horizon A, the largest comparative yield of fruiting parts obtained in any entire series (fig. 6).

Expressed in terms of total dry weight of a plant *Bromus rubens* also yielded the largest comparative amount of material of any species in horizon B soil, amounting to 62.13 per cent of the yield in horizon A. The striking difference in the extent of development of *Danthonia californica* and of *Bromus rubens* in horizons A and B of this soil series indicates again the rather exacting requirements of the climax perennial species.

Time of Seed Maturity.—The time required for seed production of the different species in the respective horizons of the soil series used was expressed in the number of days from the time of germination to the appearance of flowers and the time after that activity to the maturity of the seed.

In the Holland soil, *Stipa pulchra* in horizon A produced inflorescence 85 days after planting. All specimens reached seed maturity in 134 days. In horizon B only two panicles appeared, and these did not show until 141 days after planting or 56 days later than in horizon A (fig. 3). Moreover, in horizon B, 204 days elapsed before seed maturity, or 70 days later than in horizon A. In horizon C not a flower unfolded during the growing period of approximately 10 months.

Triticum vulgare in horizon A of this soil series produced inflorescence in 45 days and mature seed in 94 days. In horizons B and C the time required to produce mature seed was 114 and 139 days, respectively.

In the Aiken soil, *Erodium cicutarium* in horizon A began flowering 69 days after planting, whereas in horizon B of this soil series the first flowers appeared 97 days after planting. The plants in both the A and B horizons produced seed and were still growing when the experiment was concluded, approximately 235 days after germination. The fructification of *Triticum vulgare* in the Aiken soil series was less rapid in horizons A and B than in the same soil horizons of the Holland and Olympic series. There was also a difference in the time of seed maturity in horizons A and B of the Aiken soil, horizon B requiring 26 days longer than A.

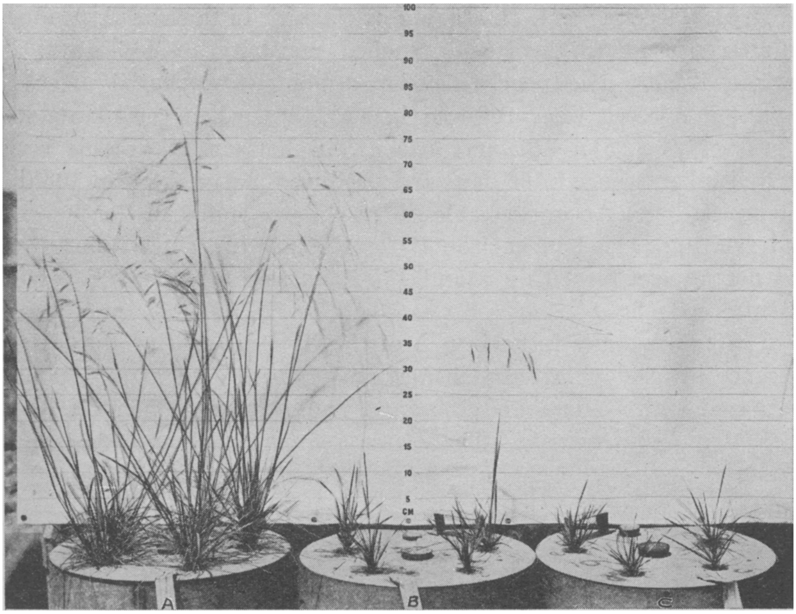

Fig. 3. *Stipa pulchra* grown in horizons A, B, and C of the Holland soil. Age of all plants, 130 days; soils naturally packed.

