THE EFFECT OF SELECTION AND INBREEDING ON GROWTH OF
ANDROPOGON FURCATUS MUHL. (BIG BLUESTEM)

by

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INTRODUCTION

The lack of fundamental research on the genetic be-
havior of the important native forage species is a direct
outgrowth of the type of agriculture practiced in this
country. Of necessity it has been an ever expanding agri-
culture in which cash grain crops were all important.
Hence, the plant breeders' efforts were largely directed to-
ward the improvement of these crops with the consequent neg-
lect of the forage species.

However, several factors have served to emphasize the
importance of our native grassland to a stable American
agriculture. Possibly of first importance, and certainly
most spectacular, has been the soil erosion both by wind
and water that has followed in the wake of broken grass-
land, destroyed forests, and continuous cash cropping. In
conjuction with this is the untold human suffering that
necessarily attends such destruction. The importance of
grass as a crop in a long-time program of profitable farm-
ing has been adequately demonstrated in European countries
where the agriculture is much older than here. Therefore,
it would appear quite essential to return certain of our
more desirable cultivated areas, as well as the marginal
and submarginal acres that are at the present demanding so

much attention, to permanent grass.

A second factor exists on our range lands where over-grazing, along with the drought of recent years, has so de-pleted the carrying capacity over most of the area as to make it imperative that something be done to alleviate this condition. The plant breeder can make an important contri-bution by breeding adapted strains of grasses that are superior in forage yield, in palatability, and in seed pro-duction. Before such a breeding program can be successful the genetic behavior of the species under consideration must be understood. It becomes necessary, then, to inves-tigate the response to inbreeding and the inheritance of such factors as leafiness, vigor, height, time of maturity, disease and insect resistance, seed production, and via-bility. The general variability of the population should be determined to enable an accurate evaluation of any im-provement in the species. With these problems in mind, a program of genetic study of the important native grasses including Andropogon furcatus Muhl.was started in 1935 by the Department of Agronomy, Kansas State College of Agri-culture and Applied Science. This paper is a report of the progress made in the improvement of this species during the past five years.

In its original condition the prairie was largely made

up of the _Andropogon_ consociation, _Andropogon furcatus_
being dominant on the moist slopes and well aerated low-
lands. This species together with _Andropogon scoparius_
constituted approximately 80 percent of the vegetative
cover. Today this once extensive grassland is a rapidly
vanishing unit of native vegetation. Man and his plow,
overgrazing, and drought have combined to destroy large
areas until the only section of any consequence that re-
maines is the Flint Hills or bluestem pasture region of east-
ern Kansas. Small localized _Andropogon_ associes are found in
eastern Nebraska and Oklahoma, relice of the once dominant
vegetation. The carrying capacity of these pastures has
been greatly reduced since 1900. Prior to that time two to
four acres were generally sufficient to graze a mature
animal from May to October, inclusive. At the present time
six or seven acres in this tall grass area are required to
graze an animal unit for the same period.

In restoring these devegetated pastures and reseeding
to grass areas that have proven unsuitable for cultivation,
Andropogon furcatus exhibits several advantages. In the
first place, it is native to the region and thus has become
adapted through a long period of natural selection to the
varied climatic conditions that obtain here. It is a vig-
orous, hardy, long-lived perennial that will produce an

abundance of palatable, high quality forage during the summer months when the tame cultivated grasses are largely dormant. In addition, _Andropogon furcatus_ will respond well to cultivation, producing an excellent yield of seed when sufficient moisture is available.

Methods of seed collection have been developed, making available ample quantities of seed of the prairie grasses for preliminary revegetation studies, but it remains for the plant breeder to develop high yielding, more aggressive strains with heavy seed to facilitate the cultural treatments that are necessary to reseeding on a commercial scale.

DESCRIPTION OF SPECIES

Andropogon furcatus Muhl. (_A. provincialis_ Lam.), commonly known as Forked Beardgrass or Bluejoint Turkeyfoot from the characteristic finger-like divisions of the terminal, spikelike racemes, and more recently known as big bluestem in contrast to little bluestem (_A. scoparius_ Michx.) is a hardy, robust perennial, described by Hitchcock (28) as follows:

Plants often glaucous; culms robust, often in large tufts, sometimes with short rhizomes, 1 to 2 m tall, usually sparingly branching toward the summit; lower sheaths and blades sometimes villous, occasionally densely so, the blades flat, elongate, mostly 5 to 10 mm wide, the margins very scabrous; racemes on the long-exserted terminal peduncle mostly 3 to 6, fewer on the branches, 5 to 10 cm

long usually purplish, sometimes yellowish; rachis straight,
the joints and pedicels stiffly ciliate on one or both mar-
gins, the joints hispid at base; sessile spikelet 7 to 10 mm
long, the first glume slightly sulcate, usually scarbrous,
the awn geniculate and slightly twisted below, 1' to 2 cm
long; pedicellate spikelet not reduced, awnless, staminate.

For purposes of clarity and implification in this
paper, the species Andropogon furcatus Muhl. will be re-
ferred to frequently as A. furcatus or big bluestem.

REVIEW OF LITERATURE

The literature contains but two references to the ge-
netic behavior of Andropogon furcatus. There are, however,
many reports on the breeding behavior of the various tame
grasses such as Phleum pratense L., Dactylis glomerata L.,
and Festuca elatior L., as well as extensive data on the ap-
plication of genetic principles to the improvement of the
naturally cross-pollinated forage and grain crops, to which
reference will be made. In addition, there is an abundance
of material on the ecological adaptation, distribution and
economic importance of Andropogon furcatus that will be re-
viewed because a consideration of these factors is essential
to the formulation of an intelligent program of breeding
and improvement.

Andropogon furcatus exhibits a wide range of adaptation
and is found over much of the temperate region of North

America. Hitchcock (28) lists it as occuring in "dry soil, prairies and open woods, Quebec and Maine to Saskatchewan and Montana, south to Florida, Wyoming, Utah, and Arizona; Mexico." It was the dominant species of the virgin prairie or tall grass region of central United States where, according to Weaver and Fitzpatrick (79), it made up 90 percent of the cover on the well watered areas and as much as 25 percent on all but the driest uplands. Sarvis (54) found that it occurred only rarely at Mandan, North Dakota, but that it was highly relished by livestock. Harvey (25) noted the prominence of A. furcatus and A. scoparius in the prairies of southeastern South Dakota where they assume facial rank, A. furcatus being the taller and far more conspicuous. Together with A. scoparius it consitiuted 80 percent of the cover of the prairie grassland of Nebraska, according to Weaver and Fitzpatrick(80), and Stieger (65) reported the A. furcatus association as dominant in that area. A similar condition was found by Aldous (2) in Kansas with A. furcatus the dominant species in the eastern one-third of the state. Schaffner (57) listed A. furcatus as the most important species in a study of the typical prairie of Clay County, Kansas with A. scoparius, Sorghastrum nutans, and Panicum virgatum following in that order. Bruner (9) stated that "The Andropogon associes constitutes the sub-climax prairie

of eastern Oklahoma and is also represented extensively in the post climax prairie of the sandy soils which occur along river courses throughout the true and mixed prairie and even into the short grass plains."

Following the droughts of 1934, Weaver and Albertson (77) reported losses of 80 percent and more of the original cover of grass on native prairie, with A. furcatus suffering least because of its deep root system. Savage (56) and Aldous (5) agreed essentially with this report; Aldous, however, cited overgrazing as an important factor in the loss of vegetation. Later studies by Weaver and Albertson (78) substantiated these earlier observations. They found that a reduction of 50 to 66 percent in basal cover had occurred during the drought period, 1934-37. This was largely due to the almost complete destruction of A. scoparius although the deeper rooted A. furcatus also suffered great losses toward the end of the period.

According to Cornelius (15) approximately 190,000 head of cattle are shipped from the short grass ranges of Texas, New Mexico, Oklahoma, Arizona, and Colorado each year to fatten for market on the nutritious grass of the bluestem section of Kansas. Aldous (3) considered the bluestem grasses valuable from a pasture standpoint because they make a major portion of their growth during June and July, and if

moisture is available, a substantial amount of forage will
be produced during August. The Forest Service, United States
Department of Agriculture, gives A. furcatus a palatability
rating of 70 percent for the eastern one-half of Kansas.
Newell (48) found the bluestems very desirable forage
species in Nebraska and stressed the importance of develop-
ing seeding methods.

Stapledon (59), in discussing the important character-
istics of forage species, stated, "The economic value of
a grass depends, in the last resort, not only upon its pal-
atability and nutritive value but equally upon its ability
to maintain itself and withstand the conditions of manage-
ment superimposed upon it."

A. furcatus is possessed of this ability to a marked
degree, being described by Aldous (4) as very vigorous,
standing close grazing, and recovering rapidly from abuse if
protected. In discussing the problems of the herbage plant
breeder, Saulescu (55) says, "In no other cultivated plant
is the breeder attended by so many difficulties. The pri-
mary reason is to be found in the many sided demands made
upon the herbage plants, the most important of which are re-
sistance to cold and disease, early ripening, then longevity,
quality, adaptability, and finally productivity." In addi-
tion to these, Cornelius (15) listed resistance to drought

and control of erosion as important characters of a valuable
herbage plant. Because of its abundant top growth and ex-
tensive root system, A. furcatus is very important in re-
ducing losses from erosion. Enlow and Musgrave (18) rated
it as one of the most desirable native species in this re-
spect, and Gross (24) listed it as first over the other native
species of Nebraska in controlling water runoff and erosion.

Observation of plants from various seed sources grow-
ing in the nursery at Manhattan, Kansas lead to the con-
clusion that A. furcatus exhibits definite habitat types
corresponding to the ecotypes of Turesson (70) and the
habitat types of Gregor and Sansome (23). The work of
Turesson, especially, has drown attention to the fact that
species in nature contain certain groups which, primarily
by reason of the influence of their environment, express a
phenotypic constitution suited to the condition of life in
their particular habitats. Gregor and Sansome (23) in dis-
cussing these habitiat types stated, "It is believed in na-
ture that the types which are unsuited to the prevailing
environmental conditions of their habitat are gradually
eliminated, and those that survive bear at least a pheno-
typic resemblance to each other. Although phenotypic uni-
formity is frequently attained by wild populations to a

considerable degree, a genetic uniformity must indeeed be
rare. Under the more severe eliminating influence of arti-
ficial selection, such a wild population can again be sepa-
rated into different growth habit groups, the individual
plants of each group being more or less uniform in appear- .
ance." Turesson (71) concluded that these habitat types are
not the result of sporadic variation preserved by chance
isolation but are due to the reaction of the genotype to a
given environment. Sylven (67) agreed closely with the
above when he stated, "... during the course of generations,
natural selection has created types of populations of great
local value to agriculture adapted to various environmental
conditions." Stapledon (60), discussing environmental in-
fluence on plant forms, stressed not only the climatic and
edaphic factors but also methods of management (i.e. graz-
ing, clipping, and fertilizer practices) as important fac-
tors in the environment. Gregor and Sansome (23) pointed
out essentially the same thing, "... the growing plant
throughout its entire life is subjected to the influence of
the interacting physical and biotic factors which together
constitute its environment."

Cornelius (15) in studying variation in A. furcatus
found significant differences in leaf area, height, and
time of maturity for plants from different states and

concluded the, "Plants from Oklahoma seed are generally more leafy, later maturing, and taller than plants from northern sources of seed." This is in close agreement with the work of Anderson and Aldous (6) on A. scoparius in which they found the variability between habitat groups to greatly exceed that variation within each habitat group.

In his work with Lolium perenne, Jenkin (32) concluded that individual plants from a fairly stable habitat differ from one another in phenotype, and that this variation is restricted to a relatively narrow range, while the genotypic variation will be much greater. Similar results for A. furcatus are reported by Cornelius (15) who found considable variation with the scotype of this species. The importance of selecting strains for relatively small regions of adaptation has been emphasized by Jenkin (34), Stevenson (64), and Anderson and Aldous (6).

Church (12) investigating A. furcatus cytologically called this species a decaploid, heterotypic metaphase showing 35 bivalents. A striking ring formation of synaptic mates was displayed at diskinesis, indicating there has been considerable chromosome instability at some time in the ancestory of the present population. He found 10 to 20 percent sterile pollen which, together with the fact that the species is a decaploid, led him to believe A. furcatus was

of remote hybrid origin as contrasted with the more recent
hybrid origin of A. scoparius. The high degree of varia-
bility in the species reported by Cornelius (15), as well
as its extensive range of adaptation, would lend credence
to this belief. Nielsen (49) listed the somatic chromosome
number of A. furcatus as 60. This is at variance with
Church's findings, but Nielsen concluded that both comple-
ments may exist and stated, "It is interesting to note that
the occurrence of 60 (Nielsen) and 70 (Church) somatic
chromosomes in this species parallels those numbers found
and reported as occurring in A. hallii, which is also poly-
morphic and systematically confusing."[1]

Hunter (30), investigating the sub-tribe Andropogoninae
cytologically found a change in the basic number of chromo-
somes of the genus Miscanthus from 36 to 42 to 64 chromo-
somes in three different species. He concluded, "... it is
possible for such a change to occur without producing any
great effect on the expression of the phenotype." Peto (53),
studying the genus Agropyron, found a polyploid series in
this genus with a basic number of seven. In the material
he examined there was a complete series from diploid to
octaploid forms with a correspondingly wide range of mor-
phological variation. In view of the appearance of

[1]Personal correspondence.

satellites, constrictions and segmentation, he concluded
that many of these species were of hybrid origin.

The technique of emasculation and hybridization has
been discussed in detail by Jenkin (35), and Vinall and
Hein (74). Since the procedure will vary for the individual
species, their methods will not be review here, although
the importance of such a technique to the study of specific
genetic characters should not be overlooked. This partic-
ular phase of the breeding program, according to Stapledon
(61), should follow only after a period of selection and
inbreeding has yielded uniform lines with which to make
hybridizations. The material reported in this paper ex-
hibits a wealth of natural variation from which to make
selections, so it is felt that the phase of controlled
hybridization has not yet been reached. Nevertheless, a
technique of emasculation and hand pollination is being
developed in anticipation of its use later in the breeding
program. The general procedure will be based on the sug-
gestions of Jenkin (35) who has had remarkable success in
the hybridization of certain Lolium species.

Inbreeding exhibits a depressing effect on the vigor
of many cross-pollinated species. Nilsson (50) found that
deleterious effects often accompany inbreeding and he
divided these effects into two classes, the first of which

he classified as partial depression, that is, the occurrence
of abnormal and inviable individuals such as dwarfs, lethals,
etc. The second effect, classified as general de-
pression was evidenced by a general decrease in vigor, dis-
ease resistance, winter hardiness, and seed production fol-
lowing inbreeding. He also found greater variations in the
inbred material than in the progenoes from free flowering.
Significant reductions in plant height, winter hardiness and
seed production are reported by Nilsson for Festuca.
pratensis Huds., Dactylis glomerata L. and Phleum pratense
L. He stated, however, that continued selection of the tall
inbred segregates should about counteract the effect of in-
breeding and thus make possible a relatively homozygous tall
strain that would suffer little loss of vigor by selfing.
Stapledon (62) observed a loss of about 50 percent in vege-
tative vigor of Dactylis glomerata L. following inbreeding,
which closely agrees with the work of Calder (10) on this
species. A loss of vigor amounting to 63 percent, as a re-
sult of inbreeding in Lolium spp. was reported by Jenkin
(33), 32 percent of the plants selfed giving defective
seedlings. Nilsson (50) and Nilsson-Leissner (51), working
independently, agreed that inbreeding Festuca rubra L. re-
sults in a marked decrease in vigor in some lines and almost
no loss of vigor in others. Hayes and Baker (26) found

that selfing <u>Phleum pratense</u> resulted in a segregation of
the progeny into lines that were as vigorous as the parents
and also lines that were much reduced in vigor. Many leth-
al seedlings appeared in the inbred progeny so the authors
concluded that "Self-fertilization in timothy, as well as
corn, is a desirable method of freeing it from undesirable
recessive characters." Hayes and Clarke (27) were able to
isolate selfed lines of timothy more vigorous than the
commercial sorts, and McRostio (46) found inbred strains, after
five generations of selfing and selection, outyielding the
open-pollinated varieties. On the other hand, Williams (82)
studying the genetics of red clover, concluded, "Self-fer-
tility has proven invaluable in connection with the study of
the genetics of red clover, but from the standpoint of crop
improvement, on account of the marked loss in vigor of growth
which invariably accompanies inbreeding, self-fertility
must be regarded as nothing less than an unmitigated ill."
He found a decided and progressive loss in vigor as a
result of inbreeding as shown by an average reduction in
total yield of 37.9 percent for the first inbred generation
and 61.8 percent for the second inbred generation when com-
pared with the cross-bred populations. There were, however,
certain inbred lines that retained their vigor to a marked
degree and which were strognly prepotent in regard to high

yielding qualities when outcrossed.

