THE EFFECTS OF NONBENEFICIAL NODULE BACTERIA ON AUSTRIAN WINTER PEA [1]

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INTRODUCTION

When typical nodules form on the roots of legumes the bacteria which they contain are presumed to be working in harmony with the plants, furnishing nitrogenous compounds manufactured from the gaseous nitrogen of the air. Apparently this is not always the case, however, for occasionally a condition arises in which there is no doubt that the nodule organisms have exerted a detrimental effect. In many other instances it is probable that the bacteria live on the roots of the legume without appreciably influencing the plant. It is to be expected that all grades of efficiency exist among the legume bacteria.

REVIEW OF LITERATURE

The nature of the association of legume and nodule bacteria has long been in doubt. By some it has been regarded as parasitism, but if it is so, it can only be considered as theoretical parasitism. Voorhees and Lipman (*12, p. 92*) [3] state:

> * * * in the very definition of the term, parasitism involves a more or less marked injury to the host, which, at best, derives no benefit from the invading organism. In the phenomenon under consideration, however, there is, under normal conditions, a distinct gain to the host plant, and hence the term "parasitism" is not applicable.

Woronine (*13*), who first discovered bacteria in nodules, referred to them as parasites. Smith (*10, v. 2, p. 97*), considered nodule bacteria as parasites, since they pass through the same stages as disease-producing organisms. Jones (*7*) attributes parasitic tendencies to mung-bean nodules growing under submerged conditions.

Eaton (*4*) has reported that nodule production on soybeans bears a direct relation to light, and Leonard (*8*), also working with soybeans, has shown that a lack of light, or interference with the organs utilizing light, reduces the beneficial effects of symbiosis in accordance with the severity of the light deficiency. Thornton (*11*) states that parasitism in nodule bacteria is induced by cutting off the carbohydrate supply.

The appearance of ill effects among legume plants growing under optimum conditions is due to another type of parasitism—a parasitism inherent in the invading organism. In cases of this kind the organism enters the roots and forms nodules, but these are not beneficial.

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[3] Reference is made by number (italic) to Literature Cited, p. 663.

Hiltner (*6*) calls attention to parasitic nodules on locust and differentiates between these and beneficial nodules by their location on the roots. The former were distributed all over the root, whereas the latter were located at the crown.

Helz, Baldwin, and Fred (*5*) citing 16 papers on this subject, reported a wide variation in the effects produced by strains of nodule bacteria of the vetch and pea group.

Briscoe [4] reported greenhouse work in which poor and good strains were used in combination, and the mixture produced as satisfactory results as the good strain alone. A means of correcting the unadaptability of strains is reported by Wunchik (*14*), who has indicated that by plant passage an unadapted strain may become better adapted to a strange host, and Allen and Baldwin (*1*) have confirmed this finding. That the organisms in nodules on the same plant may consist of both good and poor strains has been shown by Dunham and Baldwin (*3*).

EXPERIMENTAL MATERIALS AND OUTLINE OF WORK

In 1929 observations were made at Jeanerette, Iberia Parish, La., on a field of Austrian winter peas (*Pisum arvense* L.) which had been planted without artificial inoculation on the low-lying black neutral alluvial soil of that locality. After a month or so of growth it was definitely apparent that the crop would be a failure; the field contained mainly yellow stunted plants with an occasional vigorous individual. Samples of the plants were collected and sent to the senior author at Washington, D. C. The roots of most of the plants examined, whether normal or stunted, were apparently healthy, and all the plants had nodules on their roots. It was noticed, however, that the nodules on the stunted plants were small, globular in shape, and rather evenly distributed over the roots, whereas those on the vigorous plants tended to be convolute or branched and were largely confined to the crown roots. Cultures were isolated from nodules of both types of plants and tested on Austrian winter pea. These cultures produced nodules on the pea under controlled conditions and, in addition, gave rise to effects similar to those noticed on the plants from which they came. In other words, the bacteria from the stunted-plant nodules produced what might be called parasitic effects, whereas those from vigorous plants produced good plants. When these preliminary tests were completed cultures of the proper nodule bacteria were prepared on agar in test tubes and sent to Jeanerette, La. (Table 1.) There they were applied to seed by adding water to the tube, shaking thoroughly to secure a suspension of the organisms, and moistening the seed with the mixture. The seeds were sown promptly after treatment at the rate of 1 pound per each 10 by 60 foot plot. To prevent transfer of the cultures, vessels and hands were thoroughly rinsed in running tap water between each treatment. No disinfectants were used. Before the seeds were sown basic slag at the rate of 600 pounds per acre and ground oyster shells at the rate of 3,600 pounds per acre were applied each to one-third of the plots in Austrian winter pea; the remaining third were left untreated. Figure 1 shows the arrangement of the plots.

