May 20, 1950

To the Committee on Graduate Study:

I am submitting to you a thesis written by Harry W. Wellhausen entitled "Seed Coat Permeability in Certain Strains of Crimson Clover, Trifolium Incarnatum L." I recommend that it be accepted for nine quarter hours of credit in partial fulfillment of the requirements for the degree of Master of Science, with a major in Agronomy.

L M Skold

Major Professor

We have read this thesis
and recommend its acceptance:

E. Winters

J. K. Underwood

Accepted for the Committee

E. G. Watts

Dean of the Graduate School

SEED COAT PERMEABILITY IN CERTAIN STRAINS OF CRIMSON CLOVER, *TRIFOLIUM INCARNATUM* L.

A THESIS

Submitted to
The Committee on Graduate Study
of
The University of Tennessee
in
Partial Fulfillment of the Requirements
for the degree of
Master of Science

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by

Harry W. Wellhausen

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INTRODUCTION

Crimson clover, Trifolium incarnatum L., was introduced into the United States in 1818, and distributed by the Patent Office in 1855. Crimson clover has become increasingly important since 1880 when its value for agricultural purposes was first beginning to be appreciation (9). It is most widely grown in the Atlantic Coastal plains of the Southeastern states. More recently its production has been extended to the Pacific Northwest.

Seed production has been largely concentrated in Tennessee with Franklin County the largest production area. Until 1948 Tennessee produced approximately 70 per cent of the seed in the United States, since then seed production has expanded and extended rapidly to other Southern states so that Tennessee produced only 50 per cent of the total seed crop in 1949 (13).

Crimson clover is most important as a winter annual legume. It has become increasingly important in Tennessee as an early fall, winter, and spring pasture plant, for soil erosion control and green manure, and for the production of seed.

The most important and difficult part in the production of crimson clover is obtaining and maintaining a stand. Poor stands may be attributed largely to poor seedbed preparation, inadequate inoculation and low percent of hard seed, according to Alexander (2). Crimson clover seed absorb water readily and

sprout quickly. The seedlings are tender, succulent, shallow rooted, and are easily killed by lack of moisture. Kephart (9) states that crimson clover produces practically no hard seed and often germinates 90 per cent in two days.

It is a common occurrence to find heavy stands of clover seedlings two weeks after seed ripens in seasons of frequent rains. With few exceptions all seedlings die during the summer; no new seedlings develop in the fall because the permeability of crimson clover seed permits complete early germination.

In recent years many farmers have obtained excellent volunteer stands of crimson clover after a seed crop, according to Stuckey (19) and Alexander (2). Characteristics of volunteering strains have been that new seedlings would appear following each of the summer and early fall rains. Survival of such seedlings would depend upon continued adequate moisture.

Many of the volunteering strains have now been recognized as hard-seeded or reseeding varieties. Hollowell (7) reports that Dixie crimson clover is a new hard-seeded variety that has successfully volunteered under a wide range of soil and climatic conditions. Dixie is a blend of Thornton, Allen, and Hardy strains that have successfully volunteered in Georgia for more than ten years (19). Since the release of Dixie crimson clover, Alabama has recognized two additional reseeding varieties called Auburn and Autagua. Georgia (19) tests in

1945 indicate that seed of the components that go into the Dixie strain contains more hard seed than the Auburn strain by 30 per cent.

In Europe as many as six to seven different varieties of crimson clover are recognized, differing in date of bloom and color of flowers according to Kephart (9) and Pieters and Hollowell (16). In 1920 Kephart (9) reported that in America no definite varieties were recognized except a white-blossomed variety which was sold in the South and which was two weeks later in maturity than the ordinary crimson clover. Pieters and Hollowell (16) in 1937 reported a strain developed in northern Georgia known as Pitt's clover.

That seeds of many leguminous plants possess impermeable seed coats is a well-established fact. Under natural conditions, individual seeds become permeable at different periods after harvest so that any one lot of seed is capable of producing seedlings over a long period.

