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The factors affecting the method of branching in Ailanthus glandulosa.

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FACTORS AFFECTING THE METHOD OF
BRANCHING IN AILANTHUS GLANDULOSA

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The Factors Affecting the Method of

Branching in <u>Ailanthus glandulosa</u>

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INTRODUCTION

The method of branching in trees depends upon the development and growth of their buds. Most trees have a tendency to produce branches from their terminal or apical buds, while the more basal buds of the twigs remain dormant or die.

Literature on factors affecting bud growth shows: (1) maturity of the bud and its supporting tissue, (2) nutrient condition of the supporting tissue, (3) water conductive ability of the sap-wood, and (4) dormancy as factors inherent in the plant. Available moisture, wound reaction, and climatic conditions are shown to be factors in the environment that affect growth in buds.

Bergen (2) states that woody plants which have an indefinite annual growth continue to grow until their soft and immature tips are killed by frost. Growth of the shoot and its branches in the succeeding season is thereby restricted to the mature area of the shoot.

Gardner (14) shows a descending nitrogen-carbohydrate gradient corresponding with the growth of apical buds in the Bartlett pear. Harvey (15) shows a similar nutrient distribution corresponding to a similar growth of apical buds in the twigs of apple trees. Butler, Smith, and Curry (4) concur with Harvey in relating apical bud growth in the apple with the higher ratio of nitrogen adjacent to the growing buds.

They attribute the apical bud growth to the upward trans-
location of nitrogen and the downward translocation of carbo-
hydrates in the parent shoot.   Davies (8) study of regen-
eration in Salix nigra likewise shows that the total quantity
of nitrogen in the shoot is distributed so that the bud
growth takes place at the point of greatest nitrogen con-
centration.   His results show that the initial changes prior
to regeneration and development are not dependent upon the
rapid translocation of nitrogen toward the area of bud growth.
Denny and Stanton (10) show that the reserve food in twigs of
Syringa vulgaris is adequate and that renewal of growth in
the buds was due to a factor within the buds.

The experiments of Farmer (12), Eustace (11), and Roberts
(20) show a difference in the conductive ability of the wood
in various shrubs and trees.   The results of this difference
in the conductive ability upon bud performance after dormancy
have been construed differently by these workers.   Eustace
related the degree of bud failure in the apical region of
fruit tree twigs to the quantity of water contained and the
ripeness of the wood.   The greater the conductive ability
of the wood in the apical region of the shoot the greater is
the danger of frost injury to the buds.   This view is at
variance with the results shown in Farmer's experiments with
young ash and sycamore trees.   The water conductive ability
of the wood in the apices of the sycamore twigs was high and
the apical growth was characteristically strong.   Frost
injury to the apical buds was absent.   In the ash trees the

conductive ability of the wood in the apices of the twigs was low; correspondingly frost injury was frequent in the apices of the twigs. Roberts' experiments with cherries led him to conclude that climatic effects upon bud performance must be correlated with the stage of bud growth. The fruit bud in the cherry was killed by frost while the slower developing leaves were often uninjured. It is therefore apparent that high, water conductive ability is related to strong and rapid growth of buds.

The existence of a dormant stage in the winter buds of perennials in the colder climates has long been acknowledged as a factor in bud growth. The cause of this dormancy as well as the renewal of growth after dormancy has not been determined. Loeb (19), from his work on Bryophyllum calycinum, formulated the theory that the growing apex of a stem forms a definite inhibiting substance which moves toward the base and thereby inhibits the growth of lateral buds. The work of Reed and Halm (21) with cuttings of Chinese lemon suspended in moist air, verifies Loeb's inhibition hypothesis. This theory is challenged by the results of an experiment on Bryophyllum calycinum conducted by Child and Bellamy (7) . They found that isolation by means of low temperature did not impede the flow of fluids and substances in solution while it did block the inhibiting action of the growing tip. These results led them to conclude that the common phenomenon, dominance of the growing tip, was due to physiological activity of the cells within the dominant bud. The existence of an inhibiting substance in either the supporting or

the bud cells is challenged by the experiments of Denny and Stanton (9).   They succeeded in breaking the rest period in lilacs, crabapples, almonds, and snowballs by vapor stimulations of ethylene chlorhydrin, ethylene dichlorid, furfural, and propylene chlorhydrin applied to the buds.   The results of these experiments indicate that dormancy and the cause of its termination are important factors in determining bud development.

Howard (16) has shown that cut twigs of woody plants respond to treatments that break the rest period in the same manner as pot-grown plants if the cut ends are kept immersed in water.   The necessary available water supply as a factor in bud growth is evident as Farmer (12) has shown for the sycamore, and Roberts (20) for the cherry.

Experiments show that wound reaction is a factor in abnormal bud growth.   Coville (6) has shown that dormant buds of Vaccinium corymbosum were forced to develop when portions of the stem adjacent to the bud was rubbed briskly with a knife handle.   Ringing has produced a variety of results. Barker and Lees (5) found that knife edge rings did not cause dormant buds of pear and other fruit trees to develop. Broader rings caused the buds below the rings to grow until a callus had formed over the ringed area.   Summers (22) shows that the effects of pruning on twig development vary according to the type of the plant.   Pruned apple and pear shoots developed an acropetal pattern of bud growth similar to the unpruned shoots.   Pruning to the last two or three buds

upon the shoot produced negative results in all three.   It
is evident that accidental injury to buds or their adjacent
tissues may cause abnormal bud growth in trees.   It is
further evident that in the event the injury is severe enough
to cause the death of buds abnormal branching may result.

As Roberts (20) has shown in his experiment with frost
injury in cherries climatic factors must be considered in
connection with the stage of bud growth.   The experiments
of Johannsen (17) with woody shrubs, and Coville (6) with
Vaccinium corymbosum, show that uniformly low temperature
during the dormant stage of the plant was conducive to an
earlier spring growth than would have occurred in the absence
of such chilling.   Coville shows that blueberry bushes kept
at greenhouse temperatures were eight to fourteen days slower
in developing their buds than those plants subjected to the low
temperatures of winter out-of-doors.   His experiments also
show that bud failure in the terminal region of the plants
kept in the greenhouse was frequent while out door plants ex-
hibited vigorous terminal growth.   These experiments show
that low temperature during the quiescent period of woody
perennials in the colder climates is a factor in normal bud
growth after dormancy.   As previously stated from the re-
sults of Eustace's (11) and Wiggans' (23) experiments with
fruit trees and Farmer's (12) experiment with sycamore and
ash trees, low temperature after growth has actively begun in
the buds is destructive to the buds and their supporting
tissues.   It is, therefore, evident that low temperature

during the dormant stage is a stimulating factor in bud growth but low temperature after the bud has begun active growth is a destructive factor in bud growth and consequently a factor that causes abnormal branching.

THE SPECIFIC PROBLEM

Twigs or shoots of Ailanthus glandulosa, Desf. (Tree of
Heaven) do not develop terminal buds.   All elongation in
the following season is, therefore, entirely dependent upon
the development of axillary buds.   As a solitary bud is de-
veloped in the axil of each leaf, the maximum potential branch
development of each shoot is determined by the number of leaves
developed upon the shoot in the previous season's growth.   The
number of leaves on shoots or twigs is not uniform.   Keeler
(18) states that the length of Ailanthus glandulosa shoots may
vary from a few inches to more than five feet.   The statement
is too conservative; the writer has found shoots more than
ten feet in length.   Correspondingly, the number of leaves
may vary from two to nearly fifty.   It is, therefore, evident
that the number of branches theoretically possible may vary in
the same proportion.   It is a well known fact that all buds on
the tree type plants do not develop into branches.   Blakeslee
and Jarvis (3) have shown that there is a struggle for existence
among buds, and only a few succeed in developing into branches.
It is, therefore, evident that the number and position of buds
that develop into branches determine the branch-patterns.