[4] BRISCOE, C. F. INOCULATION OF SOYBEANS. Miss. Agr. Expt. Sta. Press Circ. 419, 3 p. 1932. [Mimeographed.]

TABLE 1.—*Source of the nodule bacteria cultures used in the experiments*

Stock No.	Diagram No. (fig. 1)	Host plant from which bacteria were isolated	Source of cultures
473[a]	1	Alaska garden pea	W. H. Wright, University of Wisconsin; his No. P3. 1927.
484[a]	7	do	I. L. Baldwin, University of Wisconsin; his No. 15 or 310 1927.
510	3	Austrian winter pea	Jeanerette, La 1929.
511	6	do	Do.
512	4	do	Do.
513[b]	2	do	Do.
515[b]	8	do	Do.
518[c]	5	do	Rosslyn, Va. 1930.
None[d]	[d] 0		
548		Louisiana vetch	Jeanerette, La. 1931.
549		do	Do.
549		do	Do.
550		do	Do.

[a] The complete history of this culture is not available, but judging from the response obtained with Austrian winter peas, it is believed to be a low nitrogen-fixing strain.
[b] This culture was isolated from plants that showed no benefit from the presence of nodule organisms.
[c] This culture was isolated from a slightly pink nodule apparentely produced by a nonbeneficial culture on plants showing symptoms of being adversely affected by nodule bacteria. From subsequent results it is presumed that this culture either changed its character rapidly, by means of one plant passage, or that through some unknown means an efficient organism was harbored in the nodule from which it came.
[d] Designation used for untreated areas.

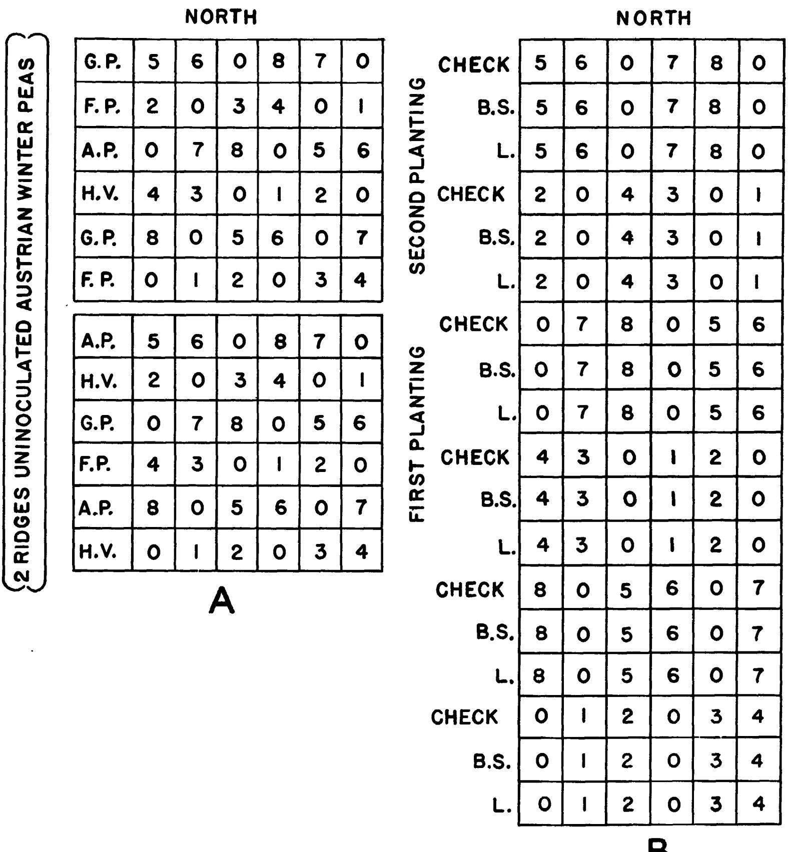

FIGURE 1.—Arrangement of plots of Austrian winter peas and other legumes at Jeanerette, La., 1930: A, Detail of plot arrangement of mixed-legume plantings; B, detail of plot arrangement of Austrian winter-pea plantings. The letters to the left of the numbers indicate the species of legume planted, or a soil amendment, as follows: A. P., Austrian winter pea; F. P., Canada field pea; G. P., garden pea; H. V., hairy vetch; B. S., basic slag; L., ground oyster shell lime

