Technical Report No. 157

GROWTH RESPONSE OF BLUE GRAMA

TO THUNDERSTORM RAINFALL

Freeman Smith

Natural Resource Ecology Laboratory

Colorado State University

Fort Collins, Colorado

TABLE OF CONTENTS

ABSTRACT

This paper is a review of literature pertinent to the growth of blue grama with respect to thunderstorm rainfall in the shortgrass grasslands of central North America. The review is not exhaustive, but it does serve to draw attention to this climatic-biotic relation.

INTRODUCTION

Blue grama (*Bouteloua gracilis* (H.B.K.) Lag.) is the major native forage species on the North American continent. It is the dominant plant in the shortgrass prairie, the largest grassland association on the continent (Weaver and Albertson, 1956). The shortgrass prairie extends far north into the provinces of Saskatchewan and Alberta of Canada and far south into the states of Jalisco and Guanajuato of Mexico. In Canada and the United States this grassland occurs along the eastern side of the Rockies. In Mexico it occurs on the eastern side of the (western) Sierra Madre. From east to west the shortgrass prairie is narrow, varying from 100 to 500 km; but from north to south it extends almost 5000 km. The total area is nearly 150 million ha.

The distribution of blue grama is continuous from central Alberta (Canada) to central New Mexico (United States). Between central New Mexico and northern Chihuahua (Mexico), its distribution is discontinuous and, in places, merges with the desert grassland. Further south its distribution again becomes continuous in the highlands of Chihuahua, Durango, Zacatecas, Jalisco, and Guanajuato between the eastern and western Sierra Madre.

No single map of the entire distribution of blue grama has been published. For Canada, Coupland (1950) presented a map of the northern boundaries of the mixed prairie (taken to be the same as those of blue grama). For the United States, the maps of Shantz and Zon (1924), Carpenter (1940), and Kuchler (1964) show the distribution of blue grama (shortgrass prairie). For Mexico, the maps of Shreve (1939, 1942) and Leopold (1950, 1959) complete the picture. Leopold refers to the shortgrass prairie as the mesquite-grassland.

THUNDERSTORM RAINFALL

The climate of the central North American grassland is thoroughly discussed by Borchert (1950). His monumental work does not include the grasslands of Mexico and Canada; however, the same climatic patterns apply (México. Servicio Meteorológico, 1939).

The *general* feature of the climate in which blue grama dominates is the pattern of rainfall. Little rain occurs between the last of September and the first of April. Nearly 75% of the annual rainfall does occur during the April through September period. The source of moisture is the warm, moist air mass that moves across the Caribbean Sea and Gulf of Mexico and carries its moisture deep into the North American continent (Benton and Estoque, 1954; Holtzman, 1944).

The *characteristic* feature of the climate in which blue grama dominates is the complete temporal and spatial uncertainty of this rainfall pattern. Will there be a rainfall season? When will it begin? How long will it last? Where will it rain? Where it rains, how much will it rain? Where it rained last, how long will it be before it rains again? The *questions* about the rainfall pattern are the characteristic feature, not the rain itself.

Let us examine with more detail the pattern of precipitation that characterizes the Great Plains. Annual precipitation varies between 300 and 500 mm. However, as mentioned previously, about 75% of this occurs during the growing season (April to September, inclusively). What is even more striking is that more than 50% of the annual rainfall occurs during June, July, and August. This distinct rainfall season is clearly defined in Mexico (México. Servicio Meteorológico, 1939; Shreve, 1944; Gentry, 1957; Gómez, 1970), in the United States (U.S. Department of Commerce and U.S. War Department, 1947; U.S. Department of Commerce, 1949; Borchert, 1950), and in Canada (Coupland, 1950).

The abrupt flow of warm, moist air from the Gulf of Mexico is ultimately related to the position of the jet stream over the Himalayas (Bryson, 1957). Due to movement of the jet stream from south of the Himalayas to north of the mountain mass (in late May) a readjustment of the global circulation (during June) brings about a pressure system that promotes the penetration of moist air north from the Gulf of Mexico to the prairie provinces of Canada (Bryson and Lowry, 1955).

The arrival of this tongue of moist air has been studied in Arizona. Based on a dew-point temperature of 13°C, the average date of arrival is about 8 July, but sometimes it comes as early as 16 June or as late as 24 July. The flow of moist air is not entirely continuous, but occurs as pulses. This advance and retreat happens about four times between the date of the first advance and that of the last retreat (about 15 September). The presence of the moist air disappears as abruptly as it appears; thus, the potential for growing-season rain on the Great Plains lasts only 3 months.

The coincidence of the flux of moist air and the high summer temperatures make for one of the most awesome mechanisms for energy exchange in the atmosphere--the thunderstorm. Thunderstorms have received attention in the past, and much has been written about their characteristics. Battan (1961, 1964) has written two excellent, popular books recently. Because of the importance of weather conditions for airplane takeoffs and landings and also because hailstorms are intimately related to thunderstorms, thunderstorms continue to command intensive study.

One usually directs his attention to the destructive aspects of thunderstorms such as flashfloods and ruined crops. Rarely does one appreciate the fact that the success of native forage production and domestic dry-land

crop production in the interior of North America depends almost entirely on thunderstorm rainfall.

Before one can fully appreciate the evolutionary success of the grasses of the Great Plains, blue grama in particular, he must be aware of the uncertainties with which the grass must contend.

