

EFFECT OF ENVIRONMENTAL CONDITIONS UPON THE NUMBER OF LEAVES AND THE CHARACTER OF THE INFLORESCENCE OF TOBACCO PLANTS¹

H. A. ALLARD

INTRODUCTION

Among tobacco growers it is a matter of common observation that the number of commercial leaves produced by tobacco plants varies considerably from season to season. It is commonly believed that drought and other conditions unfavorable to growth not only produce smaller sized leaves but also reduce the number of leaves. Since in actual field practice any count of the number of leaves is only approximately accurate, an investigation was made to determine the true number of leaves and the character of the inflorescence produced by tobacco plants under different conditions of environment.

Since the inflorescence of the tobacco plant is determinate or centrifugal in its mode of flowering there is no further production of internodes with the appearance of the terminal flower bud. The terminal blossom is the first to appear, followed by other blossoms arising from the nearest or inmost buds of the branches representing the terminal whorl. The lowest lateral branch of the inflorescence of the main stem is popularly termed the first bald sucker from the fact that it is leafless or bears only rudimentary leaves. In well-developed plants the first bald sucker is readily distinguished from the secondary axillary branches below, and is sometimes used as a convenient point from which to begin a count of the number of leaves produced by the plant.

In the following investigations a count was made of every leaf above the cotyledons. In order to do this conveniently the same leaf on each plant, counting from the cotyledons, was marked by puncturing the leaf one or two times with a heated needle. This treatment affords a quick and simple method of marking any particular leaf, and at the same time prevents the possibility of inoculating the plants with the mosaic disease.

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FIRST EXPERIMENT

In the first experiment seed of a bagged individual plant (7G) of the Connecticut Broadleaf strain designated as No. 2 was used. The seed was sowed in flats Nov. 13, 1912, and on Jan. 4, 1913, the plants were transplanted to two-inch pots. On Jan. 28 they were transplanted from these pots to a bed of rich clay-loam in the greenhouse at Arlington, Virginia. From the time the plants were transferred to two-inch pots a record was kept of all the leaves produced by marking the following leaves:

4th	leaf	above	the	cotyledons	marked	in	January.
6th	"	"	"	"	"	"	on February 13.
8th	"	"	"	"	"	"	March 1.

As soon as the young plants had become established in the bed, the moisture relations of one half of the bed were maintained at an optimum for the growth of the plants, while the other half of the bed was kept relatively dry. The moisture content of the moist soil ranged from 18 to 20 percent throughout the experiment, while that of the dry soil was kept at 10 to 12 percent.

The plants in the moist soil were as large and as vigorous in all respects as plants growing under the most favorable field conditions. The plants in the dry soil became very much stunted, reaching only half the height attained by the plants in the moist soil and blossomed about 10 days later than these.

Complete data as to the number of leaves, number of nodes, and the character of the inflorescence of the plants grown in the moist and dry soil are given in Table I.

From a comparison of the data for the two sets of plants, the following relations are brought out. From column (7), it is seen that the average number of nodes from the cotyledons up to but not including the terminal whorl of branches is the same for the normal and stunted plants, namely 32.4 and 32.9, respectively. The average number of nodes produced by the plants, inclusive of the terminal whorl, is also unchanged, namely 36.6 for the normal and 36.1 for the stunted plants. An analysis of the various elements of the inflorescence as shown in columns (4), (5) and (6) indicates somewhat different relations for the two sets of plants. From column (6) it is evident that the normal plants produced the largest number of flower branches, an average of 8.2, as compared with an average of 5.9 for the stunted plants. This reduction in the number of flower branches has taken

TABLE I

First Experiment. Number of Leaves, Number of Nodes, and Character of Inflorescence of Connecticut Broadleaf Plants Grown in the Greenhouses in Moist and Dry Soils