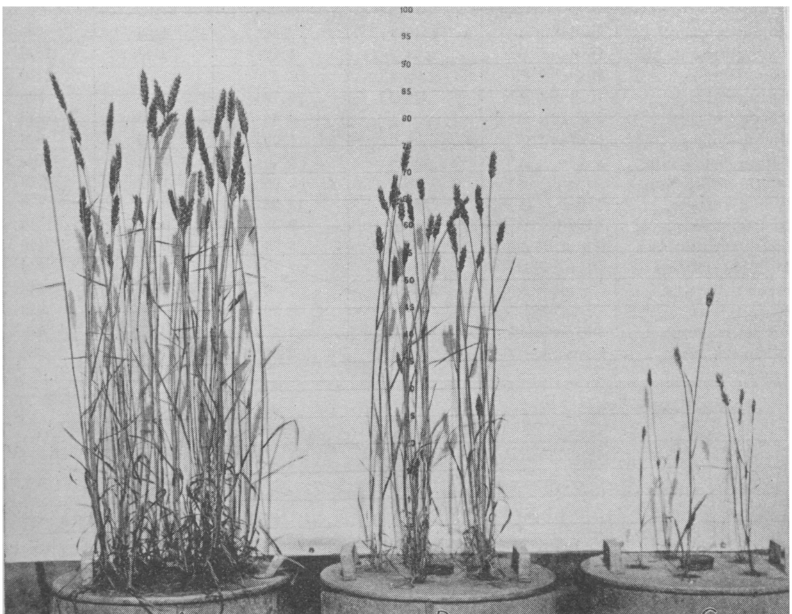

Fig. 4. *Triticum vulgare* grown in horizons A, B, and C of the Holland soil. Age of all plants, 126 days; soils artificially packed.

In the Olympic soil, *Danthonia californica* in horizon A produced inflorescence in 78 days and reached maturity in 130 days. In horizon B only two poorly developed panicles appeared after 106 days, but no seed was produced in 130 days, when the plants were harvested (fig. 5). *Bromus rubens,* in horizon A of this series, showed inflorescence in 66 days and produced mature seed in 106 days after planting. An appreciable difference was noted in the flowering and fruiting period in horizon B for this species, since inflorescence did not appear for 83 days and 135 days were required to produce mature seed (fig. 6).

Triticum vulgare in horizon A of the Olympic soil, produced inflorescence in 59 days after planting, and mature seed after 110 days, compared with 73 days and 130 days, respectively, in horizon B.

Water Requirements.—The water requirements and the growth produced in the different soil horizons are sumarized in table 6.

TABLE 6

WATER REQUIREMENTS AND GROWTH PRODUCED IN THE DIFFERENT HORIZONS OF THE THREE SOIL SERIES

Species	Soil series and horizon	Leaf length per plant centimeters	Dry weight per plant grams	Water used per plant kilograms	Water requirement per unit of dry matter cc per gram
Stipa pulchra	Holland A	1938.8	7.40	4.83	650
Stipa pulchra	Holland B	463.0	1.52	2.17	1420
Stipa pulchra	Holland C	399.8	1.22	1.36	1110
Triticum vulgare	Holland A*	896.2	20.78	6.89	300
Triticum vulgare	Holland B*	259.4	6.90	2.95	430
Triticum vulgare	Holland C*	62.0	1.00	0.60	600
Erodium cicutarium	Aiken A*	208.8	6.16	4.34	700
Erodium cicutarium	Aiken B*	30.3	1.06	1.19	1120
Triticum vulgare	Aiken A	262.9	11.08	5.27	470
Triticum vulgare	Aiken B	26.9	0.32	0.49	1540
Danthonia californica	Olympic A	2951.4	6.76	3.11	460
Danthonia californica	Olympic B*	1206.1	2.42	0.83	340
Bromus rubens	Olympic A*	2843.2	6.76	2.27	340
Bromus rubens	Olympic B*	496.9	4.20	1.73	410
Triticum vulgare	Olympic A*	101.1	2.30	0.96	420
Triticum vulgare	Olympic B*	70.5	0.84	0.32	380

*Artificially packed soils.

In all cases the water requirement per unit of dry material produced was, with slight exceptions, greatest in horizon C, intermediate in horizon B, and least in horizon A, a condition which may be accounted for by the difference in osmotic concentration of the cell sap.[5] Exceptions occurred with *Stipa pulchra* in the Holland soil, and with *Danthonia californica* and *Triticum vulgare* in the Olympic soil, in which slightly less water was required in the lower horizons.

