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THE GEOGRAPHIC VARIATION OF ASCLEPIAS TUBEROSA INTERIOR IN OKLAHOMA

A DISSERTATION

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BY

LAWRENCE JOSEPH WATSON

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THE GEOGRAPHIC VARIATION OF
ASCLEPIAS TUBEROSA INTERIOR IN OKLAHOMA

APPROVED BY

DISSERTATION COMMITTEE

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CHAPTER ONE

INTRODUCTION AND FRAMEWORK FOR THE STUDY OF ASCLEPIAS TUBEROSA INTERIOR

The major objective of this study is to analyze the distributional pattern of a specific plant subspecies in a given geographical area. In connection with this an attempt is made to relate the pattern of plant distribution to selected environmental variables.

The plant subspecies *Asclepias tuberosa interior* displays a unique and interesting pattern of flower color variation in the state of Oklahoma. This pattern, which appears to be non-random, bears a strong resemblance to the known pattern of mean annual rainfall distribution in Oklahoma. The total rainfall decreases from west to east. Light colors are found in the arid areas and darker flowers in the more humid ones. It is this specific correspondence in pattern which will be the major objective to be investigated.

In addition to the investigation of the spatial distribution pattern of flower color, some supplemental plant character variables will be included in the study. Their inclusion is somewhat exploratory; little empirical evidence presently exists to suggest that these characters display systematic variation. Such characters as plant height, leaf dimensions and flowering part measurements are included. All plant characters considered in this study are morphological or structural characters which can be identified and measured directly.

There are a number of general elements to be examined which are related to the problem being investigated in this study. Among these is a brief account of previous research on the family Asclepiadaceae (milkweed) as well as a look at prior study of the species Asclepias tuberosa and its subspecies A.t. interior. This overview presents the foundations for the present research and includes some of the basic considerations which were examined prior to the start of this study.

This chapter will also look at the theoretical considerations which are germane to a study of A.t. interior in Oklahoma. These include the concepts of systematic and unique intraspecific variation, migration, genetic processes, speciation, etc. These concepts will be examined and a number of implications to this particular investigation will be detailed so that it is possible to see the theoretical basis for this study and to better understand the general context into which the study fits.

Previous Study of A.t. interior

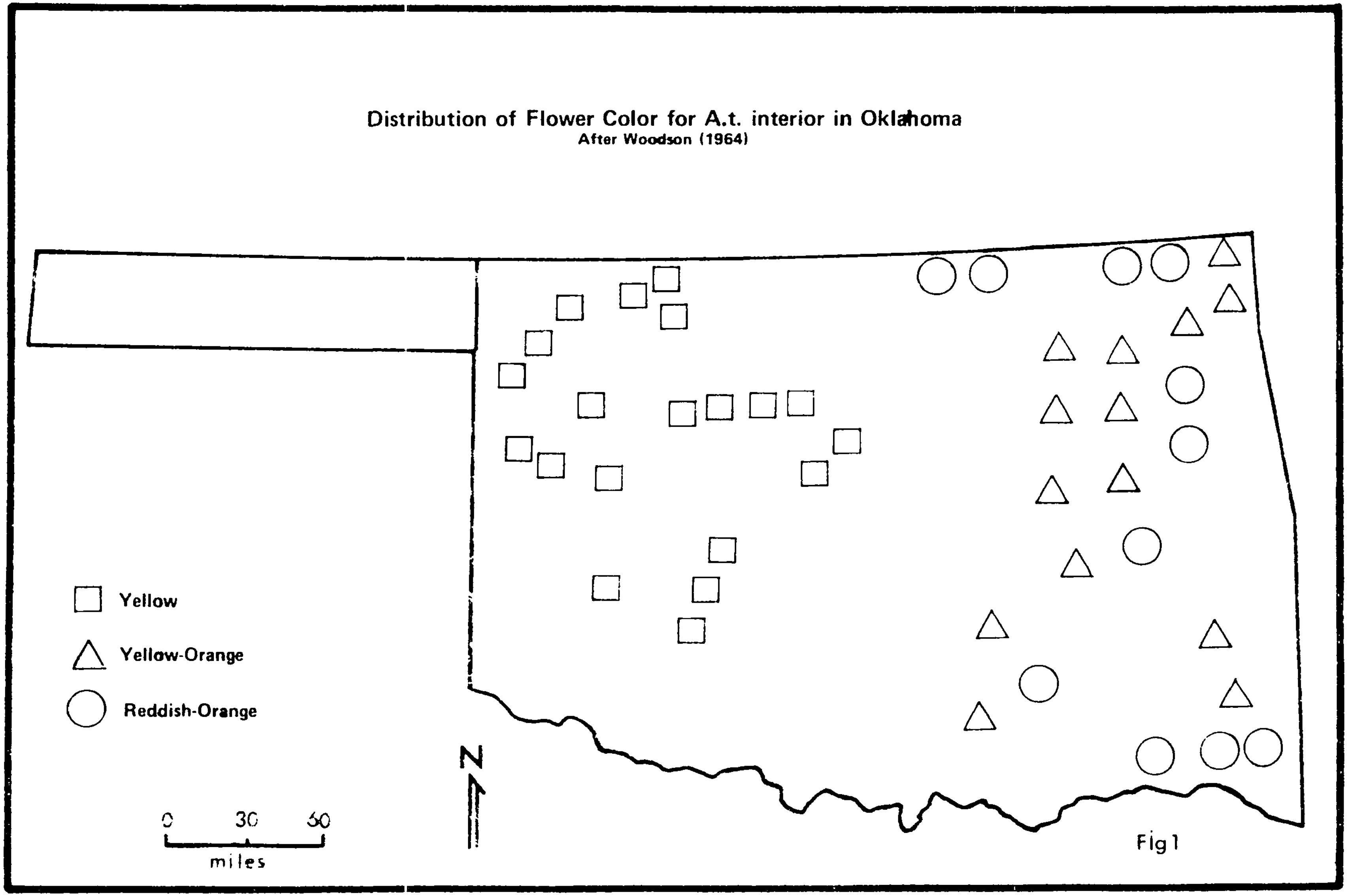
The species A.t. interior had been the subject of study by R.E. Woodson, of George Washington University, for about 20 years. During this period Woodson published a series of papers in which he presented a number of new ideas about the nature of the family Asclepiadaceae. The first paper, "Notes on Some North American Asclepiads" appeared in the Annals of the Missouri Botanical Gardens in 1944. It was to be the most general of several papers published by Woodson. A number of more specific studies followed. Among them was "Some Dynamics of Leaf Variation in Asclepias Tuberosa," which appeared in 1947. In this paper, Woodson presented taxonomic evidence indicating that three subspecies existed within A. tuberosa. These were A. t. interior, A. t. tuberosa and A.t. rolfsii. The three subspecies could be distinguished by the use of several leaf characters which were unique to each of the three subspecies. In addition, the three subspecies were found to have separate ranges. *A.t. interior* is found in an area running diagonally from upstate New York, through the central midwest and on into the southwestern U.S. It is the most widely distributed subspecies. The second subspecies, *A.t. tuberosa* is found in the southeastern U.S., while the third and least widespread subspecies is *A.t. rolfsii*. It is found along the gulf coast, eastward from Texas to Florida. It was the publication of this paper which did much to confirm Woodson's position as the major authority on the species *A. tuberosa*. He was to remain the authority for the balance of his lifetime.

While Woodson's research was primarily botanical, there is a strong spatial tone which runs through much of his later work. His final paper, "The Geography of Flower Color in Butterflyweed" deals with the distribution of flower color in the species *A. tuberosa* within the United States. (Woodson, 1964) Contained within this study are a number of statements about the subspecies *A.t. interior*. These statements are clearly spatial and there is an attempt to relate the observed pattern of flower color to the known pattern of environmental variation within Oklahoma. This attempt at explanation was, however, done in speculative terms and no attempt was made to substantiate the hypothesized relationships.

During the time Woodson spent in the field collecting the data used to write his last paper, he noted that A.t. interior displayed a well-defined spatial pattern in Oklahoma. He observed that the majority of plants found in western Oklahoma were yellow in color, that those in central Oklahoma were yellow-orange and those to the east were largely orange. He felt that the yellow colored flowers resulted somehow from the semi-arid conditions found in western portions of the state and that as moisture amounts increased, to the east, the flowers responded and became darker in hue. This proposed relationship between flower color and mean annual rainfall was stated as a hypothesis. Woodson did not test or attempt to investigate it. He merely suggested that a relationship existed and could be observed in Oklahoma.

It can be seen from the material above that Woodson left an interesting biogeographic question unanswered i.e. What environmental factors are related to flower color in _A.t. interior_? This question is strongly spatial in nature, and it is logical that a biogeographer would be interested in trying to answer it. This environmental influence question fits a number of basic biogeographic constructs. Some of these have been explored by Kellman (1974), Sneath and Sokal (1973) and in papers by Erikson, Bradshaw, Epling and others in the book _Papers on Plant Systematics_ (Ornduff, 1967). The papers in the latter volume deal with a variety of concepts of concern to biogeographers, including intraspecific variation, environmental influence and population dynamics.

Becoming more specific, the Woodson map of flower color, shown as Figure 1, illustrates an interesting flower color transition in central Oklahoma. West of a line running through the central counties of the state are found yellow flowers. East of this line the flower color is generally darker. A biogeographer might conclude that such a sudden shift in flower color could be the result of a dramatic environmental shift. This belief would appear to have some


Distribution of Flower Color for A.t. interior in Oklahoma
After Woodson (1964)
Yellow
Yellow-Orange
Reddish-Orange
N
0 30 60
miles
Fig 1

validity, as a major interface is known to exist in this same region of Oklahoma. The area to the west has long-grass prairie, populated by such dominant species as *Andropogon gerardi* and *Bouteloua curtipendula*. The forested region to the east is dominated, to a great extent, by members of the oak-hickory association(*Quercus*-*Carya* association).

The interface (ecotone) is a region of transition which has been traditionally explained in terms of climatic change. It is thought that the decreasing rainfall as one moves from east to west in the state is responsible for the change in dominant vegetation. Factors such as soil and bedrock are also considered to be important environmental controls, but they are of lesser importance than climate in determining the range of the organisms involved.

With the foregoing ideas in mind, it is quite possible to see that environmental factors exist which might be responsible for the pattern of observed geographic variation in *A.t. interior* within Oklahoma.

FRAMEWORK

The overall relationships which are considered in this study may be viewed with reference to Figure 2. This diagram depicts the basic processes of genetics and migration as well as the influence of environmental factors on intraspecific variation in general and systematic intraspecific variation in particular.

The term intraspecific refers to a process which occurs within a species. The term species is used here as commonly defined. (See Stebbins, 1966, Chapter 5)

The variation in living organisms is of two types, unique variation and systematic variation. The former may be considered that form of variation which occurs in individual organisms as a result of unique genetic or environmental circumstances. This variation is specific to individuals within a population and is not of primary concern in this study.

The second type of variation which is the subject of this study is systematic intraspecific variation. This term infers that the variation is nonrandom and occurs within a single species. Among a number of modern researchers this form of

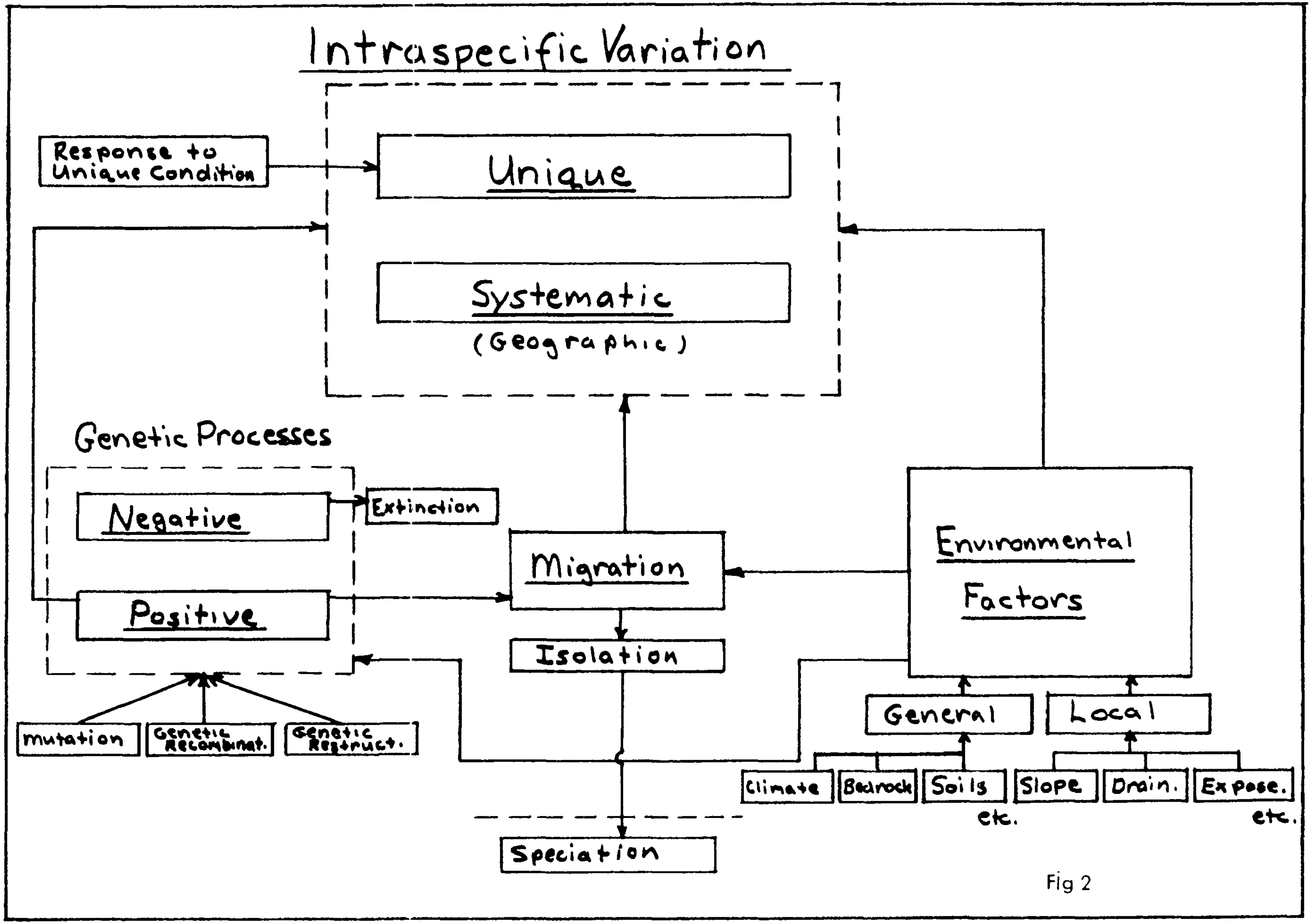

Intraspecific Variation
Unique
Systematic
(Geographic)
Response to Unique Condition
Genetic Processes
Negative
Positive
Extinction
Migration
Isolation
Speciation
Environmental Factors
General
Local
Climate
Bedrock
Soils
etc.
Slope
Drain.
Expose.
etc.
mutation
Genetic Recombinat.
Genetic Restruct.

Fig 2

study has been called geographic variation analysis. (Sneath, P.A., Sokal, R.R., 1972, pp. 376-380; Gabriel, K.R. and Sokal, R.R., 1969, pp. 259-278; Marcus, L.F., & Vandermeer, J.H., 1966, pp. 1-13). It is systematic and geographic in that given patterns of variation can be observed and measured and are associated with particular geographic areas.

A basic assumption in geographic variation analysis is that there are relations between vegetative or animal patterns and the patterns of physical environmental variables such as climate, topography, soils etc. In the general biogeographical context, Neill says "...There are patterns of distribution, and these are of special interest to the biogeographer, who wants to know how the patterns came about." (Neill, W.T., 1969, p. 7) With regard to plant patterns M.C. Kellman recently stated "...The basic supposition in such analyses is that spatial orderliness exists in vegetation and can be identified and related to underlying factors (normally environmental)." (Kellman, M.C., 1974, p. 39)

Genetic processes, migration and environmental factors have various effects upon geographic variation. The influence of these processes and factors is continuous and all of them are important and will be considered individually.

The genetic process consists of a number of subprocesses which are considered to be among the cornerstones of evolutionary development. (Stebbins, 1966, p. 2) Among these are positive or helpful genetic modifications, negative or harmful modifications and those which are neutral, neither harmful nor helpful in their effect upon organisms possessing them. The negative modifications are harmful in that they decrease the survival potential of an organism which usually leads to elimination. Those modifications which are positive or neutral tend to be passed on to progeny and become incorporated into a species and can be observed as part of geographic variation.

Among the genetic subprocesses are mutation, genetic recombination, where reproductively induced genetic modification occurs, and genetic restructuring, where the ordering of the arrangement of genes on chromosomes is modified. These subprocesses are the basic mechanisms through which the major portion of intraspecific variation originates. The modifications are then subject to the effects of environmental factors and possibly those of migration. Favorable and neutral modifications may be passed on and can be seen in geographic patterns while the negative usually lead to extinction of the organism.

The migration process as commonly defined involves the change of an organism's range. (Cain, S.A., 1944, p. 88; Haldane, J.B.S., 1966, p. 22; Seddon, B., 1973, pp. 133-140) This process has two basic components: they are dispersal and establishment. The first involves mechanisms of distribution and the latter involves survival in a new environment. Should an organism be dispersed into a new area, the survival and reproduction of that organism will indicate whether migration has taken place. Obviously, the elimination of the dispersed organism by the environment would prevent range expansion. Retreat can also take place. Unfavorable environmental changes can eliminate portions of a species and reduce the overall range. (For a detailed treatment of migration and dispersal, see Polunin, N., 1960, pp. 97-127)

Isolation as used here involves the separation of subpopulations of organisms from the main body or parent population. Such isolation would allow genetic drift to become more dominant and might produce genetic isolation. In mild separations the subpopulations could be distinct enough to be called a subspecies. In more prolonged separations, where genetic drift has had a longer period to operate and where exchange of zygotic proteins in breeding is no longer possible, a new species will have evolved. (Stebbins, 1966, pp. 99-115)

Environmental factors, as stated by Oosting and others, contain all of the elements of the physical environment which have an effect upon the growth, development and survival of an organism. (Oosting, 1956, p. 5) These elements can be divided into general factors and local factors. The general ones include climate, bedrock type, general elevation etc. while the local ones include angle of slope, degree of exposure and general orientation.

The two sets of environmental factors are known to affect all forms of life and to act concurrently. While individual factors may be critical, for individual species at particular times, groups of factors which act together are usually more important. Thus groups of factors, not individuals, are important.

The patterns of environmental variation have often been seen to correspond to the pattern of geographic variation in a number of organisms. This is a major consideration in biogeography. (Seddon, 1971, p. 1) The general implication is that knowledge of environmental conditions will enable one to predict with some accuracy the distribution of an organism. This applies to both systematic and unique variation, but has its greatest utility when applied to the former.

Environmental factors are the major mechanism by which migration is controlled. Unfavorable environmental conditions will not permit a new organism to become established in a new area, while tolerable factors may aid an organism to successfully expand its range. The environmental elements can thus be seen to control and restrict the migration process. In addition, a number of less direct relations to the other evolutionary processes exist. Genetic processes aid migration only as long as favorable environmental factors are maintained. The isolation and speciation processes are also influenced by migration.

The major focus of this study is systematic intraspecific variation (geographic variation) of <u>A.t. interior</u> in Oklahoma and the relationships between this pattern and the pattern of environmental variation. Both general environmental factors such as climate, bedrock and soil types will be considered along with specific local variables such as drainage, exposure, angle and orientation of slope, etc.

The other processes which appear in the framework will also be considered but in a less direct way. Genetic and migrational implications will enter into a number of conclusions regarding interrelations between each of the major elements but are of less immediate interest than the portions of the model discussed so far. In the case of the migration, isolation, speciation portion, for example, the model indicates some of the relationships which are possible for many organisms rather than one individual plant or animal. In fact, the process of speciation is by definition beyond the aim of the general model. A detailed examination of these processes, while important, is beyond the scope of this study and might well follow upon the conclusion of this investigation.

Morphological plant characters will be utilized in the

study rather than the physiological or genetic characters which might be employed by biologists.
Morphological plant characters give a reasonably good picture of variation without introducing factors which are complex and difficult to interpret. (See Sneath & Sokal, 1972, pp. 72-109 for a detailed discussion of character selection).

It is appropriate to stress at this point that the present research is intended to look at geographic variation as a spatial process and is not intended as a detailed study of all aspects of the life history of A.t. interior. Spatial patterns are the major focus of this study. Reproduction, physiology, genetics etc. are biological processes which are important and might be investigated best by biologists.

In summation, the model presented in Figure 2 depicts the general framework within which this study fits. It gives a general picture of the context of intraspecific variation and the subset of systematic or geographic variation. The framework enables one to view the complex of interrelations and dependencies which exist in the study of geographic variation as well as providing a background upon which the results of the study can be viewed.