The purpose of this study is to determine (1) the number
and position of axillary buds on shoots of Ailanthus glandu-
losa that develop into branches, and (2) the factors prin-
cipally responsible for the development of the buds.

THE MATERIAL

A large thicket of uncultivated <u>Ailanthus</u> <u>glandulosa</u>
served as an outdoor laboratory.   It also supplied the cut
shoots used in this experiment.   The thicket is located on
the banks of Silver Creek, Clark county, Indiana.

TECHNIQUE

The number and the position of axillary buds of unculti-
vated <u>Ailanthus glandulosa</u> shoots that developed into branch-
es was found in the following manner.   In the spring of 1930
a sample of 225 young trees was selected at random.   The
number and the position of branches developed upon these trees
were tabulated (<u>see</u>, Table 1, page 14).   The tendencies in
branching of this sample were then computed on the basis of the
normal frequency curve as expounded by Garrett (13).   In the
spring of 1931 a second sample of branching was tabulated from
436 trees.   The tendencies in branching were calculated on
the same basis as used in the first sample (<u>see</u>, Table 2, page
15).   The collective results obtained from these two, annual,
random, samples are considered fair examples of branch-patterns
developed by <u>Ailanthus glandulosa</u>.

The principal factors responsible in affecting the branch-
ing were sought both within the tree and its environment. The
relationship of those factors identified with the nature of the
plant (first, maturity of the buds; second, food reserves;
third, water conductivity; and fourth, dormancy) was measured
by forcing bud growth in cut twigs.   The influence of each
of these factors upon potential branch development was tested
in the following manner.

1. The maturity of buds and their ability to develop

Howard (16) has shown that cut twigs of woody plants re-
spond to treatment in the same manner as pot-grown plants.

was tested by forcing both whole shoots and sections of shoots into growth by placing their cut ends in battery jars containing tap water at room temperature.

2. The food reserves in the buds and their adjacent tissues was tested by forcing growth in the tip sections containing three buds.   The forcing agents were moisture and room temperature.

3. The water conductive ability of the tissues of shoots was tested by using common red ink in the water supply of the cuttings.

4. The existence of a dormant period and its influence upon bud development was tested by forcing buds into growth, by the moisture-temperature method, from the period of leaf fall until leaf development was reestablished in the following spring.

Effects of external factors (first, available moisture; second, wound reactions; and third, low temperature) upon bud growth were tested in the following way.

1. The effect of available moisture upon bud growth was tested by comparing the development of cut twigs.   Two sets of cuttings were kept at room temperature: the cutings of the first set were placed with their cut ends submerged in water, while the cuttings of the second set were kept without a water supply.   The latter set had their cut ends sealed with surgical tape to prevent evaporation.

2. The effects of bruising, ringing, notching, and bending upon the behavior of buds in the cut shoots was compar-

ed with the bud development in cut twigs when both were subjected to the forcing treatments.

3. The effects of low temperature upon bud performance was tested in two separate experiments. In the first experiment cut shoots were used. Freshly cut shoots with buds still dormant and cuttings containing growing buds were frozen in a refrigerator for twenty-four hours and then subjected to the forcing tests. In the second experiment, the bud growth found in the thicket on March 1, 1932 was compared with the bud growth found upon trees in the thicket on April 16, 1932. A ten day period of sub-freezing temperature prevailed from the fifth to the fifteenth day of March.

THE METHOD OF BRANCHING IN <u>AILANTHUS</u> <u>GLANDULOSA</u>

AS SHOWN BY THE BRANCHING IN TWO SUCCESSIVE YEARS

THE NUMBER OF BUDS THAT DEVELOPED INTO BRANCHES

The branches established by the random sample of two hundred twenty-five Ailanthus glandulosa shoots, in the spring of 1930, were distributed as follows (see, Table 1). Fifty-six shoots developed one branch each, ninety-four developed two branches each, fifty-five developed three branches each, fifteen developed four branches each, two developed five branches each, two others developed six branches each, and one developed eight branches.

The branches established by the random sample of four hundred thirty-six shoots, in the spring of 1931, were distributed as follows (see, Table 2). One hundred four shoots developed a solitary branch each, one hundred sixty-four developed two branches each, one hundred twenty-five developed three branches each, thirty-four developed four branches each, eight developed five branches each, and one shoot grew six branches.

A comparison of the method of branching found in the two samples shows a similarity in the number of branches developed by the shoots in the two seasons. The minimum number of branches established by a parent shoot in both samples was one, and the maximum number was eight. The difference in the maximum number of branches for a shoot in the two seasons was due to a single case. One shoot in the first sample had eight branches, while the largest number of branches on a

Table 1

Table 1 shows the correlation in the number of branches developed on parent shoots with the position of uppermost branch development on those shoots. (1930)

Number of branches

Position of uppermost bud development in shoot	1	2	3	4	5	6	7	8	Total
17		4	3						7
16		1	2						3
15	4	1	5	1					11
14	1	4	2	1					8
13	4	10	4	2					20
12	6	11	4		1				22
11	3	9	3						15
10	5	8	7	1					21
9	10	6	1						17
8	3	10	1	1	1				16
7	6	9	4	2					21
6	6	10	6	1		1		1	25
5	3	5	6						14
4	1	2	2	1		1			7
3	1	2	2	2					7
2		2	3	3					8
1	3								3
Total	56	94	55	15	2	2	0	1	225

Average number of branches for each shoot = 2.22±.19

Average bud position from which uppermost
branch developed on parent shoot   = 9.15±.68

Coefficient of correlation   = .-07

Table 2

Table 2 shows the correlation in the number of branches developed on parent shoots to the position of uppermost branch development on those shoots. (1931)

	Number of branches						
	1	2	3	4	5	6	Total
13	1						1
12				1			1
11			1				1
10	2	3	3				8
9	5	3	6	2	1	1	18
8	4	2	1	1	1		9
7	8	13	12	4	1		38
6	7	16	17	5	1		46
5	13	27	19	8	3		70
4	13	28	26	11	1		79
3	8	36	21				65
2	9	30	16	2			57
1	34	6	3				43
Total	104	164	125	34	8	1	436

Position of uppermost bud development in shoot

Average number of branches for each shoot = $2.27 \pm .141$

Average position of uppermost branch development on parent shoot $\qquad = 4.38 \pm .112$

Coefficient of correlation $\qquad = .22$

shoot in the second sample was six.   The average number of branches for a shoot in the 1930 sample was 2.22 and the average number in the 1931 sample was 2.27.   The mode in both samples was two.   It is evident from these data that while the number of branches established by a shoot may vary from one to at least eight, the average shoot has a tendency to establish two branches.

THE POSITION OF BUDS THAT DEVELOPED INTO BRANCHES

Two factors were observed in the position of buds which were developed into branches on the parent shoots.   First, the bud position from which the uppermost branch was established upon the shoot.   Second, the bud positions from which lower branches were established upon the shoot.

In the 1930 sample, three shoots of the two hundred twenty-five established their uppermost branches from their tip buds. The remaining two hundred twenty-two established their uppermost branches from lower buds.   The lowest position from which an uppermost branch was established was the seventeenth bud.   The average position of uppermost branch growth in the sample was the 9.15 bud (see, Table 1, page 14).