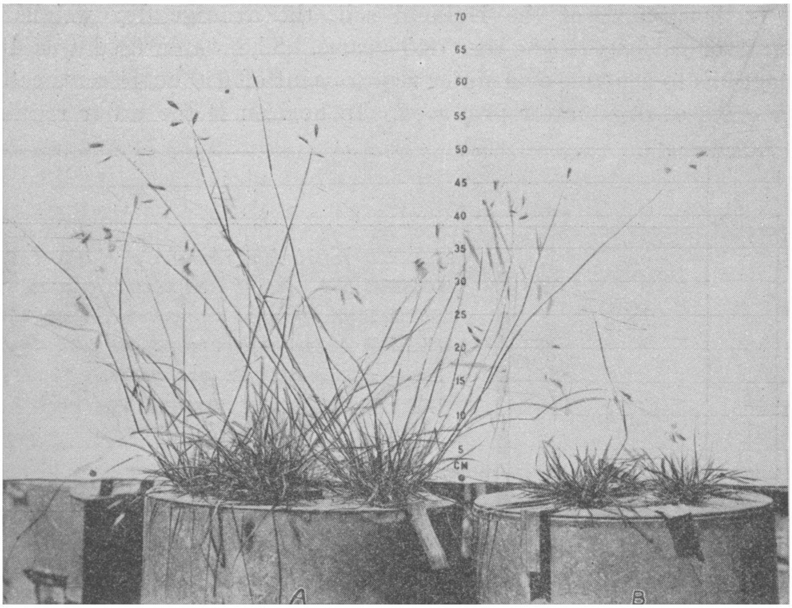

Fig. 5. *Danthonia californica* grown in horizons A and B of the Olympic soil. Age of all plants, 130 days.

Fig. 6. *Bromus rubens* grown in horizons A and B of the Olympic soil. Age of plants, 118 days.

In horizon A of the Holland soil, the average dry weight of plants of *Stipa pulchra* was 7.40 grams. The water used was 4.83 kilograms to a plant, or a water requirement of 650 cubic centimeters per gram of dry matter produced. In horizon B the water require-