The problems of sterility following inbreeding of normally cross-pollinated strains and the subsequent utilization of these inbred lines need further investigation. Especially important is the effect of continued selfing on the seed production and viability of a given strain since a progressive decrease in self-fertility would be a serious barrier to obtaining inbred lines.

Table 1 presents a brief summary of the literature in regard to seed set of various species studied.

Thus, experimental evidence would indicate that for most of the cross-fertilized forage species it will be possible to obtain inbred strains that admit at least some degree of self-fertility and that exhibit much uniformity as regards growth characters. On the basis of the results from the limited work on inbreeding, it seems doubtful if inbred lines will be of commercial value in themselves. Myers(47) suggested two possibilities for their utilization. It may be necessary to use them in hybrid combinations. Theoretically, if a sufficient number of lines are combined, relatively little reduction in vigor would be expected in F_2 and the vigor should remain rather constant in later generations, thus making possible the production of seed of the commercial crop. The synthetic variety

Table 1. Summary of the effect of inbreeding on seed set of various forage species.

Species	Citations	Effect from inbreeding	Remarks
Phleum pratense L.	Webber (81)	Wide variation in fertility of progeny	
do	Hayes and Barker (26)	Some progeny highly self-sterile Some progeny highly self-sterile	
do	Hayes and Clarke (27)	do	Inter-annular correlation of selfed seed set $r = .829 \pm .033$
do	Clarke (14)	High and low self-fertility apparently inherited. Many lines highly self-sterile	
do	Kirk (44)	Progressive increase in self-sterility	
do	Jenkin (31)	Wide variation in self-fertility	
do	Nilsson (50)	Wide variation in self-fertility	Correlation between self- and general fertility of $r = +.7212$
Dactylis glomerata L.	Wolfe and Kipps (84)	Average seed set of selfed 8.8%; open 43%	Germination of open and selfed seed is about equal. Will Admit of continued selfing.
do	Stapledon (61)	No pronounced reduction of seed production in most lines	
do	Kirk(44)	Variation from complete self-fertility apparent self-sterility	

Table 1 (cont.)

Species	Citations	Effect from inbreeding	Remarks
Dactylis glomerata L.	Nilsson (50)	Range from self-sterile to self-fertile plants	
Lolium perenne L.	Nilsson (50)	Range in seed set of 0-34%, Mean of 7.3%	Seed set of same individuals for different years, r= +.72
Do	Kirk (44)	Very low degree of self-fertility	
Do	Jenkin (37)	Highly self-sterile	Three types of chlorophyll deficients resulting from selfing
Festuca pratensis Huds.	Nilsson (50)	Range of 0-5% of normal seed set	
Festuca elatior	Beddows (7)	Reduction in seed set	22.3 times as much seed from open-pollinated heads
Bromus inermis Lyers.	Kirk (44)	Progressive increase in self-sterility with continued selfing	
Do	Keyser (42)	Apparent complete self-fertility	
Do	Waldron (75)	Range from self-fertile to self-sterile	
Do	Beddows (7)	Do	
Andropogon scoparius, Michx.	Anderson and Aldous (6)	Reduced seed set 49% to 57%	
Trifolium pratense	Williams (82)	Normally self-sterile	True self-fertility extremely rare

would exhibit considerable variability, thought by many to be a desirable character in forage plants. As an alternative, Myers suggested the use of inbred lines in controlled crosses, the hybrid seed to be used for planting the commercial crop. The criticisms of too much uniformity and the possible cost of producing sufficient seed might be raised against this procedure. It is conceivable that even the highly self-fertile inbred lines will be normally cross-pollinated when the artificial barriers to foreign pollen are removed. In this case, it would only be necessary to interplant inbred lines and permit them to hybridize. Then, too, according to Myers, there is the possibility of the production of self-sterile inbred plants by sib-pollination which could be used in the above manner.

The factors conditioning sterility and fertility have only recently been touched upon. Nilsson (50) grouped his self-sterile plants into three classes: (a) genuine sterility caused by partial or absolute lethality in the haplophase or diplophase, (b) modifactive sterility caused by environmental influence, (c) incompatibility, that is, the prevention of fertilization by genetic factors in spite of full vitality in the haplo- or diplophase. He concluded that the occurrence of self-sterility following inbreeding is due to the segregation of different factors directly

causing a decrease in fertility, or causing a general depression in vigor which again impedes fertility. Jenkin (37) found a segregation of yellow-tipped albinos, non-surviving green and surviving green resulting from selfing a normal green plant of <u>Lolium perenne</u>. He was able by appropriate back-crosses to obtain such a ratio as to suggest that his parent plant was heterozygous for two factors conditioning chlorophyll inheritance.

The problem of self-sterility following inbreeding has changed the viewpoint of several investigators. Kirk (43) first found several self-lines of red clover more fertile than his random samples of open-pollinated material and concluded that self-fertilization followed by selection provided the best means of attack in developing improved varieties. Following various difficulties incident to self-sterility and loss of vigor he later reversed his conclusion (44), stating that some method of composite crossing was probably best. In the same way, Stapledon's (60) earlier work suggested the possibilities of using some degree of inbreeding with orchard grass, but his later work (61) advocated strain building.

The actual breeding program for the improvement of grassland plants should follow three lines of attack, according to Stapledon (63). The first step is merely

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selection from a uniform habitat of the types desired, i.e.
the isolation of "aggregate strains" which breed remarkably
true within a prescribed circle of variation. The next is
the purification of these types by a method designed to de-
crease the concentration of the undesirable and to increase
the concentration of desirable plants. Following this
would come the actual strain building by the most refined
methods of breeding. "The herbage plant breeder," Stapledon
concluded, "will have done much if he can produce a strain
which will breed true to a 'throw up' of 50 percent 'ideals'
generation after generation where the ordinary seed of com-
merce is incapable of a 'throw up' of more than 15 percent.
In such a program, however, the plant breeder should be
coming along behind himself and by the adoption of methods
increasingly elaborate should aim at a product attaining
over more closely to the genetical idea of purity."

The importance of careful evaluation of the polymorphy
within the species in beginning a breeding program has been
stressed by Sylven (67). Valle (73), in discussing the
breeding of grassland plants stated, "... the main stress
at the outset should be laid upon a study of agricultural
value in cultivated types and especially the old local types
of the country concerned. At the same time wild material
from various parts of the country should be collected. The

extent to which selfing or inbreeding can be employed should be determined early and if it has a deleterious effect upon the progeny more suitable methods should be evolved."

Following the initial period of mass selection, in which some of the variability and a relatively high percent of the undesirable types are eliminated, a system of strain building should be followed. Kirk (43) defined strain building as any system of mating by which a strain is built up from carefully selected plants. It does not necessarily contemplate complete uniformity but aims to increase the population of individuals that possess the desired characteristics. Jenkin (36) stated that the word "strain" presupposes a certain amount of conscious selection and thus strain building would mean a refined system of breeding involving progeny tests and controlled crossing. Stapledon's (61) method of strain building involves the progeny testing of at least 30 unrelated parent plants and the use of the purest progeny from these plants in a mass isolation block as the new strain. Jenkin (36) concluded, "Whatever breeding tests are undertaken, the first essential is to employ satisfactory methods for the isolation of one's plants, to develop a proper technique of selfing, and to arrive at some satisfactory standard for estimating and comparing self-fertility." When it is found impractical to determine

the gross genetical consitiution of the basic plants in a
potential strain by inbreeding, Jenkin (34) has suggested a
system of diallel-crossing to determine the compatibility
of the parent plants. The F_1's are then backcrossed to
their parents and intercrossed with each other. Such a pro-
gram would take considerable time but fortunately need not
be done at once. As the plants are tested the undesirable
ones can be rejected and at the same time new unrelated plants
can be brought in and tested. Thus, "strain building"
is a continuous process and the perfected strain is not
necessarily identical with the same strain at its init-
ial establishment, although the same type is maintained.
throughout.

Upon close examination, the methods just discussed are
found to be only quantitative in nature and to aim at in-
creasing the percent of desirable types in a given strain
but not toward the development and subsequent utilization
of "pure lines." In view of the success of the inbreeding
and pure line methods that have followed mass selection in
some of the related crops, it would seem possible to reason
by analogy and to conclude tentatively that inbreeding might
be the next step in the improvement of our herbage species.
In the "fixing" of certain specific characters, such as rust
resistance and winter hardiness, or for increasing the

proportion of a desirable character that may not be in abundance in the plant population under consideration, or in freeing the material of undesriable recessives, inbreeding may be of first importance.

MATERIALS AND METHODS

The intensive breeding work on <u>Andropogon furcatus</u> was started in 1935 when the first generation of individual plants was set out for detailed study. The seed for this nursery was obtained from older observation plots in the grass nursery. These observation plots in turn were grown from seed of particularly promising plants growing in their native habitat. In making the original selections, drought resistance was considered of major importance, a considerable portion of the seed being obtained from an extremely droughty location along an old railroad right-of-way near Manhattan, Kansas. However, only the most leafy, vigorous plants having a marked ability to produce seed were included in the selections. Thus, while the material making up the 1935 nursery would, in a sense, represent the natural variability of the species, it had in reality undergone considerable selection in regard to certain characters.

Table 2 shows the general plan followed in growing the various generations of <u>Andropogon furcatus.</u> Seed was

Table 2. General nursery plan followed in grass breeding program.

Year	Generation	Source of seed	Approximate no. plants	Treatment
1935	First	Field selections from natural populations	200	
1936	Second	1935 nursery	4500	25 plants caged in muslin bags
1937	Third	1936 nursery A. Open-pollinated B. Bagged plants	2350 A. 1800 B. 550	Mass selection. Inbreeding with parchment sleeves
1938	Fourth	1937 nursery A. Open-pollinated B. Bagged plants	7000 A. 5000 B. 2000	Mass selection. Inbreeding with parchment sleeves
1939	Fourth (From second year growth, third generation plants	1937 nursery A. Open-pollinated B. Bagged plants	900 A. 600 B. 300	Do
1939	Fifth	1938 nursery A. Open-pollinated B. Bagged plants	4700 A. 3440 B. 1260	Do

obtained from individual selected plants each fall, then
taken into the laboratory where caryopsis counts were made
to determine the percent of florets containing seed. The
following February this seed was planted in four-inch as-
phalt paper squares covered with sand, and observed for time
of emergence and percent germination. The seedlings were
then spaced out in flats with 100 seedlings in a flat to re-
duce seedling competition and enable them to make vigorous
growth before transplanting to the field nursery early in
May. By starting the seedlings in the greenhouse early in
the season and providing favorable conditions for early
seedling growth, the resulting nursery plants were able to
produce considerable forage and seed in their first growing
season. This made possible the selection of desirable types
from the first season growth and hastened progress toward
the ultimate goal of an improved strain. Such a procedure
has been effective for increasing the percentage of desired
types in the population. However, the more refined methods
of strain building that follow mass selection may neces-
sitate using second or even third year growth as a closer
approximation of the genetic constitution of the plant in
question.

In the nursery the individual plants were spaced 30
inches apart each way. This plan reduced the competitional

effects of close planting and permitted normal development
of each individual plant. The use of a one-row cultivator
to control weeds and maintain the soil in good tilth elim-
inated a large amount of hand labor and consequently great-
ly reduced the nursery expenses. A small irrigation system
was used to supply water to the plants at critical times
during periods of summer drought so that a seed crop could
be produced each year. The application of irrigation water
as well as the various cultivations during the season were
uniform for all parts of the nursery. The nursery was
located on a very uniform soil as regards both soil type
and topography so that plant variation due to these factors
has probably not been of any great significance.

.The immediate goal of the breeding program has been to
eliminate by selection a high percentage of the poor, un-
productive plants found in the natural population of A.
furcatus. Plants were selected on a basis of their vigor,
leafiness, quality, disease resistance, and seed producing
ability. Field selections were based on observational com-
parisons, the seed from rather large numbers of plants be-
ing collected. Further selection was made in the laboratory
on the basis of detailed field notes taken during the grow-
ing season, percent of spikelets setting seed, and viability
of the seed. Seed from the plants passing both field and

greenhouse tests was used for the nursery plantings the following season. During the growing season all plants that were not of the desired type were removed from the nursery, thus eliminating a large amount of undesirable pollen from the plant population. This general procedure has been repeated each year since the breeding program was initiated.

While the methods outlined above probably would result in a greatly improved strain, it was felt that a more intensive method of breeding would necessarily follow. With this in mind, a system of breeding and progeny study of the inbred plants was initiated in 1936 following some preliminary trials in 1935. These preliminary trials consisted of bagging individual heads in two inch by six inch glacine bags. A total of 600 heads were bagged during the season without obtaining any seed. In 1936 large musling bags were used and the entire plant caged. A seed set of 7.2 percent was obtained in the bags but microscopic studies showed many of the meshes in the fabric to be large enough to allow pollen grains of A. furcatus to pass through. Bagging the plants in this manner made recording of detailed notes impossible on the cage plants in addition to having a marked detrimental effect on their vital functions. Since 1936, 18 by 36 inch vegetable parchment sleeves have been used as the isolating mechanism and only five or six culms

enclosed in the bags. This material is very resistant to
weathering and when properly used is highly efficient in ex-
cluding foreign pollen. The use of parchment sleeves per-
mitted the normal development of the parent plant so that
the seed obtained in these bags would more nearly represent
the true reaction of that particular plant to inbreeding.

Five generations of selection and three generations of
inbreeding have been included in this study of A. furcatus.
The plants were carefully observed during their growing
season and detailed field notes were taken on various char-
acters such as time of maturity and leaf area. Such factors
are of economic importance to the farmer in that, collective-
ly, they make up what he obtains as pounds of beef per acre,
while to the plant breeder, they are the "yardsticks" by
which progress in improvement can be measured. On the basis
of these observations, the outstanding plants have been sel-
ected to be parents of the next generation. A few heads
on the particularly promising plants were inbred to study
the effect of selfing and to obtain lines that might be
utilized later in a hybridization program.

To eliminate as much of the personal element as possible
and to obtain notes that would admit of statistical analy-
sis, the first ten plants in each progeny row were used
for detailed measurements. A plant was considered mature

when the first five culms had heads in flower. This made
possible the comparison of different plants at a definite
period in their development. Leaf area measurements, taken
at the time of maximum leafiness, were made in the following
manner: The average length of leaves in centimeters per
plant was obtained by measuring 30 leaves at random over the
plant. The measurements were taken from the ligule or col-
lar to the distal tip of each leaf so that the leaf sheath
was not included in the figure. The average width of leaves
in millimeters was obtained in a similar manner, using the
widest point on each leaf. The average number of leaves per
culm was then calculated for ten random culms per plant and
the total number of culms obtained. The product of the
average length of leaf, by the average width of leaf, by the
number of leaves per culm, by the number of culms per plant
gave a figure designated as "total leaf area." This was
larger than the actual leaf area since the leaves are tapered
in shape, but for the purposes of comparison between
plants, it was found to be sufficiently accurate. To obtain
a figure for reducing this factor to actual leaf area, 84
mature lsaves were picked at random from second generation
plants. These leaves were blueprinted and their area mea-
sured with a plainimeter. This actual area was divided by
the product of the length times the width and a factor of

.6811 ± .058 for this relationship was obtained. In other
words, the actual leaf area is 68 percent of the figure ob-
tained by multiplying the length by the width at the widest
point. The actual areas of 84 mature leaves were corre-
lated to the values obtained by multiplying the length times
the width at the widest point. The high correlation of
.9813 ± .002 shows that length times width gives a value
tha is very reliable where comparisons between plants are
to be made and where it is not necessary to know the actual
leaf area. Data relative to the lateral spread of the
plants were obtained by measuring the basal diameter of each
plant at the surface of the ground. These data were taken
during the same period leaf area measurements were obtained.

The data obtained relative to leafiness, number of culms,
height, basal diameter, time of maturity, disease and in-
sect resistance, setting of seed, viability, quality, and
their various interrelationships will be discussed in
regard to general variability, effect of selection and of
inbreeding.

PRESENTATION OF DATA AND DISCUSSION

General Variability

Andropogon furcatus exhibits a wide range of adaptation to many soil types and to a variety of climatic conditions. Its suggested ancient hybrid origin, Church (12), its decaploidy, and its apparent high degree of cross-pollination, together with its extensive occurrence, would indicate that a variety of forms could be found in the species as it exists in nature. Observation of strains of A. furcatus from Nebraska, Kansas, and Oklahoma, growing in the breeding nursery, indicate there are definite habitat types in this species corresponding to Turesson's (72) ecotypes. In general, plants from Nebraska are earlier, smaller, and less leafy than plants of southern origin, while those from Kansas are intermediate in these characters. Table 3 shows the plant height and time of maturity of A. furcatus plants from various seed sources grown in the Manhattan, Kansas nursery. Observations of these three ecotypes have shown that the taller, later maturing Oklahoma plants are also more leafy than the Kansas or Nebraska ecotypes.