In the 1931 sample, uppermost branches were established upon parent shoots from the first to the thirteenth bud position.   The average position was the 4.38 bud.   It is evident that the average position of uppermost branch development was 4.77 buds less than in the 1930 sample (see, Table 2, page 15).

These data indicate that while the uppermost branch may be
established through the development of any one of the first
seventeen buds in the shoot the chances are greatest that the
uppermost branch on a shoot will be a development of a bud
between the fourth and the ninth position.

The position of branches relative to each other, in the
cases of multiple branch development, showed the following
variation.   In the 1930 sample, nineteen of the branching
shoots did not have their branches in a regular descending
order.   The branches were separated by one or more buds
which failed to establish branch growth (see, Plate I-A).
In the 1931 sample, eighty-one shoots exhibited a similar non-
systemic order in branch arrangement.   In the remaining
cases of multiple branching in both samples the branches were
arranged in a basipetal order (see, Plate I-B).   As the
non-systemic arrangement equaled but eleven per cent of the
total multiple branching in the first sample and twenty-four
per cent of the cases of multiple branching in the second
sample, it is evident that the normal tendency in branching
was systemic.

A comparison of the shoots that established branches from
their tip buds with the shoots that failed to establish such
branches shows that non-systemic arrangement of branches is a
character accompanying the failure of the shoot in establish-
ing a branch from its tip bud.   The three shoots that
established branches from their tip buds, in the 1930 sample,
developed no other branches (see, Table 1, page 14).

A   B

Plate I

A ___ Shows a non-systemic arrangement of branches on a
       parent shoot.   Non-systemic arrangement occurred
       19 times in the 161 cases of multiple branching in
       the 1930 sample and 81 times in the 332 cases of
       multiple branching in the 1931 sample.

B ___ Shows a systemic arrangement of branches found on
       parent shoots.   Systemic arrangement was found
       142 times in the 161 instances of multiple branching
       in the 1930 sample and 251 times in the 332 instances
       of multiple branching in the 1931 growth.

In the 1931 sample there were forty-three shoots that estab-
lished branches from their tip buds (see, Table 2, page 15).
Thirty-four of these shoots established no other branches, six
developed an additional branch each from their second buds,
and three developed two additional branches each from their
second and third buds (see, Plate II).   The average number
of branches developed by the forty-six parent shoots, in the
combined samples, which established branches from their tip
buds was 1.3 .   The average number of branches developed by
the two hundred twenty-five shoots in the 1930 sample was 2.22
and the average number of branches developed by the four
hundred thirty-six shoots in the 1931 sample was 2.27 .   A
combined average of 2.25 branches for each shoot in the two
samples.   That this additional branch for each shoot in the
average of the two samples was due to failure of the tip bud
and not to a progressive degree of apical bud failure is shown
by the fact that there was no regularity in correlating the
degree of apical bud failure, below the first bud, with the
number of branches established.   The average number of
branches developed on those shoots whose uppermost branch was
a development of the second bud on the shoot was 2.3 branches
for each shoot.   The average number of branches developed by
those shoots whose uppermost branch was a development of the
seventeenth bud was 2.4 branches for each shoot.   The average
number of branches developed by those shoots whose uppermost
branch was a development of bud positions between the second
and the seventeenth varied between 1.9 and 3.0 branches for

A   B

Plate II

A. The type of branch growth resulting when the apical
    bud alone developed.   This pattern occurred in
    each of the three instances of Apical bud develop-
    ment in the 1930 sample.   It was found 34 times in
    the 43 instances of apical bud development on the
    1931 growth.

B. The type of branching found six times in the 43
    cases of apical bud development of 1931.

each shoot (see, Fig. 1).

Arrangement of branches in a non-systemic order was found only upon the shoots that failed to establish branches from their tip buds.   In the nine shoots that established branches from their tip buds and also developed branches from lower buds, the branches were in a regular descending order (see, Plate II).   The shoots that did not establish branches from their tip buds frequently developed their branches in a non-systemic order (see, Plates I-A, II, and III).

Fig. 1

Bud position on parent shoot from which
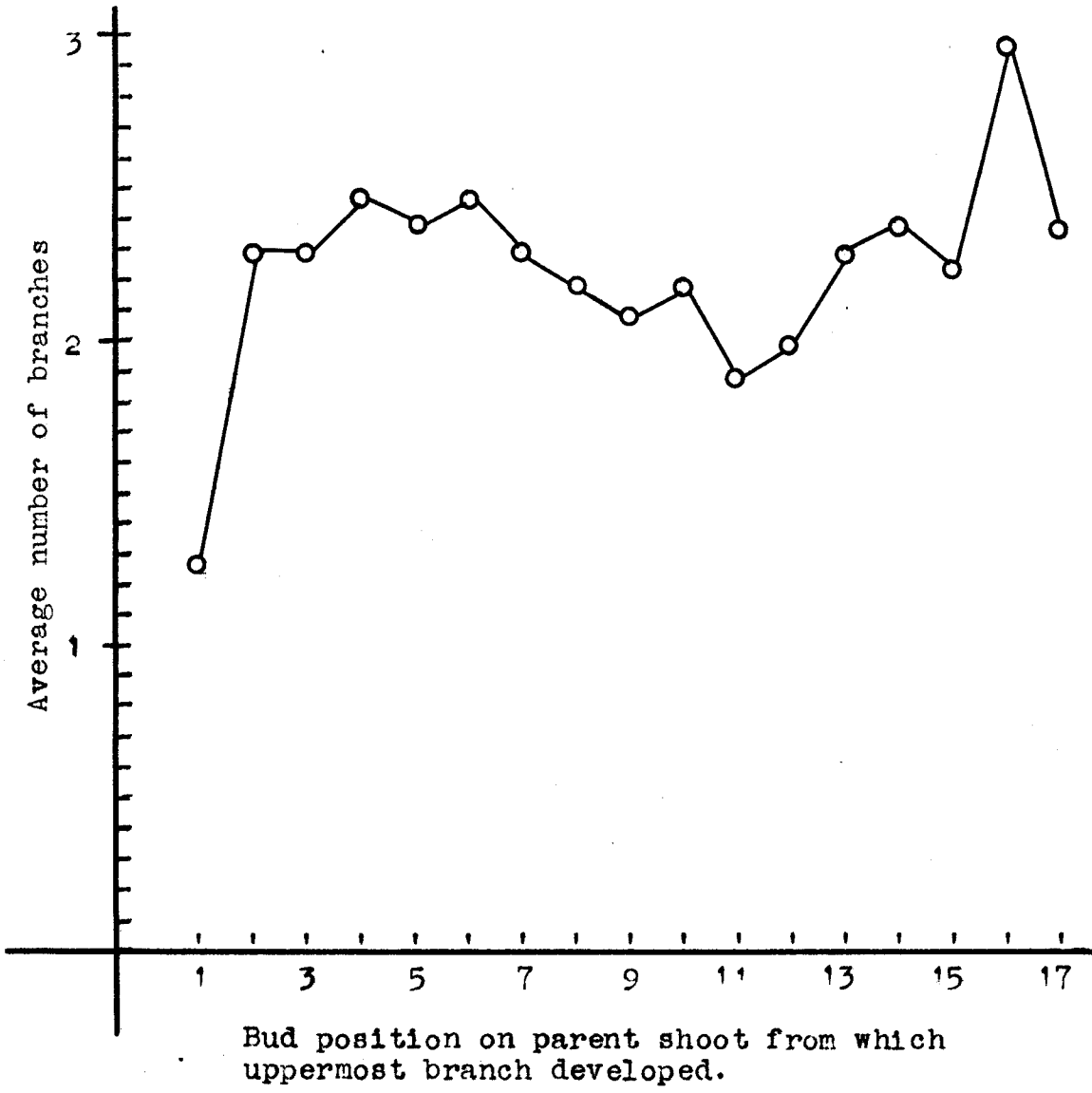uppermost branch developed.