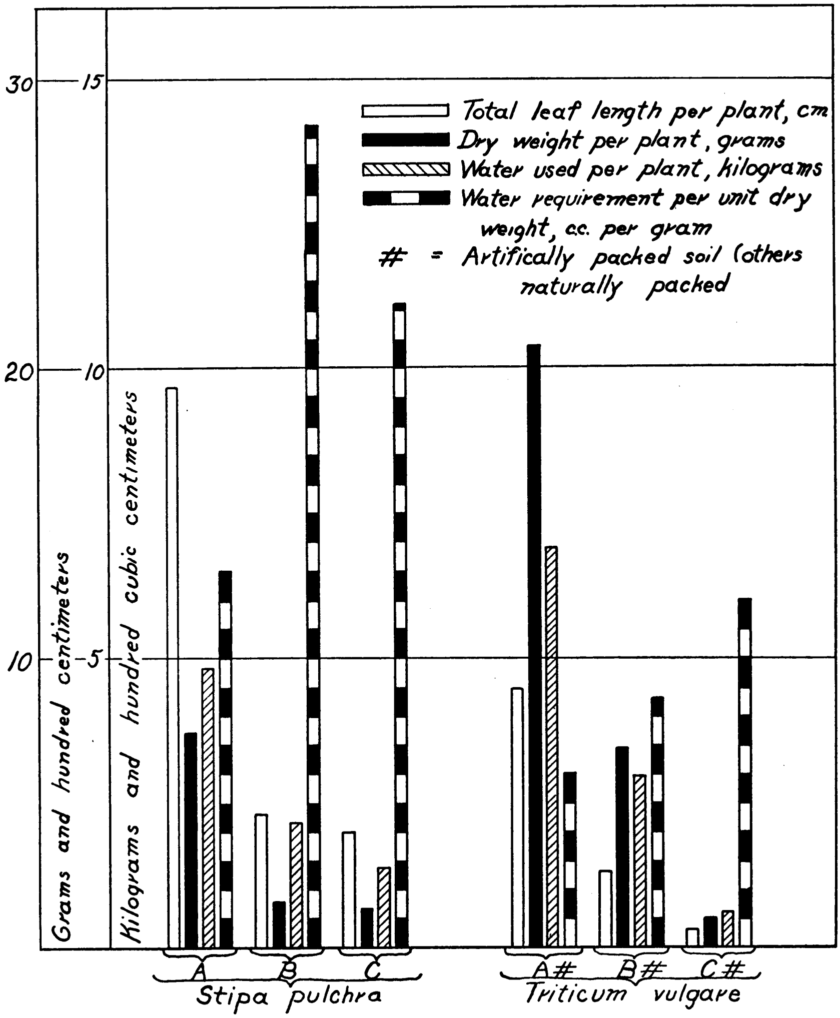

Fig. 7. Vegetative growth and water requirements of *Stipa pulchra* and *Triticum vulgare* in horizons A, B, and C of the Holland soil.

ment increased to 1,420 cubic centimeters per gram, whereas in horizon C the water used was 1,110 cubic centimeters per gram. *Triticum vulgare,* in horizons A, B, and C of the Holland soil, used 300, 430, and 600 cubic centimeters per gram respectively (fig. 7).

In the Aiken soil, *Erodium cicutarium* in the A horizon produced an average weight of 6.16 grams. The water used was 4.34 kilograms to a plant, and the water requirement was 700 cubic centimeters per gram of dry material produced. In horizon B the dry weight was