The mixed-legume plots and one of the Austrian winter-pea plots (fig. 1, B) were seeded October 22, 1930; the second sowing of Austrian winter peas, a duplicate of the first, was made November 3, 1930. The plots seeded to mixed legumes were 10 by 60 feet, and those seeded to Austrian winter peas were 10 by 20 feet. Samples of the black silt soil taken from seven representative spots in the mixed-legume planting gave a pH value of 6.75, indicating a uniform hydrogen-ion concentration. Six composites of individual samples from three different spots in the first planting of the Austrian winter peas were more variable in reaction, the pH values ranging from 6.57 to 7.88. Obviously there was little need for a neutralizing agent in this soil.

FIELD OBSERVATIONS

GROWTH AND NODULATION

On January 31, 1931, plants grown from seed treated with cultures 510, 511, and 518 were observed to be greener than those in other plots of the first planting of Austrian winter peas, in some of which the plants were turning yellow and a few were dying. On the plots containing mostly poorly colored plants, an occasional rather vigorous plant was noticed. All plants, even those in the worst condition, had nodules on their roots. As in earlier studies (*9*) it was found that on the better plants the nodules tended to branch or become convolute, whereas on most of the poor plants the nodules were smaller and globular in shape, the former type being placed rather generally around the crown, and the latter scattered more or less evenly over the roots.

On February 17, 1931, a second examination of representative plants was made. This revealed much the same condition as the first. (Table 2.) At this time there was no evidence that either the basic slag or the lime had influenced the growth of the plants or the formation of nodules.

TABLE 2.—*Growth and nodulation of Austrian winter peas and other legumes at Jeanerette, La., February 17, 1931*

Name of plant [a]	Inoculation treatment	Growth	Nodulation
Canada field pea	510	Excellent	Normal.[b]
Alaska garden pea	None	Fair	Scattered.
Hairy vetch	None	Poor	Plentiful.
Austrian winter pea (2)	512	Excellent	Normal.
Austrian winter pea	484	Poor	Scarce.
Do	484	Fair	Do.
Do	518	Poor	Do.
Austrian winter pea (2)	518	Excellent	Normal.
Austrian winter pea (3)	511	do	Do.
Austrian winter pea (6)	None	Poor	Scarce.
Austrian winter pea (2)	510	Excellent	Normal.
Austrian winter pea (3)	513	Poor	Scarce.

[a] Numbers in parentheses indicate the number of samples examined.
[b] Normal means tendency to branch and locate near the crown, all other notations in this column refer to scattered globular nodules.

Plants of Austrian winter pea from seed inoculated with culture 510 accidentally mixed with the seed of hairy vetch were very good, and plants from the latter were much better than other vetch plants from untreated seed, most of which did not exceed 4 inches in height. All vetch plants had nodules. Whether the beneficial effect of the association of vetch with Austrian winter pea was due to a transference of adapted organisms or to the utilization of by-products is not known, but it is an interesting lead to consider. The seed of Canada field peas and Alaska garden peas did not germinate satisfactorily, and the crop that was made was not satisfactory.

A better picture of the differences between excellent and poor growth and between the two types of nodulation is shown in Figure 2. Although some of the roots were broken off in removing the gummy soil and many nodules are believed to have been lost in the washing process, Figure 2 adequately illustrates the extreme variation in root system and type of nodulation resulting from treatments with beneficial and nonbeneficial cultures. No differences were observed between the untreated plants and roots and those treated with nonbeneficial cultures.

The Austrian-winter-pea plants from the ridged beds were better than those from the flat bed, but not nearly so good as plants from the areas inoculated with good cultures. Possibly the ridging limited the water supply and thereby interfered with the activities of the native nonbeneficial nodule bacteria.

During the course of the experiment, more especially in the later stages, some of the poor plants which survived the earlier effects of treatment took on renewed life. This is presumed to have been due to the spreading of good nodule bacteria by means of dust, implements, insects, man, or beast. It is reasonable to expect, and experience offers a slight basis for believing, that infections may occur with bacteria of good, bad, and intermediate efficiency, so it is quite possible that where there is an apparent turn for the better, the more efficient organisms may have obtained the upper hand or the progeny of the nonbeneficial organisms may have become better adapted to the plant while within the nodule.

