CORRELATION OF SOME SOIL PROPERTIES WITH VARIATION IN THE *ANDROPOGON GERARDI* VITMAN--*ANDROPOGON HALLII* HACK. COMPLEX IN NEBRASKA

by

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INTRODUCTION

Hybridization between Andropogon gerardi Vitman (big bluestem) and Andropogon hallii Hack. (sand bluestem) has been postulated in Nebraska (Romberg, 1954; Satterwhite, 1970), but a statewide sample based on large numbers of specimens and characters has never been analyzed. Nielson (1939) observed that A. hallii in Nebraska is polymorphic with some "races" appearing to blend gradually with A. gerardi. Correll and Johnston (1970) state that A. hallii intergrades completely with A. gerardi in Texas and its recognition as a separate species is of dubious merit. Merging the two species does not solve the nature of the variation. The problems of a taxonomic treatment of species exhibiting clinal variation are unresolved (Heywood, 1959; David and Heywood, 1963; Gregor, 1963; Wagner, 1969). Specifically the questions are: can genecological information be assimilated into orthodox taxonomic categories?; what features should be used to assign differentiated populations to these categories?; and should these features include cryptic characters such as chemical and physiological differences?

Böcher (1967) states that most taxonomists will abandon a taxonomic treatment of continuous variation because they cannot describe taxa without discontinuity. He stresses that the similarity between gradients arising from introgression and those resulting from selection may be very great. The study of genotypic variation, that is, clinal variation of organisms in relation to environmental gradients has become widespread

in recent years. The extensive literature on this subject has been reviewed by Heslop-Harrison (1964) and Langelet (1971). In most studies done by taxonomists (e.g., Benson et al., 1967), relating occurrence of hybrids to specific habitats, the measure of environmental properties is superficial--slope, aspect, elevation, soil textural class, and other properties which have no relevance to the physiology of plants. Other studies by ecologists (e.g., Whittaker, 1956) relating community ordination to environmental gradients slight the study of variation in the plants--in many cases all members of a species are placed within certain ecological limits along the environmental gradients. The assumption is made that all members of a species have similar environmental requirements. When the present study was initiated, I knew that there were tested taxonomic methods which could be used to place a morphological ranking on members of a group of varying plants and I was also aware that those environmental properties which directly influenced the growth of plants were the ones most likely to have high correlation with plant variation. These properties include light, soil water, soil air, and soil nutrients, among others. Other habitat properties such as elevation, latitude, longitude, slope, aspect, soil texture, annual precipitation, length of growing season, and depth to water table, though easily measured, have no direct effect on the growth of organisms. Whittaker (1967) recognizes that the "elevation gradient" has no relevance to plant growth and that this gradient is a complex climatic gradient for which elevation is simply one measure of relative position.

Since hybridization between the two taxa apparently has been occurring for a long time, a complete merging of germ plasm might be

expected unless selective forces in the environment were tending to keep the extremes separated. The problem then arises: what are these selective forces?

Since the plant variation cuts across physiographic and climatic zones, it seems to be independent of climatic, or topographic or geographic gradients. Logically, all observations pointed to edaphic control. Thus the problem may be stated: what edaphic properties are most highly correlated with the variation in the plants?

The approach to the problem involved 1) an analysis of the plant population and calculation of a numerical value for each specimen so as to determine its relative position in the entire range of variation, 2) an analysis of soil properties at the collection sites, and 3) testing of correlations between the plants and the soil properties.

Since the plant analysis involved the measurement of numerous characters for each plant specimen and since the occurrence of each character was to be correlated with soil measurements for each soil sample, it was considered expedient to use the IBM 360 computer to handle the voluminous data.

METHODS AND MATERIALS

Sites and Sampling

In the fall of 1971 and 1972 populations of the Andropogon gerardi x hallii complex were sampled at 45 sites throughout the state (Fig. 1). Locations are given in the Appendix. From a preliminary study I knew that the Nebraska center of A. hallii was in the Sandhills and the bluestem most like A. gerardi was in the southeastern part of the state. From preliminary study I knew that populations on roadside sites were more variable than populations from relatively undisturbed upland sites. Disturbance at a site introduces different and less rigorous selective factors into the environment (Anderson, 1949; Solbrig, 1970). Since hybridization has been occurring for perhaps hundreds of years, I thought that by sampling populations on sites which were, as far as I could determine, undisturbed, I was sampling where more rigorous selection was occurring, and I would have a better chance of discovering the selective factors. Thus, sites characterized by man's disturbances, by heavy grazing, and those located on floodplains were not sampled, with the exception of two sites discussed later.