Using Snedecor's (58) procedure for the calculation of analysis of variance, leaf area data obtained on these three

ecotypes showed a highly significant variation between means

of strains with an F value of 7.23 and a one percent level

of significance of 4.92.

Table 3. Effect of seed source on growth of Andropogon
          furcatus (1936 nursery, 1937 data).

Source of seed	No. of Plants	Plant Height Inches	Time of maturity
Holt Co., Nebraska	16	34 ± 11	July 13 ± 10 days
Anderson Co., Kansas	11	41 ± 9	Aug. 3 ± 8 days
Guthrie, Oklahoma	20	44 ± 10	Sept. 19 ± 14 days

Plate I shows the differences in growth habit, leafi-

ness, and time of maturity of typical plants in these three

strains. A similar condition was found in Andropogon

scoparius by Anderson and Aldous (6). Evans, Allred, and

McConkey (21), working with 13 strains of timothy, found the

time of heading, maturity, and general growth habit of his

strains to be determined largely by temperature and length

of day. Sufficient data are not available on A. furcatus

to reach any definite conclusions, but there are indications

that length of day has a very marked effect on time of ma-

turity of this species.

Within ecotypes of A. furcatus, there is also definite

natural variation in many characters. Although it is not as obvious as the variation between ecotypes, such variation can be perceived readily upon close observation of any one ecotype. It is this variation that has been of major interest in the selection program. It was felt that selection of desired lines within the ecotype of the area in question would result in a more dependable final strain from the standpoint of yield, palatability, resistance to drought, winter injury, and disease than if lines from ecotypes that had not been subject to the conditions of natural selection in the given area were added to the strain.

That the plants in the 1935 nursery exhibited ample variation from which selections could be made is shown in Table 4 and Plate II. Plate III shows typical differences in growth habit and vigor of two of the original parent plants in their second season of growth.

Table 4. Variability in first generation A. furcatus (1935 nursery, 1935 data).

Character	Max.	Min.	Ave.	Date data obtained
Leaf area (sq. cm.)	4511	87	1296	July 6-12, 1935
No. of tillers	49	1	13	July 6-12, 1935
No. of culms	73	3	27	July 6-12, 1935
Height (inches)	110	30	68	At maturity
Time of maturity	9/13	7/8	8/19	

Keyser (42) in a preliminary report on variability in
Bromus inermis found 121 distinct strains or types occur-
ring as natural variants. Waldron (76)reported wide var-
iation between different clones of Bromus inermis in regard
to yield, protein content, and percent of natural crossing.
For instance, his clones varied in percent to protein on a
dry basis from 7.2 to 16 percent, and he found a significant,
positive correlation of protein content with yield, al-
though there was considerable variation in this relation.

In addition to the variation in growth habit shown in
Table 4, many interesting morphological variations have
been found in A. furcatus. Paired, sessile spikelets have
occurred, that is, two sessile and fertile spikelets ap-
peared at one node on the rachis instead of the normal con-
dition of one sessile, fertile spikelet and one pedicellate,
staminate spikelet at each node. A number of plants have
been found in which the pedicellate spikelet, which is r
normally staminate, produced viable seed. This particular
character has appeared in many of the progeny from six of
the original parent plants. Polyembroyonic or twin seeds
have been found in one plant, appearing in the sessile and
pedicellate spikelets in both inbred and open-pollinated
flowers. These characters are being studied further since
sufficient data have not been collected to warrant drawing

any definite conclusions regarding their behavior.

An important factor in regard to the variability of
A. furcatus is its degree of natural cross-pollination. No
definite data as to the percent of cross-pollination have
been obtained but observation of the plants during the per-
iod of flowering indicate that the species is highly cross-
pollinated. It has many of the characters of an anemophi-
lous plant. The flowers are perfect and very small with no
showy parts. The stigmas are large, plumose structures and
usually become exserted from between the lemma and palea
after the anthers of the same flower have dehisced. Records
have been obtained of stigmas in the field remaining recep-
tive for as long as eight days if pollen is kept from them.
The two-celled anthers are semi-versatile, becoming fully
exserted before dehiscing through a terminal pore to re-
lease large masses of powdery pollen which floats readily on
the wind. The entire inflorescence usually projects above
the leaves, facilitating the transfer of pollen from one
plant to another by the wind. In addition to these morpho-
logical and anatomical characteristics, inbreeding, as will
be shown later, results in greatly reduced seed set and much
loss of vigor. These facts would indicate that the species
has been highly cross-polinated for many generations.

Thus, it appears that the species, Andropogon furcatus,

exhibits considerable variation within strains (ecotypes)
as well as between strains. From these variations within
strains it should be possible to select superior types
adapted to the environmental conditions under which they
will be grown. Such a program should aim not at complete
homozygosity for any particular strain but only to eliminate
the less desirable types from the population and thus in-
crease the percentage of high producing plants.

Effect of Selection on Leafiness

A. furcatus is of major importance in a region where
the soils contain most of the essential elements in an
available form. The forage species growing in such an area
will, in general, have an adequate supply of these essential
elements for the proper nutrition of animals that feed on
them. Total yield, for this reason, has been the factor of
major interest in the improvement of A. furcatus. At the
beginning of the experiment the problem was to devise a
means of measuring the total production of the plants with-
out interrupting their normal life cycle. In order to per-
mit seed production, it was necessary to measure the quan-

tity of forage produced by the plants without removing the
foliage. Since such terms as "non-leafy, leafy, and very
leafy" did not adequately describe the plants for purposes

of intensive selection, a more detailed method of measure-
ment has been devised. Total leaf area, measured in the
manner previously described, has given the most accurate
evaluation of plant yield short of actually weighing the
total forage produced. It is the leafy portion of this
species that is preferred by the grazing animal and since at
its most leafy stage the plant is highest in nutritive value,
total leaf area becomes a factor of major importance in
the breeding program.

In discussing leafiness, the term "total leaf area" is
used to denote the measured leaf area and not the "actual"
leaf area. To convert this figure to "actual" leaf area,
it is necessary to multiply the calcualted area by the
factor 0.6811, as mentioned earlier in this thesis. The
field measurements were made during the period of maximum
leafiness of the plants in the nursery so as to be compar-
able from year to year. Plat IV shows a plant of the "ideal"
type at about the stage of growth at which the measure-
ments were obtained. This plant, the result of four gen-
erations of selection, shows the extremely leafy, fine-
textured type of growth that is considered highly desirable
from a grazing standpoint. Leaf area measurements have been
taken on both first and second year growth of A.
furcatus during the five years of selection with the

exception of the first year material in the 1936 nursery.
The notes on first year growth include five generations of
selection, while the notes on second year growth include
only four generations. Yield data, in addition to an analy-
sis of variance between strains compared to the variance
within strains, are given in Table 5.

The yearly means in Table 5 show a highly significant
increase in leaf area following four generations of selec-
tion for both the first and second seasons of growth. The
slight advantage of the third generation over the fourth
generation in their second season of growth can probably be
explained by the abundant spring and early summer rains of
1938 and the consequent heavy growth of the established
bluestem plants in the 1937 nursery. So favorable a season
was not encountered in 1939. Such abundant growth did not
occur in the first year plants of the 1938 nursery since
they were just becoming established during and after these
rains and had not become large enough to utilize the exces-
sive moisture. In the earlier generations, high F values
were obtained when comparing variation between lines to that
within lines. This indicated there were distinct genetic
differences between the lines in regard to the expression
of leaf area. Since these lines were the progeny of in-
dividual plants, it should follow that the parent plants

Table 5. The effect of continued selection on the leaf area of _Andropogon_ _furcatus_.

Season of Growth	Generation	Nursery	Number of Plants	Mean and standard deviation (sq. cm.)	Coefficient of variation	Analysis of variance F value ≠	1% level of significance
First	1st	1935	197	1296 ± 910	70		
do	2nd	1937	510	5237 ± 2970	57	4.36	1.57
do	4th	1938	250	7497 ± 3684	48	2.20	1.88
do	5th	1939	100	12986 ± 6665	51	1.62	2.59
do	4th∕	1939	120	10095 ± 7407	73	3.89	2.40
Second	1st	1935	197	14160 ± 9350	65	3.07	2.31
do	2nd	1936	190	26004 ± 10309	40	3.67	1.88
do	3rd	1937	250	46703 ± 20350	44	2.38	1.77
do	4th	1938	330	36697 ± 12980	35		

≠ Obtained by dividing variance between lines by variance within lines. Snedecor (58)

∕ Selection from second year growth, third generation (1937 nursery).

should differ one from the other in their ability to transmit the character leaf area to their offspring. If this were true, as is indicated by the available data, it should be possible to bring about considerable improvement of the population by continued selection of the desirable types from open-pollinated lines. Table 5 shows the fifth generation selection in its first season of growth to have a mean leaf area of nearly ten times the original first generation material. The data on plants in their second season of growth is perhaps a more reliable criterion from which to make comparisons. Here the fourth generation selection is nearly 22,500 sq. cm. larger than the original unselected material. These significant increases in leaf area can be taken to mean that many of the small, non-leafy plants have been eliminated from the population by selection.

The general variability of the population has been decreased materially during the course of the experiment as is shown by the trend in the coefficients of variability for the successive selected generations. A critical examination of the data, indicates that this is due, in a large measure, to the reduced variation between different lines. In other words, continued selection toward an "ideal" type has resulted in the reduction of differences between progeny lines. This conclusion is substantiated by the results of

analyses of variance set up to show differences between
lines compared to differences within lines. There is a def-
inite trend toward decreasing F values in the successive
generations, and in addition a significant decrease in the
coefficients of variability.

While the general variability of the population has
been significantly reduced by continued selection, there has
been no reduction in the variation between individual plants
within each line. This is shown by the class frequency dis-
tributions of leaf area for 1937, 1938, and 1939 shown in
Tables 6, 7, 8. It can be seen that in 1937 there was
an average spread within lines of about eight class inter-
vals between the largest and the smallest plants. By 1939
the average spread was approximately 17 class intervals
within each row and there was very little difference between
rows. Although the median leaf areas have been increased
year by year and the variation between ten-plant lines has
become decidedly less, there has been a rather marked in-
crease in variability within ten-plant lines. It can be
seen that this increase in variability has been brought
about by the appearance in the later populations of a few
plants with extremely large leaf areas in the families that
are most variable. This variability indicates heterozygosity
within the progeny group. Heterotic vigor, then, would

Table 6. Class frequency distribution of leaf areas, 1937 nursery, 1937 data.

Sq. Cm. /10	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Total
0-125	3				1	1			1									6
126-250	4		1	2	3	3	1	1	2	1	1			1		2	3	24
251-375	3	4	1	2	6	2	3	1	3	2	2		3	2	1	4	4	43
376-500		1	2			2	2	1	1	3		1			1	2	1	17
501-625		2	1	1		1	1			2	1	4	1	1	3	1	2	21
626-750				1			1	1	3	1		2		1	2	1		13
751-875			2	1		1	1	1		1	1	1	1	2				12
876-1000		3	3	1				2			3							12
1001-1125				2				1			1			1				5
1126-1250												1	2	1	1			5
1251-1375													1					1
1376-1500							1	1							1			3
1501-1625																		0
1626-1750													1		1			2
1751-1875											1							1
1876-2000																		
2001-2125								1				1		1				3
2126-2250																		
2251-2375													1					1
2376-2500																		

Table 7. Class frequency distribution of leaf area, open-pollinated, 1938 nursery 1938 data.

Sq. Cm. /10	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Total
0-125		1	1						1									3
126-250	5	1	3					1			1							11
251-375	3		1	1	1			1			1						1	9
376-500	2	1	1			1	1		1	1	2	2		1		1	2	16
501-625			1	2	1	2	2		1	1	1	1	3	1	2	2		20
626-750		3	1	4	4	1	1	1		2	4	1	3	2	2	4	5	38
751-875				1	1	3	1	2		1		3	1	1	1	1	1	17
876-1000		2	1		1	1		2	4			1	1	1	1	1		16
1001-1125		1		2			3	1	1	2				2				12
1126-1250			1	2			2			2		1	1					9
1251-1375		1				1		1	1				1	1	1	1	1	9
1376-1500										1	1							2
1501-1625														1				1
1626-1750								1										1
1751-1875						1									1			2
1876-2000									1						1			2
2001-2125																		
2126-2250												1			1			2

Table 8. Class frequency distribution of leaf area for ten 10-plant rows, 1939 nursery, 1939 data.

Sq. Cm. /10	1	2	3	4	5	6	7	8	9	10	Total
126-250									1		1
251-375				1							1
376-500	1	1	4	1							7
501-625	1		1					2		1	5
626-750		1	2	2				1			6
751-875					2		1		3	1	7
876-1000	1			1	2	2	1			1	8
1001-1125	1	3	1			1	1	2	3	1	12
1126-1250		2	1	1	1				1	1	7
1251-1375	1	2	1	1		4	2	1			12
1376-1500								1			1
1501-1625					3		2			1	6
1626-1750				2		1		1		2	6
1751-1875	2	1		1			1				5
1876-2000					1						1
2001-2125					1	1			1		3
2126-2250						1				1	2
2251-2375								2			2
2376-2500											
2501-2625	1									1	2
2626-2750	1										1
2751-2875	1										1
2876-3000						1					1
3001-3125											
3126-3250											
3251-3400						1		1			2

explain the presence of these particularly large plants.
Since this species is highly cross-pollinated, field hybrids
could account for the large plants in these variable rows.
If these assumptions are true, then selection of these ex-
tremely vigorous, heterozygous plants as parent material
would probably not increase the uniformity of the nursery
population and certainly the first generation progeny of
these plants would be highly variable. On the other hand,
it is quite possible to find large, leafy plants that pro-
duce uniformly desirable offspring. To distinguish between
these two genetically different types, it would be necessary
to resort to progeny tests.

Thus, much of the general variability was eliminated
by the program of selection. Plate V, showing the fourth
generation in its second season of growth, illustrates the
degree of uniformity that has been obtained by continued
selection. These leafy, productive plants are in marked
contrast to the highly variable material shown in Plates II
and III. This does not imply complete homozygosity in these
lines, but indicates that many of the stemmy, non-leafy
types have been eliminated from the population by con-
tinued selection of the leafy, highly productive types.

Jenkin (36), formulating a method of strain building
for grasses, stated, "If selection for the greatest possible

vigor is practiced, then no appreciable progress toward a homozygous strain may be made." He concluded that the combination of an excessive number of parent plants into a strain may lead to a detrimental heterozygosity. However, Kirk (43) stated, "It is quite conceivable that the best way to secure herbage plants of superior traits is to bring together as wide a range of biotypes as possible." Upon close examination, these differences in opinion are seen to be more apparent than real. Jenkin and Kirk in reality attacked the same problem from opposite directions and arrived at a rather indefinite mid-point, the former sounding a warning against too much variation and the latter warning against too narrow a range in the population.

It will be recalled that the fifth generation open-pollinated plants showed no significant variation between lined (Table 5) and there was a definite trend toward reduced variation between lines from the firat generation through each of the successive generations. Thus, after five generations of open-pollinated selection of $\underline{A}$. furcatus in its first season of growth, there can be expected little further increase in yield by further selection without sacrificing too much of the desired uniformity. In this case, it will be necessary to formulate a more intensive method of selection to increase further the productivity of

the population. Plants in their second season of growth are
believed to be more reliable material from which to make
such selections. Jenkin (36) made this suggestion but pre-
sented no data to substantiate his views. In this study of
A. furcatus data were obtained relative to the variability
between individual plants in their first and second season
of growth. It was found that the coefficient of variability
within the plant lines independent of variation between
means of lines averaged 24 percent for plants in their se-
cond season of growth compared to 43 percent for plants in
their first season of growth. This shows that the plants
in their second season of growth were more uniform within
lines. If this were true then differences between lines in
the second year material would be more significant than com-
parable differences between lines having more variability
in their first season of growth. Since the plants in their
second season of growth apparently exhibit less inter-plant
variation due to external factors, they should present more
reliable material from which to make selections. To obtain
information on this point, plants were selected from the
third generation, 1937 nursery, in its second season of
growth and their progeny grown in the 1939 nursery. These
progeny were fourth generation selections comparable to
the fourth generation selections grown in the 1938 nursery.