The area that receives rain from a thunderstorm is small. The shape of the area is slightly elliptical (Fogel and Duckstein, 1969); but if regarded as circular, the radius would vary from 0.75 km to 9.0 km. Within the area receiving rain, there is always one center (and sometimes more than one) that receives the greatest amount of rainfall. This center usually has a radius between 0.5 km and 0.75 km. Radially, away from the center, rainfall amounts decrease rapidly to the edge of the area. For a single thunderstorm, differences of 300% to 500% between the rainfall at the center and the rainfall 2 km away are not uncommon.

From records of many individual storms obtained from a single rain gage, the actual rainfall amounts for a specific point follow a distribution somewhat like this for Nunn, Colorado: 55% of the rainfall amounts to less than 8 mm; 25% is between 9 mm and 15 mm; 10% is between 16 mm and 23 mm; and 10% is greater than 24 mm. Recognizing that, with respect to the distance the rain gage may be from the thunderstorm center, amounts from three to five times greater or from one-third to one-fifth as much could be measured at another location less than 2 km away.

Thunderstorms are short-lived. The average duration of rainfall is between 35 and 50 min. Some may be as short as 1 min, and a very few thunderstorm sequences may last as long as 12 hr (Sariahmed and Kisiel, 1968). A general direct relationship between duration and rainfall amount exists: the longer the storm the greater the rainfall.

The time between thunderstorm rainfall at the same location is extremely variable. For the 3-month season at Nunn, Colorado, the time between events averages between 3 to 5 days. But again, one storm may follow another in rapid succession or it may be as long as 40 days before the area receives rainfall again. While the occurrence of rainfall over large, level areas is essentially random, there is a definite preference for thunderstorms to be more frequent over areas with abrupt topographical changes and over rough terrain.

Thunderstorms have a definite seasonal preference; they also have a definite diurnal preference. The great majority of them occur between 1200 and 1800 (local standard time). There is a tendency for more nocturnal storms in the upper midwestern states.

The highest rain rates ever recorded have been from thunderstorms. Rain rates as high as 500 mm/hr have been measured for short bursts of rain and 100 mm/hr is not uncommon. A more common rain rate is about 10 mm/hr.

Evaporation rates are high during the summer months. Values that range between 2 and 8 mm per day have been reported (Striffler, 1969). Considering the average storm amount and the time between storms, one can easily see that only from large thunderstorms will water be available to plants longer than a day.

This somewhat brief description of the nature of rainfall patterns that occur during the growing season on the shortgrass plains is not meant to be exhaustive, but rather to provide the setting in which the growth processes for blue grama are imbedded. In summary, rainfall during the growing season (April through September) in the shortgrass plains begins abruptly in June, per-sists less than 90 days, and ends almost as abruptly in August. Thunderstorms occur most frequently during the afternoons. They are small in areal extent and

nearly random in location. Durations are usually very short. Rainfall is extremely variable within the area covered by the storm and extremely variable from storm to storm. The time between storms is also random and quite variable, but is almost always long enough to insure that evaporation will deplete the soil water from the most common storm.

BLUE GRAMA

Blue grama is a native, perennial, warm-season shortgrass. It is the most important grama in terms of forage; it is nutritious, palatable, and cures well in the fall while retaining much of its nutritive value for winter grazing. Blue grama is an increaser and will replace midgrasses on overgrazed ranges or during droughts. It will withstand extreme droughts, recovering with opportunistic growth during favorable growth periods.

Blue grama grows under very diverse limits (seemingly). It is found on a variety of soils from 20°N latitude to 55°N latitude and from 700 m to 3000 m in elevation. However, the range of latitude and elevation through which blue grama grows is not as diverse as one might think. The predominant factor of the environment is rainfall, and its characteristics have previously been shown to be surprisingly uniform from Zacatecas to Saskatchewan.

Such a range, however, has promoted ecotypic variation throughout the evolution of the species. General observations have been that in its more northern and southern extents (Canada and Mexico) it is decidedly a sod grass. This is generally also true throughout its extent in the United States. However, in New Mexico, Arizona, and parts of Chihuahua it clearly assumes the bunchgrass form.

Ecotypic variation in terms of growth characteristics, photoperiodism, and flowering has received much attention. Riegel (1940) reported that blue

grama in the southern Great Plains were taller, had more leaf surface, greater herbage yields, and produced more tillers than those in the northern Great Plains. He also reported that southern plants flowered later than northern plants.

McMillan (1956) studied material on an east-west basis. Since latitude was the same he concluded that the late spring frosts, short wet seasons, early beginning of dry seasons, and early fall frosts for the western edge of the transect were the environmental factors responsible for the selection of rapid growing, early maturing ecotypes of blue grama. General conclusions are that flowering, maturity, and dormancy are earliest in the west and north and latest in the east and south.

Lavin (1953) observing blue grama plants from southern Arizona to southern Saskatchewan concluded that blue grama was a short-day plant in the south and an indeterminate-day plant in the north. Olmsted (1944) also showed that while photoperiod was directly related to latitude, the number of tillers showing elongation and herbage production were inversely related to latitude (for side oats grama).

Cornelius (1947) reported that flowering dates for blue grama were inversely related to latitude. This same north-south variation pattern in flowering was identified by other workers. For average flowering dates, Riegel (1940) found that blue grama from different sources in the Great Plains flowered on the following dates: northern, 1 July; southern, 25 July; and central, 5 August.

Benedict (1940) found that if average day and night air temperatures were equal to or greater than 25°C, flowering occurred with long or short days. However, if day temperatures were 25°C and night temperatures were

15°C, no flowering occurred. This indicates that floral induction is temperature sensitive.