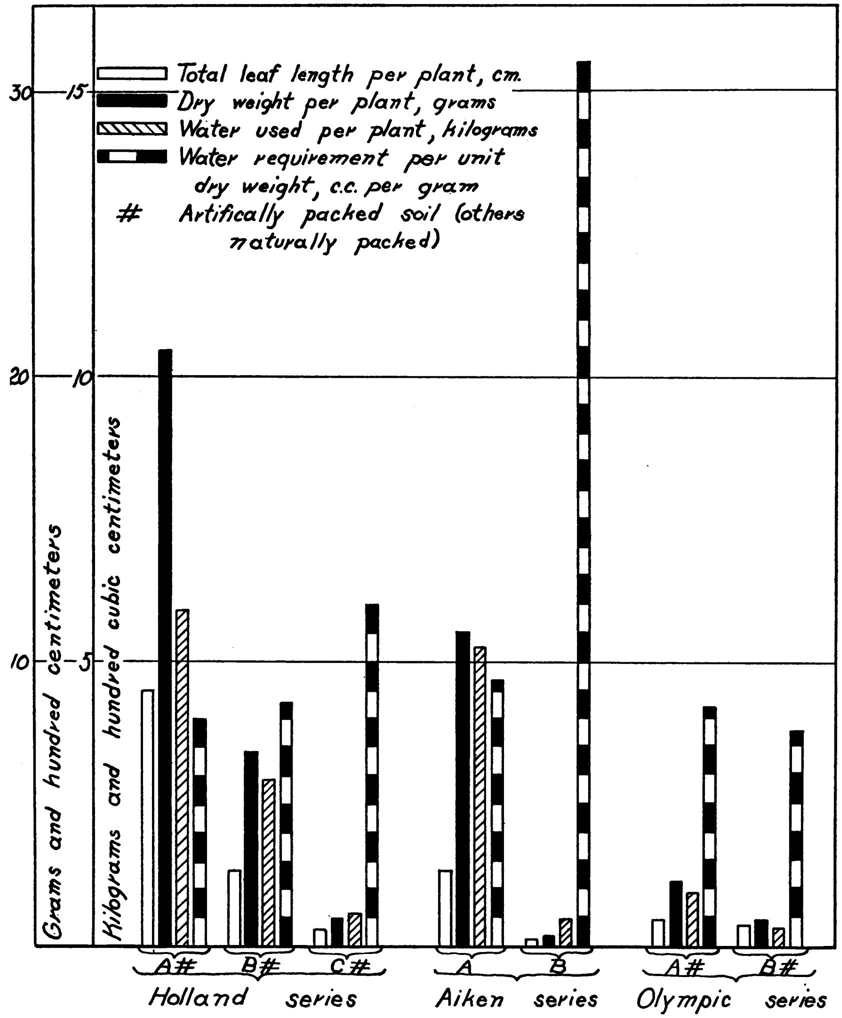

Fig. 8. Vegetative growth and water requirements of *Triticum vulgare* in the Holland, Aiken, and Olympic soils.

1.06 grams to a plant, and the water used was 1.19 kilograms, and the water required was 1,120 cubic centimeters per gram of dry matter. With *Triticum vulgare,* the dry weights in horizons A and B were 11.08 and 0.32 grams to a plant respectively. The water used was

5.27 and 0.49 kilograms to a plant, and the water requirements were 470 and 1,540 cubic centimeters per gram respectively, of the dry material produced. The latter represents the highest water requirement obtained in any of the soils (fig. 8).

In the Olympic soil, the contrast exhibited in the water requirements of the other two soil series is less striking. In horizon A, *Danthonia californica* produced 6.76 grams of dry material to the plant. The water used was 3.11 kilograms to a plant, with a water requirement of 460 cubic centimeters to a gram of dry material produced. The dry weight of the plants grown in horizon B was 2.42 grams, the water used was 0.83 kilograms, and the water requirement was 340 cubic centimeters to a gram of dry material. In spite of the fact that the vegetative growth in horizon A was much greater than in horizon B, the water requirement in horizon B was lower.[5] With *Bromus rubens,* the water requirements in horizons A and B were 340 and 410 cubic centimeters to a gram respectively. With *Triticum vulgare* the water requirement was 420 and 380 cubic centimeters to a gram in horizons A and B, respectively, the requirement again being greater in horizon A.

A comparison of the vegetative growth and the water requirements of *Triticum vulgare* in each horizon of the three soil series is shown graphically in figure 8. Although a marked contrast is shown in the Holland soil, the greatest difference was found in horizons A and B of the Aiken series. The results indicate that horizon B of the Aiken soil was the least productive of the three series studied. Horizon A of the Holland soil was the best. There were marked differences in physical characteristics of the surface soil and the subsoil in both the Holland and the Aiken soils, whereas in the Olympic soil there was little contrast.

Natural Packing vs. Artificial Packing of Soils.—Considerable contrast was found in the growth of vegetation in the soil which was naturally packed, as compared with that which was packed artificially. In the Holland soil, the rate of growth of *Stipa pulchra* at the time of seed maturity in naturally packed soil of horizon A was only 61.2 per cent of the rate in similar soil artificially packed (fig. 9). On the other hand in horizon C, *Stipa pulchra* grew more vigorously and produced more air dry material in the naturally packed phytometer, the growth in the artificially packed soil being only 35.2 per cent of that produced in the naturally packed soil. However, *Stipa pulchra* did not produce seed in horizon C regardless of soil treatment.

In the Aiken soil, *Triticum vulgare* grown in the B horizon developed much more vigorously in the artificially packed soil (fig. 9).

In terms of total leaf length, the production in the naturally packed soil was only 17.4 per cent of that of the artificially packed soil. The average dry weight of a plant in the artificially packed soil was 4.52 grams, whereas in the naturally packed phytometers it was only 0.32 grams. The water requirements also showed a marked difference, being appreciably less in the artificially packed soil. These data would indicate that it is desirable to use naturally packed soil for experimental work of this nature in order to simulate field conditions. It also becomes evident that the differences in growth yield and fructification in the different soil horizons cannot be accounted for wholly by the physical condition of the soil.