The data obtained on the progeny from selections in two-year-old material is shown in the middle line of Table 5. The progeny of plants selected in their second season of growth have an average leaf area of approximately 10,000 sq. cm. as compared to the average leaf area of 7,500 sq. cm. for the progeny of plants selected from their first season of growth. This shows a distinct advantage for the selections made from plants in their second season of growth. While seasonal differences may account for some of the variation, it should not explain all of the increase in size since in both years the plants were kept as nearly as possible under uniform growing conditions. Thus, it would appear possible to extend the usefulness of selection in open-pollinated lines by careful choice of desirable types from plants in their second year of growth.

The Effect of Inbreeding on Leafiness

Inbreeding in A. furcatus is accompanied by considerable loss of vigor in most of the lines studied. This loss of vigor may be expressed as a marked reduction in leaf area in the progeny of the plants that are inbred. Table 9 shows the percent reduction in leaf area for the entire population inbred one and two generations. Many of the plants were so small that data could not be obtained on them, hence the

percent reduction shown in Table 9 may be somewhat less than the actual reduction of vigor that occurred in the field. However, it was felt that the data were sufficiently accurate to give reliable comparisons and to indicate trends. While the greatest loss occurred in S_1, there was a further reduction of leaf area in the S_2 generation. In the 1939 nursery, which showed considerable lees reduction in vigor, there were only 12 inbred lines, while there were 30 inbred lines in the 1938 nureery. Of the 12 inbred lines in the 1939 nursery, two lines showed no reduction in leaf area compared to their open-pollinated eibs. This accounts for the lower percentage reduction in the 1939 nursery. Among the eecond season selections (from 1937 nursery, second year growth), there were no highly vigorous inbred lines. Plate VI ehows the general effect of inbreeding on the population.

Table 9. General effect of inbreeding on leaf area.

Genera-tione inbred	Percent reduction of inbred linee compared to open-pollinated sibs			
	1938 nursery		1939 nursery	
	1st season	2nd season	1st season	2nd season sel. (1937 nursery)
1 (S_1)	59.80	47.86	13.18	55.76
2 (S_2)	70.76	55.33	34.59	

The different reactions to inbreeding of various plants
in the nursery are shown in Table 10. These data have been
selected to show the variability of response to inbreeding
exhibited by A. furcatus. For example, line 1 shows the
marked loss in vigor characteristic of many lines. At the
other extreme, line 10 shows the vigorous inbred lines that
were found in a few cases. The remaining eight lines in
Table 10 show the various degrees of reduction in leaf area
that appeared in the material. These differences are pic-
tured in Plates VII, VIII, and IX. It is significant that,
in general, the open-pollinated lines having the largest
leaf area have been reduced most following inbreeding.
Moreover, the inbred lines that have suffered little loss of
vigor in S_1 have given progeny lines (S_2) that likewise are
more vigorous than the general level of the inbred popula-
tion. Stevenson (64), working with Agropyron cristatum,
found a similar condition. He stated, "The L_1[2] progeny
which showed wide segregation and marked loss in vigor be-
haved similarly in L_2 and succeeding generations, and like-
wise, the L_1 lines, which appeared strong, vigorous, and
uniform, continued to produce relatively uniform and vigorous
progenies in the succeeding generations." There are wide
differences between individual plants of A. furcatus in

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[2] First inbred generation or S_1.

regard to their ability to "throw" vigorous offspring fol-
lowing inbreeding. This would lend encouragement to the use
of inbreeding and selection as a means of establishing vig-
orous and fairly uniform lines that could be used for strain
building in this species.

Table 10. Differences in size of various inbred progeny
groups in comparison with their open-pollinated
sibs (1938 nursery).

Parent plant nos.	Mean leaf area (average of 10 plants)			
	Open-pollinated		Inbred sibs	
	Mean & S.D.	Coefficient of variation	Mean & S.D.	Coefficient of variation
1	9244 ± 3299	35	1118 ± 810	72
2	8028 ± 2422	30	2275 ± 770	33
3	5287 ± 2538	48	774 ± 692	89
4	5939 ± 1699	28	1041 ± 514	50
5	5161 ± 1917	37	1063 ± 737	69
6	5160 ± 2418	47	3185 ± 937	29
7	6125 ± 3307	54	3851 ± 1687	43
8	4617 ± 1741	37	2240 ± 829	37
9	6193 ± 1705	27	5019 ± 5039	100+
10	5519 ± 2585	46	5608 ± 3938	70

The class frequency distribution for leaf area of
plants inbred one generation is shown in Table 11. There is
considerable skewness evident in this population since in

Table 11. Class frequency distribution for leaf area, 1938 nursery, 1938 notes (selfed once).

Sq. Cm. /10	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	Total
0-125	5	7	3	4	1	7	2	7	3	7	1			4	2	3	4	5	4	9	6	3	8	5	2	102
126-250	4	2	3	4	5	3	4	3		2	4	1	2	3	5	2	4	2	3	1	2	3	2	3	3	67
251-375		1	4	2	3		2			1	4	3	5	1	2	1	1	2	3		1	3		1	2	42
376-500	1						1					2	3	1		2		1						1		12
501-625				1			1		2		1	3				2	1							1	3	16
626-750									1					1	1							1				4
751-875									2			1														3
876-1000									1												1			1		3
1001-1125																										
1126-1250									1																	1

many lines more than half of the plants were so reduced in leaf area as to fall into the lowest class. The apparent high degree of uniformity of these S_1 plants compared to their open-pollinated sibs (Table 7) can be partially attributed to the greatly reduced mean of the inbred plants. Thus, smaller variations in leaf area are much more significant in the inbreds. The S_2 population shown in Table 12 exhibits considerably more variation and has a larger mean than the S_1 material. This was expected because the S_1 parents of this population were, of necessity, the more vigorous plants in the 1938 inbred nursery since the extremely weak plants failed to produce seed. There was, then, considerable unavoidable selection for vigor in the inbred material. In addition, the 1939 growing season was more favorable for the establishment of the S_2 seedlings so that they were able to make more rapid growth.

A most obvious effect of inbreeding has been the segregation of the various inbred progeny groups into rather distinct entities making for greater variation between lines. This is clearly shown in Table 13 by the F values based on a comparison of the variation between strains to that within strains. For example, in the S_2 lines (1939 nursery) there is a highly significant F.value of 7.37 (one percent level of significance = 2.23) as compared to 1.62

(five percent level of significance = 1.97) for the open-pollinated lines. An examination of Table 13 shows that variation is consistently greater between inbred lines than between comparable open-pollinated lines. The class frequency distributions for leaf area of the inbred material, shown in Tables 11 and 12, compared to that of the open-pollinated selections shown in Tables 6, 7, and 8, indicate the the above assumptions are essentially valid. That is, following inbreeding there are rather distinct differences between progeny groups and considerable uniformity within progeny groups. In many of the inbred rows where most of the plants are greatly reduced in vigor and quite uniform, there have appeared a few rather vigorous plants with large leaf areas. The inclusion of these robust segregates in the data has lead to abnormally large standard deviations that could be quite misleading if this fact were not known (Table 10).

In the utilization of inbred lines, the questions of hybrid vigor and the degree of cross-pollination occurring between inbred lines allowed to pollinated naturally are of paramount importance. Although no qualitative data have been obtained on these points, considerable evidence has accumulated realtive to the effect on leaf area of allowing free pollination between inbred lines. Returning to Table

Table 12. Class frequency distribution for leaf area, 1939 nursery, 1939 notes (double selfed).

Sq. Cm./10	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	Total
0-125									6		1		1		3				8
126-250			1			1			2		2								9
251-375	2					2	2		2	2			2	2	1		2		15
376-500	1	3	1				1			2	1		1		4	1	5		20
501-625	2	1	1		2		1			1						2	1	2	13
626-750	1	2	1		1	1	2	2		1	2		1	1			1	2	18
751-875			1		1		3	1		1				1		2		2	12
876-1000	1	2	1			1		1	1		1		1	4		2		1	16
1001-1125	1				1			1						1			1	2	7
1126-1250	1	1					1	1				1		1		1			7
1251-1375			1	2	2	1		1		1		1			1	1		1	12
1376-1500			1	1	1	1						2	2						8
1501-1625		1		1						1									3
1626-1750							1					2				1			4
1751-1875				2				1		1									4
1876-2000				3	1		1					1							6
2001-2125	1										1	1							3
2126-2250			1										1						2
2251-2375			1			1													2
2376-2500				2								1							3
2501-2625												1							1
2626-2750													1						1
4001-4125				1*	1*														2

* Probable chance hybrids - not included in the class intervals between extremes total.

Table 13. The effect of various generations of inbreeding and open-pollination on the leaf area of _A. furcatus_.

Season of Growth	Generation	Nursery	Previous treatment	No. of Plants	Mean and Standard Deviation	Coefficient of variation	Analysis of variance	: 1% level of
							F value≠	:significance
First	4th	1938	Open-pollinated	250	7494 ± 3584	47.80	2.20	1.88
do	do	do	Inbred 1937	350	3014 ± 3114	103.30	6.05	1.61
do	do	do	Inbred 1936 & 1937	250	2192 ± 1696	77.37	4.70	1.88
do	5th	1939	Open-pollinated	100	12986 ± 6665	51.32	1.62	2.59
do	do	do	Inbred 1936 & 1937 Open-pollinated 1938	120	13794 ± 6721	48.72	3.69	2.40
do	do	do	Inbred 1938	90	11274 ± 6420	56.94	5.05	2.91
do	do	do	Inbred 1937 & 1938	130	8494 ± 4230	49.79	7.37	2.23
do	4th≠	do	Open-pollinated	120	10095 ± 7407	73.30	3.89	2.40
do	do	do	Inbred 1938	120	4504 ± 3313	73.55	5.63	2.40
Second	do	1938	Open-pollinated	330	36697 ± 12980	35.37	2.38	1.77
do	do	do	Inbred 1936 Open-pollinated 1937	360	29139 ± 12458	46.18	4.02	1.69
do	do	do	Inbred 1937	230	19134 ± 13549	70.81	4.98	1.94
do	do	do	Inbred 1936 & 1937	290	16395 ± 10975	66.94	3.37	1.76

≠ Variance between lines divided by variance within lines.
≠ Selections from second year growth, third generation (1937 nursery).

13, it will be observed that the largest mean leaf area among plants in their first season of growth, approximately 14,000 sq. cm., occurs in a group of unselected plants, the open-pollinated progeny of an S_2 population. Since the first plants were inbred in 1937, there had been no subsequent selection for increased leaf area, the plants merely having been carried along as inbred lines. These "hybrid" plants were even more vigorous than the group of plants in their fifth generation of open-pollinated selection. Nursery observations showed them to be more variable as well, indicating considerable heterozygosity among them. Apparently, then, a relatively high degree of cross-pollination had taken place when these inbred lines were allowed to pollinate naturally.

It is probably safe to assume that inbreeding results in a cumulative loss of vigor for the first generations. Following Jones' (39) Theory of Heterosis, this loss should occur until the plants become relatively homozygous for the factors governing leaf area after which it should be possible to establish lines that are comparatively stable and quite uniform in appearance. It is of interest to note in this connection the work of Jones (38) with continued inbreeding in corn. He found that after 20 generations of continued inbreeding, his lines of corn appeared to be

uniform and constant for all visable characters, yet there
was still measurable variation in yield. Peterson (52)
found he could increase the percent seed set and seed size
in rye by using stabilized inbred lines in his breeding
work. Following the suggestions from the results of random
recombination presented above, the logical procedure, after
uniform inbred lines of A. furcatus have been established,
would be to combine these lines by controlled hybridization
into a composite strain that should, theoretically, be
superior in the qualities desired.

The Effect of Selection on Number of Culms

The ability of certain plants in the nursery to produce
numerous culms was thought to be an important character for
which to select. The total number of culms produced by the
plant is directly related to its vigor and yielding capacity.
It has been observed in the nursery that those plants having
the larger number of culms were, in general, more leafy and
of finer texture. Also, they produced more seed than plants
with relatively few culms. Thus, selections have been made
with the purpose of eliminating plants having few culms.
The number of culms per plant was counted each year at the
time leaf area measurements were obtained so that they would
be directly comparable for the successive seasons.

The effect of continued selection on the number of culms is shown in Table 14. It will be observed that the 1936 nursery in its first season of growth shows a slight decrease in the average number of culms per plant. This decrease is probably due to seasonal variation although the 1936 nursery was made up of progeny from all of the 1935 nursery plants and did not represent any selection toward higher culm numbers. The continued low culm numbers shown by the 1937 nursery in its first season of growth are probably due to seasonal variation and to the shock of transplanting the seedlings to the field since there was a considerable period of spring drought in 1937 when the top soil was quite dry. These same plants in their second season of growth (lower half of Table 14) show a definite trend toward more culms per plant which trend is continued in succeeding generations. Second year data are considered to be more reliable than first year data in that the plants should have recovered from any effects of transplanting and seedling injury that may have been present the first year.

An examination of the F values in Table 14, showing differences between lines as compared to differences between plants within a line, indicates that there has been considerable increase in uniformity at the end of five generations of selection. Here, as in the case of leaf area, continued

Table 14. Effect of continued selection on the number of culms of A. furcatus.

Season of Growth	Generation	Nursery	No. of Plants	Mean and standard deviation Sq. Cm.	Coefficient of variation	Analysis of variance	
						F value≠	1% level of significance
First	1st	1935	197	28 ± 17	59	. . .2	. .
do	2nd	1936	370	25 ± 14	58	3.01	1.76
do	3rd	1937	510	25 ± 12	47	2.70	1.57
do	4th	1938	250	38 ± 14	36	2.65	1.88
do	5th	1939	100	59 ± 28	47	1.75	2.59
do	4th≠	1939	120	40 ± 19	47	2.78	2.40
Second	1st	1935	197	58 ± 29	51	5.13	2.12
do	2nd	1936	190	99 ± 43	43	4.75	1.88
do	3rd	1937	250	117 ± 48	41	3.68	1.77
do	4th	1938	1330	148 ± 49	33		

≠ Obtained by dividing variance between lines by variance within lines.

≠ Selection from second year growth, third generation (1937 nursery).

selection has decreased the variability of the entire population to the point where in the first season of growth there is no longer any significant variation between lines (F value = 1.75; five percent level of significance = 1.97). Obviously, then, a more intensive method of selection will have to be used if there is to be further substantial increase in the average number of culms per plant.

The corresponding F values for the plants in their second season growth (Table 14) suggest an alternative. In every case the differences between lines of the second year plants are relatively greater than the comparable differences between the same lines in their first season of growth. The coefficients of variability for variation among plants within lines in regard to number of culms, averaged 33 percent for first season plants and 30 percent for plants in their second season of growth. This intra-group variation was calculated for each individual line so that any variation due to differences between means of lines was excluded. Consistently lower coefficients were found among the older plants which partially explain the high F values for this material since the F values are merely a ratio of variation between lines divided by variation within lines. While the percentage difference between the two years was not as great as in the leaf area data, the figures indicate

that two-year-old plants have furnished the most reliable
criterion of their true breeding behavior.

Since these differences between lines are more distinct
in the two-year-old material, careful selection among these
plants should result in a greater degree of improvement than
selection of plants in their first season of growth. That
this may actually be the case is indicated by the results of
selections made in the 1937 nursery during its second season
of growth, the data of which are shown in the sixth line of
Table 14. The progeny of these selections have an average
of 40 ± 18.93 culms compared to 38 ± 13.7 for the progeny of
first season selections from the same nursery. Although the
difference is not statistically significant it shows a slight
advantage for the second year selections. However, when
this considered in conjuction with similar data for leaf area,
shown in Table 5, it becomes evident that second season
growth is a more reliable standard upon which to base selection

The Effect of Inbreeding on Number of Culms.

The general depression of vigor in $\underline{A}$. furcatus follow-
ing inbreeding causes a marked reduction in the number of
culms. As was shown in the leaf area data, the greatest
depression occurs in S_1 where losses of nearly 50 percent

are encountered and there are indications of cumulative
losses in subsequent inbred generations. Table 15 shows the
actual percent reduction of the inbred lines compared to
their open-pollinated sibs. The 1939 nursery had too few
lines to be representative of the general reaction of the
species to inbreeding since there were only 12 inbred lines
in the nursery, two of which showed no reduction in vigor.
These two lines came from vigorous inbreds found in the 30
lines tested in the 1938 nursery.

Table 15. General effect of inbreeding on number of culms
of $\underline{A}$. $\underline{furcatus}$.