The studies cited were results of garden or greenhouse trials. While we know that there are definite patterns of photoperiodism and flowering for blue grama under favorable conditions, we will see that the uncertainty of growing conditions makes it difficult to observe clearly the same patterns in the field.

Response to Thunderstorm Rainfall

In the majority of published articles on blue grama, some mention is invariably made concerning the opportunistic growth response of this intriguing species. Researchers have observed particular distinct or rapid responses of blue grama to growth, flowering, and seed production. For instance, Turner and Klipple (1952) measured herbage production in Colorado for four growing seasons. They observed that blue grama's ability to make prompt, full use of favorable growing conditions *whenever* they occur is the major factor leading to its dominance in the Great Plains. Emphasis is added to this point when they showed that clipping at regular intervals throughout the growing season has little effect on the total annual yield. They concluded that prediction of production is seldom reliable because blue grama growth depends largely upon the amount and distribution of rainfall.

In terms of the rapidity of response, Miller (1967), observing blue grama on a weekly interval, observed that many plants progressed from the late-boot stage to complete emergence of inflorescence and anthesis in less than a week.

McMillan (1959) observed that flowering in blue grama was decidedly dependent on availability of soil water. This observation and earlier findings

of Benedict (1940) and Lavin (1953) suggest that the flowering date is more than likely controlled by available soil water rather than photoperiod.

Miller (1967) concluded that the flowering of blue grama in the northern portions of its range is rather opportunistic as compared to the sourthern plants which appear to be more specific in their requirements for flowering.

Seed production is completely erratic. However, good seed years do occur. Wolff (1951) reported that good seed yields were associated with heavy rainfall not more than a month prior to the date of seed maturity. Flowering and seed production have received considerable attention mainly because of the interest in artificial revegetation. Natural revegetation by tillering is by far the most important means of reproduction in established stands.

The next three sections will examine in more detail the response of blue grama to the *season* of thunderstorm rainfall, to the *sequences* of thunderstorm events, and to an *individual* thunderstorm.

Response to Season of Thunderstorm Rainfall

The first part of this paper pointed out the abruptness of the season of thunderstorm rainfall. From north to south two requirements must be met simultaneously for blue grama to grow: adequate soil water and proper soil temperatures. In the highlands of Mexico soil temperatures may be conducive to growth as early as March; but because March, April, and May are dry months, no soil water is carried over from the previous winter. Growth must await the thunderstorms of June, July, and August. In contrast, the northern Great Plains' lower temperatures allow a carry-over of soil water from late winter into spring. Water is available but growth must await warmer soil temperatures.

When soil temperatures are acceptable for growth (late April or early May), soil water is being rapidly depleted. Growth can begin but fails to continue unless the thunderstorm season arrives before the carry-over soil water is exhausted.

Reference to a production study in Arizona will be made to represent the case of adequate soil temperature/deficient soil water. The thunderstorm season is slightly different in Arizona: it begins a month later (July) and continues through August and September.

Reynolds and Martin (1968) describe growth response of Rothrock and slender grama to thunderstorm rainfall. Growth begins in early July. The end of the growing season is usually around mid-September. The average growing season is about 70 days. On the average, growth starts 11 days after the first effective rain and continues for 4 days after the last effective rain of the season. In terms of foliage height 50% of the growth occurs by early August and 100% by the end of September.

Coupland's work (1950) in southern Saskatchewan represents the case of sufficient soil water/inadequate soil temperature for growth of blue grama. He found that an average soil temperature of 12°C at 15 cm was necessary for growth. Soil temperature controlled growth from mid-April until early May. From early May and for the rest of the growing season, soil water was the controlling factor. In terms of foliage height 50% of the growth occurs by early June and 100% by the end of July.

Clarke, Tisdale, and Skoglund (1947) noted the close relationship between soil temperatures and growth of blue grama. Fisher (1966) in Colorado observed blue grama to begin growth around 1 April only to die back by early May. Leaf growth resumed with the thunderstorms in June.

Whether or not herbage production in blue grama is solely dependent on rainfall during the thunderstorm season has been speculated upon. Smoliak (1956) reported the results of a study of the relation of herbage production to rainfall at Manyberries, Alberta, Canada. His finding was that the total May to June rainfall was most closely related to yearly herbage production. Preseason precipitation was not correlated with herbage production. Clarke et al. (1947) also reported a close relation between the precipitation/evaporation ratio during the growing season and yearly herbage production. Precipitation from the previous fall and winter were of less importance.

Green and Martin (1967) discuss the relation between summer rainfall and yearly herbage production in Arizona. They found that production was highly correlated with total July through September rainfall.

Observations in Colorado (Dahl, 1970) indicate that current season's production in blue grama is also dependent on rainfall received during the late summer or early fall of the preceding year. For southern New Mexico, Paulsen and Ares (1962) determined that if a thunderstorm season is preceded by a wet spring or if two years of high thunderstorm rainfall follow one after another, substantially greater production occurs during the current or second season, respectively. From a mathematical analysis of precipitation and herbage production (Rothrock and black grama) in Arizona, Lister and Schumacher (1937) predicted that in addition to rainfall during the thunderstorm season, fall rains contributed significantly to the following year's growth. We shall return to this point later in the paper for there appears to be a growth characteristic of blue grama that justifies these conclusions.

A particularly thorough study of phytomer growth of blue grama was conducted by Lang'at (1968). A phytomer is the basic unit of growth in grasses. It consists of an internode together with its leaf (blade and sheath) at the upper end and the bud and node at the lower end of the internode.