Fig. 1   shows the average number of branches developed
by the shoots in the two samples correlated to the position
of uppermost bud development (1930-1931).

Plate III

Plate III shows the dieing back of that portion of
the parent shoot that was distal to the uppermost grow-
ing bud.   Dead spurs like this were always found in both
samples whenever the tip bud did not develop into a
branch.   The length of the spur depending upon the degree
of bud failure in the apex of the shoot.

SUMMARY

The lack of terminal bud development in Ailanthus glandu-losa determines its plan of branching. Extension-growth after dormancy was dependent entirely upon the development of one or more of its axillary buds. The number and arrangement of branches established from these buds was determined by the behavior of the tip bud in the shoot. When a branch was established from the tip bud other branching was usually absent; when other branches were developed they were in a regular descending order upon the parent shoot (see, Plate II). When no branch was established from the tip bud, the average bud position from which an uppermost branch grew ranged from the fourth to the ninth bud. The number of branches varied between one and eight with an average of more than two (see, 1, page 22). Their arrangement was systemic or non-systemic (see, Plates I and III).

THE RELATIONSHIP OF THOSE FACTORS IDENTIFIED WITH THE
NATURE OF THE PLANT ((1) MATURITY OF THE BUDS, (2)
FOOD RESERVES IN THE ADJACENT SUPPORTING TISSUES, (3)
WATER CONDUCTIVE ABILITY OF THE SUPPORTING TISSUES,
AND (4) DORMANCY) TO THE GROWTH OF AXILLARY BUDS UPON
SHOOTS OR TWIGS OF AILANTHUS GLANDULOSA.

THE MATURITY OF THE BUDS

The indefinite growth habit, so unusual in trees, but
shown by Blakeslee and Jarvis (3) to be characteristic of
Ailanthus glandulosa, may easily lead one to suppose that
maturity of the apical buds is entirely dependent upon
environmental factors.   While food supply, available moist-
ure, and temperature changes do affect the development of buds
upon the distal end of the growing shoots these factors are
able to affect the apical buds only by accidental intensi-
fication.   The performance of the buds upon cut shoots forced
into growth shows that it is characteristic of the shoots of
Ailanthus glandulosa to develop its buds to the degree of
maturity that they are carried through the quiescent period in
spite of the indefinite growth habit.   Normal bud growth upon
268 shoots out of a random sample of 281 developed leaves from
their tip buds when forced into growth by the moisture-
temperature method (see Table 3).   The tip buds that fail-
ed to develop into leaves, excepting seven shoots that failed
to grow, were much smaller than other buds on that region of
the twigs.   Their supporting internodes were also less than
four millimeters in length.   This relationship of size to
maturity of buds was found to exist only in the case of the
very small tip buds.   In general, the size of buds upon a
shoot was proportinate to the diameter of the supporting
structure.   The relatively smaller buds upon shoots of lesser
diameter were able to unfold their leaves when forced into

Table 3

Table 3 shows the position of developing buds in 281 cut shoots of <u>Ailanthus glandulosa</u> forced into growth by the moisture temperature-method from the time of leaf fall until growth was resumed in the following spring. (1931-1932)

Sample taken	No. of twigs in sample	Frequency of tip bud growth	Frequency of no development	Frequency of systemic growth	Frequency of non-systemic growth
Nov. 9	16	11	5	6	5
Nov.20	18	15	2	15	1
Dec. 2	18	18	0	17	1
Dec.20	18	18	0	18	0
Dec.28	18	17	0	17	1
Jan. 8	16	16	0	16	0
Jan.16	24	24	0	24	0
Jan.31	36	36	0	36	0
Feb.10	30	29	0	30	0
Feb.20	19	17	0	19	0
Feb.25	15	15	0	14	1
Mar. 1	No sample taken -- buds were breaking (see, Plate 7)				
	Sample taken one hour after drop in temperature				
Mar. 5	22	22	0	22	0
Mar. 7 ∗	31	30	0	28	3
Total	281	268	7	262	12

∗ The development recorded was found upon the shoots when they were gathered.   Frost had killed these buds.   Lower buds could not be induced to grow by the moisture-temperature method.

growth as were those buds upon shoots of major diameter.

A comparison of the size of buds upon shoots with the time required for leaf development shows that the size of the bud, excepting the very small tip bud, is not the prime factor in shoot development.   Table 3 shows that leaf growth was found in 268 tip buds.   Lower ranking buds grew in regular order upon 262 of the shoots.   With but few exceptions, the earliest and most rapid growth was observed in the tip bud and gradually declined in a proximal direction (see, Plate IV). The tip buds were not the largest buds on the shoots.   A series of measurements made of the size of buds upon twenty-five shoots chosen at random shows the buds between the sixth and the ninth position from the tip of the shoot to have been the largest (see, Fig. 2).   The same measurements also show that the buds in a proximal direction from the ninth were larger than the corresponding buds in a distal direction.   But as shown in Plate IV, the lower ranking buds were either slower in developing their leaves or failed to begin growth altogether.   This failure to develop was not due to immaturity because leaf development from lower ranking buds was obtained when the upper buds were removed from the shoots. Similar positive results were obtained by clipping away the top of the shoot either before or after the forcing process was begun.   The only difference observed in the development of leaves from lower buds on the shoot, when the rivalry of upper buds was removed, was in the time required for leaf unfolding.   A test of the time required for growth of leaves

Plate IV

Plate IV illustrates the characteristic bud growth found in cuttings forced into growth by the moisture-temperature method.   The shoots were gathered on February 25, 1932.

A. __ shows the minimum result of a five day treatment.

B. __ shows a median result in the same number of days.
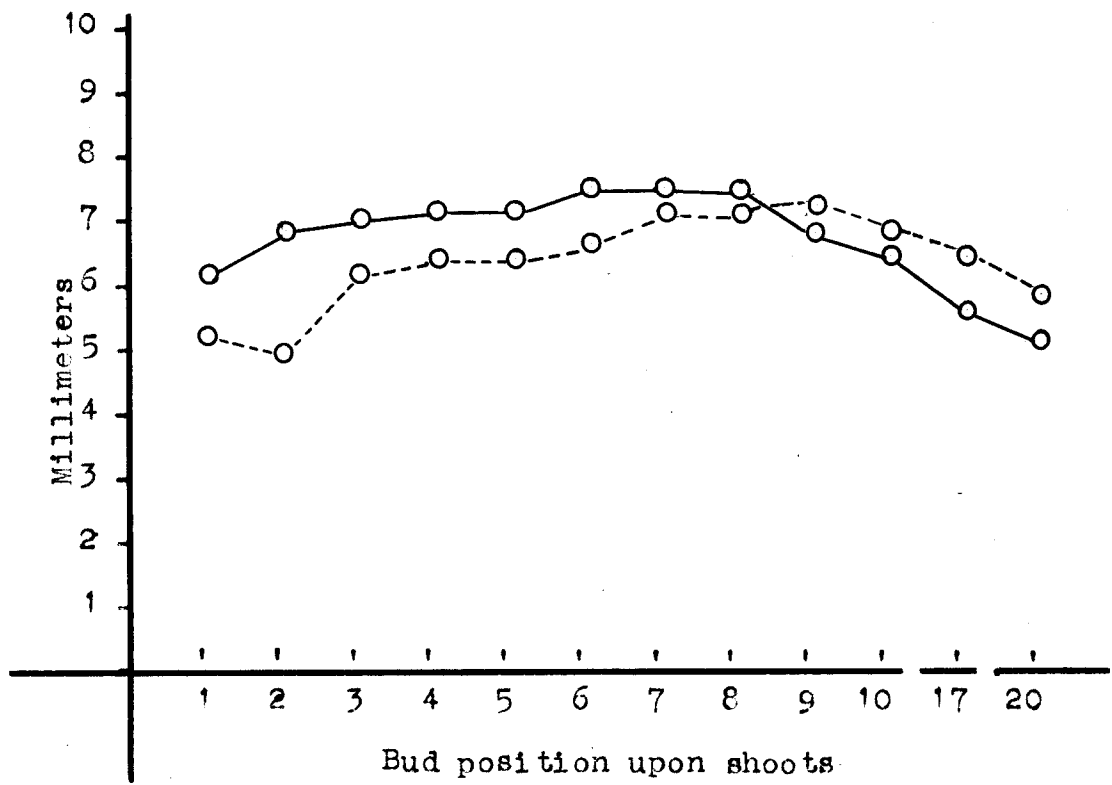
C. __ shows the maximum growth in five days.