Summary

This chapter has presented a general introduction to the problem under investigation. It has reviewed the previous work of R.E. Woodson, the authority in the study of *A.t. interior* and indicated the existence of an interesting and unanswered biogeographic question.

Secondly, it has presented a general framework for viewing the various processes involved in the study of intraspecific variation in general and systematic intraspecific or geographic variation in particular. It has given a very brief look at each of the individual processes or factors and has indicated some of the probable implications of these upon the present study.

The next chapter will present details on the methodology of herbarium and field techniques, sampling design, measurement techniques and related topics. The following chapter will deal with an analysis of the pattern of flower color variation in *A.t. interior* and its relationship to environmental variables. The fourth chapter will examine similar questions related to morphological plant characters other than flower color.

The final chapter will briefly examine the results of the study and will speculate upon suitable followup studies which might logically evolve from this investigation.

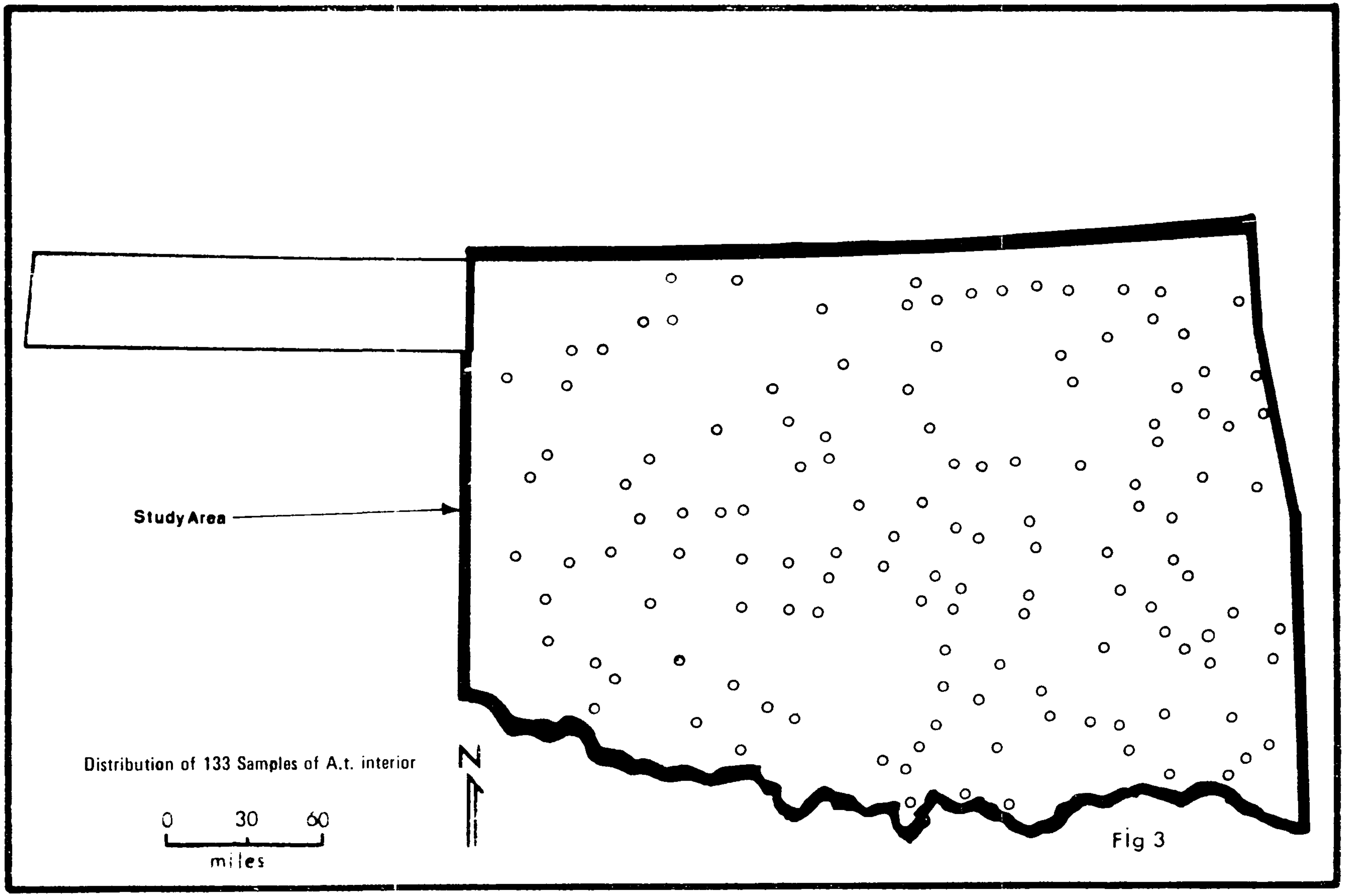
CHAPTER TWO
PLANT AND ENVIRONMENTAL DATA

This chapter describes the process of collecting the two types of data required for the study. The first part deals with plant character data and the second part with environmental data. It presents details of the work done in libraries, herbaria and the field as well as a number of the factors which were considered in selecting the plant and environmental variables which are included in the study of A.t. interior in Oklahoma. It should be noted here that the number of plant characters and environmental variables which are included in this study represent only a portion of the possible variables which could have been included. Time, cost, and practicability have essentially limited the variables to the ones described. It would be desirable to expand the size and focus of such studies if it were not for the greatly increased costs in time, money and equipment. Those variables chosen represent a logical compromise and should serve the intended research objectives.

Plant Character Data

Two groups of plant samples are considered in this study. The first is taken from Oklahoma herbaria collections and the second was gathered in the field. The majority of utilized samples are from the herbaria. The field samples have an added quality in that specific site data for these samples were gathered at the time of their collection. This gives a special accuracy dimension to this group which is not available for the bulk of the samples used. Because of the variety of collectors and collection techniques used to gather the herbaria samples it was decided it would be pointless to impose an overly rigid field sampling scheme.

Investigation began with a preliminary examination of the data available in the Oklahoma University and Oklahoma State University herbaria. Samples collected over the last 50 years were examined, using a standard key. The location of each sample was then plotted on a map(Figure 3). The preliminary mapping of sample locations and use of the identification key enabled the researcher to become familiar with the plant to be studied. This experience with <u>A.t. interior</u>



Distribution of 133 Samples of A.t. interior

Fig 3

helped the researcher to identify the plant later in the field. Mapping of the herbaria samples made it possible to judge, in a general way, the correctness of the color distribution pattern claimed for Oklahoma by Woodson. In addition, this preliminary mapping gave some idea of the density of samples which were available in the two herbaria, as well as an idea of the locations within the study area for which there were few or no samples. Plans were then made for additional samples in the field.

Examination of herbaria materials also gave an impression of the range of size, color, shape etc. to be expected in the field. It also revealed information on the blooming times of the plant in Oklahoma. This information was very valuable when field collecting trips were planned. Also, it was obviously beneficial to determine the most favorable time in which to be in the field. This enabled the researcher to collect the maximum number of samples in a minimum time span. The blooming period is a critical collecting time.

Although the two herbaria contained over 180 samples of *A.t. interior*, their distributional pattern was far from even.

There were abundant samples from some counties and none from others. To remedy this, a sampling plan was formulated which called for a density of one sample every 20 road miles or one sample per 400 square miles. County areas were then divided by 400 to determine the number of samples to be collected. Counties with few or no samples were then designated for field study.

The field work was divided into five trips. Two of the trips involved the southeastern portion of Oklahoma. One trip was taken at the beginning of the collecting period and one at the end. This division resulted from a feeling that local relief in the southeast might delay the blooming of some plants. Sheltered plants at higher elevations might bloom considerably later than those found in lower, open sites. The other parts involved trips to the southwest and northwest with a day-trip about central Oklahoma.

The trips were taken from mid-May to mid-June 1974 and portions of 38 counties were searched in an effort to collect the plant samples. Samples were collected at 42 sites, in all but a few of the counties considered. The lack of samples in the several counties might be due to intensive cultivation in a few cases or to the stress of the environment in others. The fact that samples of A.t. interior had not been found in these areas after 50 years of field collecting by botanists, makes it questionable that this organism can be found in the areas.[1] Also, the extensive search conducted during this study, with negative results, further confirms this opinion.

Collection began, typically, with a series of road traverses in a designated area. When a sampling site was located the geographic location was noted, environmental measurements were taken and individual samples were collected.

Choosing between multiple samples was not a problem. In the majority of cases, the on-site sampling was greatly simplified by the fact that little or no choice was possible, as only one plant or stand was available. In cases where a

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[1] I wish to acknowledge the contribution of Dr. George Goodman for bringing this point to my attention.

number of plants were available in several stands, the stand in the center of the area was selected. A tape was held over the stand and several individual plants were removed from the center. The rationale for this is that the central specimen represents as near to a "typical" plant as can be found in an area. It is more likely to be affected by "average" conditions in a given locality. While not truly random, this procedure is in keeping with the spirit of randomness and serves the general purpose for which it is intended.[2]

Flower color, a prime factor in this study, was determined with reference to the same publication used by Woodson: A Dictionary of Color. (Maerz & Paul, 1950) All color matching was done by the same person using shaded north light. This procedure assured that only one individual would match the flower color to the samples in the Dictionary of Color.

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[2] I wish to acknowledge the suggestion of Dr. Elroy Rice in this matter.

The color matching took place in the field at the time of collection, so that pigment fading would have as little effect as possible. Each sample was then labelled, with tape and sealed in a plastic bag to ensure that the sample would remain in good condition until the end of each day when it would be placed into a plant press. Pressing, between layers of special drying paper, began the drying process which is necessary before plants can be mounted.

Upon returning to the campus, the collected samples were put into a drying machine and allowed to "cure" for several days. The samples were then removed and placed in storage. Fumigation precautions were taken in the herbarium, to prevent the damage or destruction of the field samples. A small amount of chemicals was sprinkled in each folder before they were stored in sealed storage cabinets.

The morphological plant characters, which were considered for this study were selected to avoid a type of bias introduced by the use of too many so-called "key" characters.

Sneath and Sokal (Sneath & Sokal, 1973, p. 72) present a number of arguments in favor of using a reasonable number of unweighted characters in studies of this kind. The basic idea behind this procedure is that the over-use of key characters can lead the researcher to find what he wishes to find rather than to uncover the true relationships between and among organisms. The over-reliance upon key characters can produce an a priori bias or weight on the characters selected for a study. This weighting can lead to results which are considered suspect by some workers.

A group of 25 characters, both key characters and otherwise, were chosen for the study. (These are shown in Table 1) The plant samples were then measured using the facilities of the O.U. herbarium. This process consisted of making a series of precise measurements of stems, leaves, petals, bracts and other flowering parts. The tools commonly used for making these measurements include a meter stick for the gross measurement, a millimeter scale for smaller plant components, a microscope ocular micrometer for very small measures and a K. & E. polar planimeter for calculating

TABLE 1 PLANT CHARACTERS

	Code	Character
1.	PLL	Plant Length
2.	STL	Stem Length
3.	LSL	Lower Stem Length
4.	IND	Internodal Distance
5.	LFL	Leaf Length
6.	LFW	Leaf Width
7.	LFR	Leaf Length/Width Ratio
8.	LFA	Leaf Area
9.	BRL	Bract Length
10.	BRW	Bract Width
11.	BRR	Bract Length/Width Ratio
12.	PTL	Pedicel Length
13.	PTN	Number of Pedicels per Node
14.	SPL	Sepal Length
15.	SPW	Sepal Width
16.	SPR	Sepal Length/Width Ratio
17.	PEL	Petal Length
18.	PLW	Petal Width
19.	PLR	Petal Length/Width Ratio
20.	HDL	Hood Length
21.	HDW	Hood Width
22.	HDR	Hood Length/Width Ratio
23.	CLR	Color of Flower
24.	SHL	Stem Hair Length
25.	PTH	Petiole Hair Length

leaf area.[3]

Environmental Data

Two basic types of environmental data were used in this study. The first was collected in the field at each sampling site. The second was gathered from standard sources such as weather service bulletins, biological survey reports and the like (See Table 2 for a list of environmental variables).

The gathering of on-site environmental data began with the recording of the geographic location of each sample collected. Distance to the nearest town, highway intersection or major landmark was noted so that locational information could be recorded on an Oklahoma map.

Slope angle (ALS) and slope orientation (SLO) were measured using a Brunton compass-clinometer. Slope angle gives some idea of drainage and exposure while slope orienta-

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[3]The researcher acknowledges the assistance of Ms. Cheryl Lawson and Dr. George Goodman, O.U. Herbaria staff, in training the researcher for proper collection and herbarium techniques.

TABLE 2

ENVIRONMENTAL VARIABLES

	Code	Variable	Source
1.	AAT	Average Annual Temperature	Climatology of the U.S. #81, 1973
2.	AJT	Average January Temperature	Climatology of the U.S. #81, 1973
3.	JLT	Average July Temperature	Climatology of the U.S. #81, 1973
4.	AMT	Average Annual Maximum Temperature	National Atlas of USA, 1970, p. 105
5.	AAP	Average Annual Percipitation	National Atlas of USA, 1970, pp. 98-99
6.	AJP	Average January Precipitation	National Atlas of USA, 1970, p. 97
7.	JLP	Average July Precipitation	National Atlas of USA, 1970, p. 97
8.	AAS	Average Annual Snowfall	National Atlas of USA, 1970, p. 100
9.	ADF	Average Depth of Frost Penetration	The Weather Handbook, 1963, p. 250
10.	AJH	Average January Relative Humidity	The Weather Handbook, 1963, p. 228
11.	JLH	Average July Relative Humidity	The Weather Handbook, 1963, p. 229
12.	AJS	Average Number of Hours of January Sunshine	National Atlas of USA, 1970, pp. 98-99
13.	JLS	Average Number of Hours of July Sunshine	National Atlas of USA, 1970, pp. 94-95
14.	DLF	Average Date of Last Killing Frost	Oklahoma Biological Survey Handout
15.	DFF	Average Date of First Killing Frost	Oklahoma Biological Survey Handout
16.	MTO	Maximum Temperature Ever Observed	The Weather Handbook, 1963, p. 199
17.	MHT	Mean Annual High Temperature Frequency	National Atlas of USA, 1970, p. 108
18.	MFT	Mean Annual Freezing Temperature Frequency	National Atlas of USA, 1970, p. 108
19.	AFT	Average Number of Days with Freezing Precipitation	Climates of North America, 1974, p. 224
20.	AMD	Average Percent of Months with Severe or Extreme Drought	Climates of North America, 1974, p. 235
21.	PYP	Physiographic Province	Curtis and Ham, 1972, Oklahoma Biological Survey
22.	SLT	Soil Type	Gray, 1959, Oklahoma Biological Survey
23.	GOP	Geological Province	Branson and Johnson, 1972, Oklahoma Biological Survey
24.	VGP	Vegetative Province	Game & Fish Dept., 1943, Oklahoma Biological Survey
25.	ELV	Elevation	Johnson, 1972, Oklahoma Biological Survey

TABLE 2 Continued

	Code	Variable	Source
26.	ALS	Angle of Slope	Author's Computation
27.	SLO	Slope Orientation	Author's Computation
28.	PDX	Percent of Day Exposed	Author's Computation
29.	TDX	Time of Day Plant is Exposed	Author's Computation
30.	DRN	Drainage	Author's Computation
31.	NPS	Number of Plants per Stand	Author's Computation

tion indicates the general microclimatic realm that a given plant must survive in. North facing slopes tend to be cooler and wetter, while south facing slopes tend to be warmer and drier. (Oosting, 1956, p. 109)

Exposure (PDX and TDX), measures of the degree to which a given plant is exposed to the elements, was estimated. Site characters such as the presence of rock overhangs, shelterbelts, embankments etc. were considered as well as the time of day when the plants were shaded from insolation. Exposure measurements give an idea of the extent of influence that local factors have upon a particular organism. Some organisms are known to require shelter, while others survive best in more open environments.

General soil type (SLT) and drainage (DRN) were also estimated. In the majority of cases, the soil type was obvious. Drainage was not as easy to estimate, except during the brief periods of showers which occurred during the field activity period. The drainage estimate was made with reference to some of the previous factors as well as with the aid of local clues such as standing water, muddy conditions, extremely dry conditions etc. These two variables were measured because of their known association with certain organisms and their known effect upon geographic variation. (Dancereau, 1957; Oosting, 1956; Odum, 1959; Neill, 1969)

In addition, the number of plants per stand (NDS) was recorded. This measure indicates the number of individual plants per group if more than one plant or group was present. These data give an idea of the relative abundance of A.t. interior in Oklahoma.

Environmental data can be average, long term data which reflects the "normal" conditions to be found over an area or it can be short term data which may often reflect extremes that may not be encountered by organisms for extended periods. With two exceptions, MTO and AMD, the majority of environmental data was of the long term or average type.

The list of climatic variables AAT through AMD are as complete a group as could be gathered from standard climatic records. Sources for these data included Statistical Abstract of Oklahoma, Climatological Data (Oklahoma), the National Atlas, The Weather Handbook and a collection of informally published physical-biological maps available from the Oklahoma Biological Survey.

The variables, AAT through AMT plus MTO, MHT and MFT give some indication of the thermal regime in which A.t. interior must survive. Thermal limitations, on biotic organisms, are often critical and thus make it mandatory that these types of variables be included.

Variables AAP through JLH and AFT and AMD are concerned with various moisture conditions found within the study area. These are, perhaps, the most critical environmental variables considered in this investigation. The importance of moisture conditions upon the physiology of plants is well known (Oosting, 1956, p. 178; MacArthur, 1972, p. 129; Neill, 1969, p. 28 and Pearsall, 1950). AMD, the variable which deals with extremes of drought and their effects upon plants has been demonstrated by Cohen (1967) and MacArthur (1972).

Frost variables, ADF, DLF and DFF give some measure of the length of growing season, in an area, as well as some consideration of the depths to which frost action can be expected. MacArthur (1972, p. 130) discussed the value of growing season and frost action information in studies of the influence of the environment upon plant distributions.

Variables such as AFT, AMD and MTO are factors which might also be expected to put unusual stress on A.t. interior. They are included so that a number of "extreme" variables, which might have a critical effect, would also be examined during the process of analysis.

The variables dealing with sunshine, AJS, JLS and ELV, are indirect indicators of the amount of solar energy which is received in a given area. Because solar energy contains several forms of radiation, which are known to influence plant growth, it should be included in this study. Oosting (1956), Allard (1920), Pauley and Perry (1954) and others have reported extensively on the effects of insolation on plant responses.

The variables PYP, SLT and GOP are all associated with geological processes. The bedrock, which is the parent material for soil and which sets the limits of physiographic development is known to be important to the development of plant communities. Chemical elements transferred from the bedrock to the soil which develops on top of it are important factors which effect the growth of plants in a given geological area also. While the majority of plants are not restricted to a given bedrock-soil type, ample evidence suggests that specific plant species are at their best growing on given bedrock-soil combinations. (Oosting, 1956, Chapter 8)

Summary

Chapter three has presented the general considerations and techniques utilized in gathering the two types of data used in this study. These have included sampling design, field techniques and laboratory methods. Rationale for the use of several types of data, for the sampling methods and for a number of other factors has been given. The chapters which follow will deal with the analysis of this data and will present a number of conclusions which have been reached about the geographic variation of *A.t. interior* in Oklahoma.

CHAPTER THREE
ANALYSIS OF FLOWER COLOR VARIATION

The primary topic examined in this chapter is the flower color variation of A.t. interior within Oklahoma. An effort is made to determine the extent of the relationship between the observed pattern of flower color in A.t. interior and the known pattern of environmental variation within the state. The second objective is to consider whether evidence exists for determining the route of migration of A.t. interior through the state.