Moist Soil

Number of Plant	Height of Plants	No. of Leaves from Cotyledons up to, but not including, 1st Bald Sucker	Inflorescence			Total No. of Nodes Produced not Including Terminal Whorl	Total No. of Nodes Produced Including Terminal Whorl	Date of First Blossoms in 1913	Number of Days Intervening from Date of Transplanting to Opening of First Blossom
			No. of Lateral Flower Branches, Including 1st Bald Sucker but not Including Terminal Whorl	No. of Flower Branches in Terminal Whorl	Total No. of Flower Branches, Including 1st Bald Sucker and Terminal Whorl				
1	84 in.	30	4	4	8	34	38	March 26	57
2	90 "	29	4	4	8	33	37	" "	57
3	91 "	28	5	4	9	33	37	" "	57
4	87 "	28	3	4	7	31	35	" 25	56
5	85 "	29	4	4	8	33	37	" "	56
6	90 "	28	4	4	8	32	36	" 26	57
7	96 "	28	4	5	9	32	37	" "	57
8	95 "	29	4	4	8	33	37	" 25	56
9	90 "	28	4	5	9	32	37	" "	56
10	85 "	27	4	4	8	31	35	" "	56
Av. . .	89.3 "	28.4	4	4.2	8.2	32.4	36.6		56.5

Dry Soil

1	45 in.	31	3	4	7	34	38	March 30	61
2	42 "	30	3	4	7	33	37	" 28	59
3	48 "	30	2	3	5	32	35	April 5	67
4	48 "	30	2	3	5	32	35	" "	67
5	45 "	31	3	3	6	34	37	" "	67
6	—	30	3	3	6	33	36	" "	67
7	44 "	30	3	3	6	33	36	" "	67
8	45 "	30	3	3	6	33	36	" 1	63
9	48 "	30	2	3	5	32	35	" 4	66
10	48 "	30	3	3	6	33	36	" 6	68
Av. . .	45.9 "	30.2	2.7	3.2	5.9	32.9	36.1		65.2

place both in the terminal whorl and the lateral branches. The stunted plants produced an average of .16 branch less in the terminal whorl and an average of 1.3 less in the number of lateral branches (see columns 4 and 5).

As shown in column (3) the average number of leaves produced counting from the cotyledons up to, but not including, the leaf subtending the first bald sucker was 28.4 for the normal plants as com-

pared with 30.2 for the stunted plants. Although the first bald sucker (the lowermost branch of the inflorescence) in the normal plants occupies its true position, it is evident that this branch has been suppressed in the stunted plants. Consequently, the lowermost flowering branch appearing upon the stunted plants no longer represents the true position of the first bald sucker. More properly, it is one of the higher lateral branches of the inflorescence which now appears to be the first bald sucker.

In a second experiment the true as compared with the apparent expression of the first bald sucker is even more clearly and strikingly shown.

SECOND EXPERIMENT

In the first test stunting was brought about by maintaining a very dry soil. In the second test, the plants were grown in pots, and stunting was brought about by growing one set of plants in very small pots containing relatively little soil.

The plants used for this test were obtained from a single mother plant, and are direct descendants through three stunted generations of one of the stunted individuals of the preceding test.

The seed was sown in flats Jan. 7, 1915. As soon as the plants were large enough, they were transplanted from the flats directly to 8-inch and 4-inch pots respectively, in which they remained throughout the experiment. In this test 17 plants were grown in the 8-inch and 23 plants in the 4-inch pots. Owing to the fact that the plants in the smaller pots were very severely stunted, they grew very slowly and blossomed about two months later than the plants grown in the larger pots. Complete data as to the number of leaves, number of nodes, character of the inflorescence, etc., for the two sets of plants are given in Table II.

