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DIVERGENCE AND ADAPTATION IN ADJACENT PLANT POPULATIONS: STUDIES ON THE ECOLOGY AND PHYSIOLOGY OF THE BIG BLUESTEM (ANDROPOGON GERARDII VITMAN) - SAND BLUESTEM (ANDROPOGON HALLII HACK.) COMPLEX IN NEBRASKA

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DIVERGENCE AND ADAPTATION IN ADJACENT PLANT POPULATIONS: STUDIES ON THE ECOLOGY AND PHYSIOLOGY OF THE BIG BLUESTEM (*ANDROPOGON GERARDII* VITMAN) - SAND BLUESTEM (*ANDROPOGON HALLII* HACK.) COMPLEX IN NEBRASKA

by

Paul Warren Barnes

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DIVERGENCE AND ADAPTATION IN ADJACENT PLANT POPULATIONS:

STUDIES ON THE ECOLOGY AND PHYSIOLOGY OF THE

BIG BLUESTEM (ANDROPOGON GERARDII VITMAN) -

SAND BLUESTEM (ANDROPOGON HALLII HACK.)

COMPLEX IN NEBRASKA

BY

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DIVERGENCE AND ADAPTATION IN ADJACENT PLANT POPULATIONS: STUDIES ON THE ECOLOGY AND PHYSIOLOGY OF THE BIG BLUESTEM (ANDROPOGON GERARDII VITMAN) - SAND BLUESTEM (ANDROPOGON HALLII HACK.) COMPLEX IN NEBRASKA.

Paul Warren Barnes, Ph.D.

University of Nebraska, 1984

Adviser: Robert B. Kaul

Examination of the morphology of 95 specimens of the big bluestem (Andropogon gerardii Vitman) - sand bluestem (Andropogon hallii Hack.) complex indicates that along a local dune/meadow topographic gradient in the eastern Nebraska Sandhills, genetic variation is closely related to habitat variation and more specifically, to variation in soil moisture patterns, which in these sandy soils, is controlled by the depth to the underlying water table: sand bluestem genotypes occur on dry, upland sand dunes, big bluestem genotypes are restricted to nearby, naturally subirrigated, wet meadows, and hybrid genotypes are found in narrow dune/meadow transition zones where soil moisture levels are intermediate between dunes and meadows.

In transplant experiments, both seedlings and adult rhizome transplants of sand bluestem survive longer on the dunes than big bluestem, which showed rapid and massive mortality following brief dry periods. Also, under similar drought conditions in common gardens, sand bluestem transplants maintained significantly higher leaf water potentials than either big bluestem or hybrid transplants. These and other transplant and physiological data indicate that there may be strong selection acting to keep drought sensitive big bluestem genotypes off the dunes and restricted to more mesic sites such as the Sandhills wet meadows.

Factors excluding sand bluestem genotypes from adjacent meadows are less clear but may involve competitive abilities and/or an intolerance to flooded or saturated soils. Hybrid genotypes appear to lack the adaptive character combinations which allow them to inhabit parental habitats and are therefore confined to intermediate environments.

Comparative studies on leaf anatomy revealed that leaf thickness, photosynthetic tissue, and mesophyll surface area (A^{mes}/A) are greater in sand bluestem, but laboratory gas exchange measurements showed no inherent differences between bluestems in photosynthetic physiology, water use efficiency, or leaf chlorophyll and soluble protein contents suggesting that, in these C_4 grasses, biochemical rather than physical (anatomical) factors are more important in controlling gas exchange processes. Water relations data from both field and laboratory studies showed little difference in stomatal physiology or osmoregulation capabilities; within the bluestems the evolutionary and adaptive response to moisture stress has apparently involved non-stomatal mechanisms, such as leaf rolling and/or epicuticular waxes, which act to control water loss under drought conditions.

DEDICATION

This dissertation is dedicated to my wife, Mary, whose love, support and unending encouragement kept me going during this endeavor.

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GENERAL INTRODUCTION

Habitat-associated genetic differentiation in plant populations is well-documented (see Heslop-Harrison (1964) and Langlet (1971) for reviews). In widely distributed species, geographic variation in populations is often associated with regional climatic differences (e.g. Turresson 1925, Clausen et al. 1940, Olmstead 1944, Larsen 1947, McMillan 1959, Mooney and Billings 1961, and others). Populations can also show genetic differentiation on a more local scale, despite gene flow, if natural selection is strong (Antonovics 1971). Indeed, many studies have shown close relationships between local variation in edaphic factors, such as soil nutrient availability, salinity, and heavy metal contamination, and genetic differentiation in plant populations (e.g. Kruckeberg 1954, McNeilly 1968, Snaydon 1970, Ashton and Bradshaw 1970, Antonovics and Bradshaw 1970, and others). However, there are few reported cases where genetic differentiation and adaptation in response to local soil moisture variation have been experimentally examined.