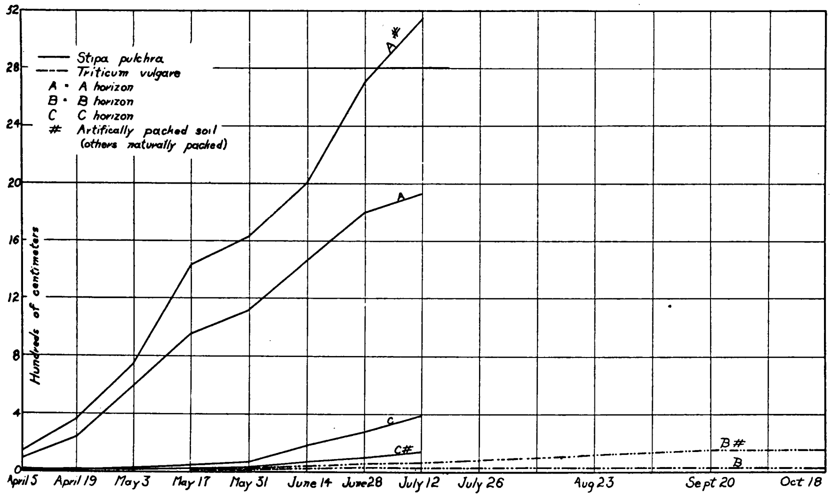

Fig. 9. Growth curves in naturally and artificially packed soils of the Holland and Aiken series. *Stipa pulchra* in Holland soil. *Triticum vulgare* in Aiken soil.

Physical and Chemical Characteristics of the Soil Horizons.—The physical analyses of the different horizons of the three soil series consisted of procuring texture fractions of the following: total sand, fine gravel, coarse sand, medium sand, fine sand, very fine sand, silt, and clay. The soil horizon samples were taken at the following depths: Horizon A, 0.1 foot to 0.3 foot from the soil surface; horizon B varied in depth from 1.0 foot to 2.5 feet from the soil surface, depending on the character of the profiles. In addition, colloidal clay determinations were made for horizons A and B, using a modification of the ammonia dispersal method of analysis as adopted by Professor C. F. Shaw, University of California.

In no case was there any appreciable difference in the mechanical analyses of horizons A and B of any soil series. Of the eight segregates there appeared to be somewhat consistently more coarse sand in horizon A, but the difference was never great. In no case did the differences in the fractions appear to account for the striking difference in plant behavior in horizons A and B. Moreover, there did not appear to be sufficient difference in the colloidal clay fractions to account for the more favorable plant development in horizon A of each of the soil series.

Through the courtesy of Professor E. L. Proebsting of the Division of Pomology, preliminary examinations of the nitrate content of horizons A and B of each of the three series have been made. The only consistent difference of seeming consequence appears to be in the larger amount of total nitrogen and of nitrate nitrogen content in horizon A of each series. These results are in agreement with those of other workers.[1] Since, however, only one set of samples was analyzed, representing conditions at the end of the growing season, the data may be interpreted merely as a probable factor of importance in plant development and vegetative succession. It appears probable that more extensive data would show the higher nitrogen content of horizon A to be the principal factor causing the larger yields and vigorous fructification.

CONCLUSIONS

The rate of growth, both of the annual and the perennial species studied, was appreciably greater in soil horizon A than in horizons of lower depth regardless of the soil series or the species used. Likewise, the amount of plant material produced in soil horizon A was consistently greater than in soil horizon C, regardless of species or soil series. This held true, also, in soil horizon B with the exception of the Olympic soil, in which the B horizon proved nearly as productive as that of the A horizon for two annual species. This deviation from the average trend may be accounted for by the fact that the soil used to represent the Olympic series was procured in grassland formation, hence the B horizon may have been subject to greater accumulation of materials from the upper horizon than in the forest soils. The number of days required for flower production and for the maturity of seed varied widely, but was much earlier in horizon A than in horizons B and C. In the latter two, the perennial species failed to produce practically any seed. Also, a difference was noted in the time of flowering and seed maturity in horizon A of the three soil series, the earliest maturity occurring in the Holland soil, followed by the Olympic, and then by the Aiken. Although there was a difference in color, the Olympic soil being the darkest, the difference in maturity cannot be attributed to greater absorption of radiant energy, since the soils were covered. The water requirement per units of dry material produced was in all cases greater in horizon C than in horizon A, and with two exceptions, in the Olympic soil the water requirement was slightly greater in horizon B than in horizon A. Artificial packing simulating in a way cultivation, tended to cause deviation from the rhythmic growth cycle procured in the naturally packed soils. This may be accounted for by the change in soil structure and in increased aeration.