Fig. 2

Fig. 2 shows the average size of buds on twenty-five shoots chosen at random.

_____ average vertical distance through bud.

- - - - average horizontal distance through bud.

from the various bud positions on long shoots was made by
selecting a random sample of twenty-five shoots and arranging
them into six groups.   Each of the four shoots in a group
was sectioned so that the top bud of the first section was the
tip bud upon the shoot.   Each group in the three lower sec-
tions was cut so that buds ranging from the ninth to the
thirtieth were top buds (see, Table 4).   The shoots were
gathered on the thirty-first day of January and subjected to
the moisture-temperature treatment for twelve days.   At the
close of this period the tip bud on the first section of each
group was unfolding its leaves, and from two to seven lower
buds were growing.   The uppermost bud on the second section
of each shoot was growing actively but was less advanced than
the tip buds of the first section.   Lower buds were likewise
active.   The uppermost bud on the third section of each
shoot was growing actively but development was less advanced
than in the two upper sections of the shoots.   Growth in
lower buds was also observable.   The uppermost bud on the
fourth section of each shoot in five of the groups was grow-
ing but the degree of development was markedly less than that
found in the three upper sections of the shoots. 2/

· This ability of lower buds to grow was also observed in the
shoot growth found in the thicket.   The destruction by frost
of apical buds of shoots in the spring of 1932 resulted in the
development of twigs from every bud position on the shoot.   In

_____

2/ The shoots were too short for a fourth section in group six.

Table 4

Group #	Section	Top bud	Bud growth found after 12 days
1	1	1	
2	1	1	
3	1	1	About to unfold its leaves
4	1	1	
5	1	1	
6	1	1	
1	2	9	
2	2	10	
3	2	11	Very active but less advanced
4	2	12	
5	2	13	
6	2	19	
1	3	17	
2	3	18	
3	3	19	Very active but less advanced
4	3	21	
5	3	22	
6	3	30	
1	4	25	
2	4	26	Active but considerably
3	4	27	less advanced than the top
4	4	28	buds on the other sections
5	4	29	
6	∨*		

Table 4 shows the bud development found on shoots cut into four sections each, after 12 days of moisture-temperature treatment. 24 shoots were gathered on January 31, 1932. The shoots were divided into six groups and sectioned so that the uppermost buds upon the sections ranged from the first to the thirtieth bud. The results show that the buds are matured.

∨* The shoots were not long enough to provide a fourth section in the sixth group.

some cases buds on the previous year's wood were growing (see,
Plate V).

It is, therefore, evident from these data that all buds of
Ailanthus glandulosa, with exception of the occasional tiny
tip buds, are mature.   The failure of some buds to develop
into shoots, after the dormant season, must be due to factors
other than lack of maturity.

A   B

Plate V

Plate V shows basal bud development upon shoots whose
tips were injured by the low temperature which prevailed
from the fifth to the fifteenth day of March 1932.

A.__ shows lower buds upon the old wood in unsuccessful
rivalry with low basal buds beneath the frost killed area
of the new wood.

B.__ shows successful twig development found upon old
wood beneath an entirely frost killed shoot.

FOOD RESERVES

The experiment with cut shoots of <u>Ailanthus glandulosa</u> to determine the maturity of their buds has shown that the stored food reserves in the cuttings are adequate to support the initial growth of buds (<u>see</u>, Plate IV). Inasmuch as all of the buds upon the cuttings did not grow when subjected to the forcing treatment it was considered possible that the necessary stored nutrient substances had been translocated to the growth region in the apex of the shoot. This upward translocation robbed the lower buds on the shoot of the necessary stored food with which to begin growth. Gardner (14) attributed a similar bud performance upon twigs of the Bartlett pear to a translocation upwards of nitrogen in the lower supporting tissues. Butler, Smith, and Curry (4) also attributed the apical bud growth of apple twigs to an upward translocation of nitrogen to the growing point. A test of the distribution of stored food, in the tissues of <u>Ailanthus glandulosa</u>, necessary to support initial bud growth was made by subjecting very short sections of shoots to the moisture-temperature treatment. Tips of shoots having but three buds grew as readily as longer shoots (<u>see</u>, Plate VI). Likewise, lower sections of shoots containing one bud were induced to grow by the same method. It was also found that lower buds that had remained quiescent on forced shoots grew when the rivalry of upper buds was removed by clipping away the top of the shoot.

Plate VI

Plate VI shows the development of buds upon short
lengths of parent shoots.   The shoots were subjected to
the moisture-temperature treatment for the same number of
days.

The bud performance upon these short sections of shoots indicates that the available stored food in the bud and its intervening internode is ample to support initial growth. Whether or not there was a translocation of nitrogen or some other substance from lower regions of the internode was not determinable by this experiment.   But the results do show that the initial growth from buds is not dependent upon food stored in the lower regions of the shoot (see, Plate VI). It is, therefore, evident that the position of the branches found upon the shoots in the 1930 and 1931 samples of branching was not due to distribution or translocation of available stored food materials in the shoots.   The fact that lower buds had the necessary available food material to support initial growth but did not grow until the rivalry of upper buds was removed shows that stored food material is not the factor that determines the number of buds that begin shoot development.   The results of bud forcing upon cut shoots shows that all buds have the necessary available stored food material, either within their own tissues or in the immediately adjacent supporting tissue, to support initial growth but only the apical buds begin growth under normal conditions.

CONDUCTION OF MOISTURE

Conduction of moisture in the shoots of <u>Ailanthus glandu</u>_
<u>losa</u> is the function of the latest formed wood tissue.
Red ink in the water supply of the cuttings caused a fairly
uniform deposit of pigment in the intercellular spaces of
this tissue.   Removal of the bark and the pith of the
immersed part of the cutting did not affect the rise of moist-
ure nor the behavior of its buds.   It was found that the red
stain was approximately proportional to the size of the shoot.
It extended upward to the tip of the shoot but no descending
path was perceptible.   Shoots that had been subjected to the
stain for several days bled more profusely when notched near
the apex than when notched near the base.