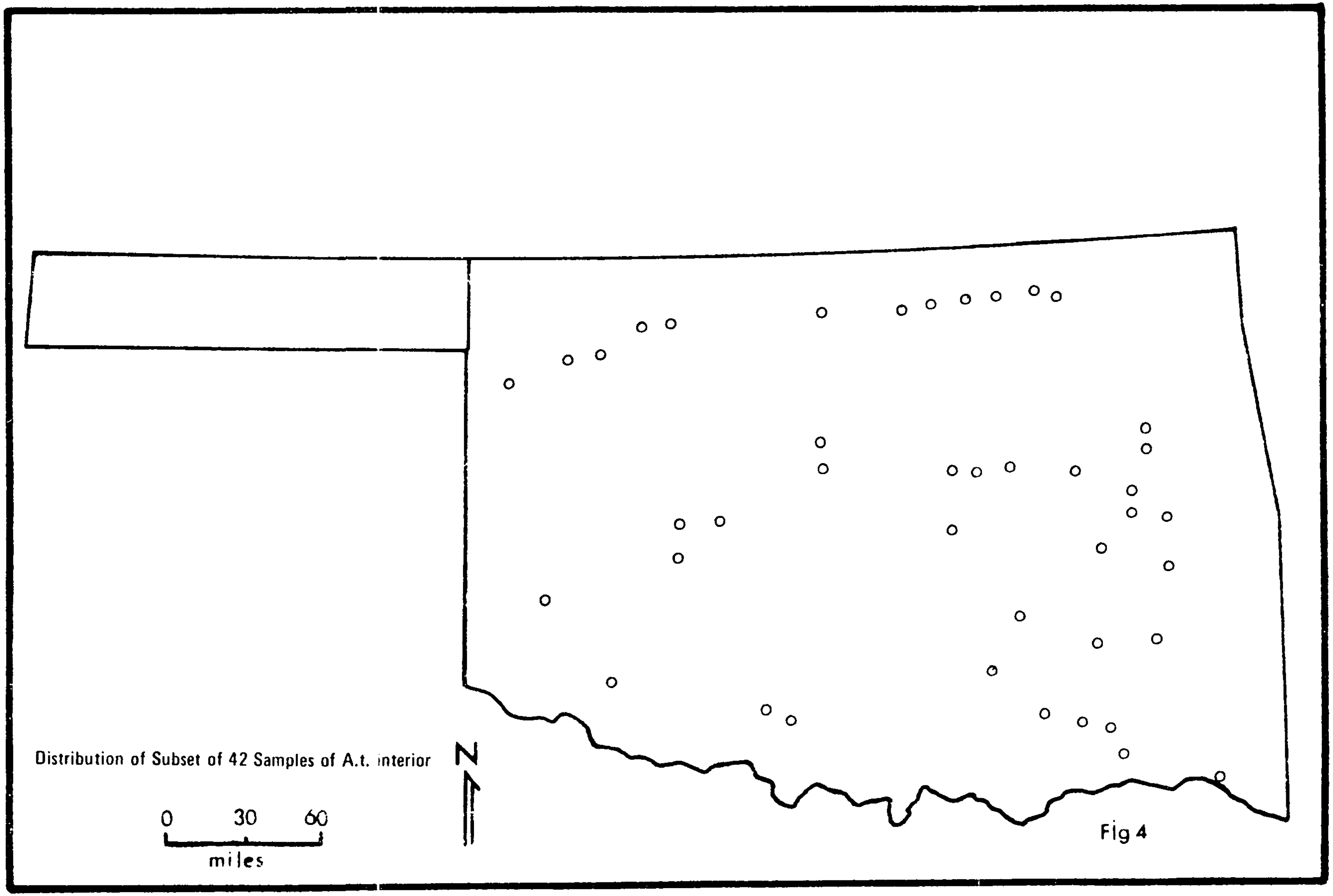
Analysis of the first objective is accomplished through the use of a number of analytical tools, i.e. trend surface analysis, correlation and regression and factor analysis. Each of the techniques is described, reasons are given for its selection, results are presented and a discussion of these is provided. Examination of the second objective involves the analysis of residuals from the regression of plant characters and environmental variables.

FLOWER COLOR VARIATION

There are a number of basic questions which can be asked about the geographic variation in flower color of A.t. interior in Oklahoma. For example: Is there a non-random pattern to the color variation? If there is a non-random pattern is it related to environmental variables? If so, which variables are they and how strong is the relationship between them and flower color variation? These questions are the ones which are under investigation in the first portion of this chapter.

Two data sets are included in this analysis. The primary set consists of all 133 samples of A.t. interior which have been included in the study. The second group, which is actually a subset, consists entirely of individuals which were collected in the field. Additional environmental information, not available for the herberia samples, was measured and recorded for this group of 42. While this subgroup is not as representative nor as well distributed as the total group, it was felt that the subgroup of 42 ought to be analyzed as well as the total set.

A number of mapping techniques can be used to plot the basic plant color information. Among the techniques is an estimation method which involves the drawing of parallel



Distribution of Subset of 42 Samples of A.t. interior

Fig 4

profiles, which are then smoothed by eye. (Nettleton, 1954) Others include the intersecting profile method and the orthogonal profile technique. (Krumbein, 1956) These are selective techniques which depend, to an extent, upon the subjective choice of the operator. In contrast are those which identify dominant spatial trends. One such technique is trend surface analysis. (For a detailed treatment of trend surface analysis in geography, see Chorley and Haggett, 1965, pp. 47-67)

Identifying Spatial Trends

Trend surface mapping is an objective statistical procedure which involves the fitting of polynomials of any desired degree to a set of data and it is preferable to estimation techniques. The basic objective in the trend surface analysis employed in this study is to distinguish the overall regional pattern of variation from the "nonsystematic, local and chance variation." (Krumbein, 1956) This result is desirable if one wishes to know the general distribution of an organism in space without the interference or "noise which local anomalies may produce. One might think of trend surface analysis as a filtering technique; one which permits the discrimination between "signal," useful information, and "static," unwanted and confusing data.

Three variables, U, V and Z are involved in trend surface analysis. U and V are independent coordinates indicating the data point position while Z is the dependent variable which indicates the value of the point described by U and V; hence

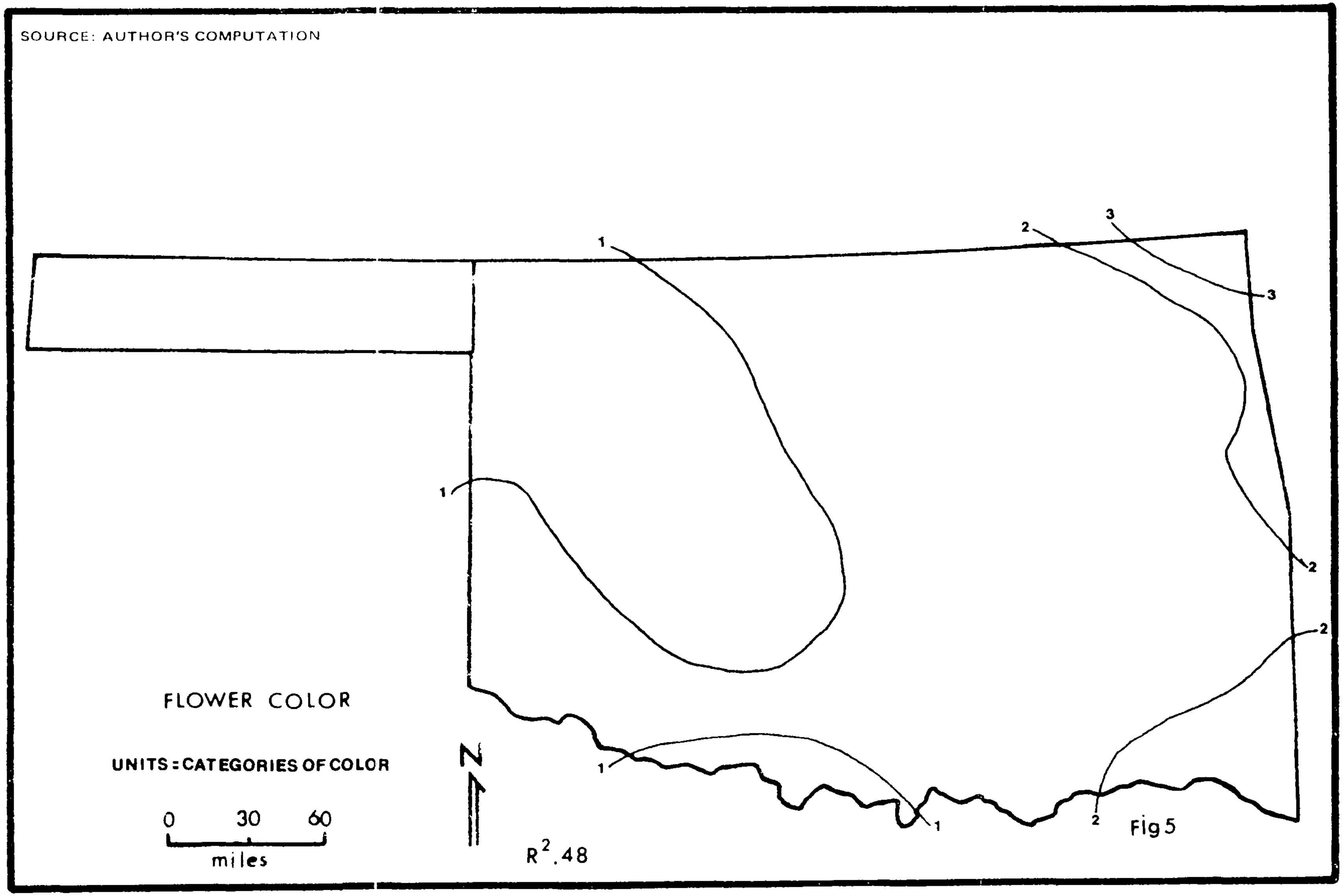
$$Z = Z\ (U,\ V) \qquad (1)$$

Using the regression equation, the Z values are estimated for each point. The R^2 values, which are calculated for each surface, provide a measure of explained variation of Z.

A sixth degree trend surface map of the color distribution of A. t. interior in Oklahoma is given in Figure 5. The sixth degree was chosen in order to account for the maximum variance possible. This was necessary as the proportion of explained variance was small with lower degree surfaces. Ideally one would use the lowest degree surface beyond which results do not improve to a significant extent. This map was computed using the larger sample of 133 observations. The flower color scores for this map are plotted on a scale of from 1 to 4. The low values indicate lighter colors (yellow) and the higher values indicate darker colors (orange).

Examination of the color trend surface map confirms Woodson's observations of the shift in flower color in _A.t. interior_ across Oklahoma. The northeast and southeast portions of the state have orange flowers, the central portion has yellow-orange ones and the flowers in the northwest and southwest are yellow. The only major difference between the Woodson map, see Figure 1, and this map appears to be the lack of a firm color demarcation line on the trend surface map in central Oklahoma. This may be due to a difference in the color coding systems used in the two studies. Woodson used a continuous scale, with over 30 possible color categories, while the present study is restricted to four categories. This limitation to four categories is justified because of pigment fading problems with the herberia samples. Many of these samples are quite old and it is not possible to determine the degree of color shift since they were collected.

In general, then, the Woodson observations on flower color distribution in _A.t. interior_ within Oklahoma were correct.


SOURCE: AUTHOR'S COMPUTATION
FLOWER COLOR
UNITS: CATEGORIES OF COLOR
0 30 60
miles
N
R^2 .48
1
1
1
1
2
2
2
2
3
3
Fig 5

Regression Analysis

The question investigated in this study deals with the relationship between the pattern of flower color variation of *A.t. interior* and the pattern of known environmental variation within Oklahoma.

Color variation is assumed to be a linear function of the environmental variables listed in Table 2. An equation was estimated for the total sample and subsample. Furthermore, in order to reduce problems which result from multi-colinearity, these environmental variables were subjected to principal components analysis, the results of which are presented in Tables 3 and 4. For each sample, therefore, a further equation was estimated in which color was assumed to be a linear function of the dominant components.

Table 3 displays the results of the principal components analysis of the large sample. The four components account for 75% of total variance. Component one might be termed a "moisture component" as the highest loadings are for precipitation or moisture related variables, i.e. AAP (.90), AJP (.85). The two insolation variables, AJS and JLS (-.90 and -.93) are also included; they represent a less direct but

TABLE 3

COMPONENT LOADINGS FOR ENVIRONMENTAL VARIABLES ON THE LARGE SAMPLE

(Components with eigenvalues greater than one)

Variables	Comp 1	Comp 2	Comp 3	Comp 4
AAT	.17	.94	-.09	.04
AJT	.32	.90	-.07	.06
JLT	-.40	.58	-.42	.11
AMT	-.17	.80	-.13	-.28
AAP	.90	.19	.17	.22
AJP	.85	.34	.09	.14
JLP	.06	-.14	.06	.37
AAS	-.45	-.83	.04	-.03
ADF	-.62	-.68	-.01	-.16
AJH	.21	-.04	-.06	.80
JLH	.91	.22	.10	.21
AJS	-.90	-.09	-.23	-.26
JLS	-.93	-.01	.09	-.15
DLF	-.06	-.71	-.25	-.20
DFF	-.02	.79	.25	-.06
MTO	-.62	-.07	-.22	-.05
PYP	-.53	-.41	-.05	.21
SLT	.16	-.01	.89	.06
GOP	-.76	.09	.33	.10
ELV	.14	.06	.08	.48
VGP	-.75	-.23	-.32	-.28
% of Accumulated Explained Variation	.43	.64	.70	.75

rather obvious connection between moisture conditions in an area and the elements which control the amount of insolation.

The second component might be called a "temperature component". The first 3 variables, AAT (.94), AJT (.90) and AMT (.80) together with AAS (-.83) have the highest component loadings. The others, related to frost are also indirect temperature indicators i.e. ADF (-.68), DLF (-.71) and DFF (.79).

The third and fourth components are somewhat less important. Component 3 is a "soil-temperature component," SLT (.89) and JLT (-.42). The final component is a "winter humidity-vegetation factor," AJH (.80) and VGP (.48).

In the principal components analysis of the subset, seven components emerged with eigenvalues greater than one. The seven components accounted for 81% of the total variance. Results of this analysis are summarized in Table 4.

The majority of variables are related to the first two components. Component one is a moisture-geophysical component. Eight of the 15 variables with high loadings are directly or indirectly related to moisture, i.e. AAP (-.92), AJH (-.92)

TABLE 4

COMPONENT LOADINGS, ENVIRONMENTAL VARIABLE FOR SUBSAMPLE

(Components with eigenvalues greater than one)

Variables	Comp 1	Comp 2	Comp 3	Comp 4	Comp 5	Comp 6	Comp 7
AAT	-.40	-.86	-.12	.13	-.14	-.04	-.00
AJT	-.42	-.83	.11	-.04	-.18	-.13	-.07
JLT	.23	-.52	-.17	.59	-.01	.18	.20
AMT	.21	-.85	.10	.10	.05	-.14	-.19
AAP	-.92	-.04	-.05	-.05	-.10	-.01	-.15
AJP	-.82	-.21	-.08	-.05	-.16	-.13	-.20
JLP	-.71	.33	-.08	.00	-.07	.26	.16
AAS	.60	.76	.06	.06	-.01	-.02	.13
ADF	.77	.54	.01	.08	.09	.03	.10
AJH	-.92	.06	.07	-.01	-.14	.06	-.08
JLH	-.91	-.23	-.11	-.07	-.09	-.03	-.15
AJS	.96	.03	.02	.15	.06	-.03	.15
JLS	.85	.04	.22	.15	-.07	-.07	.28
DLF	.51	.65	-.02	.17	-.14	-.00	.09
DFF	-.24	-.63	.26	-.09	-.52	.09	.04
MTO	.76	.18	-.12	-.03	-.06	-.13	.01
MHT	.50	.29	.02	.03	.37	-.27	.50
MFT	-.61	.02	.25	-.02	-.18	-.52	.03
AFT	.43	.02	.01	-.07	-.05	-.13	.77
AMD	-.05	.02	-.01	-.93	-.09	.05	.21
PYP	.94	.08	.01	-.06	.09	.00	.05
SLT	.36	-.87	.04	.10	.07	-.06	.07
GOP	.79	.52	.08	.04	-.01	.04	.19
ELV	.55	.74	.05	-.10	.14	-.00	.21
ALS	.83	.44	.02	-.01	-.00	-.06	.14
SLO	-.28	.09	-.66	.26	-.12	.41	.13
PDX	.08	.01	.10	.05	.89	.02	.10
TDX	-.12	.08	.88	-.00	-.07	.06	.09
DRN	.11	-.01	.88	.05	.10	-.13	.05
NPS	.12	-.12	.11	.02	.02	-.85	.02
VGP	-.16	.22	.14	.18	.23	.27	.56
% of Accumulated Explained Variation	.38	.44	.59	.68	.73	.78	.81

and AJS (.95). It is also a geophysical component as 3 variables, PYP (.94), GOP (.79) and ELV (.83) have high component loadings.

The second component might be called a "temperature-soil-vegetation component." Among the temperature variables with high loadings are AAT (-.86), AJT (-.83), AMT (-.85) and DLF (.65). The variables SLT (-.87) and VGP (.75) make up the soil-vegetation elements of this component.

The five remaining components are less important, accounting for 4%, 3%, 3%, 3% and 2% of the total variance. They might be called "exposure, temperature-drought, frost-slope, freezing temperature-drainage and temperature-number of plants per stand, components".

Results for the Large Sample. The estimated equation for flower color and the environmental variables, showing only those parameters significantly different from zero at the 5% level, using the t test, is

$$R^2 = .38$$

$$CLR = 9.05 - 0.04\ AJS \qquad (2)$$

Thus, the variable AJS, average January sunshine, is the only entered variable shown to be significantly associated with flower color in an inverse manner. This indicates that as winter sunshine increases the flower colors become lighter. This progression is what would be expected. The lighter flowers are found in the drier and clearer west and darker flowers are found in the more humid eastern portion of Oklahoma.

The effects of insolation on biological organisms are being investigated by an increasing number of researchers. Bainbridge, Evans and Rackham (1966) present a number of papers on the ecological effects of light. Among these is a paper by A.P. Hughes which stresses the importance of light upon plants; the response of flowers to light is stressed. While the flower color - light association is not considered in detail, a number of other relations are examined i.e. the relationship between light quality and duration on blooming etc. Results of this kind seem to indicate that a number of relationships between light quality and flowering exist and should be investigated further. This work also indicates that the relationships involved are complex and require very specific on-site analysis if one wishes to deal with cause and effect.

In light of the considerations presented, additional research on the relationship between flower color in _A.t. interior_ and the average number of hours of January sunshine would seem to be indicated.

The estimated equation for flower color and the four environmental components, showing only those parameters significantly different from zero at the 5% level, using the t test, is:

$$R^2 = .36$$

$$\text{CLR} = 2.42 + .60 \text{ Comp } 1 + .27 \text{ Comp } 4 \qquad (3)$$

Thus component one, a moisture component and component four, a winter humidity-vegetation component are shown to be significantly associated with flower color.

The relationship between the first component and flower color is consistent with results achieved earlier (see the flower color trend surface map and text found in the beginning of this chapter). This component combines two moisture variables with direct associations, AAP, average annual precipitation and AJP, average January precipitation, with a third moisture variable, AAS, average annual snowfall. The third moisture variable and the two insolation variables have inverse or negative relations. The two insolation varaiables are AJS, average January sunshine and JLS, average July sunshine. The insolation variables are somewhat indirect in their implications to moisture conditions. This first component accounts for 29% of the explained variation.

The association between component four and flower color is less important in that this component adds only 6% additional variation. Component 4 is positive winter humidity-vegetation component which combines variables AJH, average January humidity and VGP, vegetative province. Wintertime conditions seem to be important for this organism as is shown by component 4. This winter condition association will be reemphasized a number of times in the analyses to follow.

Results for the Small Sample. The estimated equation for flower color and the small subsample of environmental variables, showing only those parameters significantly different from zero at the 5% level, using the t test, is

$$R^2 = .67$$

$$CLR = 3.37 + .49AJH - .47JLH + .14GOP - .09MFT \quad (4)$$

which indicates that flower color is associated with four environmental variables. The first variable, AJH, average January relative humidity, has the strongest association. It accounts for 52% of the variation in flower color. The other 3 account for an additional 14%. Since the first variable seems to be the most important, it will be discussed first.

The negative relationship between AJH and flower color is similar to that for the association of color with sunshine (AJS). Its explanation is as follows. Biologists have observed, on numerous occasions, that organisms whose range extends over both humid and arid areas exhibit coloration patterns similar to that of A.t. interior. The individuals from humid areas are darker in color than from arid regions. This response pattern is called Gloger's rule. (Clarke, 1954, p. 126) While this principle has been generally applied to mammals, birds and insects, it may also apply to other organisms such as plants. Such associations may not be well known due to the general lack of spatial studies. In any case, the logic of such an assumption is as follows: generally, arid and semiarid areas, like much of Oklahoma, support fewer plants per unit area than do more humid areas. The plants which are supported are under greater stress from herbivores in the drier areas, and mechanisms which reduce the probability of being consumed by steer, horse or natural herbivores would give a survival advantage to such an organism. The lighter flower color possessed by the A.t. interior in dry portions of Oklahoma might make individual plants less conspicuous and less likely to be eliminated by grazing animals. Those of a darker shade might be more conspicuous, be consumed in greater quantities and thus have a lower survival potential than the lighter flowered plants. Thus, over a considerable time period, the lighter (yellow) colored plants would become dominant in the arid areas. In addition, since pollination in A.t. interior is accomplished by insects of several orders, such as Hymenoptera, odor is probably the chief lure and the color may make little difference in pollination success.

In the case of the darker colors which predominate in the eastern, more humid, portions of the state; the richer colors may be an advantage in attracting pollinators. It may be that plants compete for the attention of pollinators in the more lush eastern portion of the state and thus deeper color is an aid in survival and reproduction.

It is certain that a number of other explanations of the association between flower color and humidity are possible. The fact that winter humidity from this analysis and winter insolation from the previous section emerge as being related with flower color is interesting in that both variables involve a period of cold conditions. It may be that winter is a time of greater biotic stress for perennials than is generally thought. Polunin's observation that "Winter is normally a resting period when activity is at a minimum in temperate regions, though many plants are active at lower temperatures...some even below 0°C," may be correct and conditions during the so-called dormant period need further investigation. (Polunin, 1960, p. 285)

In addition, it may be that the temperature-humidity gradients may be steeper in winter. This would make the contrast between the dry-cool west and the warmer-more humid east even greater during the winter period.