CROP YIELDS

By harvest time a great many of the vigorous growing Austrian-winter-pea plants had lost a rather large proportion of their lower leaves by shedding or decay. Plant lice may have contributed to the losses, since they were plentiful on the plants of the early sowing. The pea vines, which had grown over the dividing furrows, were thrown back on their respective plots before harvesting. The vines were cut with a scythe during rather dry weather and weighed promptly after cutting.

The larger weeds were separated from the cut material, but it was not practical to remove all the little weeds and grass that had grown up in the plots where pea plants had died. It is to be expected that the weight of the grass and weeds will partly compensate for the dead pea plants and may therefore give a false picture in the tabulation of yield data. Where the growth of the winter peas was good and the vines thoroughly covered the ground, weeds and grass were largely suppressed.

FIGURE 2.—Representative Austrian winter-pea plants from plots treated with a beneficial nodule culture (right), and with a nonbeneficial nodule culture (left)

TABLE 3.—*Yields of Austrian winter peas from plots inoculated with a beneficial culture and from untreated plots*

[Planted October 22, 1930, harvested April 24, 1931]

Inoculation treatment	Yield of hay from 10 by 20 foot plot		Moisture in green pea vines	Inoculation treatment	Yield of hay from 10 by 20 foot plot		Moisture in green pea vines
	Green	Moisture free			Green	Moisture free	
	Pounds	*Pounds*	*Per cent*		*Pounds*	*Pounds*	*Per cent*
511	81	13.98	82.74	None	6	1.05	82.56
None	21	4.35	79.28	511	79	19.97	74.72
511	86	26.55	69.13	None	16	3.35	79.04

Table 3 shows the yields from uninoculated Austrian winter peas compared with those from peas inoculated with a beneficial culture. The data indicate an increase of 485 per cent in the yield from the inoculated plots as compared with that from the uninoculated. If such improvement can be made fairly consistently in these soils, it is apparent that the addition of the proper organisms will mean the difference between success and failure.

A comparison of the effects of basic slag and lime on Austrian winter peas receiving different cultures is given in Table 4. The data shown in Table 4 indicate no decided superiority in crop yield as a result of the application of basic slag or lime.

TABLE 4.—*Plot yields in pounds (green weight) of Austrian winter-pea hay per 10 by 20 foot plots, as affected by inoculation, basic slag, or lime*

[Planted October 22, 1930; harvested, except as otherwise noted, May 11, 1931]

Inoculation treatment	Yield with—			Total yield
	Lime	Basic slag	No addition	
512	80	92	75	247
510	73	86	71	230
None	61	61	50	172
513	44	55	66	165
473	43	54	45	142
None	29	33	53	115
Total	330	381	360	
484	31	45	60	136
None	35	38	44	117
511	62	72	57	191
518	55	76	63	194
None	42	45	47	134
515	46	59	55	160
Total	271	335	326	
None	62	59	51	172
513	47	52	41	140
473	50	45	36	131
None	56	52	44	152
510	47	59	48	154
512	53	62	58	173
Total	315	329	278	

TABLE 4.—*Plot yields in pounds (green weight) of Austrian winter-pea hay per 10 by 20 foot plots, as affected by inoculation, basic slag, or lime*—Continued

Inoculation treatment	Yield with— Lime	Basic Slag	No addition	Total yield
511	56	59	63	178
518	64	51	51	166
None	50	50	36	136
515	47	43	30	120
484	28	29	16	73
None	43	45	27	115
Total	288	277	223	
473	47	48	44	139
None	44	45	43	132
510	50	55	43	148
512	51	55	49	155
None	19	18	20	57
513	31	31	30	92
Total	242	252	229	
None	62	59	63	184
515	42	44	46	132
484	37	45	42	124
None	16	6	21	43
511 [a]	79	86	81	246
518 [a]	42	47	37	126
Total	278	287	290	
Grand total	1,724	1,861	1,706	

[a] Harvested Apr. 24, 1931.

Table 5 shows the relative value of the different inoculation cultures.