Genera- tion inbred	Percent reduction of inbred lines compared to open-pollinated lines		
	1938 nursery		1939 nursery
	1st season	2nd season	1st season
S_1	47.25	49.42	20.10
S_2	56.34	57.46	25.29

The data presented in Table 16 relative to the response
of different plants to inbreeding agrees closely with that
shown for leaf area in Table 10. That is, the inbred mater-
ial ranges from greatly reduced progeny groups to those
showing no reduction at all in number of culms. According
to the Theory of Dominance preposed by Jones (39), those
plants whose progeny show the greatest effects following

inbreeding should be the most heterozygous ones. If this assumption is true, there should be a positive relationship between the effect of inbreeding and the variability of the material. This has been shown to be the case by Nilsson (50) in Dactylis glomerata and Festuca pratensis and there are evidences of such a relationship in A. furcatus (Table 10). However, sufficient numbers of inbred lines have not been studied to establish definitely such a correlation.

Table 16. Differences in number of culms of various inbred progeny groups in comparison with their open-pollinated sibs (1938 nursery).

Parent plant nos.	Mean number of culms (average of 10 plants)			
	Open-pollinated		Inbred	
	Mean & S.D.	Coefficient of variation	Mean & S.D.	Coefficient of variation
1	27 ± 5.27	19.5	6 ± 2.91	48.5
2	30 ± 11.20	37.3	8 ± 2.73	34.1
3	32 ± 11.63	36.3	10 ± 2.16	21.6
4	43 ± 13.66	31.8	16 ± 6.41	40.1
5	44 ± 18.12	41.2	22 ± 11.49	52.2
6	29 ± 7.90	27.2	20 ± 7.34	36.7
7	39 ± 12.17	31.2	33 ± 20.96	63.5
8	49 ± 20.64	42.1	43 ± 40.24	93.5
9	24 ± 12.54	52.2	24 ± 15.14	63.1
10	26 ± 5.26	20.2	27 ± 17.54	64.9

Vigorous individuals that apparently were homozygous for
the factors conditioning number of culms (Table 16) appeared
in the populations studied. Such plants should not exhibit
any noticeable degeneration due to inbreeding. Their value
in a strain-bulbing program can be determined only by ap-
propriate tests.

As might be expected, variability within progeny groups
has been decreased by inbreeding. At the same time differ-
ences between progeny groups have increased materially fol-
lowing inbreeding. This is shown in Table 17 by the F
values based on variance between lines compared to that
within lines. In every case the F values for the inbreds
are higher than those for comparable open-pollinated lines.
These data are in complete accord with the figures presented
in Table 11 regarding leaf area. Thus, it would appear that
inbreeding may serve at least two purposes in the breeding
program. First, inbreeding is necessary for an accurate
evaluation of the genetic make-up of a given plant. Second,
continued inbreeding with careful selection in the inbred
progeny should result in establishing uniform lines of dis-
tinctly different growth habits. Such lines might be
adapted to the various needs that arise in a comprehensive
pasture improvement program.

Considerable heterosis was manifest by the progeny of

open-pollinated S_2 plants as is shown in Table 17. These plants had an average of 62± 23.75 culms compared to 16 ± 9.67 for the S_2 parent plants. This difference is highly significant. Furthermore, the mean culm number of the open-pollinated progeny group that had been selected for five generations toward higher culm numbers was no larger than the mean of these outcrossed progeny from the S_2 parents. This is especially significant in view of the fact that the inbreds were subject to no selection other than the natural elimination of the extremely weak plants.

The "hybrid vigor" manifest by the progeny of open-pollinated S_2 plants indicates a direct use for the inbreds. It should be possible to combine certain of them in such a manner as to utilize this phenomenon of "hybrid vigor" after the suggestions of Myers (47). He stated that if sufficient number of inbred lines were used in the initial crosses, there would be little loss of vigor in F_2 and subsequent generations. Thus, a commercial seed supply could be obtained from any of the generations following the initial crosses. It would be necessary for the original inbreds to be completely cross compatible, a fact that could be established only by appropriate crosses.

Table 17. The effect of various generations of inbreeding and open-pollination on the number of culms of A. furcatus.

Season of Growth	Generation	Nursery	Previous treatment	No. of plants	Mean and standard deviation	Coefficient of variation	Analysis of variance	
							F value≠	1% level of significance
First	4th	1938	Open-pollinated	250	38 ± 13.70	36	2.65	1.88
do	do	do	Inbred 1937	350	20 ± 12.89	64	8.60	1.61
do	do	do	Inbred 1936 & 1937	250	16 ± 9.67	60	5.77	1.88
do	5th	1939	Open-pollinated	100	59 ± 27.70	47	1.75	2.59
do	do	do	Inbred 1936 & 1937 Open-pollinated 1938	120	62 ± 23.75	38	3.22	2.40
do	do	do	Inbred 1938	90	47 ± 20.60	44	3.02	2.91
do	do	do	Inbred 1937 & 1938	130	43 ± 19.22	44	5.24	2.23
do	4th≠	do	Open-pollinated	120	40 ± 18.93	47	2.78	2.40
do	4th≠	do	Inbred 1938	120	27 ± 14.05	52	7.74	2.40
Second	4th	1938	Open-pollinated	330	148 ± 48.73	33	3.68	1.77
do	do	do	Inbred 1938 and open-pollinated 1937	360	99 ± 41.84	42	5.34	1.69
do	do	do	Inbred 1937	230	74 ± 45.65	61	7.20	1.94
do	do	do	Inbred 1936 & 1937	290	63 ± 30.22	47	4.92	1.76

≠ Obtained by dividing variance between lines by variance within lines.

↗ Selection from second year growth, third generation (1937 nursery).

The Effect of Selection on Plant Height

In the effort to breed superior forage strains, plant height has not been considered an important character upon which to base selections. It was felt that the extremely tall plants were undesirable from a forage standpoint since they were generally sparsely leaved, coarse, and stemmy. The decumbent and low growing types were also considered inferior as they were usually poor in both forage and seed production. In regard to plant height then, the only consideration in the selection program has been the elimination of these extreme types. Height measurements were taken each year at the period of maximum leafiness before the flowering culms had begun to appear. Data were obtained on average height, ie. the distance above ground reached by the bulk of the leaves in their normal position, and maximum height, or the height of the plant to the tip of the leaves held upright. This latter figure has been found to be more closely associated with yield and with the other factors studied, hence, maximum height will be used in this discussion.

The results of continued selection toward a medium height population are shown in Table 18. The most obvious fact, perhaps, has been the reduction in average plant height from 52 inches to 30 inches in the material in its

Table 18. Effect of continued selection on the maximum height in inches of A. furcatus.

Season of Growth	Generation	Nursery	No. of Plants	Mean and standard deviation	Coefficient of variation	Analysis of variance	
						F value≠	1% level of significance
First	1st	1935	198	52 ± 8.61	16		
do	2nd	1936	370	40 ± 9.00	22	7.97	1.88
do	3rd	1937	250	25 ± 5.70	23	4.45	1.88
do	4th	1938	250	23 ± 3.86	16	1.18	2.59
do	5th	1939	100	30 ± 6.47	21		
do	4th⌐	1939	120	27 ± 4.73	17	1.94	2.40
Second	1st	1935	198	64 ± 12.30	19		
do	2nd	1936	190	34 ± 6.71	19		
do	3rd	1937	250	39 ± 4.80	12	6.52	1.88
do	4th	1938	330	33 ± 4.18	12.	2.62	1.77

≠ Obtained by dividing variance between lines by variance within lines.

⌐ Selection from 2nd year growth, third generation (1937 nursery).

first season of growth. During this same period and in the
same material, total leaf area has been increased nearly ten
times (Table 5). Apparently the plants of medium height are
by far the most leafy. This substantiates observations made
in the nursery that the tall plants are generally stemmy and
sparsely leaved. It is worthy of note that the plants in
their second season of growth are not significantly taller
than they were in their first season of growth. Also, the
coefficients of variability for this character are much
lower throughout than are those for the characters, leaf
area and number of culms. Clarke(14), studying variability
in timothy, found that plant height varied least in any of
the factors on which he obtained data. Evans (20), in his
studies of timothy, concluded that the factors determining
plant height depended largely upon length of day for their
expression. Thus, the height of a species in any given
latitude might be expected to vary less than other charac-
ters more dependent upon the inherent vigor of the plant for
their expression. Analyses of variance for plant height
(Table 18) show that after the fifth generation of selection
there were no longer any significant variations between
progeny rows, whereas earlier generations had shown highly
significant differences between lines. These facts, in
accordance with the data previously presented on leaf area

and number of culms, indicate the necessity of a more-intensive method of selection if further improvement is to be accomplished. It has been found that the coefficients of variability showing differences between plants within lines for plants in their second season of growth averaged 12 percent as compared to 15 percent for plants in their first season of growth. Thus, as has been shown in the data for leaf area and number of culms, plants in their second season of growth are more uniform and more stabilized than plants in their first season of growth. The data indicate that plant height, like leaf area and number of culms, is an inherited character and that it will admit of considerable change by selection in open-pollinated lines.

The Effect of Inbreeding on Plant Height

That inbreeding has a deleterious effect on plant height is shown in Table 19. However, the reduction in height following inbreeding is not nearly as great as the reduction in leaf area (Table 9) or in number of culms (Table 15). Here again, the genotypic constitution of the mother plant is very important since many progeny lines showed no significant reduction at all while a few were decidedly reduced in height. Similar observations were made by Nilsson (50) studying the effect of inbreeding on plant

Table 19. General effect of inbreeding on plant height of
A. furcatus.

Genera-tions inbred	Percent reduction of inbred lines compared to Open-pollinated sibs		
	1938 nursery		1939 nursery
	1st season	2nd season	1st season
S_1	19.20	22.71	22.90
S_2	27.83	28.52	

height of timothy. He stated, "As regards height, it may be
said that it is on an average, and even in most individual
cases, lower in inbred families than open-pollinated fam-
ilies. ... In many cases the differences between inbred and
open-pollinated families are not significant. In three
cases the inbred progeny is significantly taller than
the open-pollinated sibs." In data on A. furcatus ten of
thirty lines studied showed no significant reduction in height
following inbreeding and two of the inbred lines were actually
taller than their open-pollinated sibs. Furthermore,
progeny of these tall inbreds were, in general, equal in
height or even exceeded the height of their mother plants.

A study of Table 20 indiciates there has been consider-
able variation in the response of various lines to inbreed-
ing. That is, some of the inbred progeny groups show con-
siderable reduction in height while others show no signifi-
cant differences between open-pollinated lines and their

Table 20. The effect of various generations of inbreeding and open-pollinated on height of
A. furcatus.

Season of Growth	Generation	Nursery	Previous treatment	No. of Plants	Mean and standard deviation	Coefficient of variation	Analysis of variance F value‡	1% level of significance
First	4th	1938	Open-pollinated	250	23 ± 3.86	16	4.45	1.88
do	do	do	Inbred 1937	350	18 ± 4.59	25	7.75	1.61
do	do	do	Inbred 1936-37	250	16 ± 4.63	29	3.4	1.88
do	5th	1939	Open-pollinated	100	30 ± 6.47	21	1.18	2.59
do do	do	do	Inbred in 1936-37 Open-pollinated 1938	120	27 ± 4.45	16	5.93	2.18
do	do	do	Inbred 1938	90	27 ± 4.72	17	10.9	2.91
do	do	do	Inbred 1937-38	130	23 ± 6.35	27	5.72	2.23
do	4th∕	do	Open-pollinated	120	27 ± 4.73	17	1.94	2.40
do	do∕	do	Inbred 1938	120	21 ± 5.02	23	2.94	2.40
Second	4th	1938	Open-pollinated	330	33 ± 4.18	12	2.62	1.77
do	do	do	Inbred 1936 Open 1937	360	32 ± 4.14	12	3.50	1.69
do	do	do	Inbred 1937	230	25 ± 6.20	24	6.80	1.94
do	do	do	Inbred 1936-37	290	23 ± 6.61	28	4.93	1.77

∓ Obtained by dividing variance between lines by variance within lines.

∕ Selection from second year growth, third generation (1937 nursery).

inbred sibs. The open-pollinated progeny of S_2 plants
(Table 20, line 5) are not significantly different in height
from the fifth generation open-pollinated selections (line
4). On the other hand, these "hybrids" are significantly
taller than their inbred parents, indicating considerable
response to outcrossing in regard to plant height. This is
in accord with the data presented regarding leaf area and
number of culms. In addition, most of the inbred groups
show larger coefficients of variability than the comparable
open-pollinated lines. These coefficients are based on the
total variation appearing in the various groups. Therefore,
the fact that they are larger in the inbred material would
indicate that the lines were segregating into definite
height groups. The F values, showing variance between lines
divided by that within lines, are in agreement with the
above conclusion since they are, in most cases, greater for
the inbreds.

<center>The Effect of Selection on Basal Diameter</center>

Plants of **A**. _furcatus_ generally have weak rhizomes,
hence the species appears in characteristic clumps or tufts
in nature. Occasional plants have been found that produce
vigorous rhizomes and spread so rapidly that they could be
classed as vigorous sod-formers. This ability to spread

vegetatively was thought to be an important character for which to select because of its relation to the rapidity with which stands could be established. Obviously a strain that could spread vegetatively as well as by seed would form a thick, protective cover for the soil that would be highly resistant to trampling and grazing much faster than one that depended upon seed alone for its propagation. Consequently, only those plants with large basal diameters have been included in the selections. The data relative to this character were obtained by measuring the diameter of the clump in inches at the surface of the ground. No measurements were made during the 1935 or 1936 seasons.

A study of Table 21 shows there has been a definite trend toward larger plant clumps in the successive generations of plants in their first season of growth. While it is true that the differences are not significant for any two consecutive years, there is a significant difference between the third and fifth generations. Apparently basal diameter is a heritable character that will respond to selection since it has been significantly changed by three generations of selection. Analyses of variance were calculated for variation between lines compared to that within lines for each of the three years (Table 21). The highly significant F value of 4.18 (one percent level of significance = 1.88)

Table 21. Effect of continued selection on basal diameter of A. furcatus.

Season of Growth	Generation	Nursery	No. of Plants	Mean and Standard Deviation	Coefficient of Variation	Analysis of variance	
						F value≠	1% level of significance
First	3rd	1937	250	2.58 ± .81	31	4.18	1.88
do	4th	1938	250	3.23 ± .72	22	3.59	1.88
do	5th	1939	100	4.56 ± 1.00	22	1.77	2.59
do	4th⁄	1939	120	3.53 ± .310	9	2.99	2.40
Second	2nd	1936	190	5.40 ± .97	17	4.38	2.28
do	3rd	1937	250	6.8 ± 1.36	20	9.04	1.88
do	4th	1938	330	5.78 ± .86	15	2.80	1.77

≠ Obtained by dividing variance between lines by variance within lines.

⁄ Selection from second season of growth, third generation (1937 nursery).

for the third generation plants substantiates the hypothesis
of heritable differences between plants and would indicate
that progeny of a single plant tend to be more like one
another than like the entire population. Continued selec-
tion, however, has eliminated much of this variation so that
the progeny rows in their fifth generation are not signifi-
cantly different. This agrees closely with the data obtained
on leaf area, number of culms, and plant height presented
in Tables 5, 14, and 18, respectively. It is probable
that further selection in open-pollinated lines will re-
sult in little increase in basal diameter.

The Effect of Inbreeding on Basal Diameter

Inbreeding has reduced the basal spread of the plants
in S_1 and S_2 as is shown by Table 22. It will be noted
that the S_2 plants have suffered less degeneration following
inbreeding than S_1 plants. Also, there is a strong tendency
for the second season inbreds to spread more vigorously than
those in their first season of growth. It was observed in
the nursery that those inbreds which were reduced the most
in leaf area and number of culms tended to produce more
rhizomes than the inbreds that were reduced least in vigor.
This may have been due to the fact that the new shoots on
the greatly reduced plants were subject to less competition

for light, moisture, and soil minerals by the old top
growth.

Table 22.   General effect of inbreeding on basal diameter
             of A. furcatus.

Genera- tions inbred	Percent reduction of inbred lines compared to open-pollinated sibs		
	1938 nursery		1939 nursery
	1st season	2nd season	1st season
S_1	30.96	11.09	30.05
S_2	23.22	5.37	28.73

Table 23 shows the effects of various generations of
inbreeding on basal diameter.   The S_2 plants are not signi-
ficantly smaller than their open-pollinated progeny nor are
they as large as the fifth generation open-pollinated selec-
tion.   Furthermore, there is no significant differences be-
tween the means of the open-pollinated group and the S_1 or
S_2 groups in their second season of growth.   Thus, for basal
diameter there is little evidence of the "hybrid vigor" that
was manifest by the leaf area, number of culms, and height
measurements.   The inbreds are somewhat more variable than
their open-pollinated sibs indicating that considerable
segregation has followed inbreeding.

As the investigation has progressed there has been less
importance attached to basal diameter as a measure of the
plant's reaction to selection and inbreeding.   In the first

Table 23. The effect of various generations of inbreeding and open-pollination on basal diameter of <u>A</u>. <u>furcatus</u>.