The other 3 variables which were found to be mildly associated with the flower color pattern of A.t. interior are generally related to the first and most important environmental variable. JLH is a humidity variable with somewhat the same factors relating it to flower color as does AjH. MFT, a measure of the amount of freezing precipitation in an area is a winter condition variable and may need to be investigated along with other winter (dormant period) conditions. The generally unfavorable effect of freezing conditions and precipitation are well known. (See Koeppe & DeLong, 1958, p. 71)

The final variable, GOP, is a measure of the geological environment in which the organism must survive. The indirect, but substantial relation between geology and vegetation is well documented. "Many of the...plant maps show patterns of distribution that can be correlated principally with (a) geological map..." (Seddon, 1971, p. 56)

The form of bedrock in a given area is known to have an effect on water balance. Areas with porous rock have higher infiltration rates than areas with less porous substrata. Physiological aridity is often the result of rapid infiltration. Effects of this can be seen in many areas of Oklahoma, e.g. the Arbuckles, Ouachitas etc. Since water-humidity variables appear to play an important part in the distribution of flower color in A.t. interior, such variables should be stressed in further studies.

The equation which is estimated for flower color and the subsample components, showing only those parameters significantly different from zero at the 5% level, using the t test, is

$$R^2 = .43$$

$$CLR = 3.14 - .79 \text{ Comp } 1 \qquad (5)$$

thus flower color is associated with component 1, a moisture-geophysical component. This component combines several high, inversely related, moisture variables such as AAP, average annual precipitation, AJP, average January precipitation, AJH, average January relative humidity and JLH, average July relative humidity. These inverse moisture relationships are consistent with previous results in that moisture increases are accompanied by color scores decreases; the colors shift from light to dark. This suggests that darker colors are in the moist east while the lighter colors are found in the semi-arid west.

In the case of the geophysical elements of component one, variables PYP, physiographic province, and GOP, geological province show a high direct relationship. These two factors are obviously closely related to each other and it is not surprising that they covary and have a relationship to flower color. Vegetative patterns have been found to be associated with these same factors in a number of other regions in Oklahoma. For example, the early geologists who worked in the Arbuckle Mountain area were known to estimate geologic factors using vegetative and physiographic clues. Their maps have been shown to have been surprisingly accurate by modern workers who use core analysis techniques (Conversation with Dr. G. Goodman).

Migration may also be considered to explain the flower color pattern in <u>A.t. interior</u> (See Model, Figure 2). It

CONCLUSIONS

Flower color has been found to be an independent component that does not covary with other plant characters. This would seem to indicate that flower color is an ideal character which lends itself to direct analysis.

It appears that specific site data are more useful than generalized environmental data in determining the association between flower color and the environment. The stronger associations shown in the subset analysis are evidence of this. This seems to indicate that local factors are more important in explaining the flower color pattern in *A.t. interior* than are the general environmental ones. This result may be due to the more detailed and accurate data which were gathered in the field for the smaller sample. The field samples were collected at the same time that detailed microenvironmental data were recorded. In the case of the herbaria samples, much of the environmental data had to be inferred from specimen sheets which varied in the detail with which local conditions were recorded. These factors would appear to account for the stronger environmental-flower color associations which were observed in this analysis.

In discussing local environments it is appropriate to note here that the habitats which support A.t. interior are somewhat similar across the state. This plant is found along roadsides, on embankments and in many kinds of waste places. The numbers of plants in western Oklahoma were significantly below those found in the eastern portion of the state. This agrees with the results reported by Woodson (1964). A habitat factor which emerged from this study is that A.t. interior is found almost exclusively along water courses in the western area of the state. This may be related to the greater abundance of water in these habitats or it may be due to the agricultural practices in much of this area. The mechanized equipment used in wheat production may disturb the normal roadside and other favorable sites so that A.t. interior survives only along the relative undisturbed stream beds. As most wheat fields are unfenced, machinery may enter and leave the cultivated area in a variety of places whereas machinery is much more restricted in its movements in the fenced eastern portion of the state.

An additional factor which might have influenced the more favorable result for the subsample is a kind of spatial bias. It could be introduced if the distributional pattern of the subsample corresponded to the distributional pattern of particular combination of environmental-plant variables. A visual inspection of the subsample distributional pattern and the patterns of the various variables involved indicates that this kind of bias does not exist. In addition, the subsample appears to be large enough and widely distributed enough to be adequately representative of the major portion of the state and to provide a reliable picture of geographic variation in Oklahoma.

SUMMARY

In summary, this chapter has described the results of the analysis of flower color in _A.t. interior_ in Oklahoma.

It presents the results of trend surface mapping; regressions of both the full and subsets of plant and environmental data; the component analysis of both sets; and the regression using component scores of the two sets of environmental data.

Flower color patterns are shown to be distributed as suggested by Woodson as well as being related to general moisture factors, geophysical variables and winter season conditions.

In general, then, results of this kind serve a major function of narrowing the field of inquiry to those specific variables which are strongly associated with a given spatial pattern. Succeeding studies can then focus on these known associations and discover specific answers to the "why" of plant character-environmental interrelations. While the data from a particular study may be species specific, generalizations to other species is both practical and appropriate. Generalizations, which evolve from quality research, are important to science and are generated following a number of studies of this type.

CHAPTER FOUR

AN ANALYSIS OF THE GEOGRAPHIC VARIATION OF MORPHOLOGICAL CHARACTERS OTHER THAN COLOR

This chapter reports on an analysis of the spatial trends in 19 additional plant characters as well as relating them to environmental variables and to environmental components. Migration evidence, in the regression residuals for the plant characters on the environmental measures, is also examined.

MORPHOLOGICAL VARIATION AND ENVIRONMENTAL FACTORS

Other less conspicuous morphological characters of _A.t. interior_ also possess distinctive geographic variation patterns. Moreover, such variation may be attributable to environmental factors. The existence of such relationships were suggested in the framework presented earlier. Detection of such variation requires, however, careful laboratory measurement, something not possible in the field. Thus geographic variation might well exist but go undetected for lack of the kind of careful scrutiny provided in studies of this type.

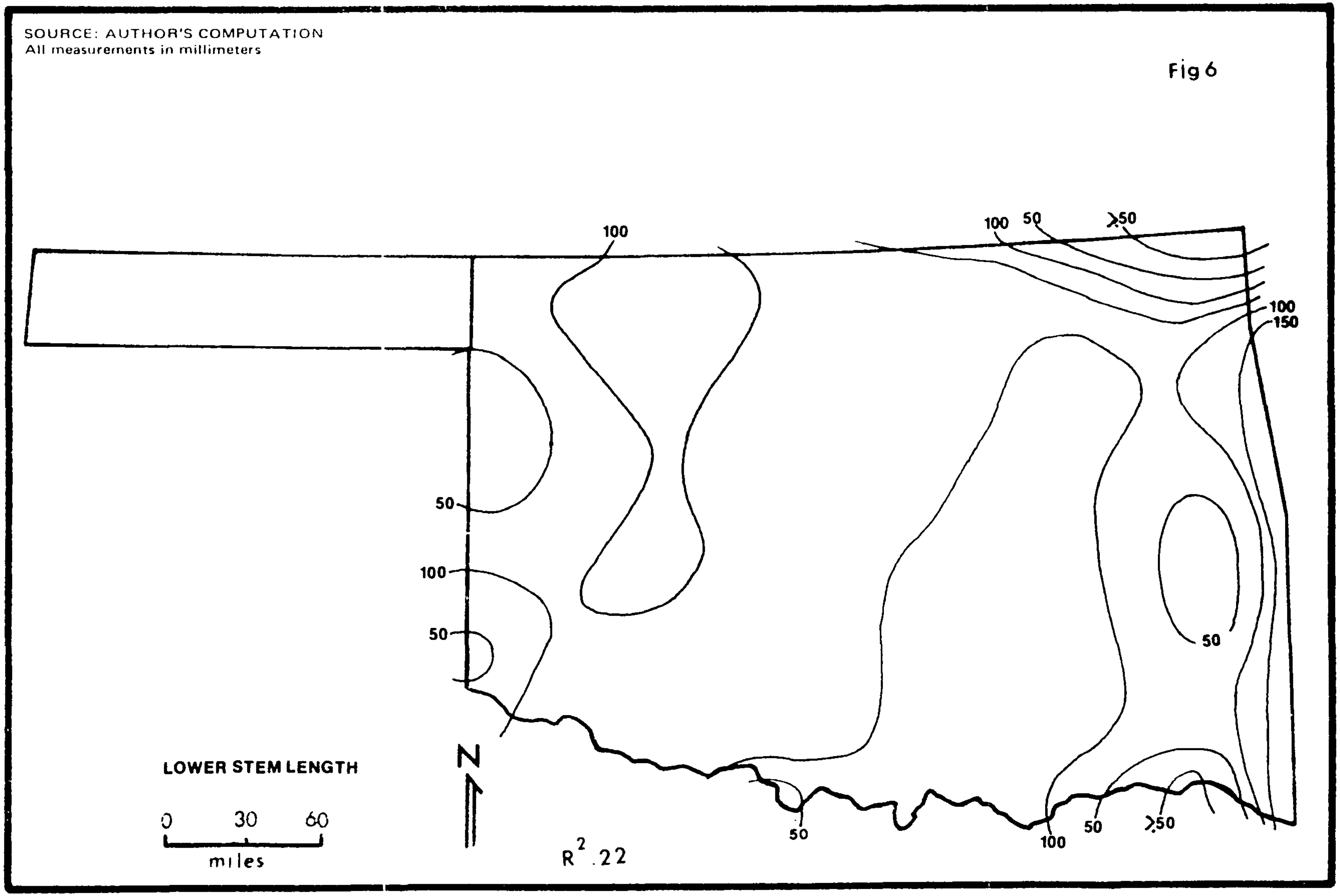
In a preliminary examination of the plant character intercorrelation matrix it was noted that 5 plant measures were highly interrelated and thus provided the same basic information as others in the set. To save computational time and effort they were not used in the remaining analysis.

Identifying Spatial Trends

Figures 7 to 25 illustrate the sixth degree trend surfaces estimated for each of the 19 plant characters. (See Chapter 3 for a discussion of trend surface mapping.)

A general examination of the complete set of maps reveals several distinct phenocontour patterns. The patterns are vertical, horizontal and a third which combines the two. The first pattern can be seen on the trend surface maps for variables LSL, BRL, BRW and SPL. The opposite or horizontal pattern can be seen on the maps for variables PLL, LFL, PTN and SPW. The remaining maps appear to have a combination of both vertically and horizontally orientated phenocontours.

Vertical banding, at first consideration, is the pattern which appears to correspond to moisture factors. The first map, of LSL, shows that lower stem length is greatest in the moist eastern part of the state. This would not be unexpected as longer stem/total height ratios are common in moist areas.


SOURCE: AUTHOR'S COMPUTATION
All measurements in millimeters
Fig 6
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100
50
>50
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150
50
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100
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LOWER STEM LENGTH
0 30 60
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R2 .22

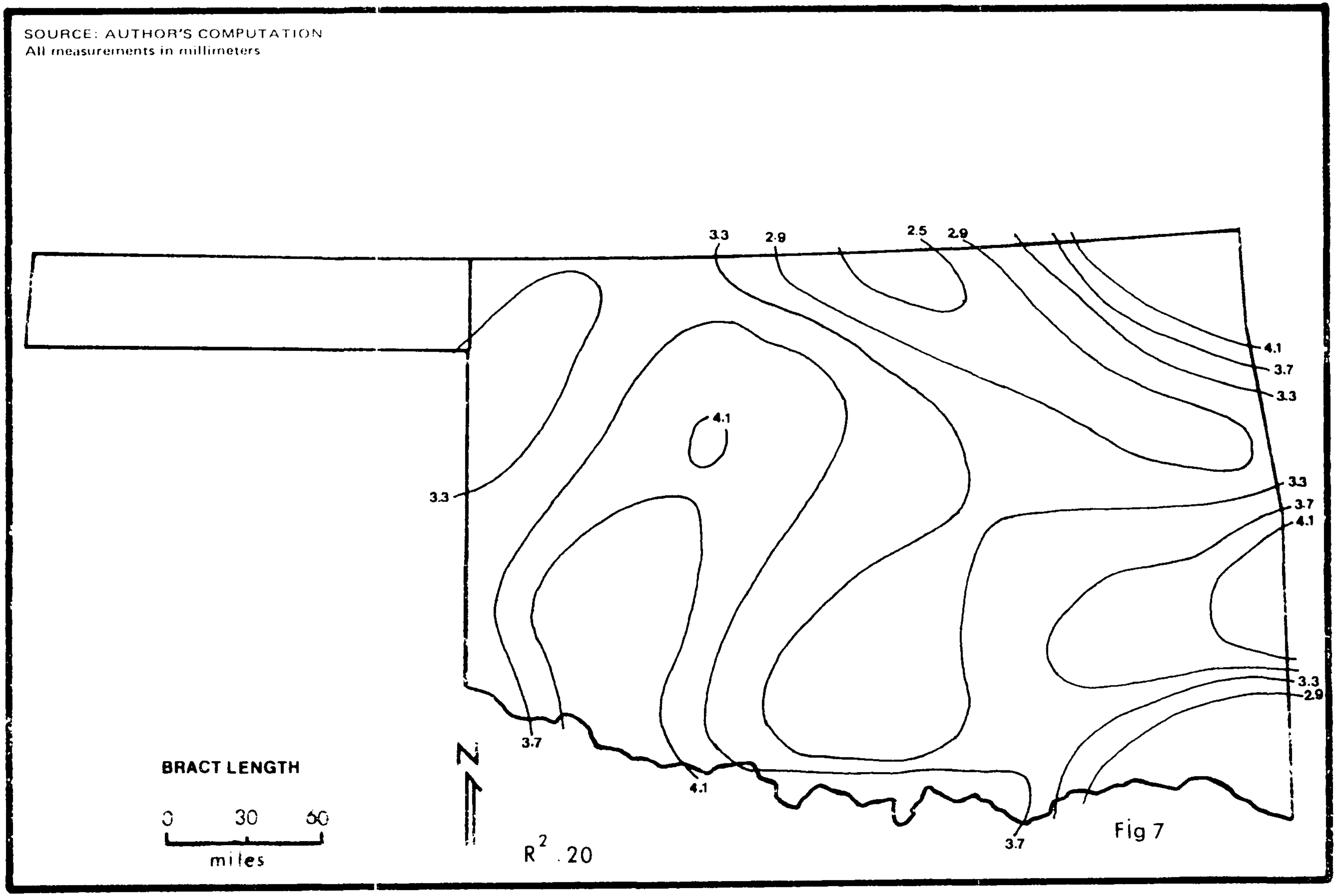
(Hidore, 1973, p. 302) The other variation is more complex and is less easily associated with the environment.

The remaining vertically banded characters, BRL, BRW, SPW and SPL are flower parts. In general, flower parts appear to be larger in the east and smaller in the west. This may also be related to the moisture conditions, which favor such modification.

The BRL and BRW maps show long-wide bracts in the east and shorter-narrow bracts in the west. This seems to contradict the general trend toward longer-narrower appendages in arid areas. (Meyer et al, 1973, pp. 455-459) This apparent contradiction appears to result from the difference in overall size rather than a change in shape.

SPL, sepal length, also exhibits this pattern. A difference in size, between moist and dry areas makes it appear that an elongated shape is found in the east when its overall size that is actually involved.

The first map in the group of horizontally banded maps is the map of PLL (plant length). The shortest plants, as shown on the map, are found in the area along the northeastern border with Kansas, while the tallest are found in the north-


SOURCE: AUTHOR'S COMPUTATION
All measurements in millimeters
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0 30 60
miles
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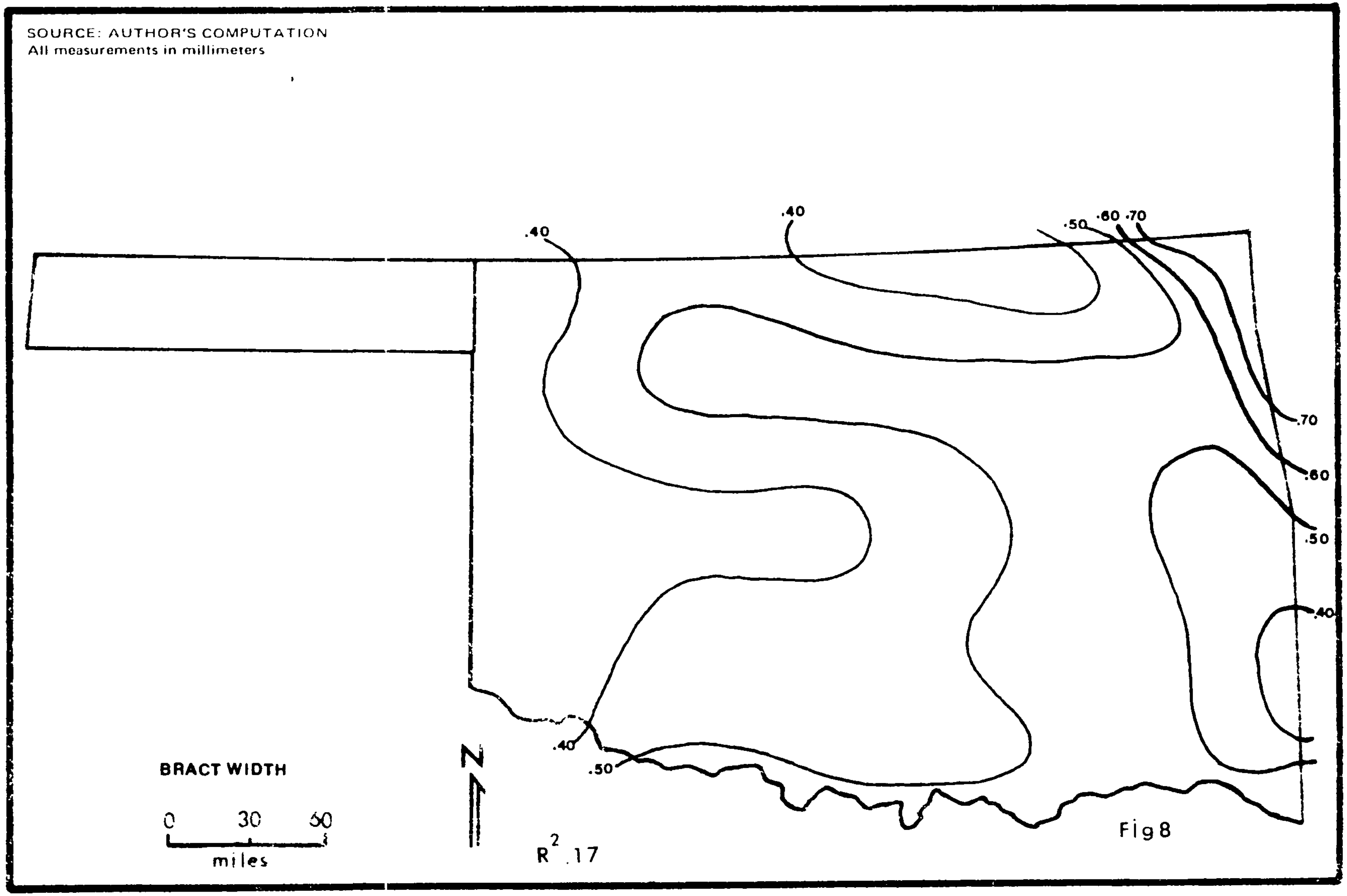
R² .20
3.3
2.9
2.5
2.9
4.1
3.7
3.3
4.1
3.3
3.3
3.7
4.1
3.3
2.9
3.7
4.1
3.7

Fig 7


SOURCE: AUTHOR'S COMPUTATION
All measurements in millimeters
.40
.40
.50
.60
.70
.70
.60
.50
.40
.40
.50
BRACT WIDTH
0 30 60
miles
N
R 2 .17
Fig 8