The research reported on here was designed to examine the ecological and physiological aspects of habitat separation in big bluestem and sand bluestem, two closely related and interfertile, native prairie grasses. These deep-rooting, C_4, perennial grasses, are normally distinguished by several key morphological differences (outlined in Chapter 1). Traditionally the bluestems have been recognized as separate species with big bluestem being Andropogon gerardii Vitman and sand bluestem, Andropogon hallii Hack. However, these grasses have been shown to be completely interfertile under artificial conditions (Peters and Newell 1961). Furthermore, the bluestems appear to show widespread,

natural, morphological intergradation (Romberg 1955, Satterwhite 1970, Kestner 1973, Gould 1975, Sutherland 1978). Because of this natural intergradation and documented interfertility, continued recognition of these grasses as distinct species has been questioned; however, to date, the taxonomic nomenclature in the bluestem complex has not been resolved (see Gould 1975, Sutherland 1978).

Irrespective of taxonomic considerations, the bluestems show very distinct differences in habitat utilization. While big bluestem, a tallgrass prairie dominant , occurs throughout North America in mesic prairie sites, sand bluestem is restricted to drier, sandy soils in the Great Plains (Hitchcock and Chase 1951). In Nebraska, the bluestems co-occur, with sand bluestem common on the dunes in the Sandhills region (a large, prairie vegetated, inland dune system) and big bluestem common in eastern Nebraska tallgrass prairie, although it is found in Sandhills wet meadows and is thus often found in close proximity to sand bluestem. These distinct distribution patterns suggest that soil moisture may be important in controlling habitat utilization; however, to date, there have been no experimental studies conducted to evaluate this hypothesis. Kestner (1973) indicated a high correlation between soil water holding capacities and bluestem distribution, although no studies were conducted within the Sandhills proper on sympatric populations. Similarly, although previous studies (Romberg 1955, Satterwhite 1970, Kestner 1973, Sutherland 1978) have documented continuous morphological variation in the bluestem complex in the field, these studies all examined populations from across geographical areas, such as Nebraska or the Great Plains. No major attempt has been made to examine and document the

nature of the variation in the bluestem complex where they co-occur in adjacent habitats.

The objectives of my research on the bluestems, which I report on here, were three-fold:

1. To examine the relationship between genetic variation and habitat variation in the bluestem complex along a local environmental gradient;
2. To experimentally evaluate the ecological factors controlling habitat assortment in adjacent populations; and
3. Determine if a physiological basis might exist which could explain population divergence by examining how populations have adapted to their respective and contrasting environments.

In Chapter 1 objectives 1 and 2 are addressed. In this chapter I 1) examine the morphological variation in the bluestem complex along a local dune to meadow topographic gradient in the eastern Nebraska Sandhills, 2) compare, morphologically, adjacent and isolated bluestem populations, 3) examine the relationship between habitat variation and bluestem variation along this topographic gradient, and 4) report on the results of reciprocal seedling and adult rhizome transplant experiments.

The third objective is addressed in Chapters 2 and 3. In Chapter 2, I report on variation in leaf thickness in the bluestem complex, which has previously not been described. I also quantitatively evaluate the anatomical basis for this variation in leaf thickness, and in an effort to determine if this variation might have adaptive significance, I examine the effects of variation in leaf thickness on photosynthetic

physiology and water use efficiency. Chapter 3 is devoted to studies of the comparative water relations and drought responses of the bluestems, both in the field and in the laboratory. I also report on preliminary studies of the variation in epicuticular waxes and suggest how this variation may be important in controlling transpiration under drought stress conditions.

CHAPTER 1

Variation and habitat assortment in the big bluestem (*Andropogon gerardii* Vitman) - sand bluestem (*Andropogon hallii* Hack.) complex along a local dune/meadow gradient in the Nebraska Sandhills

ABSTRACT

The morphological characteristics of 95 specimens of the big bluestem (Andropogon gerardii Vitman) - sand bluestem (Andropogon hallii Hack.) complex collected from six topographic positions along a local dune/meadow gradient in the eastern Nebraska Sandhills were examined to determine the relationship between genetic variation and habitat variation in adjacent bluestem populations. Based on recognized, key diagnostic morphological characteristics and comparison with isolated populations, plants occupying the sand dunes were recognized as typical sand bluestem genotypes while those occupying the meadows were recognized as typical big bluestem genotypes. Plants growing at the narrow transition zone between dune and meadow showed morphological characteristics intermediate between sand and big bluestem. Because of morphological consistency in common gardens, these plants have been interpreted as naturally occurring hybrids. Hybrid index values using 15 and 4 morphological characters satisfactorily discriminated between both adjacent and isolated sand bluestem and big bluestem populations and provide additional evidence for the occurrence of hybrids when the taxa occur in close proximity to one another.