From the data given in Table II it is evident that the plants were stunted much more severely than in the preceding test. From column (8) it is shown that the average number of nodes produced, not including the terminal whorl, is the same for both sets of plants, namely 32.4 for the plants in the large pots, and 32.8 for the smaller plants. From column (9) it is also shown that the average number of nodes produced, including the branches of the terminal whorl, is the same, *i. e.*, 35.8 for the larger plants and 35.6 for the smaller plants. From column (7) it is evident that the average number of flower branches

TABLE II

Second Experiment. Number of Leaves, Number of Nodes and Character of Inflorescence of Connecticut Broadleaf Plants Grown in Pots in the Greenhouse at Arlington, Virginia, 1915

Plants in 8-inch Pots

No. of Plant	Height to Top of Flower Head	Number of Dead Basal Leaves Above Cotyledons	Number of Leaves from Cotyledons to, but not Including First Bald Sucker	Inflorescence			Total Number of Nodes Produced, not Including Terminal Whorl	Total Number of Nodes Produced Including Terminal Whorl	Date of First Blossoms in 1915	Number of Days Intervening from Date of Transplanting to Opening of First Blossom
				No. of Lateral Flower Branches Including 1st Bald Sucker, not Including Terminal Whorl	Number of Flower Branches in Terminal Whorl	Total Number of Flower Branches Including First Bald Sucker and Terminal Whorl				
1	39 in.	1 to 10 inc.	27	5	4	9	32	36	Apr. 21	57
2	37 "	do.	30	5	3	8	35	38	" 28	64
3	43 "	do.	25	6	3	9	31	34	" 21	57
4	47 "	1 to 9 inc.	27	5	4	9	32	36	" 21	57
5	48 "	1 to 10 "	25	7	3	10	32	35	" 21	57
6	44 "	1 " 12 "	26	7	4	11	33	37	" 21	57
7	45 "	1 " 10 "	24	7	3	10	31	34	" 21	57
8	42 "	1 " 8 "	26	7	3	10	33	36	" 21	57
9	45 "	1 " 10 "	27	6	3	9	33	36	" 21	57
10	46 "	1 " 10 "	26	6	4	10	32	36	" 22	58
11	48 "	1 " 11 "	25	6	4	10	31	35	" 23	59
12	45 "	1 " 10 "	26	6	4	10	32	36	" 22	58
13	38 "	1 " 8 "	26	7	4	11	33	37	" 26	62
14	48 "	1 " 9 "	26	7	3	10	33	36	" 28	64
15	43 "	1 " 10 "	27	7	3	10	34	37	May 1	67
16	36 "	—	25	5	3	8	30	33	" 2	68
17	48 "	—	31	3	3	6	34	37	Apr. 30	66
Av. . .	43.6 "		26.4	6	3.3	9.4	32.4	35.8		60.1

Plants in 4-inch Pots

No. of Plant	Height to Top of Flower Head	Number of Dead Basal Leaves Above Cotyledons	Number of Leaves from Cotyledons to, but not Including First Bald Sucker	Inflorescence			Total Number of Nodes Produced, not Including Terminal Whorl	Total Number of Nodes Produced Including Terminal Whorl	Date of First Blossoms in 1915	Number of Days Intervening from Date of Transplanting to Opening of First Blossom
				No. of Lateral Flower Branches Including 1st Bald Sucker, not Including Terminal Whorl	Number of Flower Branches in Terminal Whorl	Total Number of Flower Branches Including First Bald Sucker and Terminal Whorl				
1	18 in.	1 to 13 inc.	No lateral branches	0	4	4	31	35	June 24	122
2	20 "	1 " 14 "	"	0	3	3	31	34	" 21	119
3	20 "	1 " 14 "	"	0	3	3	31	34	" 20	118
4	16 "	1 " 13 "	"	0	3	3	31	34	" 24	122
5	22 "	1 " 14 "	"	2	3	5	34	37	" 18	116
6	25 "	1 " 14 "	32	1	3	4	33	36	" 16	114
7	20 "	1 " 15 "	No lateral	1	3	3	33	36	" 20	118
8	25 "	1 " 14 "	32	1	3	4	33	36	" 18	116
9	26 "	1 " 14 "	30	1	3	4	31	34	" 21	119
10	29 "	1 " 13 "	29	1	3	4	30	33	" 24	122
11	17 "	1 " 17 "	31	1	2	3	32	34	—	—
12	25 "	1 " 17 "	34	1	3	4	35	38	—	—
13	17 "	1 " 17 "	No lateral	0	3	3	32	35	—	—
14	19 "	1 " 17 "	"	0	2	2	33	35	—	—
15	21 "	1 " 17 "	34	1	3	4	35	38	—	—
16	17 "	1 " 17 "	No lateral	0	2	2	34	36	—	—
17	18 "	1 " 17 "	"	0	3	3	35	38	—	—
18	19 "	1 " 17 "	"	0	2	2	34	36	—	—
19	20 "	—	33	1	2	3	34	36	—	—
20	18 "	—	33	1	3	4	34	37	—	—
21	18 "	—	No lateral	0	2	2	33	34	—	—
22	19 "	—	"	0	3	3	34	37	—	—
23	22 "	—	32	1	4	5	33	37	—	—
Av. . .	20.4 "		32	1.0+	2.8	3.3	32.8	35.6		118.6