At each site specimens were taken in the following manner: the two extremes in terms of number of inflorescences and awn length were selectively collected and then a random sample of 8 to 12 specimens representing variation between these extremes was added. This sampling method ensures that the information sought in the sample is contained within it--that variation among plants at a site, including the extremes

is sampled with a minimum of specimens. Were all plants collected at random, a much larger sample would be necessary to ensure that the extremes were collected.

When the plants were pressed, each was assigned a four digit number representing the site and the plant at the site, e.g., plant 0113 represents specimen 13 from site 1. Many clonal pairs, i.e., two culms arising from the same rhizome, were also collected and recorded as clonal specimens. The surface of the soil at each site was saturated with water. Triplicate soil cores of the top 2.5 cm of soil were taken with a Uhland soil sampler with six 2.5 x 7.6 cm rings. The apparatus was driven into the ground by hand pressure or wooden mallet, the sleeve and rings containing the soil core were withdrawn, and the core in the top ring was trimmed evenly top and bottom with a coping saw with a knife-edge blade. The rings containing the three soil cores were placed in a cylindrical pint container with metal disks separating the cores. Loose soil from the top 2.5 cm was collected in another container for other analyses. The containers were packed in boxes to minimize disturbance during travel and handling.

At site 3 the top, middle, and bottom of the dune were sampled as separate sites for both plants and soils. At sites 7, 8, and 11 plant specimens were collected every 20 paces from the top of the dune to the bottom and numbered sequentially. At each of these three sites soil samples were taken at six points on the dune: one from the level area at the top of the dune, four points on the slope of the dune, and one from the level area at the bottom of the dune.

Plant Analysis

Character Measurements

A group of characters known to vary were measured and others added as variation in them was noted. Measurements entailed counting and measuring with a mm rule or an ocular micrometer at various magnifications. Other than counting, measurements were made to at least one-fifteenth of the variation on the assumption that this would provide a degree of precision adequate for solving the problem. In all, 26 vegetative and 26 floral characters were measured on 590 specimens (Table 1, Fig. 2). Ten of these characters were ratios useful for assigning proportionality of structures to one another. The measurements were recorded on standard data sheets, transferred to standard 80-column IBM computer cards using two cards per specimen. The data were subjected to the NUTAL, GOCOR, HYBEX and FACTOR statistical programs using the University of Nebraska's IBM OS/360 model 65 computer.

Computer Program NUTAL

The output of NUTAL gives the frequency distribution in 15 classes, as well as the minimum, maximum, and mean values for each character (Table 2, Fig. 3). Although any number of classes may be chosen, 15 classes were used because relatively smooth curves are produced, there is a median class, and this number facilitates a reduction of the data into five classes needed in a subsequent program (HYBEX).

Computer Program GOCOR

The GOCOR program computes Pearson product-moment correlation coefficients of each character with each of the others. The program

was used three times to correlate 1) each plant character with each of the other plant characters; 2) like characters of clonal plant specimens; 3) the numerical value of each plant specimen with plant characters and soil characters.

The correlation coefficients among plant characters were ordered to construct groups of characters that vary together, that is, groups of characters that are considered to be consistently correlated (Fuller, 1969). Consistency refers to the sign of the coefficient.

The consistency groups are constructed in the following manner. If character 1 is positively correlated with character 2, they are put into one group; if they are negatively correlated each character is placed in a separate group. For the moment, let us assume that characters 1 and 2 are positively correlated and are put into one group. Character 3 will be put into the same group only if it is positively correlated with both 1 and 2. If character 3 is negatively correlated with both 1 and 2, it is placed into another group. If character 3 is positively correlated with 1 and negatively correlated with 2, it is said to be inconsistent and is placed into a third "discard" group.

Each character was checked with each of the characters in a group and had to be consistent with all of them before it was added to either of the two consistent groups. When all characters were checked, they formed three groups--one group of characters all positively correlated with one another; a second group all positively correlated with one another and all negatively correlated with each of the characters in the first group, and a third discard group inconsistent with those in either of the first two groups.