TABLE 5.—*Summary of the hay-crop yields of Austrian winter peas from planting made October 22, 1930, and harvested May 11, 1931*

Inoculation treatment	Plots	Average yield of dry hay	Inoculation treatment	Plots	Average yield of dry hay
	Number	*Pounds*		*Number*	*Pounds*
None	36	42.4	518	9	54.0
473	9	45.8	511	6	61.5
513	9	44.1	484	9	37.0
510	9	59.1	515	9	47.3
512	9	63.9			

Even with the larger proportion of weeds and grass in the areas inoculated with nonbeneficial bacteria, there is apparently an appreciable increment in crop yield due to cultures 510, 512, 518, and 511, whereas cultures 473, 513, 484, and 515 are not greatly superior to no treatment.

The second planting of Austrian winter peas was substantially the same in layout as the first, yet the results were not the same. The whole crop, regardless of treatment, gave no significant differences attributable to basic slag, lime, or inoculation. (Table 6.) The total yield of dry hay from the 36 plots was as follows: 1,624 pounds from lime, 1,680 pounds from basic slag, and 1,616 pounds from no treatment. The lack of variation in yields from the second planting may have been due to a scattering of good types of nodule organisms by an inundation.

TABLE 6.—*Average yields of dry hay from plots of the second planting of Austrian winter peas, sown November 3, 1930, and harvested May 22, 1931*

Inoculation treatment	Plots	Yield of dry hay		Inoculation treatment	Plots	Yield of dry hay	
		Total	Average per plot			Total	Average per plot
	Number	*Pounds*	*Pounds*		*Number*	*Pounds*	*Pounds*
None	36	1,680	46.7	511	9	444	49.3
473	9	367	40.8	484	9	400	44.4
513	9	387	43.0	515	9	411	45.7
510	9	396	44.0				
512	9	382	42.4	Total or mean	108	4,920	45.5
518	9	453	50.3				

NITROGEN IN AUSTRIAN WINTER PEA AS AFFECTED BY INOCULATION

Samples of pure winter-pea hay from a few plots were harvested February 16, 1931, dried thoroughly, and ground for analysis. The results are given in Table 7.

Comment on these results is almost unnecessary since they are of the same general nature as the other evidence given of the effect of nodule organisms on Austrian winter peas.

TABLE 7.—*Nitrogen analyses of field-grown Austrian winter-pea hay harvested at Jeanerette, La., February 16, 1931*

[Planted October 22, 1930]

Inoculation treatment	10 plants (dry weight)	Nitrogen	Total nitrogen
	Grams	*Per cent*	*Grams*
None	5.3	0.94	0.05
511	37.25	3.40	1.27
513	13.46	.86	.12
518	40.77	3.08	1.25

GREENHOUSE EXPERIMENTS

In a series of greenhouse experiments at Rosslyn, Va., Austrian winter peas were grown in sterilized sand moistened with Bryan-Crone's nutrient solution (*2*). Before the seed was sown it was sterilized with 1:500 mercuric chloride, washed thoroughly with sterile tap water, and inoculated with bacteria from test-tube cultures, the usual precautions being taken to prevent the transfer of nodule bacteria from one series to another. Each treatment was replicated 10 times and each replication usually consisted of about five plants. The data are shown in Table 8.

TABLE 8.—*Nitrogen fixation in greenhouse plantings of Austrian winter peas*

Inoculation treatment	Duration of experiment	Nodules per plant	Dry weight (50 plants)	Nitrogen	Total nitrogen
		Average number	*Grams*	*Per cent*	*Gram*
None	Oct. 28, 1929 to Dec. 12, 1929 (45 days)	----------	13.00	2.60	0.339
473		----------	12.50	3.33	.416
484		----------	12.50	2.38	.300
510		----------	15.50	3.04	.471
511		----------	23.00	2.94	.675
512		----------	21.50	3.08	.664
513		----------	21.50	2.15	.461
515		----------	23.00	2.40	.550
518		----------	20.50	3.09	.632
None	Feb. 14, 1931 to Apr. 8, 1931 (53 days)	3	15.60	1.30	.203
510		15	18.50	2.86	.532
511		16	20.75	2.74	.568
513		96	15.90	1.22	.194
518		13	26.85	2.36	.635
None	Apr. 4, 1931 to May 25, 1931 (51 days)	1	12.80	1.72	.220
512		15	13.80	2.70	.372
513		135	13.20	2.04	.269
548		90	11.40	1.66	.189
549		99	12.20	1.68	.205
550		122	11.60	1.66	.192
512+513		29	11.70	1.94	.227
513+$NaNO_3$		44	14.90	2.12	.316