in the entire inflorescence is considerably higher for the plants in the large pots, *i. e.*, 9.4 as compared with only 3.3 for the smaller plants. The average number of branches in the terminal whorl is somewhat higher for the larger plants, 3.3 for the plants in the 8-inch pots, and 2.8 for the plants in the 4-inch pots. With respect to the position of the first bald sucker, columns (4) and (5) bring out the same relations that were shown in the preceding test. Although an average of 6 lateral flower branches was produced by the larger plants, the average had been reduced to one lateral branch in the plants grown in 4-inch pots.

Owing to the fact that stunting has been extreme in this test, the data in column (4) are particularly significant. For the larger plants the average number of leaves above the cotyledons, not including the first bald sucker, is 26.4 as compared with the much higher average of 32 for the ten plants in the 4-inch pots. In many of these plants it is shown that there was complete suppression of all the lateral branches of the inflorescence.

A comparison of the data for the two experiments, as shown in Tables I and II, brings out the fact that the average number of nodes produced by the plants, exclusive of the terminal whorl of branches, has remained unchanged under all conditions of growth:

1st experiment	{	Plants moist soil,	32.4 nodes
		" dry "	32.9 "
2d experiment	{	" 8-inch pots,	32.4 "
		" 4 " "	32.8 "

If the average number of nodes, including the terminal whorl, is considered, it is indicated that the plants in the second experiment have produced somewhat fewer nodes than those in the first experiment:

1st experiment	{	Plants in moist soil	36.6 nodes
		" " dry "	36.1 "
2d experiment	{	" " 8-inch pots	35.8 "
		" " 4 " "	35.6 "

Since it has been shown that the average number of nodes exclusive of the terminal whorl has been unchanged, it is evident that the above reduction has taken place in the branches of the terminal whorl.

Unfavorable conditions reduce the size of the inflorescence quite as readily as the size of the leaves. In severely stunted plants the branches of the terminal whorl become so greatly reduced that they may be represented by single blossoms as was the case with many plants grown in the 4-inch pots in the second experiment. (See Plate XX.)

In plants stunted even more severely than those in the 4-inch pots in the second experiment, the terminal whorl is completely suppressed, and the inflorescence of the plant is reduced to the single terminal blossom of the main stem. Such plants were only 8 to 10 inches in height when blossoming finally took place, and the majority of the leaves were reduced to mere bracts.