Regrowth begins in spring from elongation of leaves formed the previous year. Tillers begin to emerge about the middle of June and continue until the end of July. An average of seven leaves per shoot are produced during the growing season. Phytomer internodes of vegetative shoot never elongated. Leaf blades made half of their growth in June and ceased elongation by the end of July. Leaf sheaths elongated slowly until the end of July, but increased rapidly thereafter.

Inflorescences were initiated about the end of June. Elongation of internodes of the reproductive shoots began with floral initiation and continued at a steady rate until the end of July when an increased rate began that was maintained until the middle of August. Many inflorescences aborted due to dry, windy conditions. Heading began around mid-July, but flowering and anthesis occurred in early August.

Miller (1967) conducted a garden experiment in Colorado in which he observed the growth patterns of blue grama from several sources representing its range from Arizona to the Dakota's. He concluded that since maximum height for all plants was reached at about the same time, the rate of elongation rather than length of growing period appeared more important. There appeared to be major differences in height growth, time, and rate of growth during the season. Taller plants made maximum growth early in the season; shorter plants grew later in the season. Growth patterns failed to

show any relation between herbage production and period of active growth or date to first anthesis.

This discussion has highlighted the seasonal pattern of growth in blue grama. The pattern is characteristic from one end of its range to the other. Pre-thunderstorm season rainfall has not been shown to be too important to current season production. Rainfall during the thunderstorm season is definitely shown to be the most important factor in herbage production. However, there is evidence to suggest that rainfall in late summer or early fall of the previous season is related to current season production. Ecotypic variation in growth patterns is not in the length of the growing season, but is displayed by the time at which most rapid growth occurs and the rate of elongation during the period of most rapid growth.

Response to Sequence of Thunderstorm Events

In the discussion of thunderstorm rainfall, the complete uncertainty of the *amount* of rainfall delivered by a thunderstorm was pointed out. Also, with consideration of the areal extent of thunderstorms and their random occurrence, the *sequence* of thunderstorm events at a particular location is particularly critical. These two characteristics together, then, essentially control herbage production of blue grama.

This aspect of the importance of rainfall amount and distribution has nearly always been recognized by investigators; however, no one has ever addressed their research to the full problem. Some attention to what researchers have called effective rainfall deserves discussion.

Effective rainfall is the amount of rainfall *at a particular time in the thunderstorm sequence* that is required to maintain soil water in a range available for uninhibited plant growth. It is not a critical value in terms

of a fixed amount; instead, it is a dynamic *process* that is a function of time, hydraulic characteristics of the soil, plant water content, stage of plant development, and evaporative demands of the atmosphere. It is sufficiently complex that researchers have paid it only lip service.

In New Mexico, Paulsen and Ares (1962) regarded 12 mm a day for 2 days in succession to be the effective rainfall to start growth. Reynolds and Martin (1968) concluded that for Arizona ranges effective rainfall was greater than 10 mm per day. Rainfall less than 10 mm was not effective unless preceded or succeeded by rains greater than 10 mm within 1 day. In Saskatchewan, using 8 mm as the threshold for the amount of effective rainfall, Coupland (1950) calculated that there were only 5% of the days between April and October in which effective rainfall occurred.

A more thorough discussion of effective rainfall is given by Green and Martin (1967). Effective rainfall is regarded as the amount which will maintain 2.5 cm of soil water per 30 cm of soil. At least 2.5 cm water per 30 cm soil is required to sustain rapid growth. During the thunderstorm season soil water within the range for rapid growth (at 7 cm in depth) will be limiting for growth within 2 to 4 days if no rainfall occurs. Single individual events as large as 8 mm do not change soil water content at 7 cm. Small events, less than 8 mm, can only maintain soil water contents adequate for growth when they are interspersed in a sequence containing events larger than 10 mm.

As one would suspect, few publications have appeared that are directed toward elucidating the effect of sequences of thunderstorm events. However, researchers have pointed out that observations do indicate response to sequences of thunderstorm events. Rauzi, Painter, and Dobrenz (1969) studied mineral and protein contents of blue grama in Wyoming. They showed that

nutrient status of blue grama was dependent on both stage of development and rainfall. Percentage Fe and Mn increased throughout the growing season while K, P, Mg, Ca, Zn, and Ca decreased. Percentage crude protein of blue grama decreased with maturity, but showed two sharp reversals that correspondend to an inmmediately preceding sequence of thunderstorm events.

Chlorophyll concentration response to rainfall is striking in blue grama. Rauzi and Dobrenz (1970) presented information showing that although chlorophyll concentration decreases from the beginning to the end of the growing season, a sequence of individual, small thundershowers spaced 1 day apart caused a trend reversal and increased chlorophyll concentration almost to the level measured at the peak of the growing season.

Sims, Lovell, and Hervey (1971) reported herbage and nutrient production of blue grama in eastern Colorado. Although their reported data suggest direct responses of nitrogen-free extract, crude fiber, crude fat, minerals, and herbage production to thunderstorm sequences, no mention is made of the dependence.

Limited data are available to clearly show growth/thunderstorm sequence dependence. Care must be taken to assure that *daily* rainfall is measured at the plots where studies are progressing. Also, because of the speed at which blue grama responds, 2-week sampling intervals are seriously questioned. Weekly intervals may suffice, but no one knows.