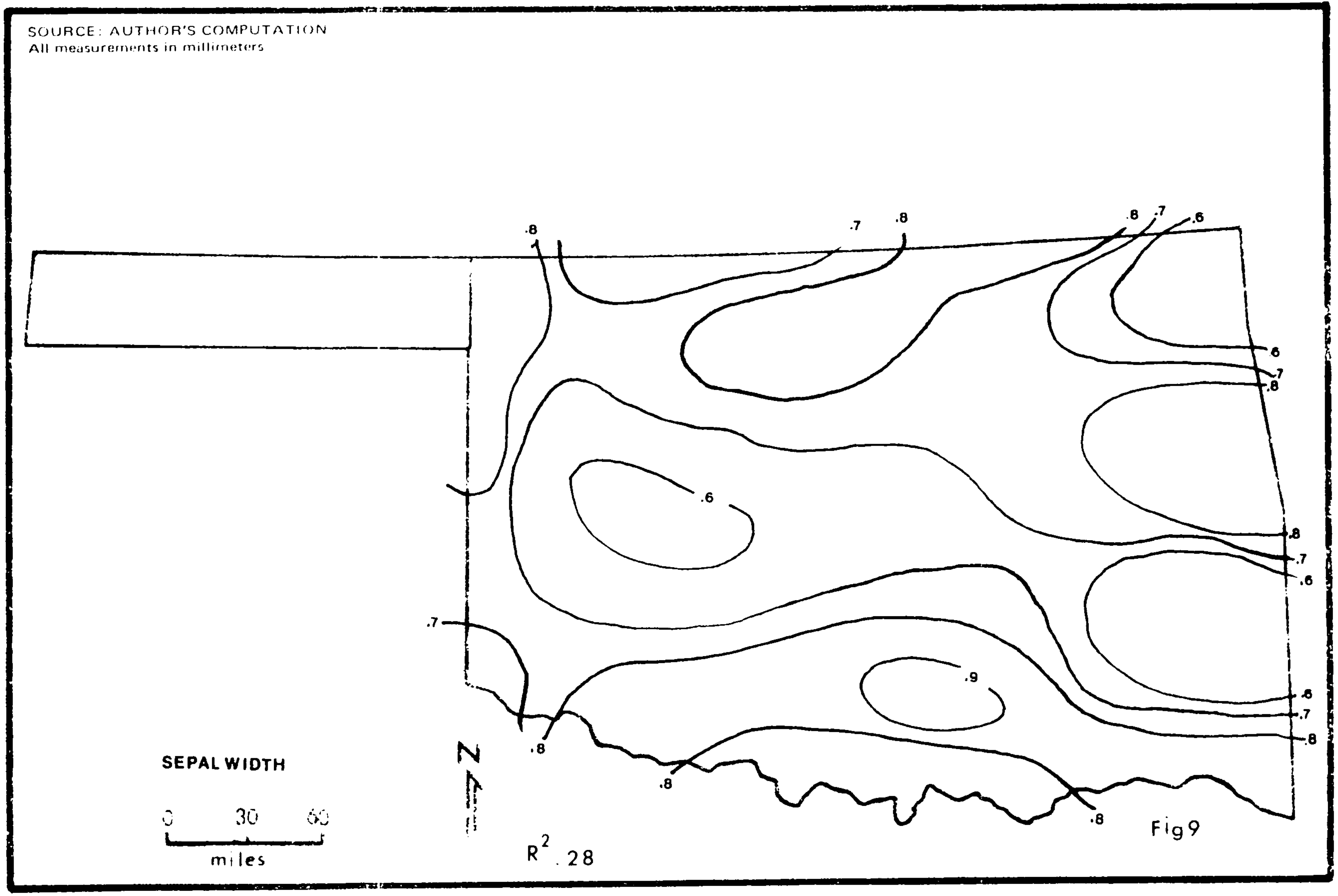
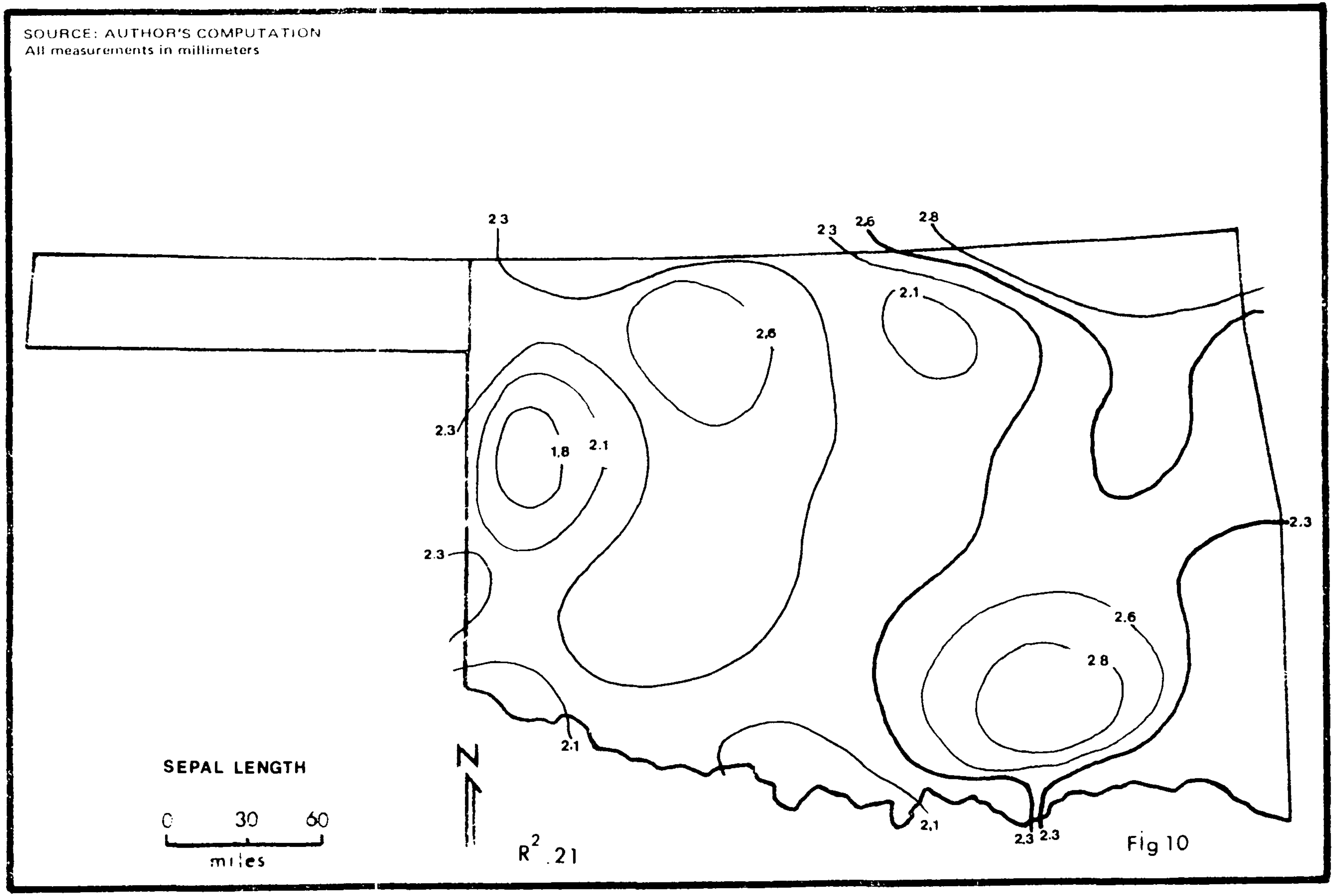
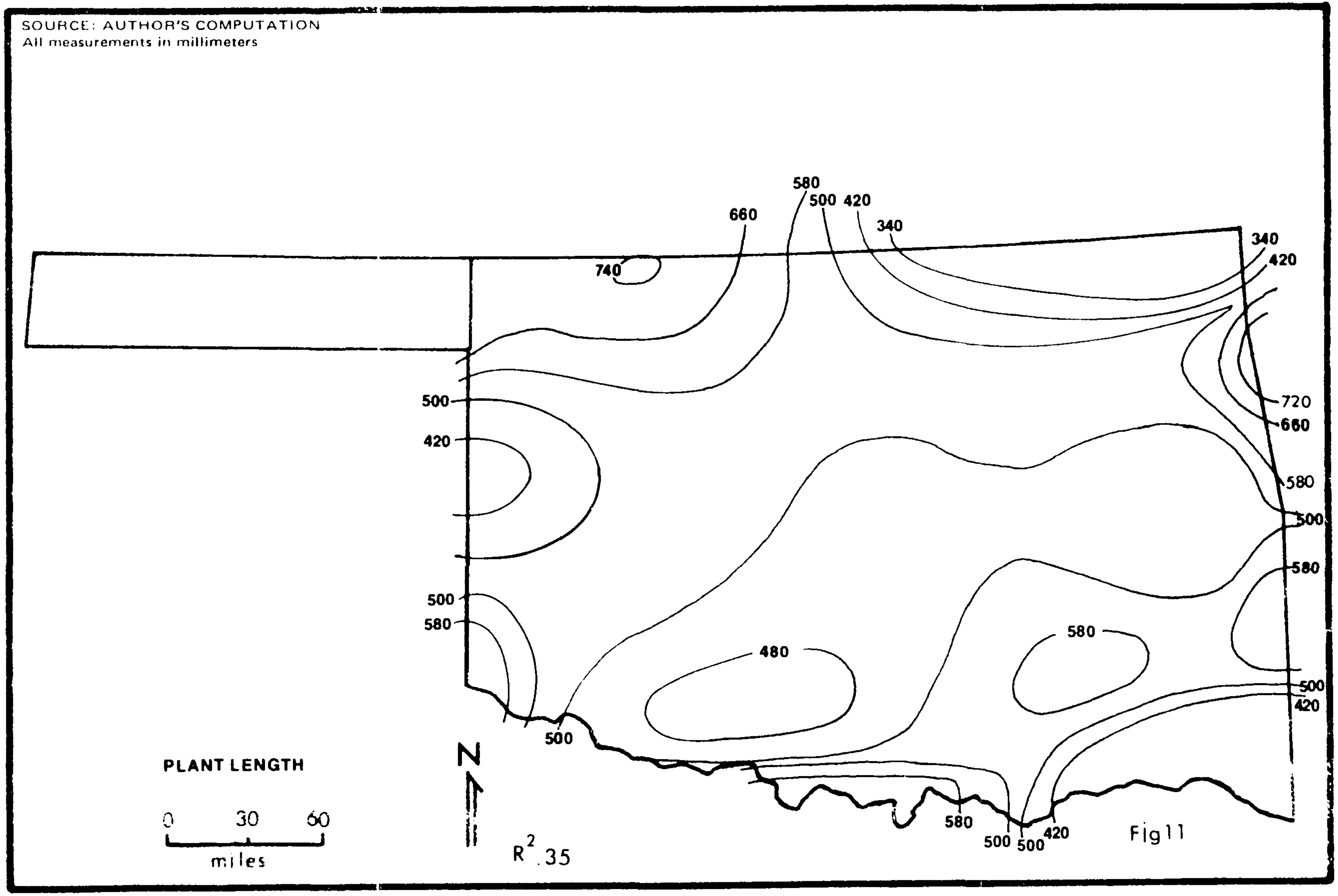

SOURCE: AUTHOR'S COMPUTATION
All measurements in millimeters
.8
.7
.8
.8
.7
.6
.6
.7
.8
.6
.8
.7
.6
.7
.9
.6
.7
.8
.8
.8
.8
SEPAL WIDTH
0 30 60
miles
N
R^2 .28

Fig 9


SOURCE: AUTHOR'S COMPUTATION
All measurements in millimeters
2.3
2.3
2.6
2.8
2.1
2.6
2.3
1.8
2.1
2.3
2.3
2.6
2.8
2.1
2.1
2.3
2.3
SEPAL LENGTH
0 30 60
miles
N
R² .21
Fig 10


SOURCE: AUTHOR'S COMPUTATION
All measurements in millimeters
580
500 420
660
340
340
420
740
500
420
720
660
580
500
580
500
580
580
480
500
420
500
PLANT LENGTH
0 30 60
miles
N
580
500 500
420
Fig11
R^2 .35

western and southwestern portions of the state. This would seem to indicate that tall plants do better in the drier portion of Oklahoma. This may indicate that the tall, robust plants are better able to survive the more rigorous climate found in these areas.

LFL, leaf length, corresponds somewhat to the same patterns of variation as the previous variable. As might be expected, taller, more robust plants tend to have larger appendages than shorter ones. The shortest leaves are found along the southwestern and western edges of the state, on the taller plants.

The third map indicates that the southeastern counties, in the Ouachita Mountains, have the largest number of pedicels (PTN). This variable is a direct measure of the number of flowers per head and one would expect that the mildest and most humid portion of Oklahoma would be favorable to flower formation. If competition for insect pollinators is a factor in survival, those with many flowers would do better. It may be that such competition is a strong factor in the southeast and plants with many flowers may have a distinct advantage.

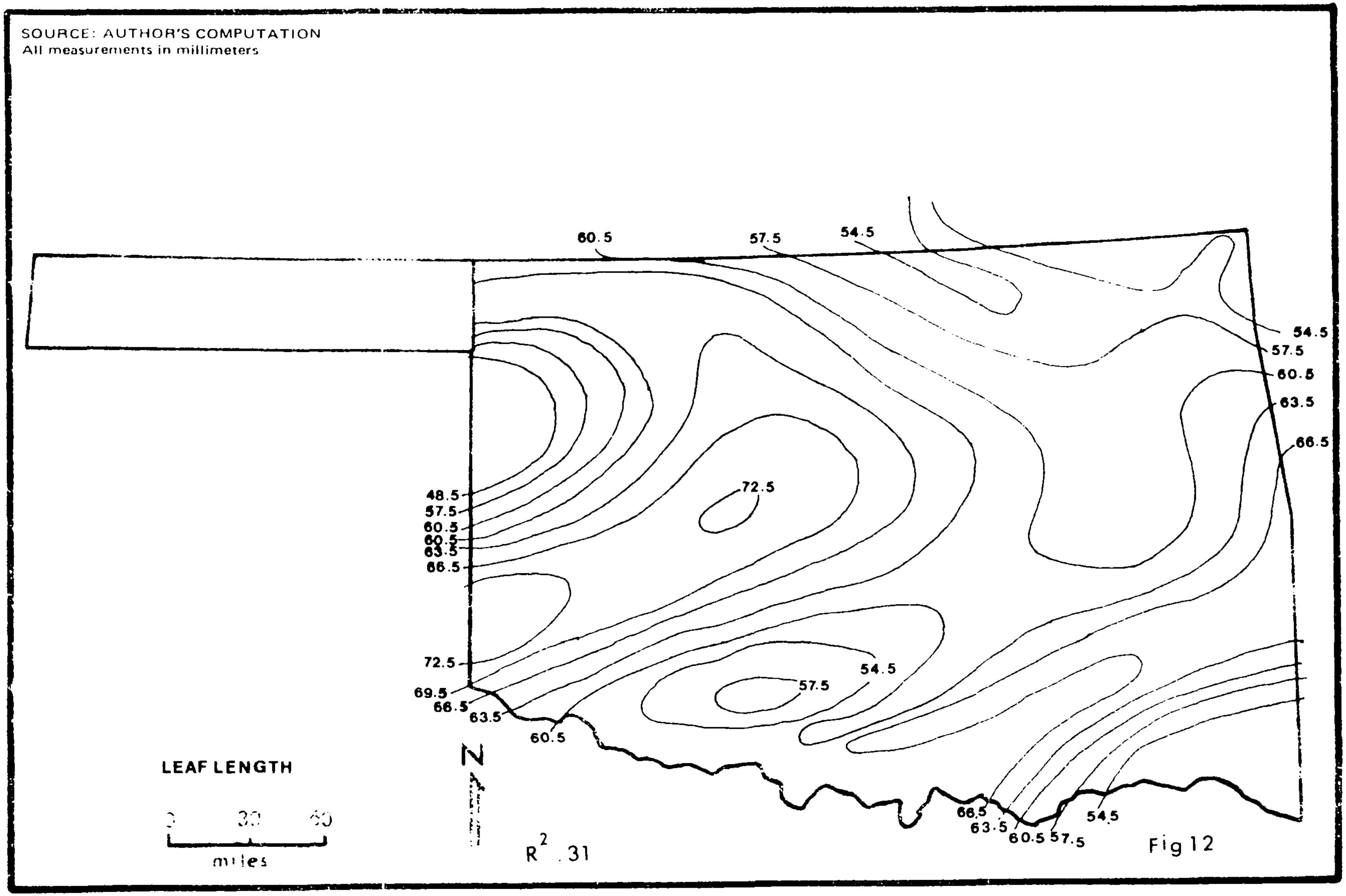

SOURCE: AUTHOR'S COMPUTATION
All measurements in millimeters
60.5
57.5
54.5
54.5
57.5
60.5
63.5
66.5
72.5
48.5
57.5
60.5
60.5
63.5
66.5
72.5
69.5
66.5
63.5
60.5
54.5
57.5
66.5
63.5
60.5
57.5
54.5
LEAF LENGTH
0 30 60
miles
N
R^2 .31

Fig 12

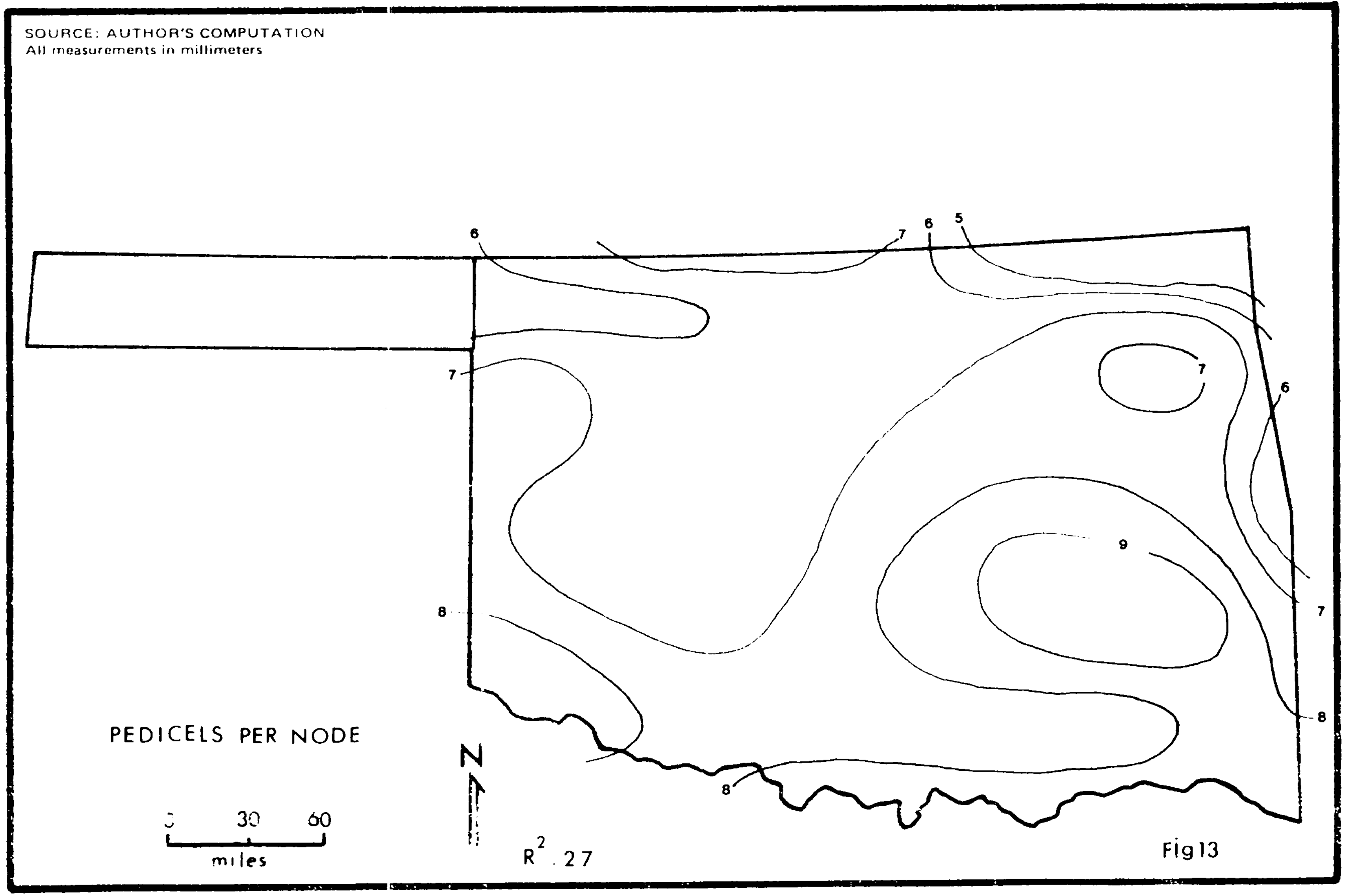
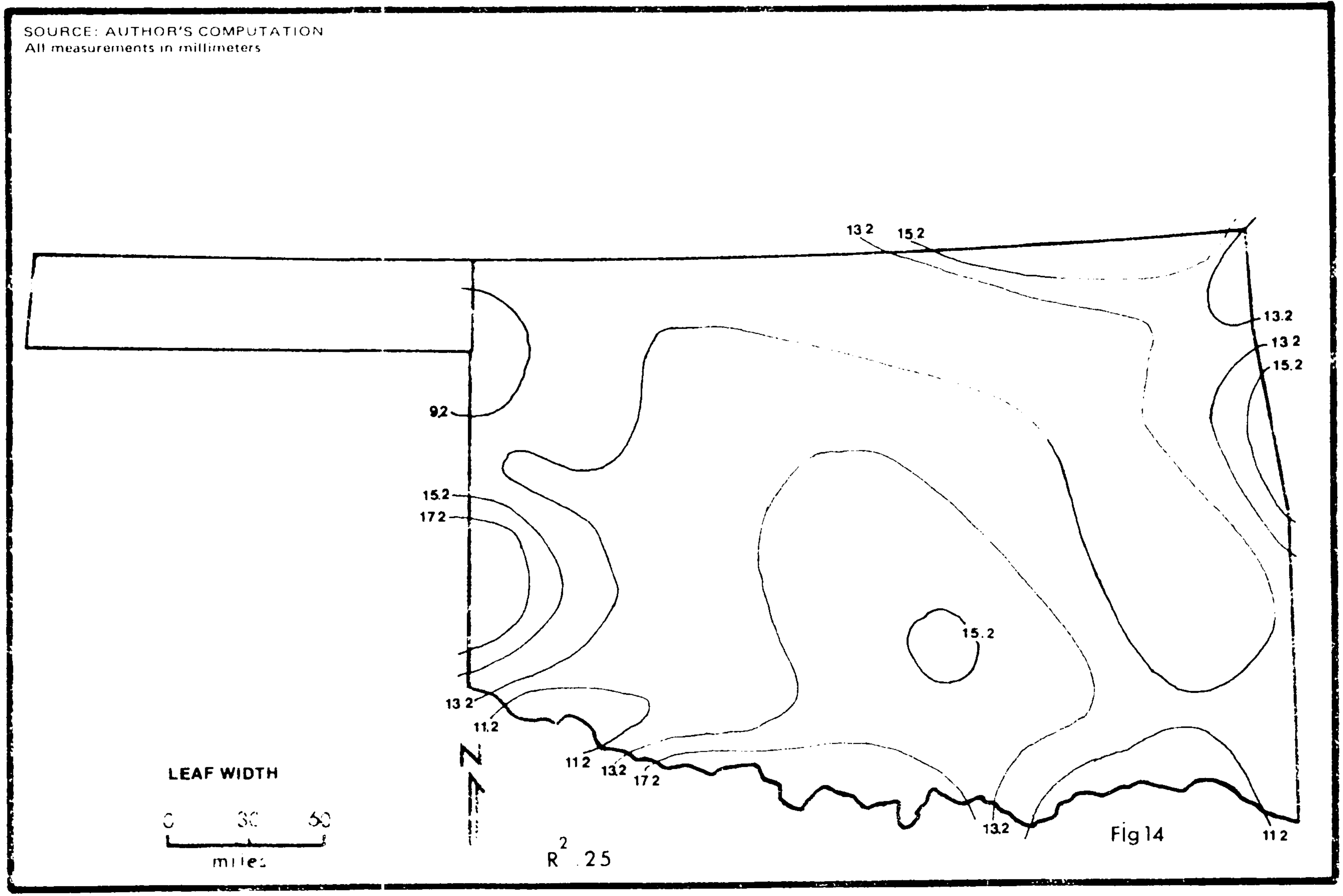

SOURCE: AUTHOR'S COMPUTATION
All measurements in millimeters
6
7
6
5
7
6
9
7
8
8
8
7
PEDICELS PER NODE
0 30 60
miles
N
R^2 . 27

Fig 13

One might also wish to consider length of growing season and its relation to number of pedicels (flowers). In the northeast and northwest where the growing season is shorter, the number of pedicels per node is reduced.