Experiments have shown that tobacco plants may be very considerably stunted before any retardation in time of blossoming takes place. Beyond these limits, however, blossoming in severely stunted plants may be delayed almost indefinitely. In fact, in the writer's experience, it has been possible to keep young tobacco plants in a practically dormant condition for periods as long as the normal life of the plant. Plants kept in a practically dormant condition for about 5 months are shown in Plates XXI-XXIII. The smallest plants in the 2-inch pots are sister plants of the same age as the large plants, and all were grown from seed sowed Nov. 13, 1912. Experiments with these dormant plants have shown that this inhibition of growth is only temporary in its effects. If such plants are transplanted to the field, vigorous growth ensues and plants of nearly normal size are produced.

In the field it is known that the number of commercial leaves is more or less variable from year to year. These variations depend upon such accidental factors as depth of transplanting, drought, height of topping, etc., and do not show the true number of leaves produced by the plants. In ordinary field practice probably not less than 6 or 8 leaves above the cotyledons are lost. As shown in Table II, the plants grown in the 8-inch pots lost from 8 to 10 leaves above the cotyledons, while those more severely stunted in the 4-inch pots lost in some instances as many as 17 leaves.

From the writer's experimental data in Tables I and II it is indicated that the number of nodes below the terminal bud is not changed by environmental conditions.

Hayes, East and Beinhart² from a statistical study of some New England types in the field, came to the conclusion that environmental conditions have little effect upon the number of leaves produced in the field.

Although in the writer's experiments it is indicated that severe stunting brings about a suppression of the flower branches of the terminal whorl, it is probable that the terminal bud does not appear until the number of nodes preceding it and predetermined in the embryo have developed.

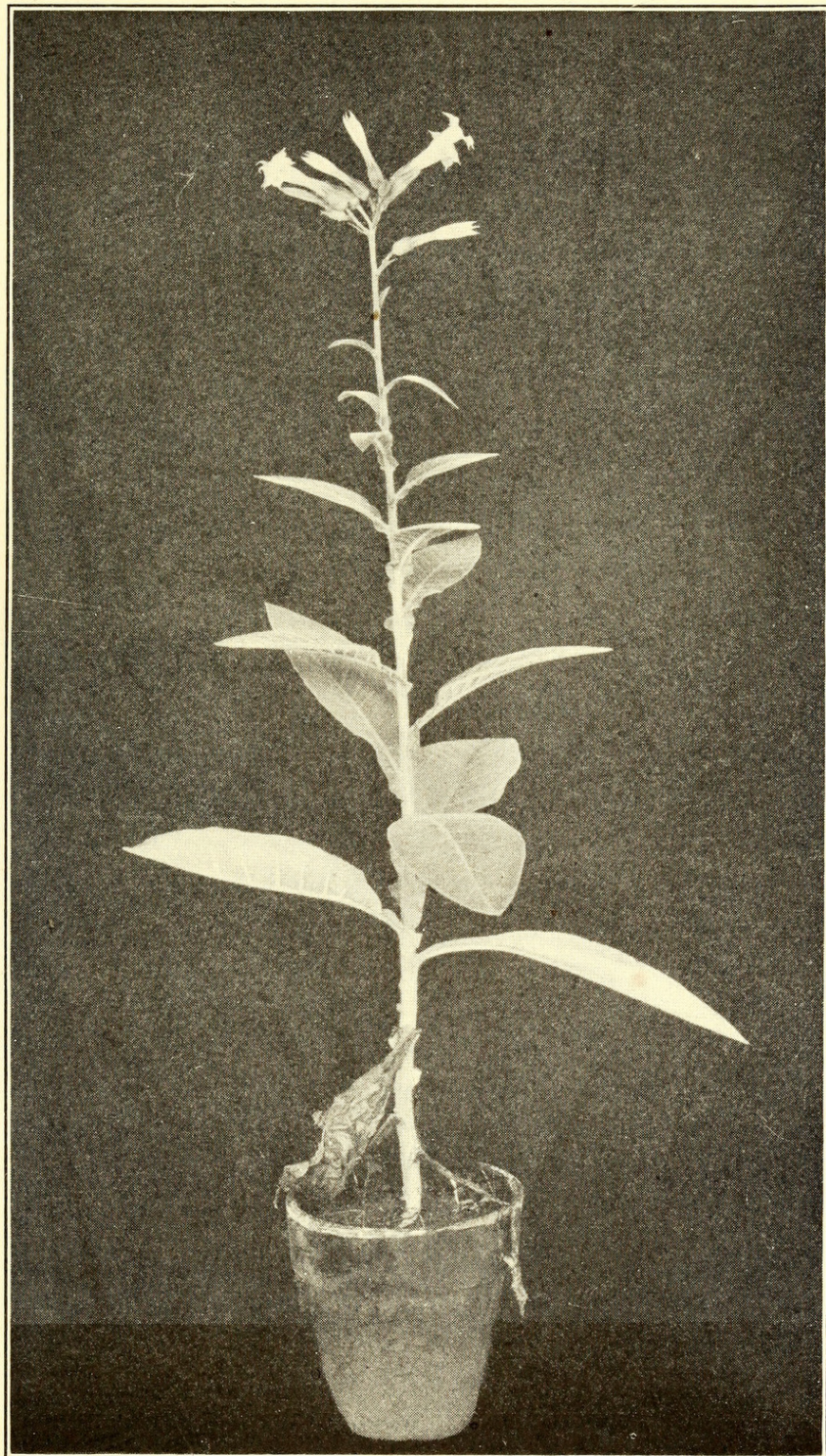
From field experiments with tobacco East and Hayes (*Am. Naturalist*, 48: 5-48, previously cited) have concluded that the conditions under which the mother plants grow may determine the number of leaves in the embryo within the normal limits of fluctuation. To establish this point beyond question, however, it will be necessary to determine all the nodes produced by the plants beginning from the cotyledons. It is clear that results based upon counts from the first bald sucker may not be entirely free from error. From the data for the experiments given in Tables I and II, it appears that the position of the first bald sucker has not been constant under all conditions.