REVIEW OF LITERATURE

Seed coat structure and reasons for dormancy of seeds of Leguminoseae have been investigated by many scientists. Crocker (3) has described the mechanisms by which seeds may be delayed in germination as follows: (a) rudimentary embryos that must mature before germination can begin; (b) complete inhibition of water absorption; (c) mechanical resistance to the expansion of the embryo and seed contents by enclosing structures; (d) encasing structures interfering with oxygen absorption by the embryo and perhaps carbon dioxide elimination from it; (e) a state of dormancy in the embryo itself or some organ of it; (f) combination of two or more of these; (g) assumption of secondary dormancy. In Leguminoseae impermability is due to the structure of the seed coat.

Malpighi, after whom certain cells in the seed coat were named, was apparently the first to study seed coat structure in the Leguminoseae family in 1687 (15). Most studies were confined to sweetclover and alfalfa. Efforts have been directed largely toward determining the nature of impermeability and developing methods of making seeds permeable. Pammel (15) in 1899 presented all the theories to date concerning the reasons for impermeability of Leguminoseae. In his studies with red clover and sweetclover he found that the "light line" was permeable to water and attributed impermeability to the

unequal layer of the cutin surrounding the seed. The light line is a band-like region of the outer tangential cell walls of the Malpighian cells just inside the modified cone-shaped structures and running transversely to the long diameter of the cells. White (21) agreed with Pammel that impermeability of some legume seeds was caused by a thickened cuticle layer. Nelson (14) working with sweet peas suggested that impermeability is due, not to hardness of the seed coat itself, but to an impermeable varnish-like film on the surface of the seed.

Coe and Martin (4), working with sweetclover, reported in 1920 that absorption of water was not prevented by either the "cuticular" layer or the cone-shaped structures of the Malpighian cell walls beyond the light line but by the light line itself. In the coats of the impermeable seed, the light line was usually broader with fewer and smaller canals crossing it, the outer tangential walls of the Malpighian cells were thicker below the light line, the lumens of the Malpighian cells were closed in the region of the light line, and the main cavities of the Malpighian cells were more reduced and further below the light line than in the coats of permeable seeds. Thus, it was found that impermeable and permeable seeds differ mainly in the amount of thickening which occurs in the outer tangential walls of the Malpighian cells.

Later Martin and Wyatt (11) (1944) in studies on Melilotus alba and M. officinalis came to the general conclusion

that the cuticle, the light line and the thickened walls of the macrosclereids form an almost continuous barrier to water absorption. Hamby (5) concluded that the impermeable region of the seed coat of Melilotus alba is formed by a layer of tightly appressed suberin caps and that permeability of naturally soft seeds occurs through the opening of a cleft at the strophiole.

Several investigations were made on possible inheritance of impermeability. Lute (10) concluded from two years investigation on inheritance studies of alfalfa seed that individual plants produce seeds varying in permeability in successive years. One group produced approximately the same percentage of hard seed, one group lower and a third much higher than the parents. She suggests a possible genetic influence which may be obscured by climatic factors.

Harrington (6) states that extreme hardness is not a hereditary characteristic of varieties or strains of different clovers. Experiments conducted six successive years proved that the percentage of hard seed has been as great in lots grown from 20 per cent hard seed as from lots grown from 90 per cent hard seed. Pieters (17) studied the progeny of five plants of Lespedeza cuneata that showed a high percentage of permeable seed. Descendents varied from year to year in the percentage of permeable seed. Germinations were high in 1930, very low in 1931, fairly high in 1932, and low in 1933.

James (8) was the first to carry on an extensive study

of the impermeability inheritance in a small seeded winter annual legume. His three years' study with three reseeding strains of crimson clover indicate a reversal in permeability of soft and hard seeded lines. Parents differing from 44.8 per cent to 60.3 per cent in permeability produced progeny differing only 0.3 per cent to 3.7 per cent in permeability. James (8) concluded that it appears doubtful if impermeability is inherited unless the possible inheritance factors are masked by environmental factors to the extent that the different effects cannot be separated.

Pieters and Hollowell (16) reported that even though crimson clover is highly self-fertile, it is not self-tripping. James (8) concluded that the high percentage of cross-pollination of crimson clover eliminates the possibility of impermeability or the reverse being inherited as a pure line characteristic. His conclusions are based on his findings from natural crosses of red-flowered plants on recessive whites which indicated cross-pollination to the extent of 68 per cent.