Response to a Single Thunderstorm Event

No one knows how long it takes for blue grama to respond to a single thunderstorm event. It is reported that blue grama grows in spurts corresponding to favorable conditions (Bement, personal communication). Observations by researchers in the field suggest that visible response to effective rains occurs within 72 hr.

To address this section of the paper to specific literature on the response of blue grama to single thunderstorm events cannot be done because no such studies have been found. Instead, it would be interesting to consider the growth responses that have been observed in laboratory studies of other plants and also to consider field measurements of soil water tension inmediately after simulated thunderstorm rainfall.

Recent work by Hsiao, Acevedo, and Henderson (1970) shows just how fast plants do respond to soil water increases. Working with maize, they showed that with plants growing at -2 bars soil water tension, the growth response (leaf elongation) when water was added to the soil was *instantaneous*. Plants growing at -3 bars soil water tension responded within 5 min. Presumably, if plants are experiencing greater soil water tensions, more time elapses between the time of rainfall and the growth response. However, assuming a lag time of 5 min per bar and a linear relation, growth response of a plant enduring -40 bars would occur within a few hours. These figures for response time are indeed impressive even if they are doubled.

Simulated rainfall experiments (Smith, unpublished) show that after rainfall simulation stops, soil water tension at the 10-cm depth remains below -15 bars for only about 4 hr. (At 5 cm, soil water tensions remain below -15 bars for only 0.5 hr.) This rapid change of soil water tensions impresses one with the rapidity with which blue grama must respond to take advantage of thunderstorm rainfall. Obviously, blue grama must be able to respond very quickly to single thunderstorm events. The nature of this response has not received detailed study. Many intriguing questions await exploration. I will entertain some of these questions in the sections on survival.

SURVIVAL

For blue grama, survival has many facets. There is a facet of survival that applies between periods of effective rainfall during the thunderstorm season. There is a facet of survival that applies between yearly thunderstorm seasons. In discrete jumps there are also facets of survival in terms of centuries, millenia, and myriads. Most discussion will concern the first two facets of survival: survival between events and sequences of thunderstorm rainfall and survival between years.

It seems appropriate to review here some of the plant adaptations that may be of particular significance for survival in all of the aspects to be discussed. Daubenmire (1968) lists these factors in terms of competition:

1.	Seed production and dispersal	9.	Plasticity
2.	Vegetative reproduction	10.	Vigor and size
3.	Reproductive potential	11.	Time of initial growth
4.	Genetic variability	12.	Time of root penetration
5.	Life form	13.	Nutrient-uptake ability
6.	Longevity	14.	Period of growth
7.	Reserves	15.	Growth rate
8.	Drought resistance	16.	Compensation point

In considering the different facets of survival we shall return to this list to attach varying importance to several factors.

Survival Between Events and Sequences

Survival between events and sequences of events is promoted by two phenomena, one corresponding to the event and one corresponding to the non-event (the time between events). Corresponding to the event is the

phenomenon of opportunistic photosynthesis and growth, Corresponding to the non-event is the phenomenon of drought resistance.

Competition may be defined as the simultaneous demand for the same resources in a common environment when these demands are in excess of the immediate supply (Risser, 1969). Clearly, this applies to soil water as a resource. Simultaneous demands on this resource come from the atmosphere, the soil, and the plant. I submit that, in importance, this form of competition far exceeds intra- and interspecific competition in blue grama.

Opportunistic photosynthesis and growth of blue grama during very brief periods suitable for rapid growth has been frequently cited for its success and survival. Attention has already been given to the short time that soil water is available in the appropriate range and also to the almost immediate physiological response to an abrupt impulse of water. Now let us examine what the plant must do during these briefs periods.

In the presence of sunlight, chlorophyll, and water the photosynthetic reactions produce sugars. For all sugars produced in one part of the plant, elsewhere in the plant concentration gradients must exist to move these carbohydrates. Multiple demands for sugars must occur to maintain concentration gradients that will promote removal of the sugars in the leaf, thus, allowing the process to continue. There are two driving forces in the system: the rate of production (photosynthesis) and the rate of removal of carbohydrates (respiration and storage). Thus, any internal or external factor affecting either the production or removal of sugars will affect the general level of carbohydrate reserves in the system (Cook, 1966).

The differential demands arise from different growth rates of other plant parts and organs and are preferentially satisfied depending on distance, position, vascular connections, and relative ages of parts (Wardlaw, 1968).

In general, lower leaves provide carbohydrates for roots, and upper leaves provide carbohydrates for shoot apices. Middle leaves provide carbohydrates both ways. Once leaves have fully expanded and matured, they continue to photosynthesize; but since they cannot store any carbohydrates, the roots and stems receive the excess. Actively growing leaves retain all their assimilates and import from older leaves. Tillers import assimilates from older shoots (Williams, 1964). Demands by flowers and fruits, particularly, have precedence over all other plant parts. Roots and buds receive carbohydrates only when all other demands are satisfied.

The major function of carbohydrate reserves is to satisfy physiological demands for regrowth in the spring, during stress periods, and for regrowth following removal of plant parts, i.e., natural death and grazing (Cook, Stoddart, and Kinsinger, 1958).

At all locations in the plant, once carbohydrates are available, they are metabolized in the growth processes of cell division and cell elongation. During these processes, respiration occurs and carbon dioxide is released. Carbon becomes bound in structural cellulose, and some is stored in starches.