While conduction was not uniform even in shoots of the
same size, it was found that the average shoot brought directly
from the thicket conducted moisture at the rate of approxim-
ately one half of an inch an hour.   The rise of the stain was
noticeably more rapid in the apical region of the shoots.
Farmer (12) associated high conductive ability of the wood in
the apical region of the sycamore with its characteristic,
strong, terminal growth habit.   The cuttings of <u>Ailanthus</u>
<u>glandulosa</u> show a natural tendency toward vigorous apical
growth (<u>see</u>, Plates IV and VI).   But the branch-patterns
found upon the trees in two successive seasons show a charac-
teristic failure of shoot development from tip buds (<u>see</u>,
Tables 1 and 2, pages 14 and 15).   Farmer (12) found a

similar dying back in the apices of young ash twigs and associated this bud failure with the low water-conductive ability of its sapwood.   As the ink stains in the sapwood of _Ailanthus_ shoots showed rapid conduction, and as they likewise indicated the upward path of water to be as near the basal as the apical buds, it is evident that water-conductive ability of _Ailanthus glandulosa_ buds is not a principal factor in affecting the growth of its buds.

DORMANCY

The existence of an annual quiescent period for many of
the woody perennials has been demonstrated by experiment.
Coville (6) studying the influence of cold upon the sub-
sequent growth of Vaccinium corymbosum and other plants, con-
cluded that trees and shrubs of cold climates become dormant
at the close of the growing season without the necessity of
exposure to cold, and that the resumption of growth was in-
stigated by agents that ended dormancy.   While dormancy in
many trees and shrubs has been demonstrated, extant literature
does not include such a study made of Ailanthus glandulosa.
It is, therefore, still to be proven that this species of tree
has a resting period.

The forcing of bud growth in moisture-temperature treated
cuttings, brought to the laboratory from the period beginning
with leaf fall in November until resumption of leaf growth in
the following March, indicates that Ailanthus glandulosa is
dormant for a short period (see, Table 5).   The first
shoots gathered in November and subjected to the treatment
gave no indication of growth for several weeks.   After
forty-one days of moisture-temperature treatment some of the
tip buds developed to the point of leaf unfolding.   Five of
the shoots brought to the laboratory on the ninth day of
November and three gathered on the twentieth day of the same
month could not be forced by this treatment.   The eighteen
shoots gathered on the second day of December unfolded leaves

Table 5

Table 5 shows the minimum and the maximum number of days required for the development of one or more buds, in the 281 forced shoots, to the stage of growth shown in Plate VI-A.

Treatment begun	Number of twigs used	Number of days required for apical bud development	
		Minimum	Maximum
Nov. 9	16	41	5 failed to develop
Nov. 20	18	33	3 failed to develop
Dec. 2	18	31	33
Dec. 20	18	26	30
Dec. 28	18	22	27
Jan. 8	16	20	21
Jan. 16	24	19	23
Jan. 31	36	15	17
Feb. 10	30	10	12
Feb. 20	19	5	7
Feb. 25	15	3	6
Mar. 1	*		

* The tip buds on the shoots in the thicket were developed to the stage shown in Plate VII.

from one or more apical buds in thirty-one to thirty-three
days.   The eighteen shoots gathered on the twentieth day
of December began to unfold their first leaves in twenty-
six to thirty days.   Eighteen shoots gathered on the
twenty-eighth day of December began to unfold their first
leaves in twenty-two to twenty-seven days.   The sixteen
shoots gathered on the eight day of January unfolded their
first leaves in twenty to twenty-one days.   Twenty-four
shoots gathered on the sixteenth day of January unfolded
their first leaves in nineteen to twenty-three days.   Thirty-
six shoots gathered on the thirty-first day of January un-
folded their first leaves in fifteen to seventeen days.
Thirty shoots gathered on the tenth day of February unfolded
their first leaves in ten to twelve days.   Nineteen shoots
gathered on the twentieth day of February unfolded their first
leaves in five to seven days.   Fifteen shoots gathered on
the twenty-fifth day of February unfolded their first leaves
in three to six days.   No shoots were gathered on the first
day of March because bud growth in the thicket was actively
established (see, Plate VII).

These results indicate that Ailanthus glandulosa is in a
resting state for some time after leaf fall but is easily
aroused by changing temperature, and possibly by moisture
supply.

The position of bud development upon the shoots was, as
previously shown in connection with the study of bud maturity,

Plate VII

Plate VII shows the bud development found in the thicket on the first day of March 1932.

A.__ shows a near maximum development of buds.

B.__ shows a near minimum development of buds.

characteristically apical (see, Plate VIII).   Likewise,
the position of growing buds on shoots in the thicket on the
first day of March was also characteristically apical (see,
Plate VII).   Therefore, dormancy in Ailanthus glandulosa
is evidently linked with a dominance of the uppermost bud.
This dominance was characteristic but not absolute.   The
bud development on 268 cut shoots showed twelve instances of
non-systemic development (see, Table 3, page 27).
Dormancy in Ailanthus glandulosa is evidently due, as Denny
and Stanton (10) found in Syringa vulgaris, to a condition
within the bud itself.   Domination of an accidental upper
bud in place of the tip bud shows that dominance in buds is
determined by position in Ailanthus glandulosa and is not
confined to the morphological tip bud (see, Table 4, page
32).

Plate VIII

Plate VIII shows the results of twenty-seven days
of Moisture-temperature treatment of shoots gathered on
the twenty-eighth day of December 1931

A.__ shows the behavior of lower buds upon the larger
part of the sample.

B.__ shows the behavior of buds upon a small part of
the sample.

MOISTURE, WOUND REACTION, AND TEMPERATURE IN
THEIR RELATION TO THE BRANCHING IN <u>AILANTHUS</u>
<u>GLANDULOSA</u>

MOISTURE

When cut shoots were kept at room temperature but not subjected to moisture treatment no buds developed.   Even six foot shoots whose cut ends were sealed with surgical tape to prevent evaporation were unable to produce visible growth in any of their buds.   This bud failure could not have been due to immaturity as the shoots were a part of a random sample selected for the various tests.

It is evident from this lack of bud growth upon cuttings kept at room temperature but not treated with water that the shoot does not contain the quantity of water necessary for leaf development.   Bud development in Ailanthus is evidently conditioned by the rise of soil water in the plant.   But as shown in the moisture-temperature treated cuttings (see, Plate VIII) water conductivity of the sapwood was high. Bud growth was apical in both the cuttings in the laboratory and in the shoots found growing in the thicket on the first day of March 1932.   As the bud failure found in both the 1930 and the 1931 samples of branching was distinctly apical, it is evident that lack of moisture did not cause this failure or all of the buds upon the shoots would have failed.

WOUND REACTION

Mutilations, such as the removal of the pith or the cutting away of the bark from the upper portion of the shoot, did not affect the growth behavior of buds upon shoots so mutilated. However, when the leaf scars were removed with the bark of the apical region, the buds in the mutilated area did not develop. Instead the buds immediately below the mutilated area began vigorous growth. The vigor of growth in the buds declined gradually in a proximal direction.

It was shown in the study of bud maturity that the cutting away of the upper portion of a shoot resulted in the development of one or more buds immediately below the injury (see, Table 4, page 32).

Rubbing or lightly bruising of tissue adjacent to buds, which Coville (6) found effective in producing bud growth in Vaccinium corymbosum, did not not effect growth in buds of Ailanthus glandulosa shoots. The upper buds still developed while lower buds, whose adjacent tissue had been lightly bruised, remained quiescent.

Severe bruising of the tissue adjacent to low basal buds caused the following change in bud development upon the shoots. When a severe bruise was made above a basal bud the bud began to grow in unison with the apical buds. When severe bruises encircled the shoot more buds above and below the bruised area were aroused but the apical buds continued development.