Thornber (20) reported that treating seed of alfalfa with water at 85 degrees Centigrade for six minutes increased the germination by reducing the percentage of impermeable seed. Harrington (6) found that the soil, season, climate, color, and size of red clover seed had no influence upon the percentage of impermeable seeds.

McKee (12) reported no serious damage on crimson clover through swelling and subsequent drying for several days, but

if the radicle emerged, injury increased in proportion to the length of drying time. Some of the legumes with hypogeal cotyledons that were sprouted with the radicle and plumule both well started into growth recover rapidly after subsequent thorough drying. This is not true or only partially so for legumes with epigeal cotyledons. These data and observations help to explain the difficulty in obtaining and maintaining stands of crimson clover.

Stitt (18) found that unhulled seed required 5 to 10 per cent more soil moisture for radicle emergence than hulled seed. Hulled seed absorbed 18 per cent more moisture in 36 hours than unhulled seed when placed on blotting paper. On mulched plots hulled seed resulted in 35 per cent stand as compared with 10 per cent stand for unhulled seed.

Hollowell (7) reported that the seed and plants of the Dixie variety cannot be distinguished from common crimson clover, and that this variety may be readily contaminated by either cross-pollination or mechanical mixtures. Hollowell (7) designated Dixie as a hard-seeded variety. On the basis of this statement and a few germination tests with unhulled seed of this variety, the Tennessee Crop Improvement Association established seed certification standards in 1947 requiring a minimum of 60 per cent hard seed in mature stripped head samples as a prerequisite for certification of Dixie crimson clover seed. The question was also raised as to methods by

which the reseeding habits could be maintained in Dixie crimson clover. The need for further information as to the validity of such hard-seed requirements led to the initiation of the studies reported herein.

EXPERIMENTAL PROCEDURE

During the seed harvesting seasons of 1948 and 1949, mature stripped head samples of unhulled crimson clover seed were collected from common crimson clover and from the three classes of the Dixie variety, namely, Registered, Certified, and Approved. Registered seed is the progeny of Foundation seed which is made up of equal amounts of the Allen, Thornton and Hardy strains; Certified seed is the progeny of Registered seed or volunteer stands; and Approved seed is the progeny of new seedings of Certified or Approved seed. Samples of Dixie crimson clover collected were limited to the number of certified seed growers producing this variety.

Germination tests were made in accordance with the methods approved by the Association of Official Seed Analysts (1). This consists of placing seeds between folds of moist blotters at a temperature of 20 degrees Centigrade. The first series of tests in 1949 were made in the State Seed Laboratory and all others were made in the Tennessee Crop Improvement Association seed laboratory. In 1948 tests were made with unhulled, hand hulled, and machine hulled seed, whereas in 1949 all tests were made with unhulled seed. In 1948 tests were of 14 days' duration. All subsequent tests were of 21 days' duration. These tests were made approximately one month after harvest; however, in 1949 a re-test was made five months after harvest.

EXPERIMENTAL RESULTS

Samples collected from each class of Dixie crimson clover were limited in number in 1948 because only a few farmers produced this strain in Tennessee. In view of the fact that there were so few samples of each class and so little difference in germination between classes, the results have been grouped in Table I. Germination tests on the basis of 14 days' duration ranged from 2 per cent to 18 per cent with a mean permeability of 7.6 per cent. Unhulled and hand-hulled seed in 1948 showed no difference in germination, averaging about 7 per cent, whereas the germination was 90 per cent or better for machine-hulled seed.

Table II presents the germination record of four samples of common crimson clover seed obtained in 1948. Two samples collected from new seedings germinated 57 per cent and 51 per cent, whereas samples from volunteer stands germinated 28 per cent and 36 per cent.

The 1949 performance of common crimson clover seed is shown in Appendix A. One month after harvest, four samples (269, 287, 288, and 303) of common crimson clover seed germinated less than the average germination of Dixie crimson clover seed (Table III), whereas five months after harvest only one sample (269) germinated less than the average germination of Dixie crimson clover seed (21-day germination period).