In the first experiment, culture 510 apparently gave poor results, so far as dry weight and total nitrogen are concerned, yet the percentage of nitrogen rather closely parallels that of the other beneficial cultures. Considering matters on the basis of total nitrogen apparently fixed by nodule organisms, it will be noted that the plants from only one culture (484) contained less nitrogen than the control. Apparently the so-called nonbeneficial cultures were slightly beneficial when the quantity of nitrogen fixed is considered. However, in the second experiment the nitrogen fixed by the nonbeneficial culture (513) was actually less than that of the control and much less than that of any of the three beneficial cultures employed, and in the last experiment this nonbeneficial culture was slightly better than the control. When the two types of organisms (512 and 513) were used together the total nitrogen fixed was not greater than that fixed by the nonbeneficial organism alone. However, the addition of 0.1 per cent sodium nitrate to the solution originally used to moisten the sand (subsequent waterings being made without nitrogen additions) helped the plants inoculated with a nonbeneficial organism considerably.

SOURCE OF THE NONBENEFICIAL ORGANISMS

The fact is evident that nodule bacteria beneficial and detrimental to Austrian winter peas exist in some of the soils around Jeanerette, La., the nonbeneficial ones evidently predominating. In seeking an explanation for the presence of these organisms it was found that plants of Louisiana vetch (*Vicia ludoviciana* Nutt.) grew plentifully and luxuriantly around the fields and in waste places. The roots of these wild plants are well populated with nodules. It is therefore reasonable to believe that the organisms causing these nodules are abundantly present in the soil. It is customary to consider that the organisms of the common vetch will cross-inoculate with garden peas, field peas, Austrian winter peas, and other legumes, although data concerning the group relations of Louisiana vetch have not been worked out. However, acting on the supposition that the bacteria of this legume are related to those of the Austrian winter pea but not satisfactorily adapted to the latter, the writers made isolations from nodules for comparison with the nonbeneficial bacteria obtained from Austrian winter peas.

After the cultures from Louisiana vetch were purified they were applied to Austrian winter pea and Louisiana vetch seed in the greenhouse under controlled conditions, as indicated in Table 8. These cultures produced nodules on their specific hosts. The results with Austrian winter peas indicate that these Louisiana vetch nodule organisms produce the same effect as those of the nonbeneficial type whose effects have been previously noted in this paper. From April 4 to May 25, 1931, the Austrian winter-pea plants grown from seed treated with three cultures of nodule organisms of Louisiana vetch had much the same appearance as those from seed treated with a nonbeneficial culture isolated from Austrian winter pea nodules. (Fig. 3.) As compared with the control, Louisiana vetch organisms (548, 549, and 550) contributed no nitrogen to the Austrian winter peas; in fact they caused a slight loss. (Table 8.)

Nodules produced by Louisiana vetch cultures were plentiful, scattered, and globular. Nodules of this type are shown in Figures 4 and 5 in comparison with nodules produced by beneficial and nonbeneficial cultures from Austrian winter peas. Characteristic nodule assemblies are more distinct in greenhouse samples than in field samples. (Fig. 2.) Table 8 shows that the average number of nodules per plant is considerably higher when poor cultures of Austrian winter peas and Louisiana vetch were used than when beneficial organisms were used. The close similarity of response of Austrian winter peas to nodule organisms from Louisiana vetch and from apparently parasitized Austrian winter peas is indicative of the origin of the unadapted strains present in the soils studied.

SUMMARY

Cultures of nodule bacteria from poor and vigorous Austrian winter-pea (*Pisum arvense*) plants from Jeanerette, La., have been compared with nodule bacteria from closely related legumes in field and greenhouse tests.

Drainage obtained by ridging the soil had but little effect, and lime and basic slag had practically no effect on the crop produced.

A favorable well-defined effect in quantity and quality of crop was evident in Austrian winter peas treated with efficient nodule bacteria in soil known to contain inefficient nodule-producing organisms.

Evidence has been presented which shows that the nodule organisms of the Louisiana vetch (*Vicia ludoviciana*) reduce the yield of Austrian winter pea on account of their unadaptability to this host.