Since we have discussed the nature of phytomer growth in some detail, we can relate the basic principles of distribution of carbohydrates as shown above. The vegetative shoots have internodes that never elongate during the current season. Therefore, in light of their proximity to the source of carbohydrates in terms of distance, position, vascular connections, and relative ages; their demands for growth are met first. Knowing that concentration of carbohydrates in roots is always low (Sims et al., 1971) and accepting the fact that carbohydrate transfer to roots is inversely proportional to the growth rate, it seems very probable that once the growth spurt corresponding to a brief event period slows down, carbohydrates are immediately

transferred to the roots. The results of Sims et al. (1971) show that the concentration of root carbohydrates is almost a constant value. This suggests that for non-event periods root carbohydrates accumulated in a short period are used to sustain plant processes until the next event.

If and when reproductive shoots begin elongateing, their demand for carbohydrates takes precedence over both tillers and roots. Only after the reproductive shoots have matured or have been killed by drying winds do carbohydrates again accumulate in the roots.

Survival during non-events is a matter of drought resistance. Levitt (1964) presents one of the clearest views of drought resistance that can be found. He clearly differentiates between the two components of xerophytism-- drought resistance and drought growth. Drought resistance embraces adapta- tions leading to survival during drought. Drought growth embraces growth adaptations leading to growth, development, and reproduction during drought.

Drought resistance can be considered to be made up of two of its own components--avoidance and tolerance. Avoidance is the ability to exclude the drought factor from its tissues. Tolerance is the ability to survive the prenetration of its tissues by the drought factor. In higher plants the drought factor is met mainly by avoidance, but also with tolerance.

A plant can avoid drought in two ways, either by water conservation or by water absorption. Conceivably, a plant could tolerate drought by having a greater rate of photosynthesis than a drought-intolerant plant.

In terms of avoidance, characteristics that enhance this ability are a high root/shoot ratio and an ability to limit water loss when absorption is reduced. This involves both stomatal control and a protective epidermis. Avoidance is a great advantage during short-term drought, but for extreme

drought or long-term drought survival depends on tolerance. Tolerance will allow the plant to survive the most severe periods in the living state without growing and to continue active growth during the less severe drought.

A plant that can successfully avoid drought is able to maintain its turgor pressure. Since growth occurs with turgor pressure, the plant can continue growth and development.

In regard to drought resistance, blue grama possesses a variable mix of avoidance and tolerance. Characteristics of avoidance mechanisms are manifest in the buliform cells in the leaves of the gramas. As drying proceeds, the buliform cells lose water and the leaf curls, thus, reducing water loss. The high root/shoot ratio in gramas also is an avoidance characteristic that promotes rapid water absorption. Thus, for non-event droughts blue grama appears to be able to avoid drought. Contrary to blue grama's apparent ability to reduce water loss, studies have shown blue grama to be an extremely inefficient user of water in terms of production per unit of water.

Though subject to controversy, I submit that blue grama also has a high degree of tolerance. No studies have been performed to determine at what soil water tension growth is curtailed. I suspect that significant growth continues at soil water tensions of -20 to -30 bars.

Summarizing, survival of blue grama between events and sequences of events seems to be almost entirely due to extremely rapid photosynthetic response to impulses of rainfall, very fast translocation of carbohydrates to roots, and physiological quiescence during non-events.

Survival Between Years

The role of winter survival and regrowth will be discussed in this section. Winter hardiness is intimately related to reserve carbohydrate. Fisher

(1966) found that root reserves were lowest at the beginning of the growing season (due to low winter precipitation and exhaustion of reserves through respiration) and that there was no significant decrease throughout the growing season. Many researchers have concluded that once carbohydrate needs of new leaves are satisfied, additional carbohydrates are not of particular importance to the plant except for regrowth (Jameson, 1964; May and Davidson, 1958).

In the preceding section the role of reserves in the spurts of growth and regrowth was touched upon lightly. The role of reserves is considered to be more important for survival during non-events than for regrowth per se.

Reserves can only accumulate when rate of production exceeds rate of use. The major period of carbohydrate accumulation in grasses appears to be between flowering and dormancy. The observation that late summer or early fall rains were of particular benefit for the succeeding year's growth has already been presented. Assuming that the rains occurred after flowering and between dormancy, their importance in the promotion of accumulation of reserves before dormancy is obvious.

Studies have been reported that show that growth of blue grama is related to the previous year's growth if the previous year was a *good* year. Partial explanation has been provided by Stubbendieck and Burzlaff (1970) who examined the nature of phytomer growth of blue grama over two seasons. Of the 16 phytomers characteristic of a mature reproductive culm, 7 had been initiated during the previous growing season. The leaf of the eighth phytomer was the first to be initiated when spring growth began in April. The last phytomer to be initiated (no. 14) was intiated near the middle of June. Internodes of phytomers 8 through 14 elongated to produce the reproductive culm. The internodes of phytomers 15 and 16 were located directly below and between

the nodes to which the rachises of the spikes were attached. The culmination of growth of a culm as carry-over from the previous year's growth may explain part of the relation between two successive year's production.

This particular ability of blue grama to form about 16 phytomers per year, growing about half of them during the current season and carrying over half of them for the succeeding season, is an intriguing strategy for survival between years.

For blue grama the hardening period begins in midfall and continues until the date of permanent soil freezing. Carbohydrates provide the energy for the development of frost resistance, maintenance of resistance during winter, and regrowth in the spring. Frost resistance may be impaired by warm, wet periods during the hardening period.

Hardening period is controlled by many factors. Those that appear most important are shorter day lengths, generally lower temperatures alternating between 20°C during the day and 0°C at night, and adequate light for high photosynthesis rates (Tysdal, 1933). Although hardening is not of specific concern in this paper, the interested reader will find an excellent review in Smith (1964).