The average permeability (21-day germination period) of common crimson clover one month after harvest was 44.0 per cent

TABLE I

GERMINATION OF ALL CLASSES OF DIXIE CRIMSON CLOVER SEED GROWN FOR CERTIFICATION IN TENNESSEE IN 1948

Lab. No.	Percent Germination by Days		
	3	7	14
1	2	2	2
2	1	3	4
3	3	3	4
4	6	10	12
5	4	5	7
6	3	4	4
7	4	4	6
8	7	8	8
9	6	8	12
10	2	5	8
11	3	3	4
12	8	8	8
13	12	14	18
14	7	9	9
15	13	14	14
16	5	5	7
17	7	8	15
18	0	0	2
19	6	7	8
20	3	5	14
21	3	4	4
22	5	6	6
23	2	2	3
24	4	4	4
Average	4.8	5.9	7.6

TABLE II

GERMINATION OF COMMON CRIMSON CLOVER SEED GROWN IN TENNESSEE IN 1948

Lab. No.	Class of Seed	Percent Germination by Days		
		3	7	14
25	New seedings	38	50	57
26	New seedings	40	46	51
	Average	39.0	48.0	54.0
27	Volunteer stands	18	24	28
28	Volunteer stands	21	33	36
	Average	19.5	28.5	32.0

as compared with 64.1 per cent five months after harvest.

The germination record of the different classes of Dixie crimson clover is shown in Appendices B, C, D, and E. Examination of the germination of all classes of Dixie crimson clover seed shows that nine samples, 262, 263, 270, 271, 272, 277, 281, 294, and 295, germinated more than the average germination of common crimson clover seed one month after harvest (Table III), whereas five months after harvest only five samples, 263, 270, 271, 272, 277, germinated more than the average germination of the common crimson clover seed. The decrease in germination of sample 306 from 41 per cent one month after harvest to 8 per cent five months after harvest cannot be accounted for.

It is impossible to make reliable germination comparisons between seedings of Foundation and Registered seed because of an inadequate number of samples and the extreme variability of samples 263 and 272. Appendices B, D, and E present data of crops of Dixie crimson clover seed that may be from one to six generations removed from volunteer stands. The data in these appendices are summarized in Table IV in comparison with Dixie crimson clover seed grown from volunteer crop. One month after harvest samples of seed from volunteer stands germinated 28.3 per cent as compared with new seedings that germinated 31.8 per cent. Five months after harvest seed from these same samples from volunteer stands averaged 31.8 per cent

TABLE III

AVERAGE PERCENT GERMINATION OF FIVE GROUPS OF CRIMSON CLOVER SEED ONE MONTH AND FIVE MONTHS AFTER HARVEST IN 1949

Grown from	No. of Samples	7-Day Germination Period			21-Day Germination Period		
		One Month After Harvest	Five Months After Harvest	Germination Increase 1 to 5 Months	One Month After Harvest	Five Months After Harvest	Germination Increase 1 to 5 Months
Dixie							
Foundation	1	18.0	35.0	17.0	35.0	43.0	8.0
Registered	5	23.8	51.2	27.4	40.4	57.2	16.8
Volunteer	19	22.0	27.0	5.0	28.3	31.8	3.5
Approved-Cert.	26	21.6	31.8	10.2	30.0	37.8	7.8
Average	51	21.9	32.0	10.1	30.3	37.6	7.3
Common	16	32.4	58.3	25.9	44.0	64.1	20.1
Difference Dixie and Common		10.5	26.3		13.7	26.5	

TABLE IV

AVERAGE PERCENT GERMINATION OF DIXIE CRIMSON CLOVER SEED GROWN FROM VOLUNTEER CROP AND NEW SEEDINGS

Progeny	No. of Samples	7-Day Germination Period			21-Day Germination Period		
		One Month After Harvest	Five Months After Harvest	Germination Increase 1 to 5 Months	One Month After Harvest	Five Months After Harvest	Germination Increase 1 to 5 Months
Volunteer[1]	19	22.0	27.0	5.0	28.3	31.8	3.5
New Seedings[2]	32	21.8	33.1	11.3	31.8	40.8	9.0
Difference		-0.2	6.1	6.3	3.5	9.0	6.5

[1]From Appendix C.

[2]From Appendices B, D, and E.

germination and 40.8 per cent germination from new seedings. The average permeability of seed samples from volunteer stands was 3.5 per cent less one month after harvest and 9.0 per cent less five months after harvest than the average permeability from new seedings one to six generations removed from volunteer stands.