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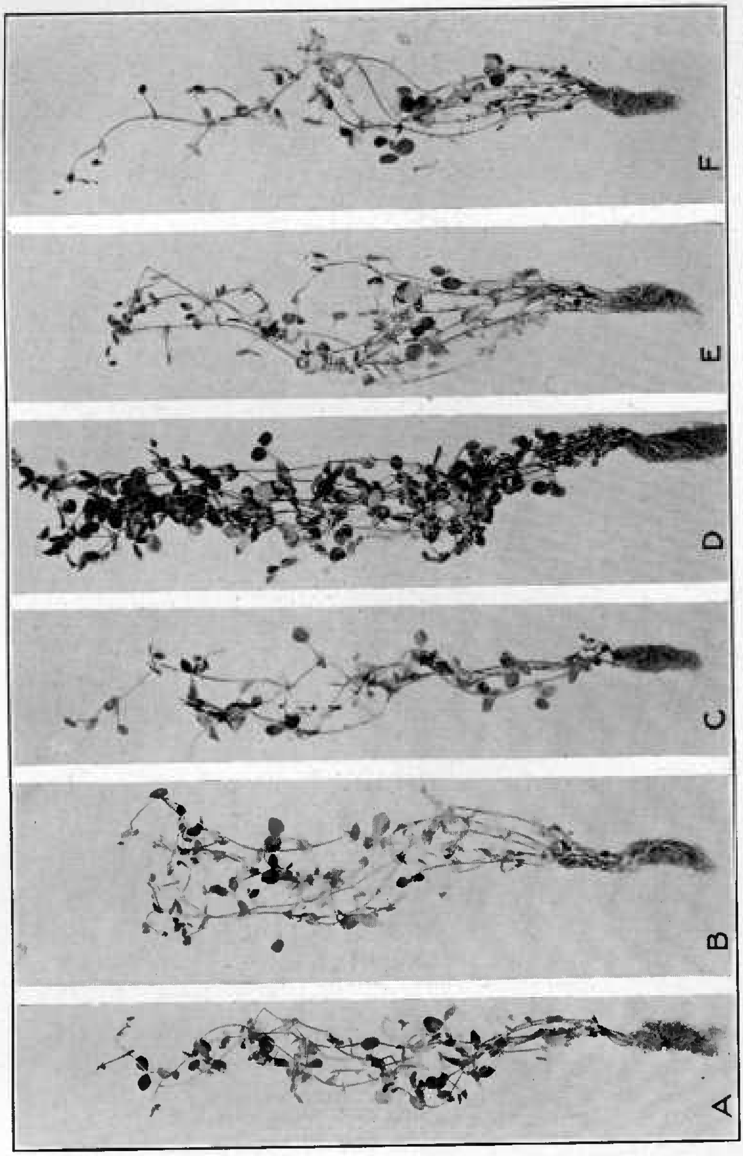

FIGURE 3.—Typical single-pot clumps of Austrian winter-pea plants treated with nodule organisms as follows: A, None; B, nonbeneficial culture 513; C, Louisiana vetch culture 548; D, beneficial culture 512; E and F, Louisiana vetch cultures 549 and 550