Season of Growth	Generation	Nursery	Previous treatment	No. of Plants	Mean and Standard Deviation	Coefficient of Variation	Analysis of variance	
							F value≠	1% level of Significance
First	4th	1938	Open-pollinated	250	3.23 ± .72	22	3.59	1.88
do	do	do	Inbred 1937	350	2.23 ± .84	37	2.38	1.61
do	do	do	Inbred 1936-37	250	2.48 ± .81	32	2.04	1.88
do	5th	1939	Open-pollinated	100	4.56 ± 1.00	22	1.77	2.59
do	do	do	Inbred 1936-37 Open in 1938	120	4.35 ± .98	22	4.02	2.18
do	do	do	Inbred 1938	90	3.19 ± .80	25	2.39	2.91
do	do	do	Inbred 1937-38	130	3.25 ± .27	8	8.83	2.23
Second	4th	1938	Open-pollinated	330	5.78 ± .86	15	2.80	1.77
do	do	do	Inbred 1937	250	5.14 ± 1.37	26	5.90	1.88
do	do	do	Inbred 1936-37	330	5.47 ± 1.49	26	3.48	1.77

≠ Obtained by dividing variance between lines by variance within lines.

place an accurate measure of basal spread is difficult to
obtain because the plant clumps are not uniformly round.
Thus, the measured diameter may not be proportional to the
actual area occupied by the plant. The difference in size
of any two plants is likely to be quite small and could very
easily be due to edaphic factors or to error in measuring
as well as to hereditary differences. As will be shown
later, there is a close relationship between number of culms
and basal diameter and since number of culms has proven
quite reliable as a measure of the plants from a breeding
standpoint, it is felt by the writer that it should be used
in preference to basal diameter.

The Effect of Selection on Time of Maturity

Aldous (4) has shown that the bluestem grasses are
very nutritious in their leafy stages of growth but as the
plants mature and become stemmy they are greatly reduced
both in nutritive value and in palatability. He found the
calcium content decreased from 0.55 percent in the immature
stages to 0.33 percent in the mature plants. Similarly the
phosphorus content varied from 0.30 percent to 0.10 percent
in the same plants. Evans (20) reported that later maturing
Phleum pratensis plants had a higher protein content and
maintained their green color longer than earlier maturing

varieties. Thus, time of maturity is an important factor
in determining the forage value of a particular strain.

In the Flint Hills area plants of A. furcatus begin to
flower about the first of July and continue until frost.
As was shown above, they lose much of their forage value as
soon as the flowering culms appear. Theoretically, by selec-
tion of the late maturing plants it should be possible to
obtain lines that would be correspondingly later in produc-
ing flowering culms. Such lines would yield more seed since
the later maturing plants would escape most of the hot winds
that are so common during late July and August in the area
where A. furcatus is important. The increase length of
the growing season of such a strain should make possible the
production of greater total yields of forage.

The date of appearance of the fifth culm bearing an in-
florescence was arbitrarily chosen to represent the time of
maturity of each plant. This made possible a direct com-
parison of the various generations since all plants were put
on the same basis. By the time the fifth inflorescence ap-
peared the plants were usually quite stemmy and had lost
much of their forage value.

The results of continued selection of the late maturing
plants are shown in Table 24. Detailed data were not ob-
tained in 1935 and 1936 on the first year material. However,

Table 24. The effect of selection on the date of maturity of <u>A. furcatus</u>.

Season of Growth	Generation	Nursery	No. of Plants	Mean and Standard Deviation	Range (Days)	Analysis of variance	
						F value≠	1% level of significance
First	3rd	1937	190	Aug. 28 ± 9.0	58		
do	4th	1938	250	Sept. 7 ± 9.0	55	3.73	1.86
do	5th	1939	230	Sept. 1 ± 4.0	30	3.25	1.89
do	4th⌁	1939	139	Sept. 5 ± 7.0	30	1.21	2.39
Second	1st	1935	195	Aug. 11 ± 10.0	71	--	--
do	2nd	1936	171	Aug. 17 ± 9.0	62	5.08	2.31
do	3rd	1937	250	Aug. 12 ± 10.0	55	3.27	1.88
do	4th	1938	330	Aug. 13 ± 9.0	58	3.80	1.77

≠ Obtained by dividing variance between strains by variance within strains.

⌁ Selections from second year growth, third generation (1937 nursery).

observational notes in 1935 showed that the plants had
started to head by July 3 and by August 5 nearly all of the
198 plants in the 1935 nursery had produced heads. At the
end of five generations of selection of the late maturing
plants (Table 24) the mean heading date was September 1 for
the plants in their first season of growth. Thus, there
was an apparent change toward a later heading date of nearly
a month in the first season material, although the type of
data obtained in 1935 make definite conclusions impossible.
However, data on the plants in their second season of growth
(Table 24) indicate there has been no significant change in
the mean heading date for the established two-year-old
plants, In other words, continued selection of the later
plants in open-pollinated lines has not significantly
changed the mean date of maturity of the established plants.
There was a significant decrease in the range of days over
which the plants matured, brought about, for the most part,
by the elimination of the extremely early and extremely late
lines. Further than that there has been no measurable
change in time of maturity of A. furcatus following selec-
tion of the late maturing plants. This is not in agreement
with the preliminary work of Anderson and Aldous (6) on A.
scoparius and Cornelius (15) on A. furcatus. These writers
tentatively concluded that is should be possible to change

the time of maturity by continued selection in open-pollinated lines. There conclusions, however, were based on a comparison of the time of maturity of one-year-old plants to that of two-year-old plants. It has been shown in the present investigation (Table 24) that such a comparison is not accurate since the younger plants are consistently later maturing. Sufficient data are not available to explain the failure to obtain later maturing lines by election of open-pollinated plants but there are certain indications that will be discussed below.

Evans (19), after extensive experiments with Phleum pratensis concluded that the time of heading, blooming and maturing of this species is determined largely by temperature and length of day reactions and that in any locality some F. pratensis plants mature earlier than others because they are adapted to shorter days. He was able, by open-pollinated selection, to obtain both early and late varieties of this species.

It is quite possible that the same two factors, i.e., temperature and length of day, condition to a large extent the time of maturity responses of A. furcatus. This assumption is substantiated by the fact that many of the seedlings started in the greenhouse in late February produced normal appearing inflorescences during April and May when the days

are equal in length to those of the normal heading period in
August and September. Apparently these seedlings are re-
sponsive to a very definite photoperiod which initiates the
chemical and physiological changes necessary to bring about
heading. There is little resson to believe that the mature
plants are not subject to similar photoperiodic responses
so that plants in a single ecotype would tend to exhibit
nearly the same variation in time of heading in successive
generations. There should be definite modificatory effects
from such factors as temperature, moisture, root development
and soil differences that might cause individual plants to
vary from the mean but such variations would not be heredi-
tary. On the other hand, it has been observed that it takes
from 20 to 35 days on an average for a plant to complete the
flowering process so that there would be ample opportunity
for pollen from the later flowers on an early plant to fer-
tilize the earlier flowers on a late plant. The progeny
from such a cross would be quite variable in time of maturity.
The inbred progeny of such plants should show segregation
into definite maturity groups, but, as will be discussed
later, the inbred lines have shown less segregation in this
character than the open-pollinated sibs.

Table 25 shows the data obtained on progeny rows grown
from parent plants that varied in time of maturity from

July 21 to September 5. While the progeny from the early
plants tend to be somewhat earlier than the progeny from
late plants there is no consistent relationship in the data.

Table 25. The behavior of various progeny rows in regard
to time of maturity.

Parent Plant No.	Time of maturity		
	Parents*	Progeny row (10 plants)**	
		Mean	Range
1	7-21	8-8	41 days
2	7-28	8-10	35 "
3	7-30	8-1	34 "
4	8-5	8-7	20 "
5	8-5	8-9	14 "
6	8-8	8-12	34 "
7	8-8	8-13	27 "
8	8-12	8-25	24 "
9	8-17	8-12	29 "
10	8-19	8-7	27 "
11	8-19	8-19	20 "
12	8-24	8-18	37 "
13	8-26	8-8	21 "
14	8-27	8-18	30 "
15	8-29	8-18	21 "
16	8-31	8-22	17 "
17	9-5	8-25	9 "

* 1937 nursery, 1938 notes.
** 1938 nursery, 1939 notes.

It appears that the progeny from the early maturing plants
have approximately the same average data of maturity and ex-
hibit about the same amount of variability as the progeny
from the late maturing plants. However, there are signifi-
cant differences in time of maturity between progeny groups

as an examination of the F values in Table 24 will show.
This means there is greater variation in time of maturity
between lines than between plants within a line. Also,
highly significant interannular correlations have been found
for date of maturity (1935 nursery r = .657 ± .041, 1938
nursery r = .401 ± .063; one percent level of significance
= .267 and .143, respectively). In other words, plants ma-
turing early in their first season of growth tend to mature
relatively early in their second growing season.

The data regarding time of maturity of big bluestem
plants from Nebraska, Kansas, and Oklahoma grown in the Man-
hattan, Kansas nursery and presented in Table 3 indicate
that this species has very definite temperature and length
of day reactions. The plants from Nebraska headed first
because their required temperatures and length of day
occurred earlier in the season at the Manhattan nursery.
This agrees closely with the work of Evans (19) on timothy.
He found that selections of this grass varying in time of
maturity headed in different latitudes when the length of
day and aily temperature exceeded the minimum required by
that selection. Although open-pollinated selection has not
significantly changed the time of maturity of A. furcatus
it should be possible to isolate late maturing plants and
by progeny studies obtain a relatively true breeding, late

maturing strain. Such a program probably would involve the
isolation of these late maturing plants into a block so
that they could intercross freely with no danger of contam-
ination by pollen from the late flowers that appear on early
maturing plants. While studies of the inbred population do
not substantiate this, it is possible that the extreme lack
of vigor exhibited by many of the inbreds may tend to ob-
scure any trends that might otherwise be manifest.

The Effect of Inbreeding on Time of Maturity

Inbreeding has affected the time of maturity of $\underline{A}$.
$\underline{furcatus}$ only in so much as it reduced the vigor of certain
plants to the point that they were unable to produce heads.
That is, the inbred plants which were vigorous enough to
flower did so at the same time as the open-pollinated plants.
The data in Table 26 show there were no significant dif-
ferences between the open-pollinated plants and their inbred
sibs in regard to date of heading. In fact, in the second
year data both groups had the same mean heading date.
Neither is there any indication of marked segregation in
the inbreds regarding time of maturity. That is, the dif-
ference between lines shown by the F values in Table 26 are
no greater for the inbreds than for the open-pollinated
progeny groups. Had there been definite segregation, as

Table 26. Effect of various generations of inbreeding and open-pollination on time of maturing, A. furcatus.

Season of Growth	Generation	Nursery	Previous treatment	No. of Plants	Mean and Standard Deviation	Range	Analysis of variance	
							F value≠	1% level of significance
First	4th	1938	Open-pollinated	250	Sept. 7 ± 9	55	3.37	1.88
do	do	do	Inbred 1936 & 1937	180	Sept. 14 ± 9	46	2.67	2.00
do	5th	1939	Open-pollinated	230	Sept. 1 ± 4	30	3.25	1.89
do	do	do	Inbred 1937 & 1938	146	Sept. 5 ± 6	30	3.18	2.19
Second	4th	1938	Open-pollinated	330	Aug. 13 ± 9	58	3.80	1.77
do	do	do	Inbred 1936 & 1937	320	Aug. 13 ± 10	58	2.47	1.79

≠ Obtained by dividing variance between lines by that within lines.

was found in the character leaf area (Table 11) the F values for the inbreds would have been somewhat large.

Approximately 850 of the 1875 inbred plants in the 1938 nursery or about 45 percent failed to head at all in their first season of growth. This was due apparently to the extremely weak condition of many of the plants. Three hundred forty-three plants, or 18 percent, failed to survive the winter season for the same reason since no winterkilling was observed in the open-pollinated lines. In the second season of growth 151 inbred plants failed to develop flowering culms. A similar condition was observed in the S_1 plants of the 1939 nursery where nearly 55 percent of the inbreds failed to produce heads because of their extreme lack of vigor.

Thus, while many of the inbred plants did not head, the remainder flowered at about the same time as their open-pollinated sibs. This substantiates the observation the inbreeding had no effect on time of maturity except indirectly through the greatly reduced vigor of many of the inbreds. As was metioned above, there has been no measureable seqregation in the inbreds. Apparently, then, time of maturity in A. furcatus is conditioned largely by some external factor or factors such as length of day and temperature. However, additional data will have to be obtained before

any definite conclusions can be reached regarding the ef-
fect of selection and inbreeding on time of maturity in
this species.

Seed Production

Important characters to consider in the improvement of
any pasture grass are its seed setting capacity and its
flowering habits. Facts relative to these two characters
are necessary since upon this information depends the method
of strain building employed. This is especially true of _A.
furcatus_ which cannot spread vigorously by means of
rhizomes or stolons but must depend largely upon seed for
its propagation. _A. furcatus_ is, in nature, quite variable
in its seeding habits. It is a general characteristic of
the perennial forage plants to be relatively poor seed pro-
ducers. _A. furcatus_ is no exception although with favorable
climatic conditions it will produce an abundant seed crop.
In unfavorable years when it is heavily grazed it often
fails to develop heads. However, there is no basis for the
popular belief that the bluestem grasses seed only once in
seven years since plants in the nursery at Manhattan have
been known to produce seed each year for at least five
years.

The hot, dry winds so common in late summer and early

fall have a very detrimental effect on seed production.
This was clearly evident from the appearance in the nursery
of many blasted heads during this period. It was noted also
that very little pollen was produced and that most of the
flowers remained closed during hot, dry days of the flowering
season but whenever a short period of relatively cool, damp
weather occurred an abundance of pollen was released and
large numbers of receptive stigmas were extruded. Thus,
climatic conditions evidently play an important part in af-
fecting seed production.

In 1935 and 1936 data were obtained on seed production
by determining the number of caryopses per plant. This was
done by removing the glumes with a rubber mat, hand-operated
thresher. Five hundred caryopses were counted and weighed
and the total number obtained from the ratio of the weight
of 500 caryopses to the total weight. While this system
showed differences between plants, it was not exact enough
to permit detailed comparisons nor did it show the percent-
age of florets that were filled. Consequently, in 1937 a
more detailed system was adopted to determine the relative
seed production of the various plants. The open-pollinated
and inbred seed were harvested in separate bags and taken
into the laboratory. During the winter months the percent-
age of fertile spikelets that produced seed was determined

by counting the number of caryopses in three random samples
of 100 spikelets each and averaging these three counts.
Such a procedure has been quite satisfactory from the stand-
point of determining the exact seed set of potential parent
plants. In addition to the caryopses obtained in this manner
have been used for germination tests. Progeny for each suc-
cessive nursery usually were obtained from plants that
proved superior in seed set and in germination although in
a few cases plants having excellent forage qualities were
selected for continuation in spite of being low seed pro-
ducers. Such plants will be blended into a strain with
plants that are good seeders and progeny of this strain will
be selected with the view of maintaining a high seed set as
well as retaining the superior forage qualities of the bet-
ter plants.

Table 27 shows the average seed set for the various
treatments since 1937 in both open-pollinated and inbred
selections. Considering only the open-pollinated data, it
can be seen that there is much variability in seed set, both
intra- and inter-seasonal in nature. The greatly reduced
seed set of the 1938 nursery can be directly attributed to
the extremely unfavorable weather conditions encountered in
the fall of 1938. Very little seed was produced until after
the first of September because of the hot winds and

Table 27. Percent of spikelets filled in <u>A</u>. <u>furcatus</u> (1937-1939, inc.).

Year Seed Obtained	Treatment	Number of caryopses per 100 spikelets (Ave. of 300)				Average
		Open-pol-linated	Inbred 1936*	Inbred 1937	Inbred 1936-37	
1937	(Open-pollinated	45.9 ± 20.7	50.59 ± 21.07			48.25
	(Inbred	7.03± 7.37	8.76 ± 10.07			7.89
1938	(Open-pollinated	17.56± 9.71	15.63 ± 9.33	13.3 ± 9.42	9.95 ± 8.65	14.11
	(Inbred	1.11± 1.62	.33 ± .61	1.93 ± 3.18	2.7 ± 3.32	1.51
1939≠	(Open-pollinated	37.40± 14.52	37.30 ± 13.56	25.10 ± 17.82	20.10 ± 15.07	30.2
	(Inbred	7.40± 6.20	10.60 ± 9.20	4.50 ± 6.43	3.40 ± 3.18	6.47

* Heads enclosed in cheesecloth bags which were not pollen proof.

≠ Selections from plants in their second season of growth (1938 nursery).

usually dry weather of July and August. Somewhat higher
seed set was obtained in 1939 as there was a short period
during the latter part of August when conditions were quite
favorable to pollination.