The 1949 performance of common crimson clover seed and the progeny of different classes of Dixie crimson clover seed given in Appendices A, B, C, D, and E are summarized in Table III for the 7- and 21-day germination periods. The average permeability of the progeny of all classes of Dixie crimson clover one month and five months after harvest was 30.3 per cent and 37.6 per cent respectively as compared with the average permeability of 44.0 per cent and 64.1 per cent respectively of common crimson clover seed one and five months after harvest. The mean germination difference between Dixie and common crimson clover seed one month after harvest was 13.7 per cent, whereas five months after harvest the mean germination difference was 26.5 per cent. Thus in four months' time the mean germination of common crimson clover seed increased 20.1 per cent and Dixie crimson clover seed only 7.3 per cent (21-day germination period).

The common crimson clover seed consistently averages more permeable seed than Dixie crimson clover seed one month and five months after harvest for 3, 7, 14, and 21-day germination periods. This cumulative average germination percent

of the two strains of crimson clover is shown graphically in Figure 1.

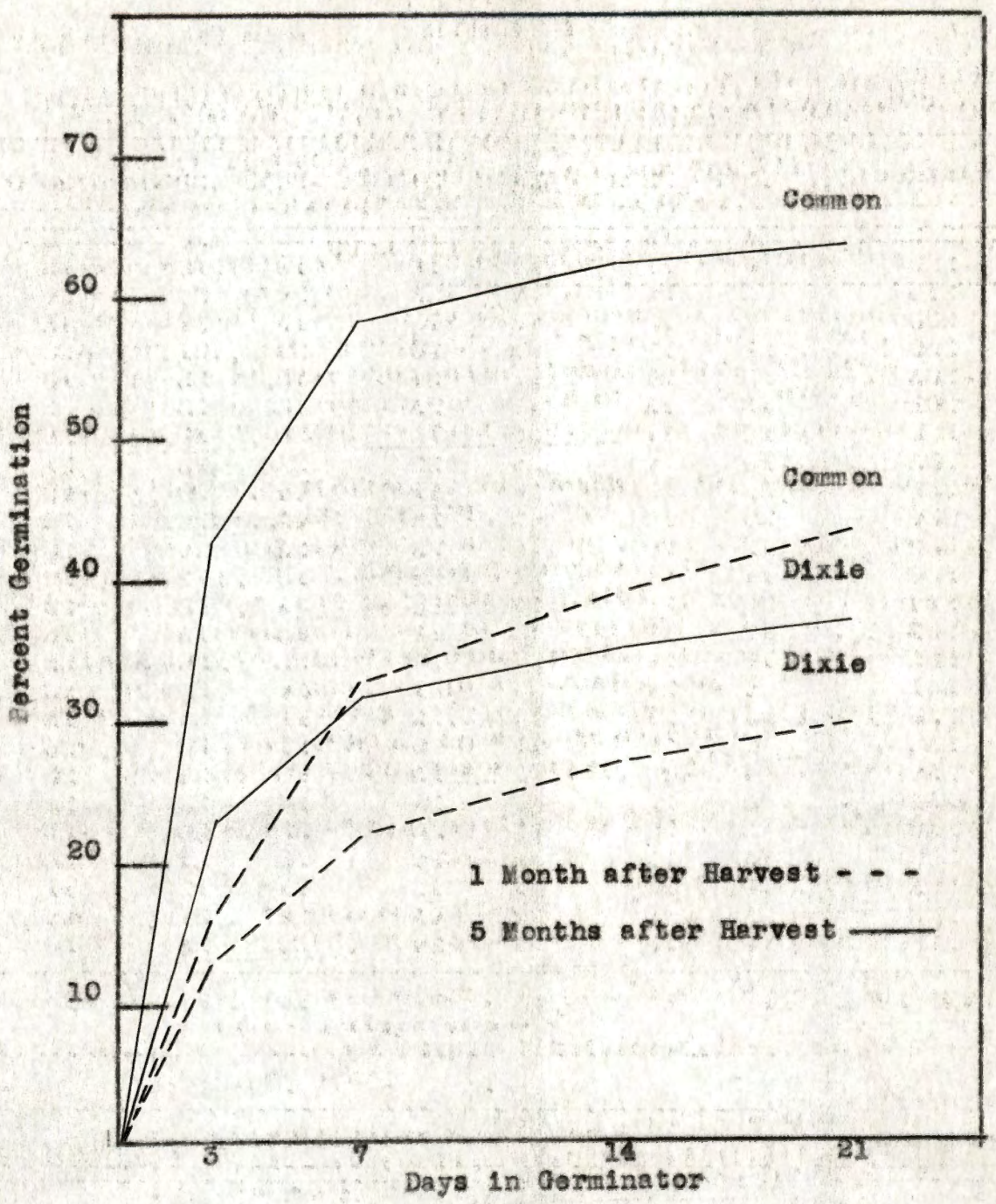


Fig. 1. Cumulative Germination Percent of Common and Dixie Crimson Clover in 1949.

DISCUSSION

Many farmers have reported excellent volunteer stands from common crimson clover even under adverse conditions. Mean germination of 54 per cent of seed from new seedings of common crimson clover suggests the possibility that the present reseeding varieties may have developed as a result of a process of natural selection over a period of years. This process would be very slow because of the high percentage of cross-pollination that normally takes place under field conditions.

It is a well-known fact that hard seed become more permeable with age. The rapidity with which this takes place would be affected by storage conditions and the degree of seed impermeability. The results of germination tests five months after harvest indicate that impermeability is retained longer in the seed of Dixie crimson clover than in the seed of common crimson clover. This has also been demonstrated by farmers who have reported that seedlings of Dixie crimson clover appear four or five times during the season following seed harvest, whereas it is unusual for seedlings of common crimson clover to appear more than once.

Samples of the Dixie strain from mechanically harvested and recleaned seed obtained and tested by the State Department of Agriculture germinated 80 per cent or better with a relatively small percent of hard seed. From this it is quite obvious that scarification in mechanical harvesting and reclean-