In addition to morphological variation, the bluestems showed variation in other characteristics, which previously has not been described: in comparison to big bluestem, sand bluestem leaves are thicker, show a higher adaxial stomatal density and show lower absorptances to photosynthetically active radiation (400-700 nm), apparently because of a greater epicuticular wax accumulation.

Along this topographic gradient, habitat assortment in bluestem genotypes is closely related to soil moisture levels which, in these sandy soils, are controlled by the depth to the underlying water table. Rapid and massive mortality of big bluestem seedlings and adult rhizome transplants on the dunes suggest that there is strong selection acting to keep big bluestem genotypes off dune sites and restricted to moister sites such as adjacent, subirrigated meadows. Factors restricting sand bluestem genotypes to the dunes are not clearly understood but may be related to competitive abilities and/or an intolerance to saturated soils. Hybrid genotypes were found in narrow dune/meadow transitions where soil moisture levels are intermediate. Seedling survivorship patterns, seedling biomass data, and the lack of correlation in adult morphological characters suggest that these plants may lack the adaptive character combinations which allow them to inhabit parental habitats.

INTRODUCTION

Big bluestem (Andropogon gerardii Vitman) and sand bluestem (Andropogon hallii Hack.) are two closely related, native, North American prairie grasses. The grasses are deep rooting (Weaver 1954, Weaver and Albertson 1956), warm-season (C_4) (Waller and Lewis 1979) perennials. Identification of the grasses is generally based on several morphological differences; whereas sand bluestem is strongly rhizomatous, has glaucous foliage, shows very villous inflorescences, and awns of the fertile spikelet are absent or very short, big bluestem is weakly rhizomatous, has dark to light green foliage, inflorescences are less villous, and awns are long (Hitchcock and Chase 1951, Gould 1975). Variation in other morphological characteristics such as ligule length, anther length and leaf venation patterns has also been described (Romberg 1955, Kestner 1973, Sutherland 1978).

Intergradation between big bluestem and sand bluestem has long been recognized. Natural hybridization between these grasses was first suggested by Romberg (1955). Statewide surveys in Nebraska by Satterwhite (1970) and Kestner (1973) documented continuous morphological variation between the taxa, which they interpreted to be the result of extensive introgressive hybridization. Because of this widespread intergradation, Gould (1975) has considered big bluestem and sand bluestem to be varieties in a single species, Andropogon gerardii. Indeed, the bluestems were shown to be fully interfertile by Peters and Newell (1961), who artificially crossed the species and obtained fertile hybrids which were intermediate in morphology. The work of Peters and Newell (1961) and Newell and Peters (1961) has resulted in the

production of the synthetic hybrid, "Champ bluestem": (Newell 1968b) which is commercially marketed. Despite the above information, the bluestems continue to be recognized as separate species. The morphological data which I present in this chapter for adjacent populations clearly indicate that continued recognition of the bluestems as distinct species is not warranted.

Irrespective of the taxonomic considerations in this complex, the bluestems are ecologically quite distinct. Whereas big bluestem, a dominant of tallgrass prairie (Weaver 1954), is broadly distributed in North America (Hitchcock and Chase 1951), sand bluestem is restricted to sandy soils in the Great Plains (Hitchcock and Chase 1951) although it has been reported to occur as far east as Illinois (Birkenholz et al. 1980). Both bluestems are found in Nebraska, but sand bluestem is restricted to coarse textured soils in the Sandhills region, while big bluestem is confined to mesic Sandhills subirrigated meadows or to finer textured soils in higher precipitation areas outside the Sandhills (Keim et al. 1932, Tolstead 1942, Satterwhite 1970, Kestner 1973). These findings suggest that the distribution of these grasses may be related to moisture availability. Indeed Kestner (1973) found a high correlation between bluestem morphology and the moisture holding capacities in soils. However, other than these correlative data there is very little information on the comparative ecology of these taxa.

This chapter is the first in a series of three chapters which examines the ecological and physiological aspects of divergence and habitat separation in the big bluestem - sand bluestem complex. Although Kestner's (1973) work documented state-wide variation there was