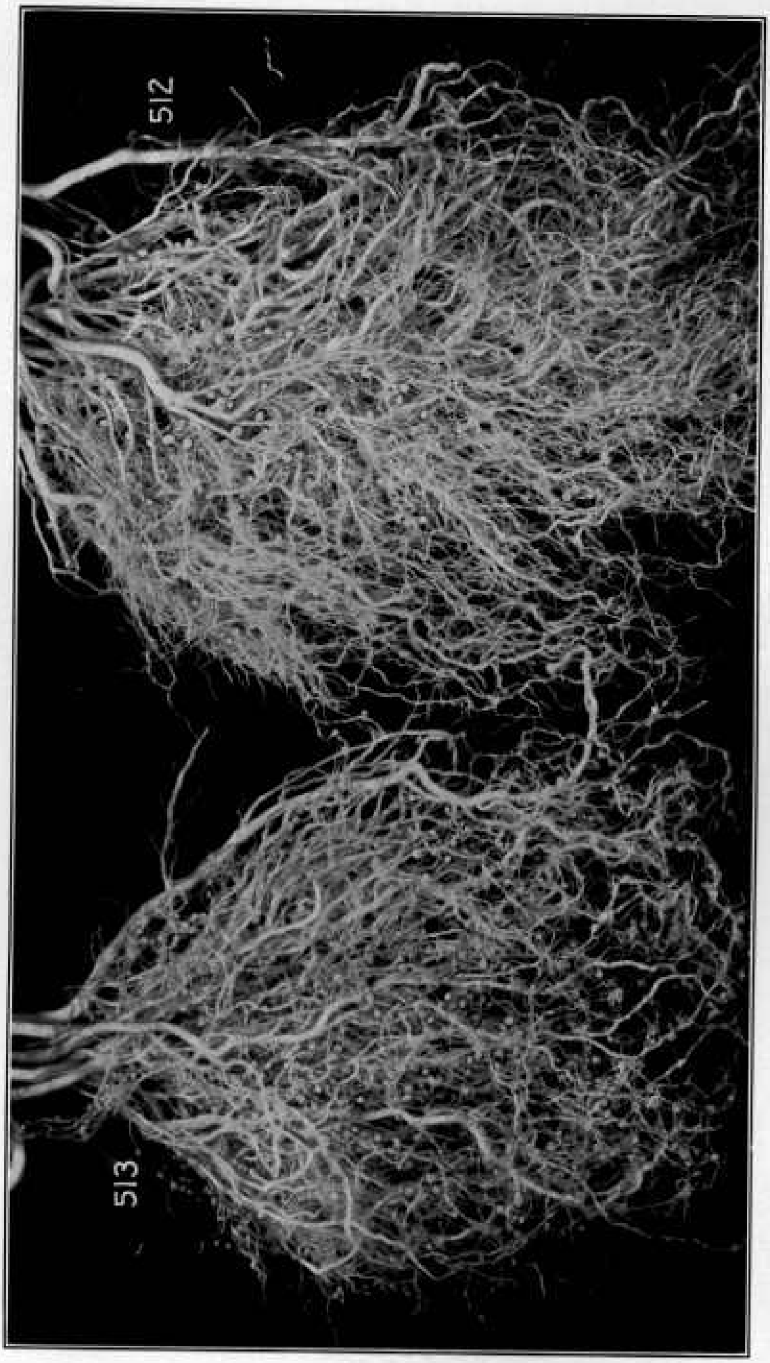

FIGURE 4.—Beneficial culture 512 and nonbeneficial culture 513 on Austrian winter peas grown in greenhouse

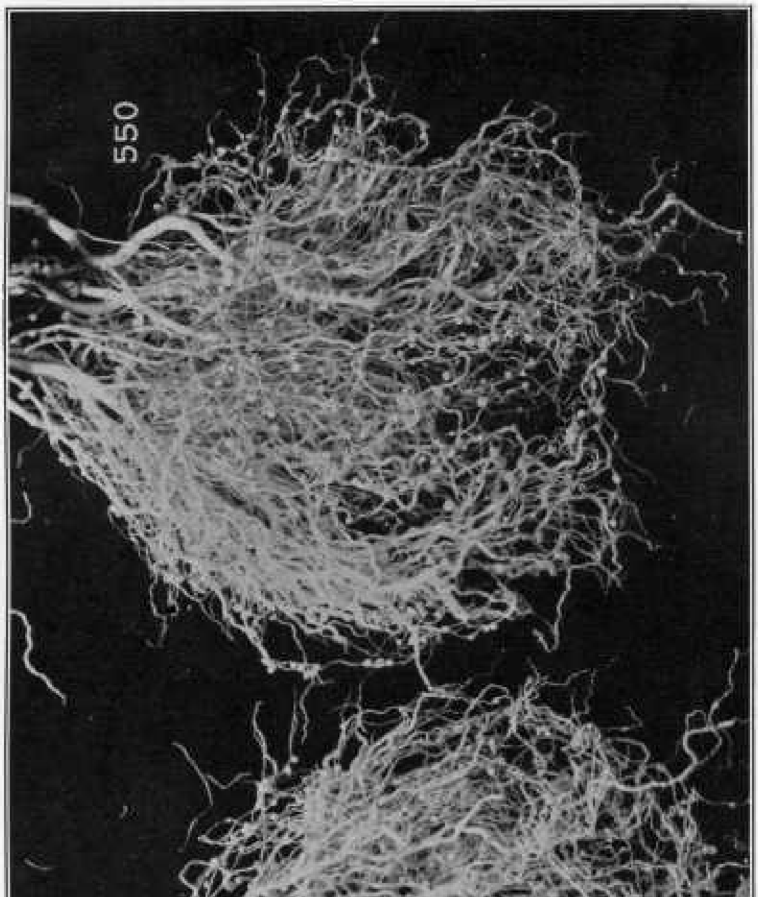

FIGURE 5.—Nonbeneficial types of nodulation produced by two different isolations from nodules of *Vicia ludoviciana* on Austrian winter pea in the greenhouse

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