Thus, counting from the cotyledons up to, but not including, the first bald sucker, the normal plants in experiment I produced an average of 28.4 leaves. In the second experiment the average for a similar count was only 26.4, amounting to a difference of two leaves. Counting all the nodes below the terminal blossoms, however, the average for both sets of plants was the same, namely 32.4 for the plants in experiment I and 32.4 for those which averaged only half as tall in experiment II. As the limits of minimum growth are approached it is evident that the first bald sucker can no longer be relied upon for comparative studies.

Between the limits of minimum growth and maximum growth all degrees of ontogenetic expression with respect to capsule and seed development may be noted. Reduction in size of plant is accompanied by a more or less proportionate decrease in the number of seed pods borne by the plant.

It has not yet been shown that the physiological environment

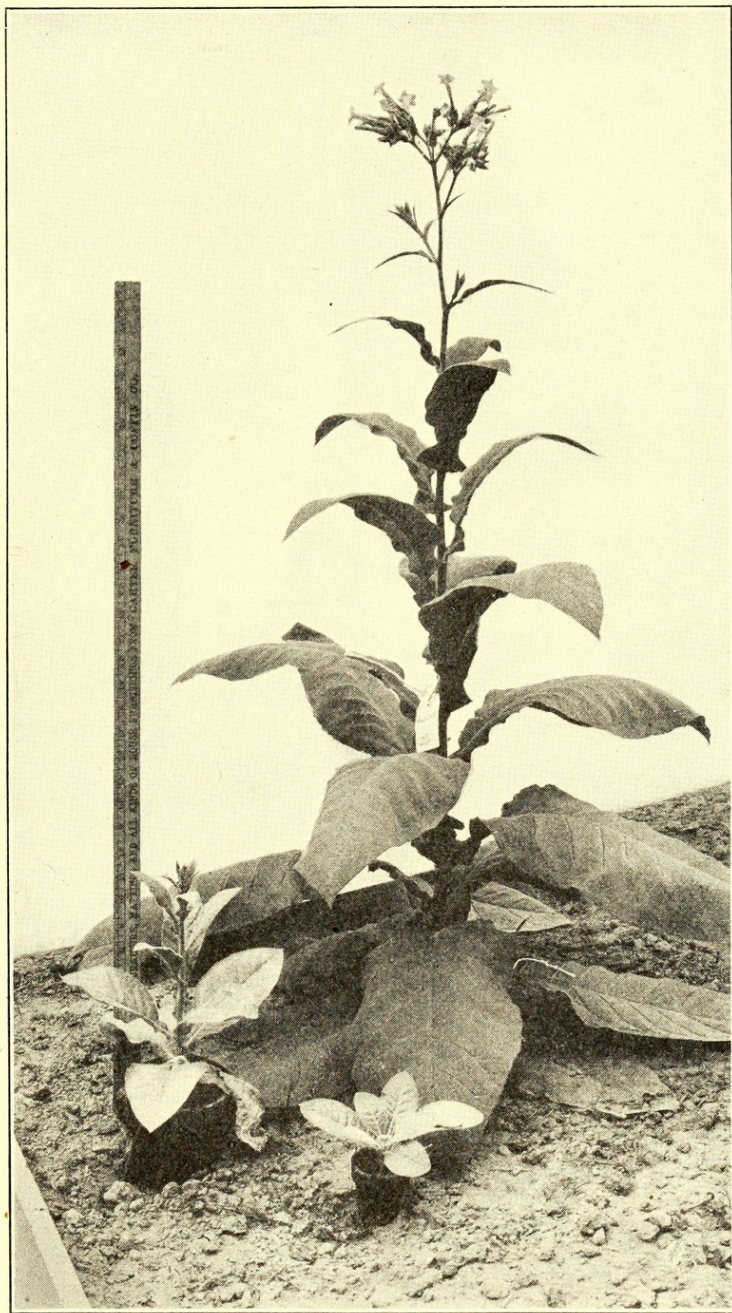
² Hayes, H. K., East, E. M., and Beinhart, E. G., "Tobacco Breeding in Connecticut." *Conn. Agr. Exp. Sta. Bull.* 176: 40-42. May, 1913. See also, East, E. M., and Hayes, H. K. "A Genetic Analysis of the Changes Produced by Selection in Experiments with Tobacco." *American Naturalist*, 48: 5-48. 1914.



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furnished by a stunted plant capable of supporting but one capsule is any less favorable to normal seed development than that furnished by a plant of maximum size producing great numbers of capsules. If it is assumed that nutritional differences during some initial period of embryonic development determine leaf number, it is reasonable to expect that capsules developed at different stages of the reproductive period on the most completely nourished plants will show a slightly higher or lower leaf number.

SUMMARY

Very severely stunted tobacco plants have been studied in comparison with plants of normal size grown under optimum conditions of soil moisture. The average number of nodes produced above the cotyledons, exclusive of the branches of the terminal whorl, has remained constant under all conditions. Unfavorable conditions reduce the size of the inflorescence. Stunting may be carried to such an extreme that the branches of the terminal whorl may be entirely suppressed, so that the inflorescence of the plant is reduced to the single terminal blossom of the mainstem.

The position of the first bald sucker is not constant under all conditions. Although it may occupy its true position in normal plants, it is one of the higher lateral branches of the inflorescence which appears to be the first bald sucker in stunted plants. In very severely stunted plants, all the lateral branches of the inflorescence may be suppressed.

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EXPLANATION OF PLATES XX-XXIII

PLATE XX. Stunted Connecticut Broadleaf Plant grown in 5-inch pot.

PLATE XXI. Plant No. 7 grown in moist soil in Experiment I.

PLATE XXII. Plant No. 7 grown in dry soil in Experiment I.

PLATE XXIII. Plant of 1st generation of cross Md. Mammoth ♀ × 70-Leaf Cuban ♂.



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