The final group of trend surface maps show a combination of both horizontal and vertical banding. It may be that the factors which affect character quality are different in different regions of Oklahoma. What may be a dominant environmental factor in one area is not as important in another i.e. water factors may be critical in the southwest and west while exposure, length of growing season etc. may be more critical in the north and northwest.

The two variables, LFW and LFR, are obviously related. While the contours do not correspond exactly, the overall pattern is similar. The widest leaves are found in the north and east as are the largest ratios of length to width. The narrowest leaves are found in the west and so have the smallest ratios. This general pattern is probably related to the general trend towards more foliage in moist areas and less foliage in the dry areas.



SOURCE: AUTHOR'S COMPUTATION
All measurements in millimeters
13.2
15.2
13.2
13.2
15.2
9.2
15.2
17.2
15.2
13.2
11.2
11.2
13.2
17.2
13.2
11.2
LEAF WIDTH
0 30 60
miles
N

R^2 .25

Fig 14

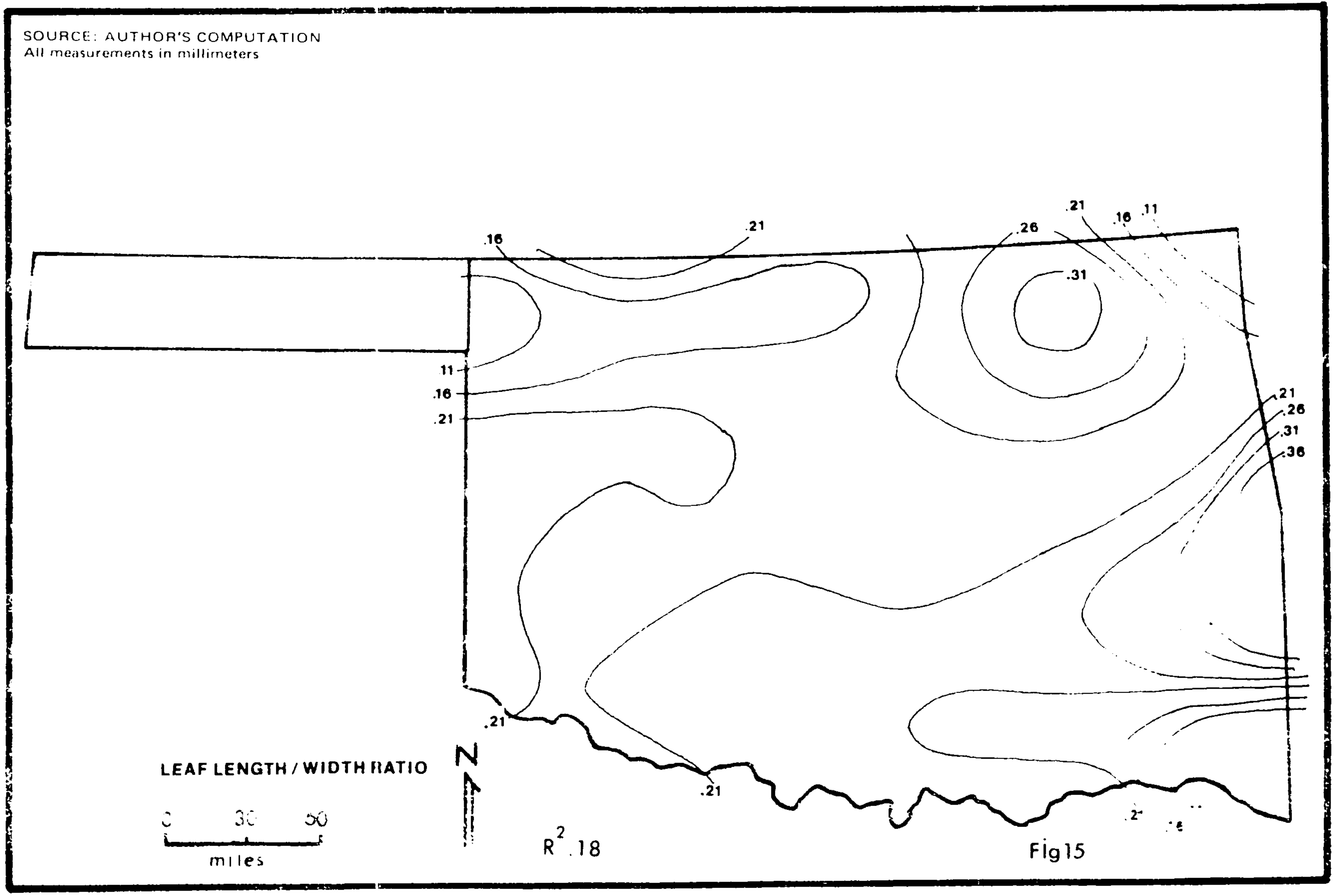

SOURCE: AUTHOR'S COMPUTATION
All measurements in millimeters
.16
.21
.21
.16
.11
.26
.31
11
.16
.21
.21
.26
.31
.36
.21
.21
LEAF LENGTH / WIDTH RATIO
N
miles
R2 .18

Fig15

Another set of variables, PEL and PLW, do not have similar patterns. PEL, petal length, is shortest in the southeast and increases in all directions within the state. PLW, petal width, is greatest in the east and decreases to the west. This indicates that flowers have short-wide petals in the east and longer-narrower petals in the west. These characters may be related to moisture conditions as PEL & PLW vary in a way similar to such previously considered variables as SPL.

Two of the hood measures, HDL and HDW, show the same pattern as other flower part characters. The long, narrow hoods are found in the west while the shorter, wider hoods are common in the east. HDR, hood length-width ratio also reflects this pattern.

Pedicel length (PTL) and length of petiole hair (PTH) have a common pattern. The longer pedicels are found in the southern portion of Oklahoma as are the longer petiole hairs. A dissimilarity is evident in that the longest pedicels are not in the same portion of southern Oklahoma. The longest pedicels are found in the south central and southeast while the longest petiole hair is found in the southwest.

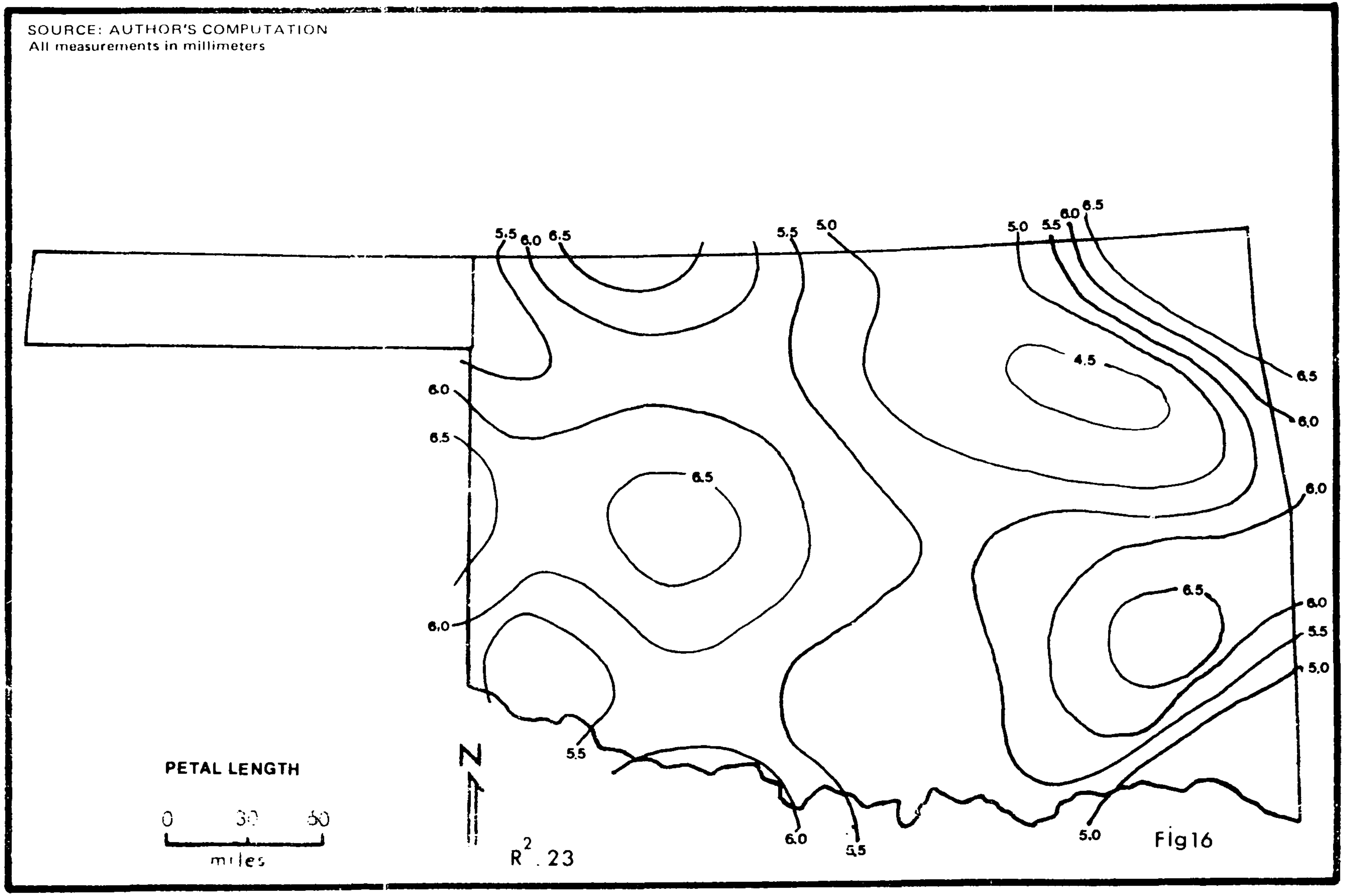
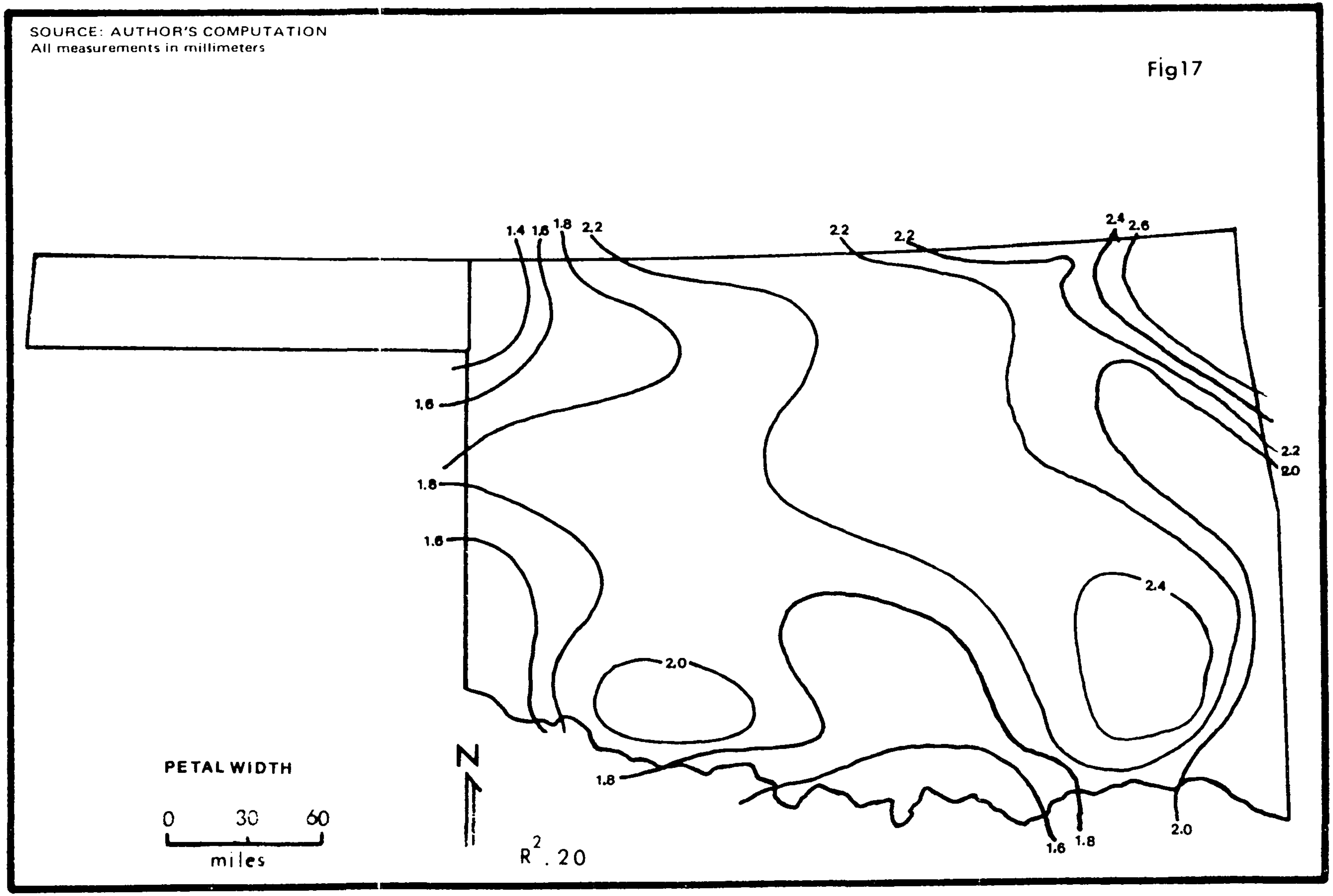
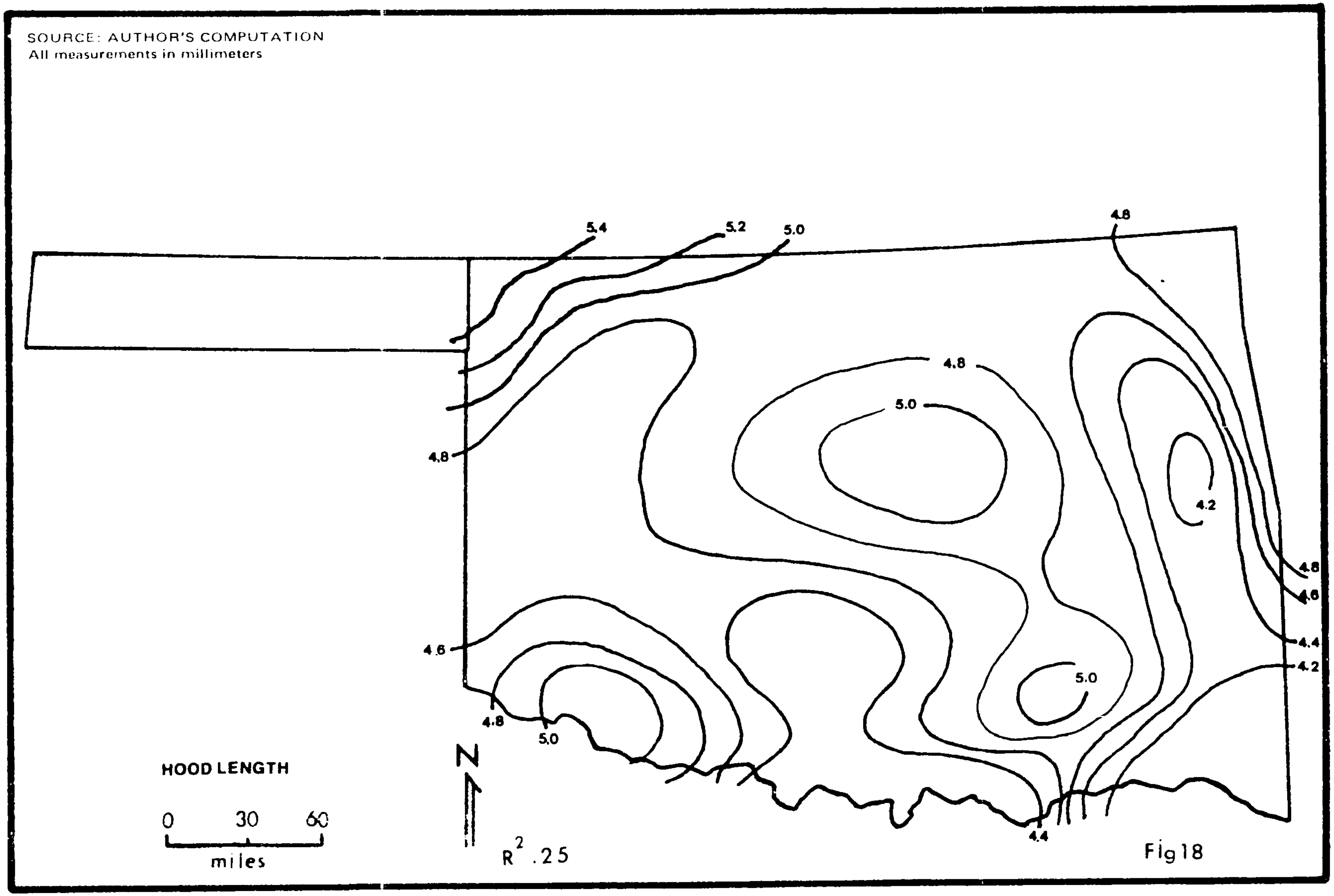
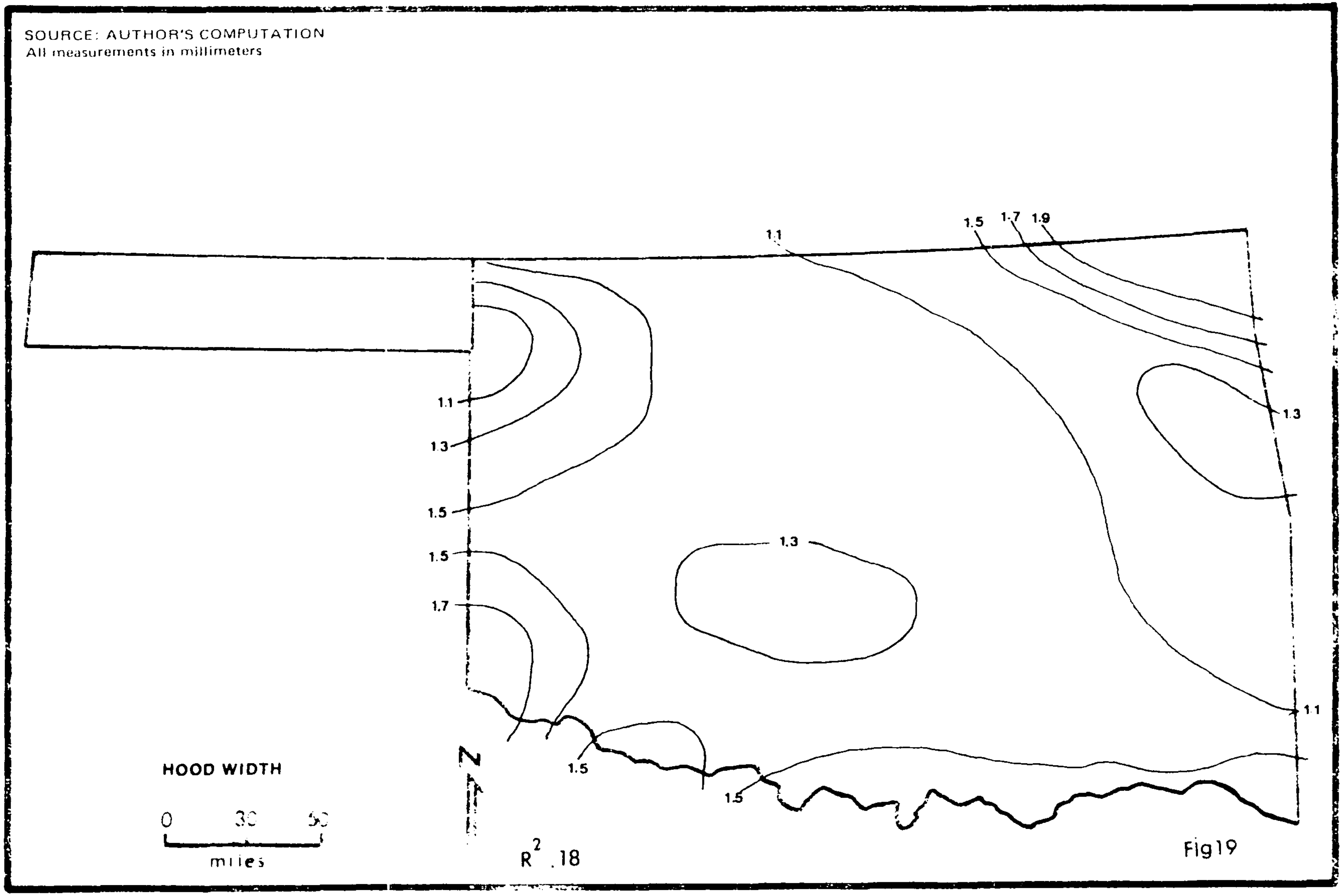