Considering frost resistance which is a desirable defense against both beginning-of-season frost and end-of-season frost, Levitt (1956) and Dexter (1956) both summarized from experiments that high K or P in the soil increased frost resistance while high N invariably decreased it. This leads one to speculate that it could be that the lower levels of N in the Great Plains soils actually promotes survival of many of its grasses.

The relation between N and hardening (winter survival) is closely related to the fact that N stimulates leaf production, but at the expense of reserves (McIlroy, 1967). High N during growth period may cause these

-24-

reserves to be reduced to a level that is unable to satisfy plant needs during the winter.

There has been evidence of blue grama mortality after nitrogen application (Rauzi, Lang, and Painter, 1968). In this particular study the researchers attributed the decline in blue grama to subnormal rainfall. However, considering the evidence provided by Levitt (1956) and Dexter (1956), one wonders if the plants had succumbed to winter death because the nitrogen had decreased their frost resistance.

Concluding this section, important aspects of survival between years need repeating. First, the most important aspect of year to year survival seems to lie in the growth of only one-half of the phytomers per season, reserving the other half for regrowth in the succeeding year. Second, one appreciates the importance of reserves for winter survival and the benefit of rains after flowering. Finally, the detrimental effect of mid- or late-fall rains is also recognized. As an aside, low nitrogen is a particularly beneficial feature of blue grama range. In combination, then, the particular growth of phytomers and the particularly dry falls and early winters afford a reasonable guarantee of survival between years.

Survival Between Centuries

Seed production in blue grama is very erratic. Germination and successful establishment is even more erratic. It has been generally known that blue grama can assume dormancy during periods of water stress and resume growth as conditions become favorable. Furthermore, during a favorable growing season floral induction and initiation of flowering culms is a continuous process throughout the favorable period. It has also been observed that floral induction can take place and remain in an induced state while the

plant assumes dormancy. Growth can then resume and flowering can take place without any further floral induction. This is the explanation for the sometimes completely erratic flowering of blue grama; flowering can take place from floral induction that occurred sometimes during the previous season.

Flowering in blue grama has been observed to depend on soil water and cool temperature during blossoming and seed formation (Hoover et al., 1947). Also, Branson (1941) and Brown (1943) concluded that seed production was directly related to soil water.

Temperatures below 15°C are also detrimental during flowering and pollen shed (Jones and Newell, 1946). Thrips, gall midges, and leafhoppers have been known to affect seed production of blue grama (Kneebone, 1957).

Coupland (1950) reported that reproductive culms were only produced in favorable years; then, they appeared in June, and anthesis occurred during the first half of July. Late summer rains increased seed production. Seeds ripened by the end of August and were shed by the end of September.

The evidence appears that tillering is the predominant mechanism of survival between centuries. Bement (personal communication) has observed that seedling occurrence in blue grama is extremely rare and that reproduction in an established community is by tillering. Riegel (1940) found that, in general, herbage yield of blue grama was inversely related to seed yield. Tillering was greater in southern plants.

The small probability of germination and establishment by blue grama is clearly indicated by Riegel's (1940) description of greenhouse require-ments. Water was *never* deficient at the surface of the soil for almost 25 consecutive days. Hyder (personal communication) has made similar statements as to these requirements. The probability of 25 consecutive days of effective

rainfall *at the same location* is very very small. Regarding such stringent requirements for establishment from seed, the almost complete dependence on tillering for vegetative reproduction and survival between centuries is easily understood.

Survival Between Millenia

As one would expect, the further into the future we project out thoughts, the less we have to substantiate them. In the earlier discussions of survival for the periods considered, the implicit assumption was that the environment did not change. Over a thousand years this is a distinct possibility. Complete reliance on tillering solves survival from century to century, but does it with little change in the genetic material. The incorporation of new combinations of genes can *only* come by sexual reproduction. Therefore, the strategy for survival between millenia is the production of seeds.

Survival Between Myriads

Just to speculate on survival between spans that cover 10,000 years, let me conclude with McMillans's (1959) ideas. Following the retreat of the glaciers, the Great Plains grassland was repopulated from distinct distributions of grasses from basically different gene populations. The available genetic potential provided the great source of genetic combinations from which genetic potential was able to match environmental potential. If blue grama is to survive between myriads, it will be by the same strategy: "variants which make each stand of grassland at any given time [must be] fundamentally different from any other stand ..."

LITERATURE CITED

Battan, L. J. 1961. The nature of violent storms. Anchor Books, Doubleday, Garden City, New York. 159 p.

Battan, L. J. 1964. The thunderstorm. New Amer. Libr. World Lit., New York. 130 p.

Benedict, H. M. 1940. Effect of day length and temperature on the flowering and growth of four species of grasses. J. Agr. Res. 61:661-671.

Benton, G. S., and M. A. Estoque. 1954. Water vapor transfer over the North American continent. J. Meteorol. 11:462-477.

Borchert, J. R. 1950. The climate of the central North American grassland. Ann. Ass. Amer. Geogr. 40:1-39.

Branson, L. R. 1941. An analysis of seed production on native Kansas grasses during the drought of 1939. Kansas Acad. Sci., Trans. 44:116-125.

Brown, H. R. 1943. Growth and seed yield of native prairie plants in various habits of mixed-prairie. Kansas Acad. Sci., Trans. 46:87-99.