Bending of shoots did not cause a change in the growth behavior of their buds. Very little bruising can be caused by bending of _Ailanthus_ shoots because they are brittle and break easily. The bud failure found in the 1930 and the 1931 samples of branching was not the result of broken shoots (_see_, Plates I and III).

The bud performance upon mutilated, moisture-temperature treated shoots indicates that some of the non-systemic branch development found in the two samples may have been due to accidental bruises. Such bruises severe enough to cause stimulation might occur from the rubbing or striking together of branches, or buds might be destroyed by the same action. It is scarcely possible that even severe bruises could cause the dying back of shoots so frequently found in the two test samples of branching.

TEMPERATURE

The effect of low temperature, during the quiescent
period, upon the subsequent growth of Ailanthus glandulosa
buds agrees with the conclusion of Coville (6), that uniformly
low temperature during the resting stage of woody perennials
is an adjunct to renewed growth of their buds in the spring.
When freshly cut shoots, gathered in early January, were
frozen in a refrigerator for twenty-four hours and then sub-
mitted to the moisture-temperature treatment, bud develop-
ment was accelerated and vigorous.   The apical buds were
dominant and no abnormal effect of the frost could be ob-
served.   This relation of low temperature during the winter
to bud performance is shown also in the results obtained by
forcing cuttings into growth from the time of leaf fall in
November until the time of normal resumption of bud growth in
the following spring.   As previously shown in the study of
bud dormancy (see, Table 5, page 41), the time required for
leaf development gradually diminished during the winter. The
low temperature may have been responsible, as Coville has
suggested, for the quicker response shown by the buds as the
season advanced.

The effect of low temperature upon buds of Ailanthus
shoots after active growth had been established was dis-
astrous.   When shoots were first subjected to the moisture-
temperature treatment until the buds developed to the point
of breaking and then placed in the refrigerator, they could

not be forced into further growth by the moisture-temperature treatment but quickly withered and died.   A similar frost effect upon the growing buds was observed in the thicket.   The apical buds were growing vigorously on the first day of March, 1932 (see, Plate VII).   On the fifth day of the same month the temperature dropped rapidly and remained uniformly low for a period of ten days.   During this period temperatures as low as - 10°c were recorded by the United States Weather Bureau of Louisville, Kentucky.[3]   On the sixteenth day of April, a tabulation was made of the position of growing buds on a random sample of 573 shoots (see, Table 6).   The tip bud was found to be growing on only nine of the shoots and the uppermost bud growth found upon the other 564 shoots was as follows: Thirty were developing their second buds; eighty-nine were developing their third buds; one hundred fourteen were developing their fourth buds; seventy-three were developing their fifth buds; fifty-seven were developing their sixth buds; forty-nine were developing their seventh buds; forty-five were developing their eighth buds; thirty-eight were developing their ninth buds; twenty were developing their eleventh buds; ten were developing their twelfth buds; eleven were developing their thirteenth buds; seven were developing their sixteenth buds; one was developing its eighteenth bud. Inasmuch as the bud failure found in the thicket, after the unseasonable, sub-freezing temperature corresponds to the

[3] The weather bureau is less than five miles from the Ailanthus thicket.

Table 6

Table 6 shows the arrangement of growing buds found upon 573 _Ailanthus glandulosa_ shoots growing in the thicket on the sixteenth day of April, 1932.

Position of the uppermost growing bud on the shoot	Number of shoots	Frequency of non-growing buds in the growth area
1	9	0
2	30	5
3	89	17
4	114	22
5	73	20
6	57	23
7	49	13
8	45	4
9	38	8
10	20	6
11	14	3
12	10	0
13	11	2
14	7	1
15	3	0
16	2	1
17	1	0
18	1	0

Entire shoot dead, buds upon old wood growing. *   9

Total 573   Total 125

Average " dieback" = 5.07   Average frequency of non-systemic growth in the growth

Average uppermost growing bud   = 6.07   area   = .22

_____

* The nine cases of entire failure were not included in the calculation of averages.

accelerated apical bud development found upon shoots prior
to the period of extreme low temperature, it is evident that
frost was the effecter of this bud failure (see, Plates IX
and VII).

The importance of unseasonable climatic conditions as a
factor in affecting branch-patterns in Ailanthus glandulosa
is shown by the bud growth found in 1932.   The shoots used
in the temperature-moisture forcing tests were from the same
thicket and of the same year's growth as the random sample of
growing shoots found in the thicket on the sixteenth day of
April.   The 281 shoots gathered from the ninth day of
November 1931, until the twenty-fifth day or February 1932,
and forced to grow, developed 97.7 per cent of their tip buds
(see, Table 3).   Bud development in these forced cuttings
was typically apical (see, Plates IV and VIII). . This bud
development was normal as it corresponds to the natural
growth found upon shoots in the thicket on the first day of
March (see, Plate VII).   After the subfreezing temperature
from the fifth to the fifteenth day of March, the random
sample of 573 growing shoots in the thicket on the sixteenth
day of April showed tip bud growth in only 1.25 per cent of
the shoots (see, Table 6, page 52).   Instead of the apical
bud development shown in the cut shoots, the typical bud de-
velopment found on the trees was below the tip (see, Plate
IX).   The average uppermost bud to develop was the sixth.
The range of this bud failure extended in some instances to
the previous season's wood.   Nine shoots were found to be

Plate IX

Plate IX shows bud growth found in the thicket on the sixteenth day of April 1932. The degree of apical bud failure in this shoot is one bud position greater than the average apical bud failure found on a random sample of 573 shoots. The unequal rivalry of buds was typical.

dead and buds were developing upon the old wood (see, Plate
V-A).   If the bud failure shown in the cuttings was a fair
average due to immaturity, frost was responsible for an aver-
age dying back of 4.95 buds per shoot in the 1932 shoot growth.