SOURCE: AUTHOR'S COMPUTATION
All measurements in millimeters
PETAL LENGTH
0 30 60
miles
N
R^2 .23
4.5
5.0
5.5
6.0
6.5

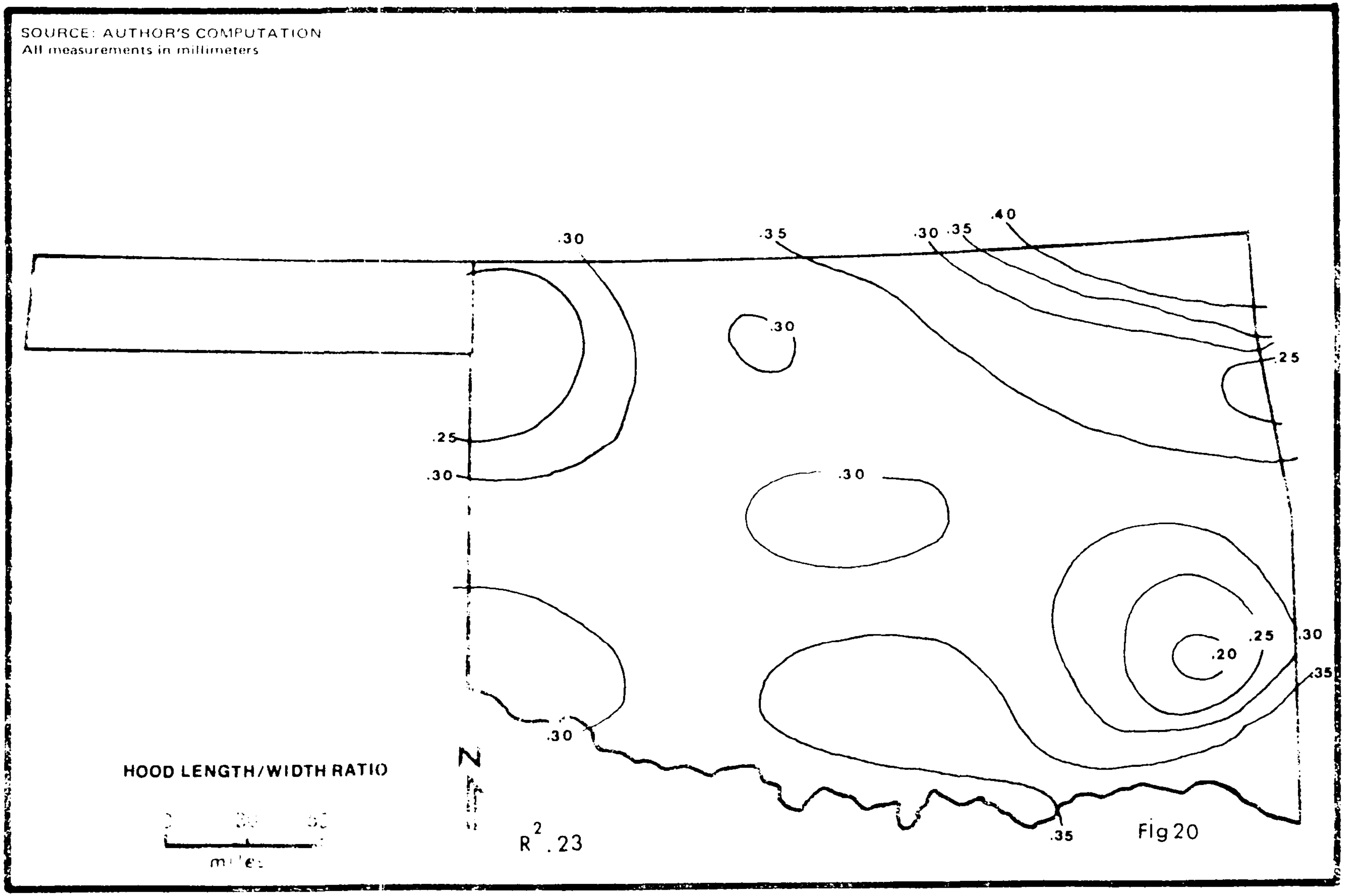
Fig16



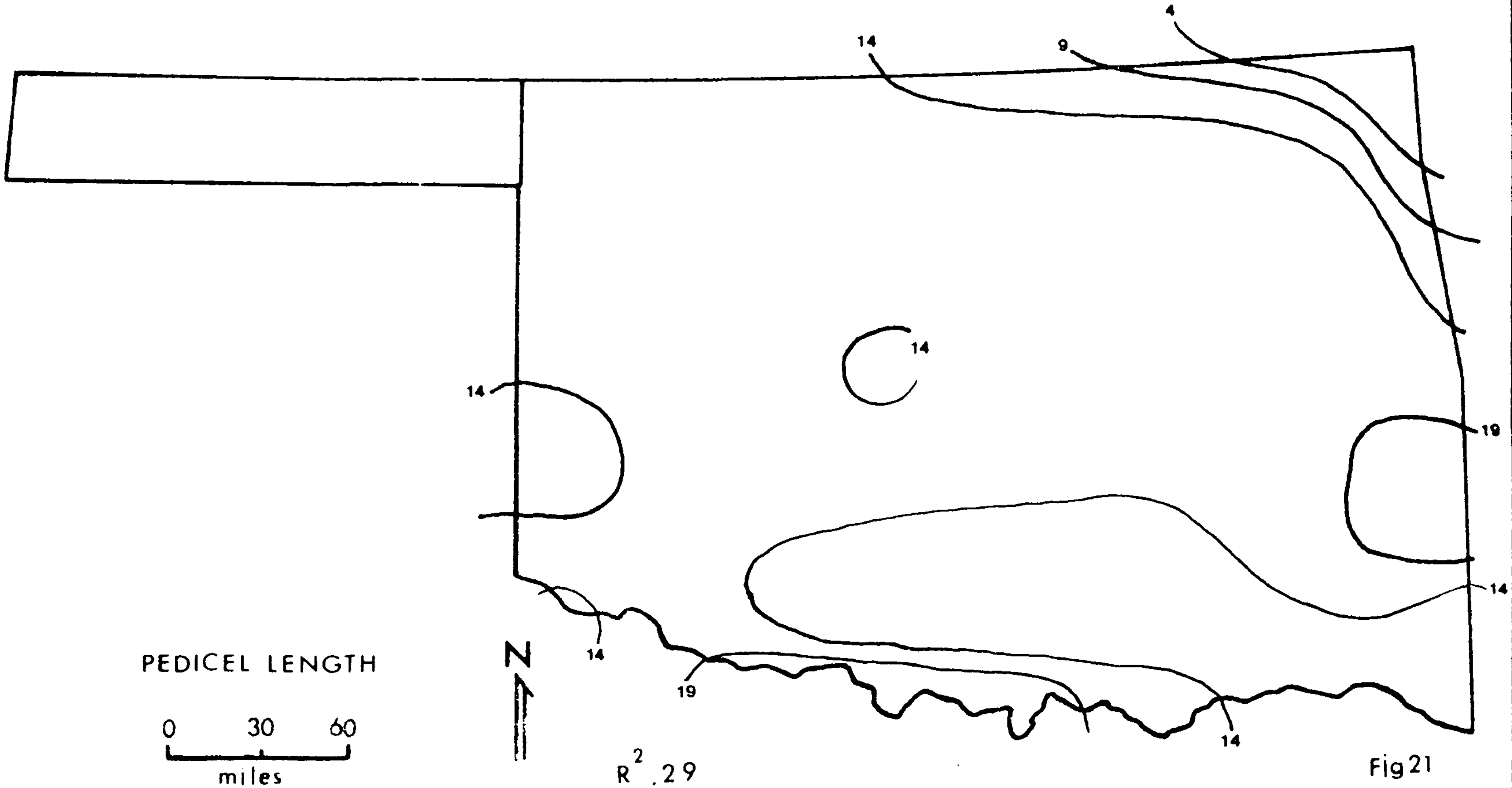
SOURCE: AUTHOR'S COMPUTATION
All measurements in millimeters
Fig17
1.4
1.6
1.8
2.2
2.2
2.2
2.4
2.6
1.6
1.8
1.6
2.2
2.0
2.4
2.0
1.8
1.6
1.8
2.0
PETAL WIDTH
0
30
60
miles
N
R^2 .20


SOURCE: AUTHOR'S COMPUTATION
All measurements in millimeters
5.4
5.2
5.0
4.8
4.8
5.0
4.2
4.8
4.6
4.4
4.2
4.6
4.8
5.0
5.0
4.4
HOOD LENGTH
0 30 60
miles
N
R^2 .25
Fig 18


SOURCE: AUTHOR'S COMPUTATION
All measurements in millimeters
1.1
1.5
1.7
1.9
1.1
1.3
1.5
1.5
1.7
1.3
1.3
1.1
1.5
1.5
HOOD WIDTH
0
30
60
miles
N
R^2 .18
Fig19


SOURCE: AUTHOR'S COMPUTATION
All measurements in millimeters
HOOD LENGTH/WIDTH RATIO
.30
.35
.30
.35
.40
.30
.25
.25
.30
.30
.25
.30
.20
.35
.30
.35
miles
N
R² .23
Fig 20

SOURCE: AUTHOR'S COMPUTATION
All measurements in millimeters



PEDICEL LENGTH

R^2 .29

Fig 21

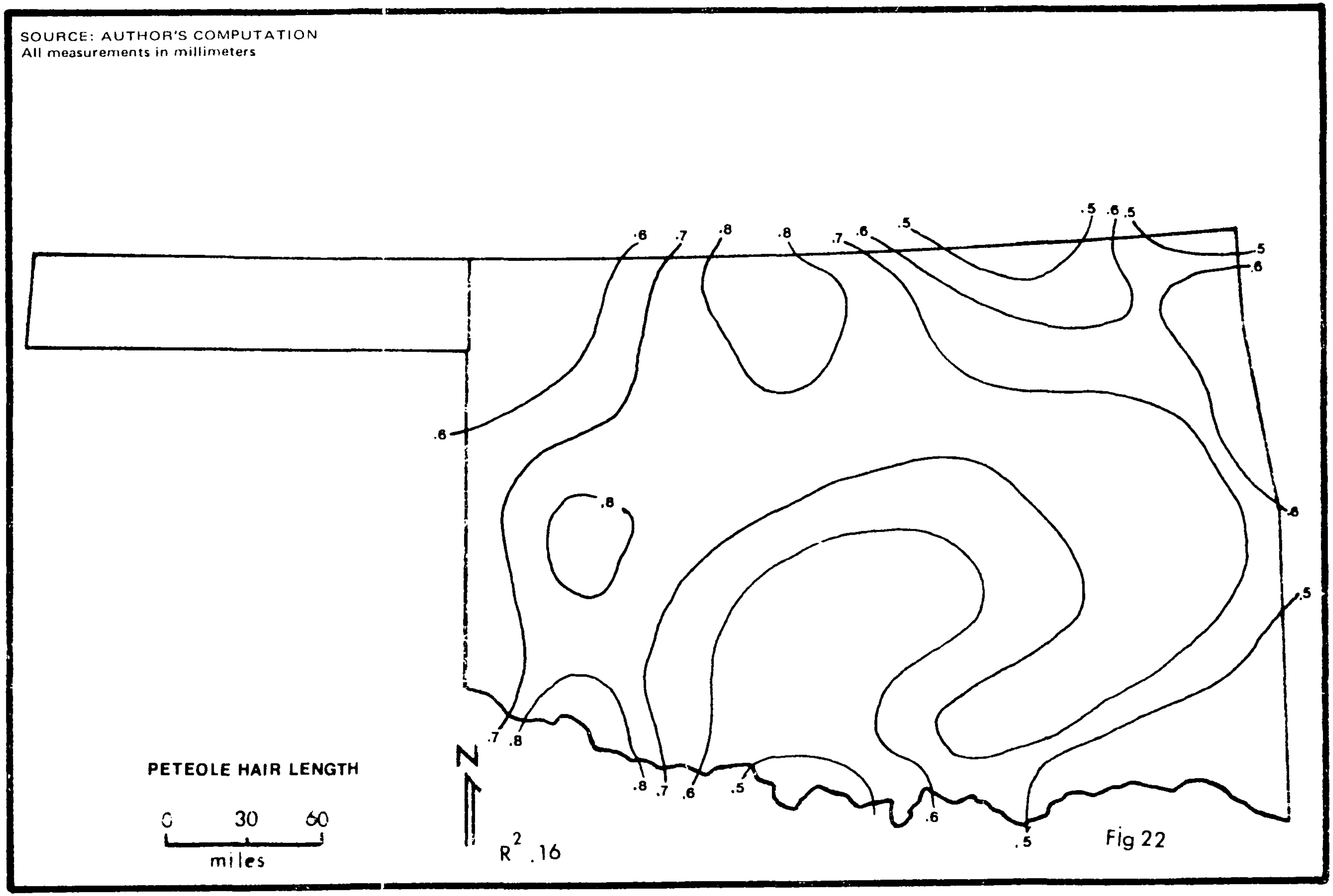
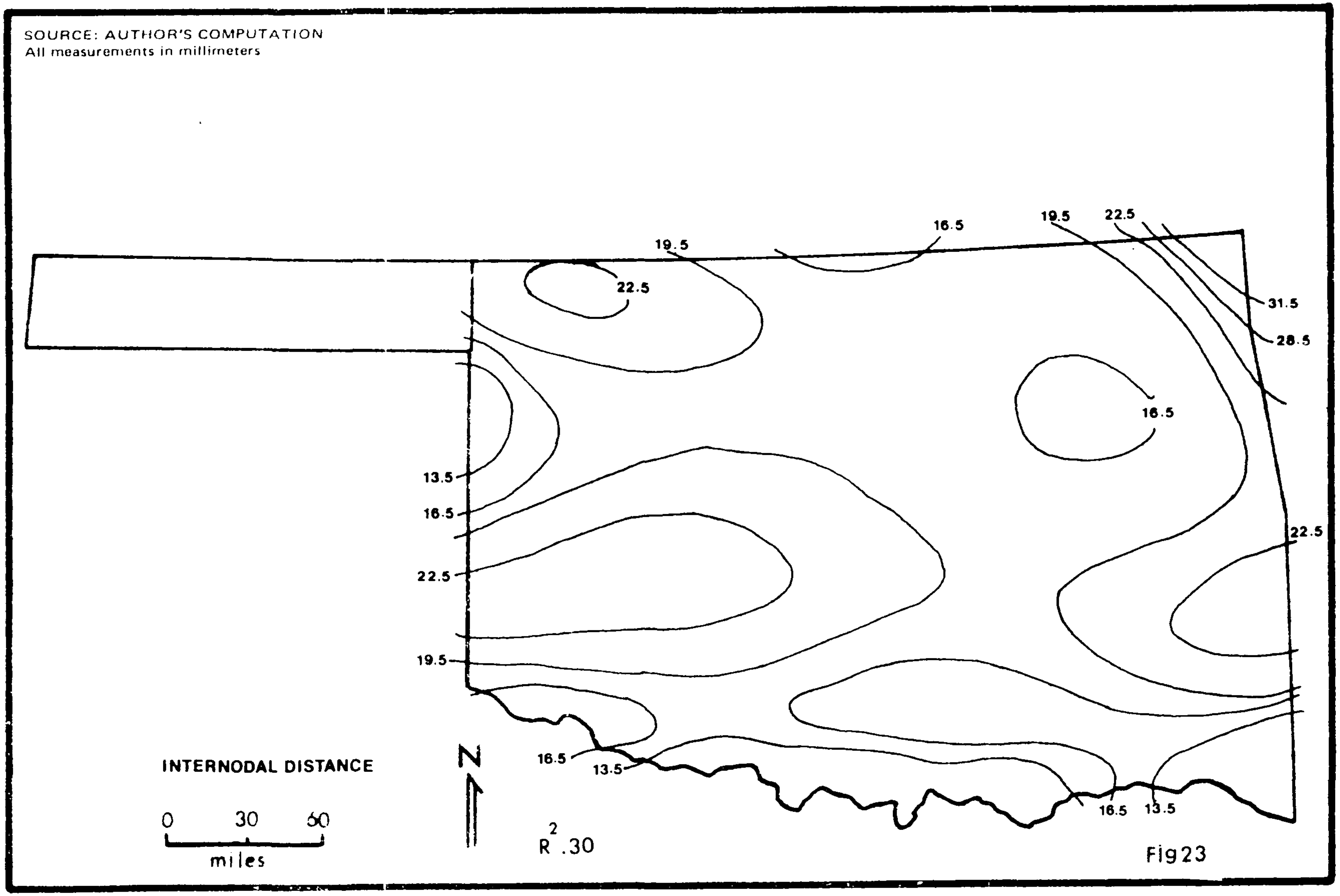

SOURCE: AUTHOR'S COMPUTATION
All measurements in millimeters
PETEOLE HAIR LENGTH
0 30 60
miles
N
R^2 .16
.5
.6
.7
.8