The important point, however, is the extent of varia-
bility between plants in any one year. For instance, in
1939, seed set in the open-pollinated plants ranged from
0 to 84 percent of the spikelets filled. The later plants
matured more seed as a rule, since most of the heads that
appeared early in the season were blasted. However, it has
not been possible to obtain significant, positive correla-
tions between seed set and time of maturity because of the
appearance of early segregates that were able to produce a
large amount of seed. This high seed production may have
been the result of climatic conditions favorable to fertil-
ization early in the season or they may be from rather late
appearing heads on these early plants. While some of this
variability no doubt is due to environment, a considerable
portion of it must be genetic in nature since the plants
were grown under rather uniform conditions. Furthermore,
it is quite evident that the most desirable plants from a
forage standpoint are not the highest seed producers. This
is shown by a comparison of the seed set of two lines, one
selected for leafiness, quality, uniformity, and total

forage production, and the other selected for height, vigor, and coarseness with no attempt to obtain quality. The former line gave an average seed set in 1939 of 31±8.06 compared to 52 ± 11.01 for the coarse non-leafy strain. It may be necessary to sacrifice somewhat in seed production to obtain a highly superior forage strain. On the other hand, it should be possible to obtain a strain high in both seed set and forage value by carefully testing and blending the tested parental types into a composite strain.

Further evidence that seed set is controlled genetically may be obtained from abnormalities that have appeared in the various generations. Viable seeds were found in the pedicellate and normally staminate spikelets of six of the original parent plants of the 1935 nursery. This character has appeared in subsequent generations in the progeny of these six plants. The fact that pedicellate seeds have been found in a few plants of families other than those from the original six plants indicates that this character has been carried as a genic factor in the pollen. A second abnormality has appeared in the form of twin seeds produced by an S_2 plant in the 1938 nursery (Plate X). The seeds range in morphology from two complete endosperms held together at the germ end by the partial fusion of the pericarp tissue, to one endosperm with two embryos embedded in it. The seeds

are viable and germinate readily. Sixty twin plant progeny
were grown in 1939, 14 of them producing twin seeds in
open-pollinated heads. Of these 14 plants three have pro-
duced twin seeds in the inbred heads. Although chromosome
counts have not been obtained on these plants, only two of
the 60 twin plants show morphological evidence of being
haploids. While the embryology of this character has not
been determined, its expression may be controlled by several
recessive genetic factors or possibly one factor with modi-
fiers. Such a conclusion seems reasonable on the face of
the evidence now available since the character has appeared
in only a few of the progeny and since it exhibits such a
variety of forms. Second generation inbreds have been found
that contain this character. After further purifica-
tion they will be crossed with plants having normal seeds
in an effort to determine the mode of inheritance.

Inbreeding in A. furcatus has resulted in a marked and
progressive decline in seed set (Table 27). Reductions of
as much as 84 percent in seed set under the bags have been
observed in the first inbred generation while subsequent
generations show even greater reduction. In addition,
cross-fertility appears to be much less following inbreeding
since the second generation inbred plants (1939), when al-
lowed to cross-pollinate, set only 46 percent as much seed

as the open-pollinated lines in the same nursery. Whether this reduction in seed set is due to increased self-sterility following inbreeding or merely to the greatly reduced vigor of the inbreds cannot be determined from the available data although both may be contributing factors. That unfavorable conditions within the bag are of little importance in determining seed set is indicated by the wide variation in seed set of the bagged plants. Furthermore, various writers, among them Nilsson (50), Beddows (7), and Jenkin (33), have shown that self-fertilized species give almost complete seed set when bagged if reasonable precautions against mechanical injury are taken. Observations in the Manhattan, Kansas nursery have shown that temperatures within the bag average less than one degree higher than outside temperatures and pollen taken from within the bags at various times and observed under the microscope appeared to be quite normal.

Kirk (43), studying the effects of continued inbreeding on various crops, found progressive reductions in self-fertility in alfalfa and brome grass and concluded that selfed-line breeding in these two crops was not feasible. Valle (73) concluded that selfing in timothy could lead to no practical results since he was unable to obtain any self-fertile lines. Jenkin (31) studied self-fertility in 50

plants of timothy and found 43 of these of very low fertil-
ity. On the other hand, a few plants were highly self-fer-
tile and gave vigorous progeny following inbreeding. Wolfe
and Kipps (84), working with orchard grass, enclosed whole
plants in cotton bags, sing heads in paper bags, and several
heads in paper bags. The seed set in all three methods was
low, averaging from four to fifteen percent as compared
to forty-five percent in open-pollinated heads.

In the present investigation it was found that 33 per-
cent of the plants bagged failed to produce seed while the
remaining 67 percent ranged in seed set per plant from one
percent to forty-two percent. To determine if inbred plants
that failed to set seed during their first growing season
they were selected or if they were at variance to the gener-
al behavior of the line, three plants from each selected
progeny row were bagged the following year and the percent-
age of spikelets containing seeds in each plant was deter-
mined. Of the fifteen progeny lines studied in the above
manner, eleven showed differences between the three plants
of less than one percent in seed set. Furthermore, none of
the eleven lines gave more than two percent seed set for any
one plant. The remaining four lines showed considerable
segregation ranging in seed set from six to thirteen percent

Thus there has been considerable uniformity in the response
to inbreeding manifest by the progeny of a single plant in-
dicating the ability of a given plant to impart in its off-
spring definite seeding characteristics. While the bulk of
the population apparently has been highly self-sterile, a
few plants have appeared that give promise of considerable
self-fertility. From these plants and from sib matings in
the self-sterile progeny groups, inbred lines will be de-
veloped that may be used in various recombinations to test
for hybrid vigor.

Germination and Time of Emergence

From the standpoint of establishing stand of A.
furcatus both percent germination and time of emergence are
important. A rapid rate of emergence is especially desir-
able since in the area where big bluestem is adapted the
soils are relatively dry and drought, especially in the sur-
face soils, is always eminent. Furthermore, big bluestem
seedlings are rather weak in comparison to many of the
weeds and other grasses with which they must compete for
moisture so that the ability to germinate quickly and estab-
lish a root system in contact with deeper soil moisture
would enable the grass seedlings to better survive such com-
petition.

A summary of the germination percentages obtained since
1937 is shown in Table 28. Seed from the 1936 nursery was
germinated in the laboratory on moist filter paper but each
year since that time it has been germinated on soil to sim-
ulate more nearly conditions that exist in nature. The first
two generations were planted early in January. Follow-
ing emergence of the seedlings much injury was encountered
from damping-off, in many cases replanting was necessary to
obtain a sufficient number of plants for the field nursery.
In addition, seedlings started so early became quite large
before they could be set out in the nursery. Consequently,
they were subject to considerable root injury while being
transplanted. It was found that by starting the seedlings
as late as the last of February the losses from damping-off
are practically eliminated and the seedlings did not become
so large as to be seriously injured by transplanting to the
field nursery.

In Table 28 it can be seen that there were no signifi-
cant differences between the germination of open-pollinated
and inbred seed. In 1939 the inbred seed showed slightly
higher germination percentages than the open-pollinated sibs
but in no case were the differences significant. Neither has
there been any significant differences in the range of
germination in the open and inbred sibs, both showing a

Table 28. Showing the percent germination of A. furcatus following various treatments.

Nur-sery	Year*	Treatment	Percent germination for each generation of inbreeding			
			Open	Inbred, 1936	Inbred, 1937	Inbred, 1936-37
1936	1937	Open	28 ± 15.05			
		Inbred	26 ± 15.35			
1937	1938	Open	50 ± 19.66	37.5 ± 18.40		
		Inbred	47 ± 20.85	4.0 ± 23.60		
1938	1939	Open	39 ± 21.66	40 ± 22.83	38 ± 25.92	33 ± 19.99
		Inbred	58 ± 21.43	42 ± 24.25	49 ± 17.85	44 ± 19.48
1938	1940≠	Open	41 ± 16.01	43 ± 14.41	64 ± 8.12≠	54 ± 9.11≠
		Inbred	42 ± 21.20	42 ± 17.17	66 ± 29.73≠	46 ± 12.80≠

* Year in which test was made.
≠ Second year growth selections.
≠ Figures based on only 5 plants so they are not comparable to other figures in the table.

spread of three to eighty-two percent in the 1938 nursery,
a spread that is typical of the other generations as well.
Furthermore, there has been no difference in time of emer-
gence of the seedlings from inbred and open-pollinated
material although there has been a range between individual
plants of four to twenty-three days in time of emergence.
For the first three or four weeks of growth the inbreds ap-
pear as vigorous as the open-pollinated seedlings but after
a short period they begin to exhibit the characteristic lack
of vigor of most of the inbred lines. The fact that there
has been no appreciable effect on germination or on the size
of the seeds of the bagged heads would indicate that there
has been little detrimental effect on the seed due to any
abnormal conditions within the bags.

Nilsson (50), studying fertility in timothy and orchard
grass, found that germination after isolation was not signi-
ficantly different from germination after free flowering
although variance was somewhat greater in the open-pol-
linated material. He obtained highly significant correla-
tions between germination of isolated and non-isolated seed
from the same mother plant. A highly significant correla-
tion of .336 ± .0118 was found between germination percent-
ages of open-pollinated and inbred sibs of A. furcatus in
the 1938 nursery, 1939 seed crop. However, there was no

significant relationship between seed set and germination
nor could any correlation be found between germination and
time of maturity. Williams (82) concluded that inbreeding
had no direct effect on the size and quality of the seed of
red clover although Kirk (43) found progressive decreases in
self-fertility following inbreeding of brome grass and
alfalfa as well as decreased viability and seed set of the
inbreds. Wolfe and Kipps (84) showed that the germination
percentages of open and selfed lines of orchard grass were
essentially the same. They found, however, that inbreeding
significantly reduced the size of the seed after one genera-
tion of inbreeding and concluded that this was due to the
reduced vigor of the inbred plants.

As would be expected when a cross-fertilized species
is inbred many chlorophyll deficient seedlings have appeared
following inbreeding A. furcatus. Most common, perhaps,
and one that has always proven lethal, are the albino seed-
lings that are white or white tinged with purple, depending
upon the presence or absence of anthocyanin. These plants
have never survived beyond the second leaf stage.

A second type of chlorophyll deficient that has been
quite common is the true virescent seedling. Many of these
can be distinguished from the lethal albino only by the fact
that they are able to develop chlorophyll in the second and

third seedling leaves and thus are able to survive. There
have been several degrees of virescence observed in the
greenhouse ranging from the almost pure white types to those
that were only slightly lacking in chlorophyll upon emergence.
Many of these types failed to survive beyond the seedling
stage while others were able to develop into nearly
normal plants.

Sufficient numbers of these chlorophyll deficients have
not been studied to arrive at any definite conclusions as to
the mode of inheritance though they most certainly must be
carried in the gene population as recessive. Their fre-
quent appearance in the inbred progeny might lead to the
assumption that "inbreeding is a desirable method of freeing
the population from undesirable recessive character,"
Hayes and Barker (26), although it would seem that desirable
characters as well, might be lost. These chlorophyll de-
ficient seedlings have appeared in a few lines in their third
generation of inbreeding indicating that there are several
recessive factors affecting their expression.

Nilsson (50) classed these chlorophyll deficient types
as examples of diplontic sterility caused by absolute or
partial lethality in the diplophase. He found such types in
meadow fescue, orchard grass, and timothy. Clark (13) con-
cluded that white seedlings in inbred timothy were due to at

least three comlimentary recessive factors all of which must be present in a homozygous condition for the albinos to appear. Working with Lolium perenne, Jenkin (37) was able to obtain three types of chlorophyll deficient seedlings from selfing a normal green plant. He listed them as (1) yellow tipped albino, (2) non-surviving green, and (3) surviving green. From appropriate outcrosses and backcrosses he was able to show that at least two pair of factors were involved in the expression of these three types. Thus, there is considerable variation exhibited by the material in regard to germination percentages, time of emergence, appearance and condition of the seedlings. It should be possible to utilize these variations in the selection program to obtain strains that are superior in their ability to produce stands of vigorous, aggressive seedlings that compete more successfully with the weeds and weedy grasses.

Disease and Insect Resistance

There has been little serious injury to A. furcatus during this investigation from disease and insect attacks. Grasshoppers have caused some injury to individual plants by chewing through the rolled flag leaf protecting the young head. Chinch bugs have been observed harboring in the plants but no damage could be attributed to them.

Several different kinds of smut have been observed on
this species but the injury resulting from them is negligi-
ble. Dr. C. L. Lefebvre[3] has identified the following
species for the author:

1. Sorosporium everhartii on A. furcatus
2. Sorosporium provinciale on A. furcattue
3. Sphacelotheca andropogonis on A. furcatus

In addition to these three, Cornelius (15) reports the oc-
currence of Sphacelotheca occidentalis on A. furcatus and
A. hallii. He states that, in general, there is less than
one percent of the florets affected by these various smuts.
Although little damage has resulted from these smuts to
date, this susceptibility should be kept in mind in the
breeding of superior strains so that any resistant lines can
be utilized.

Considerable damage in the nursery has resulted from
occasional epidemics of leaf rust (Puccinia andropogonis).
This fungus spreads very rapidly after becoming established.
Its principal effect is to cause drying and shriveling of
the leaves, thus greatly reducing both yield and palatiability
of the affected plants. An unusually uniform infection
was encountered during the growing season of 1939 so there
was ample opportunity to check the response of various lines
to this disease. The plants were rated on a scale of one to

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[3] Personal correspondence

seven, those in the first class being entirely free from
rust pustules, while those in the seventh class were so com-
pletely rusted as to prohibit production of seed.

The first pustules were observed on the leaves about
June 5, 1939 after which they increased rapidly so that by
July 12 they had spread through the entire nursery. Two
readings were obtained, the first July 18 and the second
September 9. Analysis of variance for differences between
lines compared to differences within lines shows a highly
significant variation between different lines in the open-
pollinated selections (F value = 5.17, one percent level of
significance = 1.77). Means of ten-plant lines ranged from
1.9 to 5.3. This would indicate that some lines carry re-
sistance to this rust organism. The inbreds were quite
similar to the open-pollinated lines in regard to rust re-
action. They showed comparable significant differences be-
tween lines (F value = 5.17, one percent level = 1.55) with
a range of 1.9 to 5.3 between the means of ten-plant progeny
groups. The distinct differences between lines in both the
open-pollinated and inbred material indicate that there are
definite factors conditioning the reaction of a given plant
to leaf rust. The progeny from rust-free plants of the 1937
nursery showed a class mean of 2.6 compared to a mean of
3.18 for the entire nursery and 4.7 for the progeny other

than those from rust-free parents. Thus, there is consider-
able evidence for the inheritance of rust resistance.

Clark (13) found resistance and susceptibility of
timothy to leaf rust conditioned by one factor with possible
modifiers. While no conclusions can be drawn concerning the
mode of inheritance of resistance or susceptibility in _A._
furcatus, this inheritance probably is not linked with major
growth factors since no difference could be observed between
the open-pollinated and inbred groups in regard to amount of
infection. Resistance in the plants to the rust organism
is exhibited in various manners. There are differences in
the total numbers of sori per given leaf area. In some
cases only the lower leaves of the plant would become badly
infected while the leaves at the top of the plant would have
but few scattered pustules of the rust. On some plants the
pustules were large and vigorous but on others they were
small, poorly developed, and often failed to break the sur-
face of the leaf. A more detailed investigation will be
necessary to determine the exact behavior of the organism
as well as the nature of the resistance mechanisms involved.
Meanwhile, careful selection appears to offer the first approach
toward resistant lines.

Interrelationships of Characers

Variation in a group of plants is in itself of little significance. However, the manner of variation, i.e., the degree of association of different variates, the response of the age of the plant on these relationships, is extremely important from the standpoint of breeding superior strains.

Considerable evidence has been obtained relative to the correlations existing between the various characters studied in A. furcatus. Anderson and Aldous (6) investigating the breeding behavior of A. scoparius, found highly significant correlations between certain characters such as leaf area, number of culms, and plant height. Cornelius (15), studying variability is A. furcatus, reported highly significant correlations between the characters he observed. Brown (8) concluded that variation in Poa pratensis was not random but that there was a strong tendency for morphological characters to remain together in groups. He found significant correlations between leaf width and number of florets per plant as well as between leaf width and number of rhizomes.

For convenience in discussion, the correlations in A. Furcatus were divided into two groups. Group 1, the inter-annular correlation shown in Table 29, evaluate the

Table 29. Interannular correlations in A. furcatus.