The shifting of the growth area caused by the apical bud
failure was associated with a change in the arrangement of de-
veloping buds upon the parent shoots.   The basifugal
arrangement of developing buds characteristic in the shoots
forced into growth, was affected either directly by the action
of the frost upon the buds themselves or indirectly by the
frost in shifting the growth area in the shoots.   In the 281
cut shoots forced into growth, there were twelve cases of non-
active buds interposed in the growth area of the shoots (see,
Table 3, page 27), and bud development in these shoots was
characteristically apical and basifugal (see, Plates IV and
VIII).   In the random sample of frost injured shoots in the
thicket on the sixteenth day of April, growth vigor did not
decline in this basifugal order (see, Plates V, IX, and X).
The average per cent of non-systemic growth was approximately
eighteen per cent greater than the average found for the 281
shoots cultivated in the laboratory (see, Table 3, page 27 and
Table 6, page 52).   It was also observable that the rivalry
of buds in shoots was more equal if the growing buds were in
the tip area.   In those cases where the dying back extended
no farther than the first bud, close rivalry of the immediate-
ly lower buds was the rule (see, Plate XI).   When the
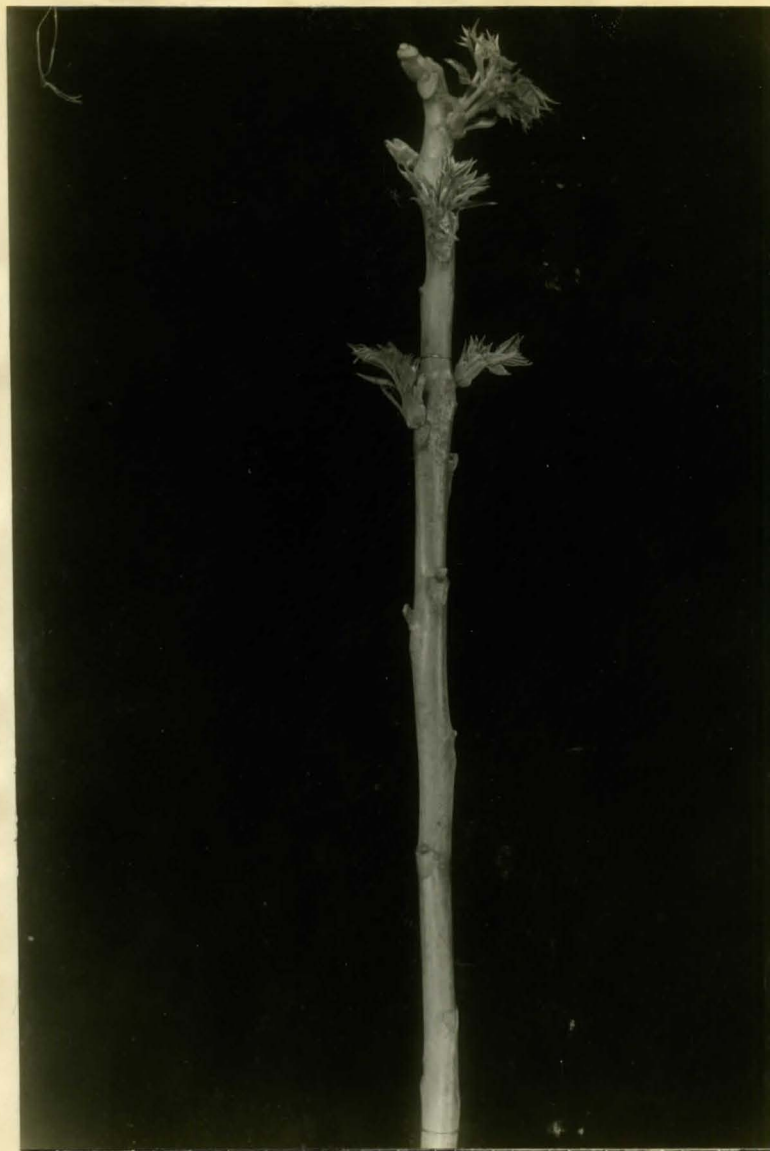dying back extended lower on the parent shoot, the rivalry was

Plate X

Plate X shows the unequal rivalry found in the buds
of a shoot when the action of frost killed the tip buds
and shifted the growing area in the shoot.   The photo-
graph was made on the sixteenth day of April, 1932.

Plate XI

Plate XI shows the typical development of buds in a
shoot that had its tip bud killed by frost.   The photo-
graph was made on the sixteenth day of April, 1932.

less equal (see, Plate X).

The temperature after the sixteenth day of April was never low enough to seriously hamper bud growth in the thicket.   The rivalry shown between the buds on that date culminated in the development of the successful buds into branches.   On the twentieth day of June, new shoot-growth was far enough advanced to show the branch-patterns resulting from the bud development found on the sixteenth day of April.   In general the patterns corresponded with the strongest bud growth shown at the earlier stage of development.   The close rivalry shown by the buds near the apex of shoots resulted in the development of branching shoots of similar size (see, Plates XI and XII-A).   Less equal rivalry shown by lower buds in shoots, where a longer section of the tips was frost killed, resulted in the development of scattered branches (see, Plates XII-B and XIII).   It is, therefore, evident that the principal cause of these branch-patterns was frost.
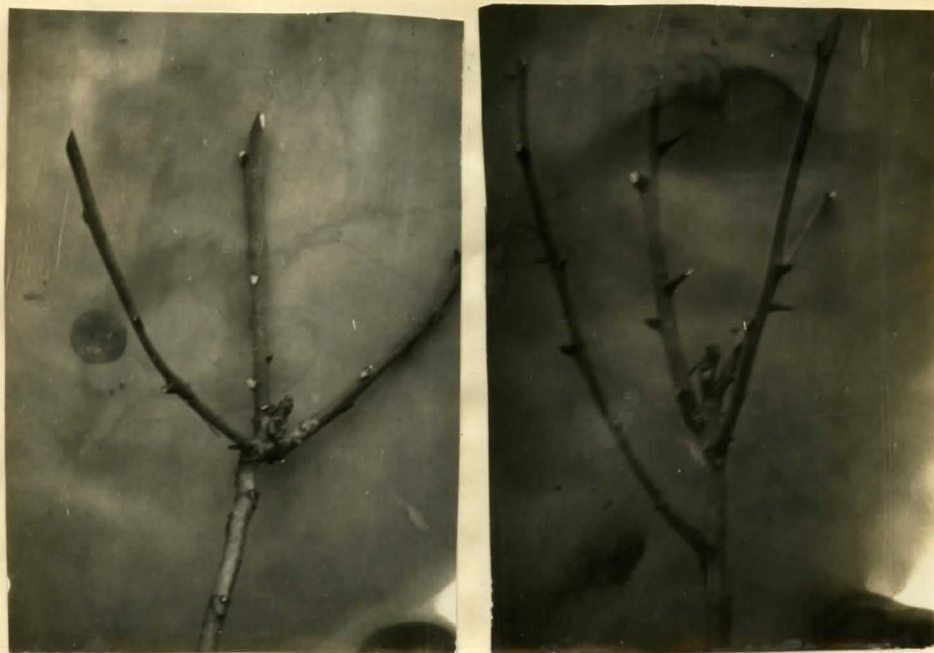
A   B

Plate XII

Plate XII shows two patterns of branching found in the thicket on the twentieth day of June, 1932.

A.__ shows the result of close rivalry in three upper buds.

B.__ shows the result of nearly equal rivalry in four buds.

<center>A</center> <center>B</center>

<center>Plate XIII</center>

Plate XIII shows two patterns of branching found in the thicket on the twentieth day of June, 1932.

A.__ shows a widely scattered pattern of branching.

B.__ shows failure of one bud in the active growth-area.

SUMMARY

The number and arrangement of branches developed in
Ailanthus shoots in the two successive seasons of 1930 and
1931 varied with the behavior of the most apical bud.   When
a branch was established from the apical bud of a shoot, other
branch development upon the shoot was infrequent.   If other
branches were established, the order of their arrangement was
basifugal (see, Plate II).   When no branch was established
from the most apical bud on a shoot, branches developed from
lower buds.   In this type of branching the average was more
than two branches for each shoot (see, Table 1, page 14, and
Table 2, page 15).

The establishment of branches from tip buds was infrequent.
Only 46 in 661 shoots exhibited this type of branching.   The
average bud position from which uppermost branches were estab-
lished varied in the two seasons by 4.7 bud positions.   The
average degree of bud failure in the shoots of the combined
sample was 6.8 for each shoot.

Buds upon cut shoots developed in a basifugal order.   The
most apical bud on the shoot was dominant in 97.7 per cent of
the shoots.   Immaturity of the tip bud was responsible for
the slight failure shown in these buds (see, Table 3, page
27).

Death of the tip bud or death to the apical part of the
shoot resulted in active development of lower buds (see,

Table 4, page 32).

Frost injury caused an average dying back of approximately five buds per shoot in the 1932 growth of shoots.

CONCLUSION

The principal inherent factor in <u>Ailanthus</u> bud development is its basifugal habit of growth. The principal external factor conditioning the inherent habit in bud growth is frost. Inasmuch as the position and number of branches developed upon parent shoots was determined by the action of frost in shifting the growth area in shoots, frost is the principal cause of the method of branching in <u>Ailanthus</u> <u>glandulosa</u>.

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