Computer Program FACTOR

The principal concern of factor analysis is the resolution of a set of variables in terms of a small number of categories or factors (Harman, 1968). This resolution is accomplished by the analysis of the correlations among variables. A satisfactory solution will yield factors which convey all the essential information of the original set of variables. Thus, the chief aim is to attain scientific parsimony or economy of description. In other words, factor analysis reduces and rearranges a large set of data to a smaller set of factors which may be considered as new characters accounting for the observed interrelations in the data (Nie, Bent, and Hull, 1970). Relationships among characters are handled in terms of Pearson Product-moment correlation coefficients computed after the data have been transformed into z-scores. The print-out includes a correlation matrix, the eigenvalues associated with the initial factors, the per cent variance contributed by each factor, the cumulative per cent of variance, and the "varimax" rotated factor matrix.

The factors generated by the program are said to be orthogonal to one another, that is, uncorrelated, and represent the best combination of variables--best in the sense that the particular combination of variables accounts for more of the variance in the data as a whole than any other combination of variables. The first factor is the best summary of relationships exhibited in the data. The second factor is defined as the second best combination and it is orthogonal to the first factor. The second factor is the combination of variables that accounts for the most residual variance after the effect of the first factor is removed from the data. Subsequent

factors are defined until all the variance in the data is exhausted. If no variable is perfectly determined by the rest of the variables in the data, the solution requires as many factors as there are variables.

The eigenvalue is a measure of the relative significance of a factor. Inherent in the program is an arbitrary cutoff of factors with reduced significance in terms of contribution to the variance of the sample; factors with eigenvalues less than 1.000 are not considered further in the analysis by the program. When the factors have been defined, the characters in the factor are rotated to find the best clustering within each factor and are assigned a coefficient or loading value which is an indication of the significance of each character within a factor. Only characters with loading values above 0.5000 are considered to be significant. This cutoff point is chosen since it best facilitates assignment of a character to only one factor; with a higher cutoff point many characters will not be assigned to any factor, and with a lower cutoff point they will be assigned to more than one factor. The consistency of characters was again tested.

The parsimony inherent in factor analysis reduces the probability of including bias into the plant analysis. The logical selection of plant characters from the rotated matrix, such that those selected are independent measures of genetically-based phenomena, increases the likelihood that an interpretable pattern will exist when the plant specimens are assigned numerical values. These values are calculated by the next program.

Computer Program HYBEX

The HYBEX program is a sophistocated extension of the hybrid index method of Anderson (1949) and is similar to the HYBIX program of Fuller (1969). The range of each character is divided into five classes and assigned a number from zero to four. Characters in one of the previously mentioned consistency groups are assigned zero as the low class and four as the high class, and those of the other group assigned four as the low class and zero as the high class. This type of assignment is necessary because the characters of one group are all negatively correlated with all the characters of the other group. The high values of one group are associated with the low values of the other.

In HYBEX I arbitrarily assigned the low values to the characters representing the A. hallii extreme. The number assigned to a specific character of a plant specimen is called the hybrid value. The sum of the hybrid values of all characters of a specimen is the hybrid index. Inferences about the nature of the plant population may be drawn from a frequency distribution of hybrid indices.

Soil Analysis

A total of 46 physical or chemical properties was measured or calculated on each of the 62 soil samples (Table 12). These properties were known to vary with soil texture (Kohnke, 1968).

Physical Properties

The volume of water held by the soil cores at various tensions was determined on a low pressure, porous-plate apparatus (Richards and Fireman, 1943). The soil core in the aluminum ring was placed into the brass container and saturated from the bottom with distilled water. The following day excess water around the core was drained, the apparatus was sealed and air pressure applied to the apparatus. Water drained from the core through the porous plate (which is impervious to air)

into a buret graduated in 0.05 ml increments. The volume of water in the core was recorded when no further drainage was evident. Trials were run at eight tensions equivalent to 5.2, 10.6, 21.5 43.1, 86.2, 172, 344, and 688 cm water on undisturbed cores of 62 samples plus trials on ten replicate samples. Tensions were maintained by a column of water for the first five tensions and a column of mercury for the last three tensions. When drainage equilibrium was attained at the highest tension, the soil core was weighed, oven-dried at 105C, and weighed again. The water content at the end of the trial was calculated, and cumulative water content determined by adding the volume drained at each pressure. The volume of water held by the samples at tensions greater than 688 cm water was determined on a porous membrane apparatus (Richards, 1947) at tensions equivalent to 2390, 5131, 10,680, and 15,530 cm water.