These studies are significant in that they indicate the importance of keeping intact the horizon A soil layer, which, according to preliminary studies in nutrients by displacement, is richer in total nitrogen and in nitrate nitrogen than the underlying horizons. The removal of the A horizon tends not only to decrease the luxuriance of growth of the vegetation, but greatly retards, if it does not actually prevent, the reestablishment of the climax and subclimax plant cover.

Where soil horizon A has been largely or wholly removed by erosion, these studies point to the fact that it would be a mistake to attempt to establish a cover of perennial grasses with a view to binding the soil and preventing further soil transportation. The normal stages of plant succession must each play its part. For several years the cover will normally consist of annual species. Accordingly, the management of the areas must at first concern itself with annual vegetation, regardless of whether seed is introduced or the invading cover is to be fostered in way of natural revegetation.

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The titles of the Technical Papers of the California Agricultural Experiment Station, Nos. 1 to 20, which HILGARDIA replaces, and copies of which may be had on application to the Publication Secretary, Agricultural Experiment Station, Berkeley, are as follows:

1. The Removal of Sodium Carbonate from Soils, by Walter P. Kelley and Edward E. Thomas. January, 1923.
4. Effect of Sodium Chlorid and Calcium Chlorid upon the Growth and Composition of Young Orange Trees, by H. S. Reed and A. R. C. Haas. April, 1923.
5. Citrus Blast and Black Pit, by H. S. Fawcett, W. T. Horne, and A. F. Camp. May, 1923.
6. A Study of Deciduous Fruit Tree Rootstocks with Special Reference to Their Identification, by Myer J. Heppner. June, 1923.
7. A Study of the Darkening of Apple Tissue, by E. L. Overholser and W. V. Cruess. June, 1923.
8. Effect of Salts on the Intake of Inorganic Elements and on the Buffer System of the Plant, by D. R. Hoagland and J. C. Martin. July, 1923.
9. Experiments on the Reclamation of Alkali Soils by Leaching with Water and Gypsum, by P. L. Hibbard. August, 1923.
10. The Seasonal Variation of the Soil Moisture in a Walnut Grove in Relation to Hygroscopic Coefficient, by L. D. Batchelor and H. S. Reed. September, 1923.
11. Studies on the Effects of Sodium, Potassium, and Calcium on Young Orange Trees, by H. S. Reed and A. R. C. Haas. October, 1923.
12. The Effect of the Plant on the Reaction of the Culture Solution, by D. R. Hoagland. November, 1923.
14. The Respiration of Potato Tubers in Relation to the Occurrence of Blackheart, by J. P. Bennett and E. T. Bartholomew. January, 1924.
16. The Moisture Equivalent as Influenced by the Amount of Soil Used in its Determination, by F. J. Veihmeyer, O. W. Israelsen and J. P. Conrad. September, 1924.
17. Nutrient and Toxic Effects of Certain Ions on Citrus and Walnut Trees with Especial Reference to the Concentration and Ph of the Medium, by H. S. Reed and A. R. C. Haas. October, 1924.
18. Factors Influencing the Rate of Germination of Seed of Asparagus Officinalis, by H. A. Borthwick. March, 1925.
19. The Relation of the Subcutaneous Administration of Living Bacterium abortum to the Immunity and Carrier Problem of Bovine Infectious Abortion, by George H. Hart and Jacob Traum. April, 1925.
20. A Study of the Conductive Tissues in Shoots of the Bartlett Pear and the Relationship of Food Movement to Dominance of the Apical Buds, by Frank E. Gardner. April, 1925.