ing was the cause of this increase in seed coat permeability.

Hollowell warned that the reseeding habit of Dixie can be maintained only by permitting repeated volunteering of this strain; first, because of possible contamination through cross-pollination with other non-reseeding types and, second, because the Dixie strain is heterozygous for reseeding characteristics.

The extreme variation from 13 to 86 per cent in permeability of seed from new seedings one to six generations removed from volunteer parents and the greater mean permeability of seed from new seedings compared with seed from volunteer stands both indicate that continued volunteering is necessary to maintain the reseeding habit of Dixie crimson clover.

Additional studies should be made to determine the comparative degree of seed-coat impermeability of common crimson clover as compared with Dixie crimson clover at periods longer than five months after harvest.

SUMMARY

Samples of unhulled seed of common crimson clover and of different classes of Dixie crimson clover were obtained to compare permeability of seed. Sixteen samples of common crimson clover seed had a mean germination of 44.0 per cent one month after harvest, compared with fifty-one samples of Dixie crimson that had a mean germination of 32.0 per cent. Five months after harvest the mean germination of the same samples of common crimson clover seed was 64.1 per cent and Dixie crimson clover seed was 37.6 per cent. Thus the mean difference in permeability between common and Dixie crimson clover was 13.7 per cent one month after harvest and 26.5 per cent five months after harvest.

Nineteen seed samples from volunteer fields of Dixie crimson clover were compared with 26 samples from newly seeded fields one to six generations removed from volunteer parents. The mean difference in permeability between samples from volunteer parents and samples from fields one to six generations removed from volunteer parents was 3.5 per cent one month after harvest and 9.0 per cent five months after harvest.

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APPENDIX

APPENDIX A

GERMINATION OF COMMON CRIMSON CLOVER SEED GROWN IN TENNESSEE IN 1949

	Percent Germination by Days							
	3		7		14		21	
	Months after Harvest							
Lab. No.	1	5	1	5	1	5	1	5
269	17	36	23	28	28	29	28	30
285	14	42	28	55	31	60	41	61
286	15	36	30	44	37	47	45	48
287	9	60	18	69	21	70	24	72
288	15	60	17	65	18	67	18	67
289	13	37	23	52	40	60	52	60
300	17	22	56	55	75	68	82	69
301	24	55	36	67	39	70	44	72
302	14	30	35	40	45	46	50	48
303	9	28	17	32	20	38	24	41
304	17	52	29	66	36	71	36	74
314	24	65	30	70	34	71	34	71
317	5	42	27	71	35	75	42	75
318	29	47	46	68	53	76	58	79
319	21	58	30	67	33	70	37	70
320	5	9	74	85	86	89	89	89
Average	15.5	41.8	32.4	58.3	39.4	62.9	44.0	64.1