The volume of water drained from soil at a given tension is a function of the diameter of the soil pores according to the equation of capillarity (Kohnke, 1968):

forces directed downward = forces directed upward

$$hDg\pi r^2 = s2\pi r \cos\alpha$$

where h = pressure in cm water

D = density of the liquid, 0.998 g/cm^3

g = acceleration due to gravity, 981 ergs/g-cm

πr^2 = cross-sectional area of the cylindrical capillary, cm

and s = surface tension of the liquid 72.75 dynes/cm

$2\pi r$ = line of contact between liquid and tube, cm

$\cos\alpha$ = cosine of the angle of contact

For water the angle of contact is so small that cosα is assumed to be 1. The equation reduces to:

$$r = \frac{0.187}{h} \qquad d = \frac{0.294}{h}$$

where r = radius of pore, cm

d = diameter of pore, cm

Since different conventions of terminology are used by soil scientists, ecologists, and plant physiologists, equivalents of pressure, tension and corresponding capillary diameters are presented in Table 3.

The pore size distribution was calculated from the amount of water drained from a given volume of soil at increasing tensions (Kohnke, 1968; Smith et al., 1944). From the 12 datum points the following physical properties were calculated: volume of pores in the 13 size classes both on a volume basis (P_V) and a weight basis (P_W). These pore size classes were then grouped into the four categories: 1) aeration pores, greater than 69μ diameter; 2) capillary conduction pores, 9-69μ diameter; 3) pores with water readily available for plant growth, 0.2-9μ diameter; and 4) pores with water not readily available for plant growth, less than 0.2μ diameter. From the volume and weight of the soil cores, bulk density and water content at saturation both on a volume basis (P_V) and a weight basis (P_W) were calculated.

Particle size distribution of each sample was determined by the hydrometer method (Bouyoucos, 1962).

Chemical Properties

The chemical analyses included tests for available phosphorus (modified Bray and Kurtz Method No. 1), extractable potassium

(equilibrated extraction method), nitrate-nitrogen (phenoldisulfonic acid method), and soil reaction (pH), (Knudsen and Hassan, 1969).

All soil data were transferred to standard 80-column IBM computer cards for further analysis.

Computer Program NUTAL

The NUTAL program was used to locate errors in the data. Errors in copying are detectable in many cases because a large number of empty classes will show up in the frequency distribution for a character when an incorrect maximum or minimum is recorded. Several such errors were found and corrected and the program was rerun. Histograms of the data give the frequency distribution of each soil character throughout the sample. I was not concerned with the frequency distribution per se, but I was concerned with the shape of the histograms because I was seeking high correlations between soil properties and plant specimens.

Plant-Soil Correlations

The hybrid index of the plant specimens was punched onto a new set of computer cards as a plant character. Duplicate cards of the soil characters at a site were made for each plant specimen at a site resulting in a total of five cards for each plant specimen--two with plant characters, one with hybrid indices, and two with soil characters. The sets of five cards were arranged in sequence according to sites. Correlations of plant characters with soil characters were accomplished using GOCOR. All characters were read by the program as comparable characters so that the coefficient of character 1 with 53 is the correlation of a plant character with the hybrid index, and a correlation of character 53 with 55 is the correlation of the hybrid indices with a

soil property. In this manner coefficients were obtained between plant characters and hybrid indices, plant characters and soil characters, and hybrid indices and soil characters. The highest correlations of soil characters with the hybrid indices were sought. Scatter diagrams of hybrid indices against soil characters were made to determine if the correlations were linear or curvilinear.

RESULTS

Plants

The 45 collection sites were renumbered according to distance from the northwest corner of the state (Fig. 1). Of the plants collected, 590 specimens were intact, having all 52 characters present to be measured. The characters measured on each specimen are listed in Table 1 and several characters are illustrated in Fig. 2.

Computer Program NUTAL

The frequency distributions from NUTAL of the plant characters based on 590 specimens are shown in Table 2. Histograms of these data were constructed for each character (Fig. 3). Several histograms have empty classes because the range of variation was not equally divisible into 15 classes. The shapes of the curves indicate how the characters are distributed in the sample and give evidence as to the nature of the plant complex.

A normal curve indicates that a character is distributed in a normal Gaussian manner. A normal distribution is evident for characters 1, 6, 7, 11, 12, 14, 19, 20, 23, 25, 27, 29, 34, 35, 36, 38, 43, 47, 48, 49, and 51.

A skewed curve indicates that either a) juveniles are included in the sample; b) a disproportionate number of plants from one extreme are collected; c) the character is distributed in the population in