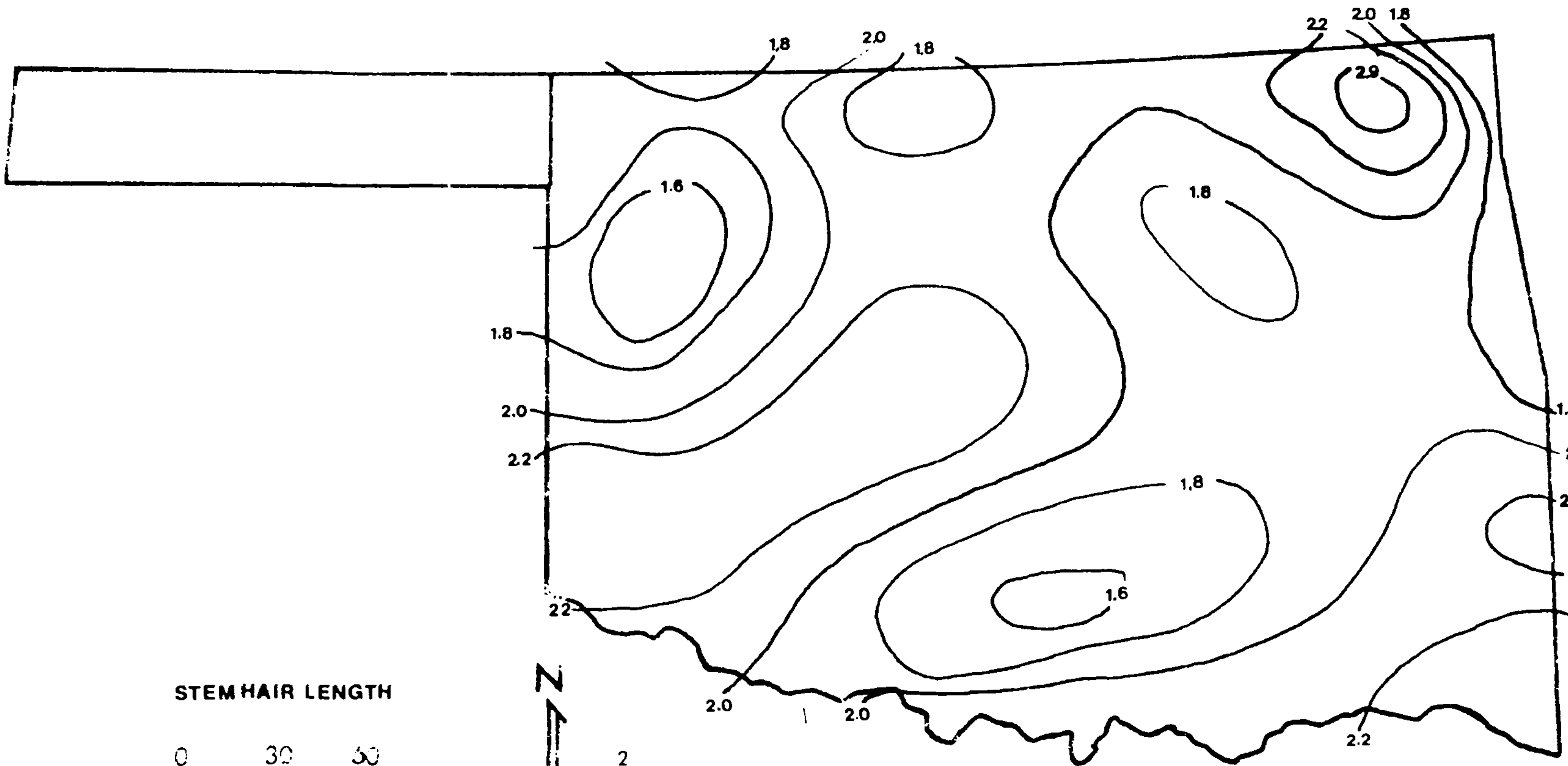
Fig 22

The final two variable maps, IND and STL, are somewhat distinct from other plant characters. IND, internodal distance, is a measure of the spacing of stalks on the stem and it gives an idea of the foliage density of individual plants. The plants in the north tend to have greater distances between nodes than do plants in the south. The greatest internodal distances are found in the northeast while the smallest one is found in the southeast. This pattern suggests that moisture and temperature may have important environmental association. Plants in the south and east having a good supply of water and a longer growing season while those in the north and west contend with drier and cooler conditions. These factors are known to effect vegetative response. (Polunin, 1960, pp. 423-460)

STL, stem hair length, varies from shorter in the north to longer in the south. There does not appear to be a significant difference between eastern and western areas. This suggests that the stem hairs might be longest in areas where temperature factors are critical. Clarke states "...temperature (may) impose a north-south gradation on the distribution


SOURCE: AUTHOR'S COMPUTATION
All measurements in millimeters
19.5
16.5
19.5
22.5
22.5
31.5
28.5
16.5
13.5
16.5
22.5
22.5
19.5
16.5
13.5
16.5
13.5
INTERNODAL DISTANCE
0 30 60
miles
N
R 2 .30
Fig23

SOURCE: AUTHOR'S COMPUTATION
All measurements in millimeters



STEM HAIR LENGTH

0 30 60
miles

R^2 .27

Fig 24

of many plants and animals." (Clarke, 1954, p. 172)

In addition, there is a possibility that similar plant characters might produce similar spatial patterns. In the case of this study, the possibilities of this kind were reduced initially by the selection of characters which were dissimilar. This was done in order to obtain the maximum amount of new information about variation from each individual character. (See Sneath and Sokal, 1973, about the avoidance of similar characters in numerical studies.) However, some plant characters which were roughly similar did have some correspondence in their distributional patterns. For example, the petal widths and widths of the bracts which subtend them have a similar pattern. The widest petals and bracts are found in the northeast and the narrowest are found in the west. Also, the length/width ratios for leaves and hoods showed correspondence in that their respective ratios are greatest in the eastern portion of the state.

In summation, it is evident that characters other than flower color display patterns of geographic variation in Oklahoma. The general picture conveyed by the trend surface analysis is that _A.t. interior_ is tallest in the drier areas of the state and shorter in the more humid portions. It appears to be more verdant, having more leaves per plant, in the more humid areas as well as having more flowers per head. The major vegetative and flowering parts of _A.t. interior_, i.e. bracts, leaves, hoods etc., tend to be long and narrow in the semi-arid west and to be shorter and wider in the more moist eastern portions of the state. And finally, only a few roughly similar plant characters appear to have similar geographic distributions over the state.

Regression Analysis

The relationship between variation in plant characters and variation in environmental measures can be evaluated through regression analysis as stated in Chapter Three. In this case the nineteen additional plant characters are regressed on the environmental variables in turn. As in the previous analysis two sets of regressions are performed; those with the large set of 133 observations and those with the subset of 42.

Plant character variation is considered to be a linear function of the environmental variables in Table 2. An equation was estimated for each plant character in each of the two samples. Furthermore, in order to reduce problems which result from multi-colinearity, principal components analysis was utilized, the results of which are presented in Tables 3 and 4. For each variable and for each of the two samples, therefore, a further equation was estimated in which each of the plant characters is assumed to be a linear function of the dominant components. (See Chapter 3 for details of the results of principal components analysis of the two sets of environmental variables)

Results for the Large Sample

The results in Table 5 show only those parameters significantly different from zero at the 5% level, using the t test. Analysis of Table 5 indicates that the variation in plant characters is not strongly tied to the environmental variables which have been used in the portion of the study. In only one case, PLL, is there more than 19% of the variance in plant characters explained by the environmental vari-

TABLE 5

REGRESSION OF PLANT CHARACTERS ON ENVIRONMENTAL VARIABLES - LARGE SAMPLE

Plant Characters	Intercept	Environmental Variables										R^2
		JLT	AMT	AAP	AJH	JLH	AJS	JLS	MTO	GOP	VGP	
PLL	-1025.9					24.14				10.47		.11
IND	15.5										.34	.05
LFL	341.0	-3.38										.07
LFW	61.2		-.67									.07
LFR	.7					-.01						.03
BRL	22.7	-.24		.02								.07
BRW	-1.2						-.01					.07
PTL	69.5								-.48			.04
PTN	9.5			-.06								.06
SPL	3.6				-.01							.04
PLL	17.1		-.12				-.01					.10
PLW	-2.2							.01				.05
HDL	12.6								-.07			.03
STL	-45.2								.41		.11	.10

Coefficients are significant at the .05 level.

ables. While little variance is actually explained, it may be interesting to examine the general picture presented by the variables which enter the equations most frequently. Of the 18 significant environmental variables, those directly or indirectly connected with moisture entered most frequently. This result is generally consistent with previous results for flower color and suggest that similar factors are responsible for character variation other than color. The variables related to temperature factors entered equations almost as frequently as those for moisture. This is again consistent with flower color results. Thus it can be stated that moisture-temperature factors appear to play a role, though a minor one according to this analysis, in relations between morphological variation and environmental conditions.

The results shown in Table 6 are for the regression of plant characters on environmental components for the large sample. Those parameters significantly different from zero at the 5% level, using the t test, are shown.

The low level of explained variance provided by any one component makes it somewhat difficult to draw specific con-

TABLE 6

REGRESSION OF PLANT CHARACTERS ON ENVIRONMENTAL COMPONENTS - LARGE SAMPLE

Plant Characters	Intercept	Components				R^2
		Comp 1	Comp 2	Comp 3	Comp 4	
PLL	515.9	24.89				.04
IND	19.0			.84	1.00	.08
LFL	62.5		-1.84	2.01		.07
LFW	12.3		-.92			.06
BRL	3.5	.18				.03
BRW	.45	-.03				.05
PTL	16.4	.64				.03
PTN	7.3	-.36	-.35			.08
SPL	2.3				-.09	.04
SPW	.64				-.05	.04
PLL	6.1	.24			.16	.09
PLW	2.1	.08				.03
STL	1.9			.08		.04

Coefficients are significant at the .05 level.

clusions about the relationships. However, an examination of the overall relations which appear, though rather weakly, may be of some value. For example, component 1 enters into the calculations the most frequently. Component 1 is called a moisture-geophysical component and its association with variation in plant characters has been shown in previous computations appearing earlier in the text. Its reemergence in this phase of the analysis again points out the relative importance of such associations to the understanding of geographic variation of A.t. interior.

The other components 2, 3 and 4 appear a few times but it is difficult to assess the nature of the relationships which these associations suggest.

Results for the Small Sample. The data summarized in Table 7 are for the regression of the plant characters on environmental variables for the small sample.

The strongest relationship between a plant character and the environment is found between BRW, bract width and 7 variables, AJS, PYP, SLT, GOP, VGP, PDX and NPS. The seven variables account for 63% of the variance in bract width for A.t.

TABLE 7

REGRESSION OF PLANT CHARACTERS ON ENVIRONMENTAL VARIABLES

SMALL SAMPLE

Plant Char-acter	Inter-cept	Environmental Variables																			R^2
		AAT	AMT	AJT	AJH	JLH	AJS	DLF	DFF	MTO	MHT	PYP	SLT	GOP	ALS	PDX	TDX	DRN	NPS	VGP	
PLL	-1596.2	35.25																			.15
STL	87.0																		2.56		.13
IND	14.7												.55					-1.75		.84	.30
LFW	48.6								-3.52						.11						.29
LFR	7.9				-.04					-.04											.34
BRL	2.8												.17								.12
BRW	-.5						.01					.01	.05	-.02		-.01			.01	.01	.63
PTL	20.6																-1.21				.11
PTN	5.4										.04			-.23							.20
SPL	-9.61			.15											-.03		-.27				.29
SPW	-2.1	.03																			.11
PLL	9.2							-.74													.14
HDR	-1.9	.03						.06			-.01								.01	.01	.35
SHL	1.6																	.19			.15
PTH	-5.5				.08			-.14													.20

Coefficients are significant at the .05 level.

interior in Oklahoma. The first variable, average January sunshine, accounts for 15% of the variance while the others each account for 10% or less. It should be noted that 5 of the 7 variables which enter the equation are local site variables. This result again stresses the importance of local factors rather than general ones.

Roughly speaking, the relationship appears to be an edaphic one. The variables PYP, SLT, GOP and VGP are commonly thought to be associated. The soil type, vegetation type, the bedrock upon which the soils develop and the generally physiography are commonly considered to be interrelated. (Clarke, 1954, pp. 71-76; Oosting, 1956, pp. 194-204; Meyer et al, 1973, p. 431-464)

Variables AJS, average January sunshine and PDX, percent of exposure, are measures of general and specific insolation. The fact that a winter condition, AJS, is again identified with variation is quite interesting and consistent with previous results.

HDR, hood length-width ratio, has some of the variation explained by variables AAT, DLF, VGP, MHT and NDS. They account for 35% of the variation in the hood ratio.

Others with coefficients of determination in this same range are LFR (.34), SPL (.34), IND (.30) and LFW (.29).

In the first case (HDR), temperature appears to be a key factor. Three variables, AAT, DLF and MHT are temperature measures. The other two, VGP and NPS, are strongly related to the general temperature regime. (Seddon, 1971, pp. 76-81) SPL, sepal length, may also have a temperature related association. The three variables ALS, TDX and JLT may be related by the fact that the effect of July temperature would be strongly modified by the other two factors; ALS, angle of slope and TDX, time of day when exposed. A plant on a steep south facing slope with complete exposure would be under considerable stress during the periods of intense heat common in July.

LFW, leaf width, is shown to be associated with slope angle, ALS, and the occurence of the first frost, DFF. These two factors have been shown frequently to be associated with plant development (Meyer et al, 1973, p. 438-441).

IND, internodal distance, is found to be related to VGP, SLT and DRN. This association is also consistent with the generally understood relationship between the vegetative province, the soil type and the drainage found in given areas. In his discussion of edaphic effects on vegetation Oosting states, "Soil water probably affects plant growth much more commonly than any other...factor," and "...topography...has a significant influence upon all plant communities..." (Oosting, 1956, p. 178 & p. 204). The basic consideration involved here is that vegetative communities have soil and drainage requirements which must be met in order for them to survive in a given area. This relationship is indicated by the results which show that such relationships exist for A.t. interior.

The last set of associations between LFR, leaf length-width ratio and AJH, average January humidity and MTO, maximum temperature ever recorded, indicate the importance of both winter conditions and temperature extremes in studies of perrenial organisms.

The remaining relationship values are somewhat lower and indicate a weaker association between the plant characters and the environment and are not discussed in detail. Overall associations, however, may be more important to an understanding of the relationships being considered in this study. Viewing Table 7 again, it can be observed that out of the 42 variables in the smaller sample 10 are directly related to the temperature and moisture conditions which have appeared to be significant previously; while the remaining 23 might be classed as geophysical. Variables like SLT, GOP and VGP are physical variables and appear several times, as do the field variables such as DRN, TDX and NPS. In fact, approximately 30% of all of the independent variables which entered equations significantly are variables measured in the field. This fact, which has emerged from the data analysis is important and will be discussed later.

In general then, it can be said that the analysis of the subset has revealed much about the general nature of the relation between <u>A.t. interior</u> and 19 environmental variables as well as again stressing the importance of local rather than general environmental conditions.

Table 8 displays the results for the regression of plant characters on the small scale of environmental components. Only those parameters significantly different from zero at the 5% level, using the t test, are shown. Examination of this table reveals that while a substantial amount of char-

TABLE 8

REGRESSION OF PLANT CHARACTERS ON ENVIRONMENTAL COMPONENTS - SMALL SAMPLE

Plant Characters	Intercept	Components				R^2
		Comp 1	Comp 2	Comp 4	Comp 7	
PLL	557.1				35.52	.10
IND	21.2			-1.80		.11
LFW	12.8		1.50		1.10	.22
BRL	3.7	-.38				.12
PTL	17.2			-.94		.13
PLL	6.5	-.25				.10
HDW	1.5			-.08		.11
STH	3.1	-.78				.17

Coefficients significant at the .05 level.

acter variance is unaccounted for by any one component, the explained variance is somewhat higher than for the regressions using the components for the full set. This is likely because of the additional site information which is contained in the 42 element data set.

Variable LFW, leaf width, has the strongest association with components 2 and 7. The two components appear to be composed mainly of temperature related information and suggest that leaf width may be realted to temperature conditions.

STL, lower stem length, has a mild relationship with component 6, a freezing temperature frequency and drainage component. The remaining associations are better than the ones in the previous section, but explain too little of the variation to rate individual interpretation.

Examining the overall results reveals that component 4, a July temperature and drought frequency component, enters significant equations most often; with components 1 and 7 the next most frequently entered. High summer temperatures and the occurence of drought are obviously related. The plant variables which are associated with this fourth component are IND, PTL and HDW; variables which have previously been shown to vary with moisture conditions. Component 1 is also a moisture component and its relationship with BRL, bract length, and PLL, length of petal, is consistent with previously observed results.

The final component frequently entering the equations, is component 7, which is shown to be correlated with LFW, leaf width, and PLL, plant length. Component 7 is primarily a temperature component and its association indicates that LFW and PLL have a temperature related variation pattern. This relationship was also shown to exist previously.

In summing up the results of component regression, the relationships appearing from this analysis tend to reenforce the information which has emerged in previous sections. This reenforcement suggests that the answers to the variation questions, posed in this paper, lie along the general route being taken in this research study. Also, that microenvironmental data are more useful than general data in the study of plant character/environmental variable relationships.

SUMMARY

Chapter Four has presented the results of a detailed look at 19 plant characters of A.t. interior and how they vary over the state of Oklahoma, of how they were associated with two sets of environmental variables, and of the relation to component scores from the two data sets.

The results of these analyses suggest that other morphological characters in addition to flower color, exhibit patterns of spatial variation within Oklahoma. They show that moisture, temperature and some geophysical variables are related to the variation of some plant characters over the state. These findings support those of the previous chapter on flower color variation, where similar environmental variables were involved. An implication of this is that morphological variation in general appears to be a response to similar types of environmental factors.

Bract width (BRW) has been shown to be almost as strongly related to the environment in this chapter as flower color was found to be in the previous one. This supports the validity of one of the basic assumptions of this chapter.

It is quite possible that the spatial variation and strong environmental association for such inconspicuous characters as BRW would not be known without studies of this kind.

These analyses also reenforce one of the conclusions of the last chapter regarding the need for very specific and accurate local information. The results of the regression of the smaller set which contained this type of information were found to be stronger than the results of the larger, more generalized sample. In addition, the field variables emerged a number of times both in the original data regressions and the component regressions.

The trend surface maps, though of somewhat less importance, give a formerly unavailable picture of the nature of geographic variation in the 19 additional plant characters. This information may be useful to those working on problems related to Oklahoma vegetation or to environmental-morphological associations.

In this chapter, as in the previous one, the associations revealed by the analysis are interesting and give a clearer picture of plant character-environmental relationships. However, the strengths of the correlations are such that it is difficult to come to substantial conclusions about the relationships under study. The other components of the general model, Figure 3, need to be considered and this may be accomplished in followup studies which may grow out of this investigation. The genetic components would seem to need emphasis as well as an imporoved look at both local and general environmental factors. In the case of bract width (BRW) it is likely that genetic factors, selection and possibly migrational components could play major roles in determining the pattern of bract width variation.

It should be noted however that flower color, a conspicuous character which has been suggested in some cases to be associated with plant survival, would seem to be a more important character than bract width. This seems obvious only because we have little knowledge of the relationships between morphological characters and the environment. Numerical studies of other plants would appear to be desirable so that it will be possible to determine if strong associations exist between morphology and environmental factors and to what extent they may determine world plant patterns.

CHAPTER FIVE
CONCLUSIONS

The major objective of this study was to examine the geographic variation (systematic intraspecific variation) of *A.t. interior* in Oklahoma. This included an examination of flower color variation and the variation of a number of other plant character variables. A consistent pattern of variation was found between flower color and several environmental variables, and between bract width and a number of environmental measures.

The strengths of these associations were stronger than those between the remaining plant character variables and the environment. However, the general consistency of results suggests that a followup study would be advisable.

The most immediate research step which might follow this study would be a much expanded version of the same basic thing. However, the second study would include samples collected in the field exclusively. This would allow the researcher to include the types of microenvironmental data that have yielded better results in this study. In addition, such a study would include additional on-site measurements i.e. soil moisture, soil pH, a more precise measurement of exposure and light factors. These variables would give a clearer picture of the local factors which appear to be important. This approach would also allow for the use of a more refined color scale, as all samples would be measured in the field against the same scale as was used by Woodson. And lastly, a number of specially selected sites, in different parts of the state, would be designated for mass collecting. A study of these mass sample might give some clues to the range of variability which can be expected over small areas. The sites selected might be in close proximity to a high order weather facility or such a facility might be set up at the collection sites. The very detailed data, collected at such facilities, would be far superior to the general data now available for most of Oklahoma.

A Major Followup Study

The present study has been restricted to Oklahoma because of a number of factors. A primary consideration is that Oklahoma was singled out, by R.E. Woodson, as a good place in which to do further research. Now that some of this has been accomplished and answers have been found to a number of Woodson's questions, one might wish to go beyond the borders of Oklahoma and to examine a larger issue.

Woodson's contention that there are three subspecies of Asclepias tuberosa was based upon a series of leaf measures. (Woodson, 1944) One might question the division of a species based upon a single character. A study of many characters, using numerical methods, might lead to a better understanding of both the species and to geographic variation in general. Such a study would involve a much larger effort than has been undertaken on this study. It would also involve an expanded time frame and a need for financial support. A number of the considerations, just mentioned with regard to Oklahoma, would be incorporated into the study. It might be wise to introduce a number of additional techniques, such as chromosomal counts and the like, in order to deal with the genetic aspects of variation. Such a large scale study would benefit from the expanded viewpoint often a part of multidisciplinary efforts.

A major question which naturally follows the above proposal involves disciplinary boundaries. Where does biogeography end and botany begin? Which research methods and tools are appropriate? Who is qualified to investigate which question and how much training must a researcher have before investigating a given phenomena? The answer to this question is rather complex and controversial. In general, it seems that the presence of strong spatial implications would automatically put a question into the biogeographic sphere. In the case where the implications were incidental or relatively unimportant the answer would be less clear.

A somewhat simplistic solution might lie in the area of interdisciplinary research where each researcher can contribute in his area of specialization. This can involve cumbersome and often uncomfortable situations, but the benefits of such an approach would seem to make such work both rewarding and interesting.

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