Genera-tion	Nur-sery	Years data were obtained	Factor	Correlation coefficient*	1 % level of significance≠
Fourth	1938	1938-1939	Leaf area	.379 ± .041	.163
First	1935	1935-1936	Number of culms	.345 ± .045	.181
Fourth	1938	1938-1939	Number of culms	.671 ± .037	.163
First	1935	1935-1936	Maximum height	.495 ± .077	.267
Fourth	1938	1938-1939	Maximum height	.413 ± .039	.163
Fourth	1938	1938-1939	Basal diameter	.487 ± .051	.163
First	1935	1935-1936	Time of maturity	.657 ± .041	.267
Fourth	1938	1938-1939	Time of maturity	.401 ± .063	.181

* From correlation chart devised by Dr. G. A. Wiebe, Div. of Cereal Crops and Diseases, Bur. of Plant Indistry, U. S. D. A.
≠ From Snedecar (58)(Table 7.2).

tendency for plants that are large in a given character one
year to be large in this character the following year, and
the tendency for plants that are comparatively small in
their first season of growth to remain small during subse-
quent seasons. A high interannular correlation should be
obtained for any given character if environmental and other
modifying factors are kept constant since any plant will
have the same genetic complex during its entire life.
Theoretically, then, any departure from a high correlation
would indicate the degree of variability in such factors as
climate, soil, competitional effects, developmental varia-
tion in the plant itself, and differential responses of the
plant to these environmental factors at various stages in
the growth cycle. While the correlation coefficients in
Table 27 are all highly significant, the fact that most of
them are rather low in value indicates there is consider-
able seasonal variation in the material. Obviously, then,
the external factors play an important part in the develop-
ment of the plant. These highly significant interannular
correlations shoud lend credence to the selection of first-
year material as a means of improving the species, especial-
ly in an unselected and highly variable population. After
much of the hereditary variability has been eliminated by
selection it is possible that seasonal variation in the

first-year plants would completely mask any hereditary dif-
ferences and thereby make first-year selection unreliable.
Analysis of variance data supporting this point have already
been discussed (pages 48 and 61).

The second group of correlations measures the degree
in which two variates tend to be associated in value. Thus,
two variates that are closely correlated in a group of
plants may be controlled by similar genetic factors or by
different genetic factors that react similarly in a given
environment. Selection, environmental factors, and the age
of the plant probably have affected these correlations but
sufficient data have not been obtained to determine the
exact influence of each of these factors. However, there is
evidence to indicate that selection has played a major role
in affecting these relationships. A summary of the correla-
tions obtained in this study is shown in Table 30 and dis-
cussed below.

It will be seen that total leaf area has been signific-
antly correlated to number of culms, in fact, these two
factors were correlated more closely than any of the other
characters observed. This is important from a practical
standpoint as it should be possible to use the factor, num-
ber of culms, as a substitute for the measured leaf area
and thus greatly reduce the time and expense required to

Table 30. The correlation of various factors in _A. furcatus_ (open-pollinated).

	Nursery	Year of data	Number of culms	Maximum height	Time of Maturity	Basal Diameter
	(1935	1935		.288 ± .065		
	(1937	1937	.766 ± .028	.405 ± .049	.034 ± .005	
Leaf area	(do	1938	.778 ± .018	.352 ± .040	.236 ± .024	
	(1938	1938	.662 ± .036	.307 ± .037	-.211 ± .037	
	(do	1939	.673 ± .030	.405 ± .046	.101 ± .054*	
	(1939	1939	.695 ± .052	.257 ± .093	-.108 ± .061*	
	(1935	1935	.496 ± .054			
	(1937	1938	.017 ± .033*		-.279 ± .049	
Plant Height	(1938	1938	-.036 ± .055*			
	(1938	1939	.113 ± .017*		-.167 ± .057*	
	(1939	1939	-.117 ± .099*			
	(1937	1938				.331 ± .041
No. culms	(1938	1938				.486 ± .048
	(1938	1939				.408 ± .040
	(1939	1939				.478 ± .069

* Not significant.

take notes on the plants and to analyze the data. As was
expected no trends were exhibted by the correlations since
both leaf area and number of culms were correspondingly h
changed by selection. To substantiate this data a correla-
tion of 0.809 ± .020 was found for leaf area and number of
culms in the second generation inbreds of the 1938 nursery
in their second season of growth. Such a correlation would
be expected since the expression of these two factors is so
closely related to the vigor of the plants.

In the second group of correlations shown in Table 30,
total leaf area and plant height, while still showing high-
ly significant correlations for each of the years, were not
as closely correlated as total leaf area and number of culms.
It would seem that the taller plants were the more leafy
but plant height, as used in this study, measured only
the height of the leaves held upright. It should be noted
also that the relationship of height and leaf area was
significantly increased n the 1937 nursery over the 1935
nursery by the elimination of the tall, sparsely-leaved in-
dividuals through selection. The relatively low correlation
coefficients in this group were due in a large part to a few
short, extremely leafy plants that were present in the pop-
ulation. The low correlation found in the 1939 nursery
could easily be caused by seasonal variation and the smaller

numbers involved, only 100 plants being included in this
data whereas 250 plants were measured in each of the other
years. Apparently plant height is a much less reliable
criterion of total leaf area or plant yield than is number
of culms. The second generation inbreds in the 1938 nursery
gave higher correlations between total leaf area and plant
height than was found in the open-pollinated lines, correla-
tions of 0.562 ± .046 and 0.734 ±.027 being obtained for the
1938 nursery in its first and second season of growth.
This increase in correlation value may have been due to the
fact that most of the low leafy plants mentioned above were
greatly reduced in leaf area but only slightly reduced in
height following inbreeding, thus, increasing the relation-
ship between these characters as compared to the corres-
ponding open-pollinated material.

Time of maturity and total leaf area were significantly
correlated in the selected population at the beginning of
the experiment. That is, the later plants tended to be
more leafy while the plants that matured early in the sea-
son were rather sparsely leaved. As the average leaf area
per plant became progressively greater in later generations
and as the sparsely-leaved individuals were eliminated by
the selection program, the correlation between time of
maturity and total leaf area decreased until by 1939 it had

become non-significant and negative. The fact that there was a small negative correlation the last year of selection indicates that leaf area was somewhat greater for the earlier plants although such slight differences could be entirely seasonal in nature and not due to any genetic change in the plants. No effect of inbreeding on the reationship of total leaf area to time of maturity could be observed. Correlations of -0.278 ± .018 and -0.192 ± .063 were obtained for these factors in the 1938 nursery in its first and second season of growth. These do not differ significantly from the corresponding correlations in the open-pollinated sibs (Table 30).

Maximum height and number of culms showed a highly significant correlation of 0.496 ± .054 in the unselected 1935 nursery. Following the elimination of the extremely tall types and the increase in number of culms by selection in the open-pollinated material, subsequent correlations for the 1937, 1938, and 1939 nurseries were not significant. Thus, after the extremely tall plants were eliminated, there was no longer any measurable tendency for the taller plants to have more culms. At the same time there was a strong tendency for the plants with larger leaf areas to have more culms and also for plants with larger leaf areas to be somewhat taller. While much of the variation in these

relationships may be due to external factors, it would appear that plant height in the selected material was more closely related to total leaf area than to number of culms. On the other hand, selection has increased the uniformity of both plant height and number of culms, while at the same time decreasing the former and increasing the latter, thereby minimizing any correlation that might exist between these two factors. A low but highly significant correlation of $0.308 \pm .033$ was found in the S_2 plants for number of culms and maximum height in the 1938 nursery. Apparently the taller plants tend to have more culms in the inbred material although it is in all probability merely an expression of vigor since the inbred plants are, in general, so greatly reduced in both of these characters.

Plant height and time of maturity have been negatively correlated both in 1938 and 1939. This is in accordance with what was observed in the nursery, i.e. the earlier plants tended to be somewhat taller than the later, more leafy plants. This is true in the inbred nursery as well ($r = -.271 \pm .021$ for 1938 S_2 plants).

Number of culms and basal diameter have shown highly significant, positive correlations during each of the generations studied. This would be expected since the individual plants form rather, dense bunches in the nursery and the

larger bunches could obviously contain more culms than the smaller bunches. Inbreeding did not affect this relationship appreciably since the 1938 nursery in its first and second year of gorwth showed correlations of 0.514 ± .047 and 0.468 ± .046, respectively. In both the open-pollinated and inbred populations the correlations are slightly though not significantly higher for the plants in their first season of growth. It would appear that there are considerable competitional effects in the older plants from shading and crowding that may reduce this relationship.

SUMMARY AND CONCLUSIONS

Andropogon furcatus is one of the most valuable native forage species in the tall grass area of the United States. It is important because of its wide distribution and adaptation, its perennial habit of growth, and its ability to produce large quantities of highly nutritious and palatable forage during the summer grazing season.

Investigation of the genetic behavior of this species was started in 1935. It was found to be extremely heterozygous in nature and to be divided into definite ecotypes which, in turn, were highly variable within themselves. This highly variable condition would be expected since the species is a decaploid of remote hybrid origin and is

highly cross-pollinated. That this variability is genetical-
ly controlled by genic interaction with the environment is
shown by the fact that highly significant variations have
been found between progeny groups of different plants. The
effects of selection and inbreeding on the variability of a
Manhattan, Kansas ecotype are discussed in this thesis.

When it is necessary that the plant mature normally
and produce seed, measured leaf area has been found to be
the best single criterion of total yield and quality of for-
age. Four generations of continued selection in open-
pollinated lines toward larger leaf areas has resulted in an
average leaf area in the first season of growth ten times
as great as that of the unselected material of the first
generation. At the same time there has been a significant
decrease in the general variability of the population. One
and two generations of inbreeding has resulted in decreases
in leaf area of 48 and 55 percent respectively for plants in
their second season of growth. Some lines are greatly re-
duced in vigor while others are not affected appreciably by
inbreeding. Distinct evidence of heterosis following free
pollination of inbred lines has been found. Data from
analysis of variance studies and from actual selections of
plants in their second season of growth indicate that such
plants are more reliable criterions of their true genetic

make-up than plants in their first season of growth. Thus,
while in relatively unselected material first-year selec-
tions may prove satisfactory for a few generations, it will
be necessary to resort to selection in second and third year
material to reach the ultimate degree of improvement by this
method.

It has been possible to increase significantly the
number of culms and basal diameter by open-pollinated selec-
tion. Here, as in leaf area, there is a tendency toward
uniformity within progeny groups and the general variability
of these two closely related characters has been reduced by
selection. Inbreeding has had a depressing effect on these
characters and studies indicate that both of them are def-
initely influenced by the genetic make-up of the plant.
However, basal diamether has been considered of minor impor-
tance because of the difficulty of obtaining accurate meas-
urements and because of the extremely small differences be-
tween plants.

Plant height is a heritable character and will admit
considerable change by selection in open-pollinated lines.
It has been the least variable of any of the characters
studied and it has shown the least reduction following in-
breeding. The only aim of the selection program regarding
plant height was the elimination of the extremely tall and

extremely short plants. This was accomplished by the third
generation of open-pollinated selection after which there
was no significant change in plant height.

Lateness of maturity has been considered an important
character for which to select. However, four generations
of open-pollinated selection toward later maturity within this
ecotype has not significantly changed the mean time of ma-
turity. The reasons for this are not clear from the avail-
able data. Inbreeding has not effected time of maturity ex-
cept in so much as it has reduced the vigor of some of the
plants to the point that they were unable to produce heads.
The plants that headed did so at the same time as their
open-pollinated sibs.

Seed production, as measured by the percentage of
spikelets containing caryopses, has shown much variability
and it is indicated that this variation is influenced by
the genetic constitution of the plant. Seed set is greatly
reduced following inbreeding and there are indications that
this reduction is due to genetic factors rather than any
abnormal conditions within the bags.

There has been no significant difference between the
germination percentage of open-pollinated and inbred seed of
A. furcatus nor has the time of emergence varied signi-
ficantly between the open-pollinated and inbred sibs.

There has been considerable interplant variation in these characters that is important from the standpoint of selection. Various types of chlorophyll deficient seedlings have appeared in the inbred material.

Disease and insect injury as a rule are not serious in this species although considerable injury to the foliage may result for leaf rust (Puccinia andropogonis). Preliminary studies indicate there are significant differences in the degree of resistance of various lines to infestation by this fungus.

Highly significant interannular correlations have been found for leaf area, number of culms, maximum height, basal diameter, and time of maturity indicating that there are definite factors which interact with the environment to determine the expression of these characters. The second group of correlations measure the relationship between two variates. Significant positive correlations of leaf area to number culms and plant height were found but leaf area and time of maturity exhibited no definite relationships. Also, there were no significant correlations between plant height and number of culms except in the unselected material. Number of culms was significantly correlated to basal diameter. A limited number of correlations in the inbred data are presented in the discussion.

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EXPLANATION OF PLATE I

　　　　_A_. _furcatus_ plants grown in the Manhattan,
Kansas nursery from Kansas, Nebraska, and Oklahoma
seed showing differences in growth habit, leafi-
ness, and time of maturity. (Photograph taken
9-24-36).

Plate I
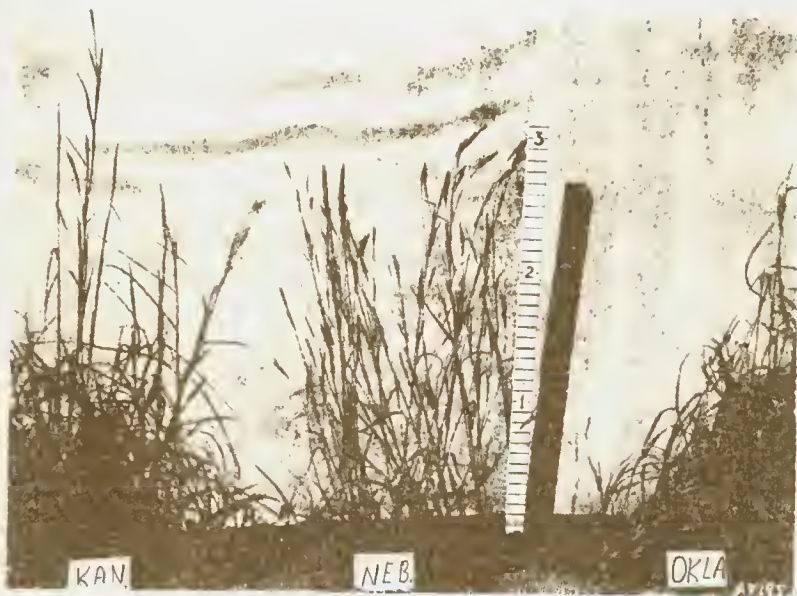
EXPLANATION OF PLATE II

A. furcatus plants in the 1935 nursery show-
ing varation within the ecotype in regard to
height, leafiness, and number of heads in the ma-
ture plant. (Photograph taken 9-11-35).

Plate II

EXPLANTATION OF PLATE III

Variation within the ecotype of A. furcatus
plants in their second season of growth in the 1935 nursery.
The vigorous leafy plant on the right, KBB85 has given
some excellent progeny while KBB76 was discarded after the
first generation. (Photograph taken 6-12-36).

Plate III

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Plate IV

EXPLANATION OF PLATE V

General view of the A. furcatus plants in the
1938 nursery in its second season of growth showing
the uniformity of the plant lines. This was the
stage at which notes were taken. (Photograph taken
6-23-39).

Plate V

EXPLANATION OF PLATE VI

The general effect of inbreeding on A. furcatus. The plants to the left of the measuring stick were open-pollinated selections while those on the right were inbred one generation. (Fourth generation selections in their second season of growth. Photograph taken 6-23-39).

Plate VI

EXPLANATION OF PLATE VII

The effect of inbreeding on A. furcatus. Two
rows from the same parent plant. The row on the
right is from inbred seed, that on the left from
open-pollinated seed. The inbred progeny row is
typical of the extreme loss in vigor encountered in
many of the inbred progeny. (1939 nursery, fifth
generation. Photograph taken 9-1-39).

Plate VII

EXPLANATION OF PLATE VIII

The effect of inbreeding on A. furcatus. Two
rows from the same parent plant, that on the left shows
the medium loss of vigor encountered in some inbred
rows. The open-pollinated sib is shown on the right.
(1939 nursery, fifth generation. Photograph taken
10-3-39).

Plate VIII

EXPLANATION OF PLATE IX

The effect of inbreeding on A. furcatus. Two
rows from the same parent plant, that on the right
being the inbred row. It shows no appreciable loss
in vigor following inbreeding. (1939 nursery, fifth
generation. Photograph taken 10-3-39).

Plate IX

EXPLANATION OF PLATE X

Seedlings from twin seeds (top row) and normal
seeds (bottom row) showing the paired coleoptiles and roots
of the seeds having two embryos. The paired seedlings
are apparently normal in vigor and growth when com-
pared to the single seedlings of the same age. (Photo-
graph taken 2-18-39).

Plate X

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