APPENDIX B

GERMINATION OF APPROVED DIXIE CRIMSON CLOVER SEED GROWN FROM APPROVED OR CERTIFIED SEED IN TENNESSEE, 1949

	Percent Germination by Days							
	3		7		14		21	
	Months after Harvest							
Lab. No.	1	5	1	5	1	5	1	5
259	15	29	21	34	26	37	29	40
262	27	42	31	47	38	51	44	52
267	5	11	7	12	11	13	11	13
268	17	23	18	24	29	24	29	26
270	2	20	52	70	79	80	82	81
273	9	32	18	37	28	39	38	40
274	4	18	11	27	16	36	20	39
278	1	30	13	50	21	56	29	56
279	9	21	11	23	15	24	17	25
281	4	24	22	51	34	58	48	59
282	15	24	21	26	22	26	22	28
283	13	15	18	15	19	17	19	18
284	20	55	33	58	37	59	38	61
290	11	44	14	53	16	53	16	53
293	12	20	20	27	37	34	38	36
294	20	16	43	33	47	56	56	63
295	22	22	39	41	44	50	48	51
297	19	24	24	33	28	38	31	42
299	16	11	23	19	26	25	34	29
305	12	17	15	27	19	29	23	29
307	19	20	19	21	19	22	19	24
308	25	15	28	20	28	21	28	25
309	16	18	17	19	17	21	17	22
310	23	24	24	27	24	28	24	29
322	9	11	11	16	12	19	12	21
323	7	17	8	18	8	19	8	21
Average	13.5	23.2	21.6	31.8	26.9	35.9	30.0	37.8

APPENDIX C

GERMINATION OF CERTIFIED DIXIE CRIMSON CLOVER SEED GROWN FROM VOLUNTEER CROP IN TENNESSEE, 1949

	Percent Germination by Days							
	3		7		14		21	
	Months after Harvest							
Lab. No.	1	5	1	5	1	5	1	5
258	9	27	14	33	18	39	24	41
261	10	15	12	15	16	16	16	17
264	24	25	26	27	29	28	30	29
266	6	12	12	13	12	13	12	13
271	6	19	49	59	70	65	74	66
276	16	29	18	31	19	31	19	33
277	10	48	59	72	77	77	80	77
280	8	11	14	11	15	11	16	12
291	13	19	15	25	17	26	17	28
292	14	13	18	21	20	25	21	29
296	16	19	22	31	28	41	30	47
298	6	11	21	32	28	44	36	48
306	21	6	32	6	37	6	41	8
311	5	12	8	18	10	18	11	18
312	14	9	16	9	19	10	19	10
313	22	25	24	29	27	31	27	32
321	13	31	21	38	25	44	25	45
324	13	14	19	23	19	24	19	25
327	16	9	19	21	19	23	21	26
Mean Germ. (Per cent)	12.7	18.6	22.0	27.0	26.6	30.1	28.3	31.8

APPENDIX D

GERMINATION OF CERTIFIED DIXIE CRIMSON CLOVER SEED GROWN FROM REGISTERED SEED IN TENNESSEE, 1949

	Percent Germination by Days							
	3		7		14		21	
	Months after Harvest							
Lab. No.	1	5	1	5	1	5	1	5
263	15	47	32	74	46	80	51	81
265	3	18	5	20	8	20	9	20
272	4	31	39	78	72	85	75	86
275	5	31	15	49	23	60	32	63
326	21	22	28	35	35	35	35	36
Average	9.6	29.8	23.8	51.2	36.8	56.0	40.4	57.2

APPENDIX E

GERMINATION OF REGISTERED DIXIE CRIMSON CLOVER SEED GROWN FROM FOUNDATION SEED IN TENNESSEE, 1949

	Percent Germination by Days							
	3		7		14		21	
	Months after Harvest							
Lab. No.	1	5	1	5	1	5	1	5
260	7	15	18	35	28	42	35	43