Bryson, R. A., and W. P. Lowry. 1955. The synoptic climatology of the Arizona summer precipitation singularity. Bull. Amer. Meteorol. Soc. 36:329-339.

Bryson, R. A. 1957. The annual march of precipitation in Arizona, New Mexico, and northwestern Mexico. Univ. Arizona Inst. Atmos. Phys. (Tucson), Tech. Rep. Meteorol. Climatol. Arid Region No. 6.

Carpenter, J. R. 1940. The grassland biome. Ecol. Monogr. 10:617-683.

Clarke, S. E., E. W. Tisdale, and N. S. Skoglund 1947. The effects of climate and grazing practices on shortgrass prairie vegetation. Dominion Dep. Agr., Tech. Bull. 46.

Cook, C. W., L. A. Stoddart, and F. E. Kinsinger. 1958. Responses of crested wheatgrass to various clipping treatments. Ecol. Monogr. 28:237-272.

Cook, C. W. 1966. Carbohydrate reserves in plants. Utah Agr. Exp. Sta., Utah Resources Ser. 31.

Cornelius, D. R. 1947. The effect of source of little bluestem grass seed on growth, adaptation and use in revegetation seedings. J. Agr. Res. 74:133-143.

Coupland, R. T. 1950. Ecology of mixed prairie in Canada. Ecol. Mongr. 20-271-315.

Dahl, B. E. 1970. Plant water-use efficiency as affected by grazing. Presented at Annu. Meeting Amer. Soc. Range Manage., Denver, Colorado.

Daubenmire, R. 1968. Plant communities. A textbook of plant synecology. Harper and Row, New York. 300 p.

Dexter, S. T. 1956. The evaluation of crop plants for winter hardiness, p. 203-239. *In* Vol. 8, Advances in agronomy. Academic Press, New York.

Fisher, A. G. 1966. Seasonal trends of root reserves in blue grama and western wheatgrass. M.S. Thesis. Colorado State Univ., Fort Collins. 55 p.

Foger, M. M., and L. Duckstein. 1969. Point rainfall frequencies in convective storms. Water Resources Res. 5:1229-1237.

Gentry, H. S. 1957. Los pastizales de Durango. Estudio ecológico, fisiográfico, y florístico. Instituto Mexicano de Recursos Naturales Renovables. México, Distrito Federal. 375 p.

Gómez, A. A. 1970. Unión ganadera regional de Chihuahua. Boletín Meteorológico No. 8. 294 p.

Green, C. R., and S. C. Martin, 1967. An evaluation of precipitation, vegetaion, and related factors on the Santa Rita Experimental Range. Univ. Arizona Inst. Atmos. Phys. (Tucson), Tech. Rep. Meteorol. Climatol. Arid Reg. No. 17.

Holtzman, B. 1944. Sources of moisture for precipitation in the U.S. U.S. Dep. Agr. Tech. Bull. 589.

Hoover, M. M., J. E. Smith, Jr., A. E. Ferber, and D. R. Cornelius. 1947. Seed for regrassing Great Plains areas. U.S. Dep. Agr. Farmers' Bull. 1985. 37 p.

Hsiao, T. C., E. Acevedo, and D. W. Henderson. 1970. Maize leaf elongation: Continuous measurements and close dependence on plant water status. Scince 168:590-591.

Jameson, D. A. 1964. Effect of defoliation on forage plant physiology, p. 67-80. *In* Forage plant physiology and soil-range relationships. Amer. Soc. Agron. Spec. Pub. No. 5. Madison, Wisconsin.

Jones, M. D., and L. C. Newell. 1946. Pollination cycles and pollen dispersal in relation to grass improvement. Nebraska Agr. Exp. Sta. Res. Bull. 148.

Kneebone, W. R. 1957. Blue grama seed production studies. J. Range Manage. 10:17-21.

Kuchler, A. W. 1964. Potential natural vegetation of the conterminous United States. Amer. Geogr. Soc. Spec. Pub. No. 36. New York. 116 p.

Lang'at, R. K. 1968. Developmental morphology of the shoots of *Bouteloua gracilis* and *Andropogon hallii* in relation to grazing. M.S. Thesis. Colorado State Univ., Fort Collins. 57 p.

Lavin, F. 1953. Geographic variations in the response of blue grama grass to photoperiod. M.S. Thesis. Univ. Chicago, Illinois.

Leopold, A. W. 1950. Vegetation zones in Mexico. Ecology 31:507-518.

Leopold, A. W. 1959. Wildlife in Mexico. The game birds and animals. Univ. California Press, Berkeley and Los Angeles. 568 p.

Levitt, J. 1956. The hardiness of plants. Vol. 6. Monogr. Amer. Soc. Agron., Academic Press, New York. 334 p.

Levitt, J. 1964. Drought, p. 57-66. *In* Forage plant physiology and soil-range relationships. Amer. Soc. Agron. Spec. Pub. No. 5. Madison, Wisconsin.

Lister, P. B., and F. X. Schumacher. 1937. The influence of rainfall upon tuft area and height growth of three semidesert range grasses in southern Arizona. J. Agr. Res. 54:109-121.

McIlroy, R. J. 1967. Carbohydrates of grassland herbage. Herb. Abstr. 37: 79-87.

McMillan, C. 1956. Nature of the plant community. I. Uniform garden and light period studies of five grass taxa in Nebraska. Ecology 37:330-340.

McMillan, C. 1959. The role of ecotypic variation in the distribution of the central grassland of North America. Ecol. Monogr. 29:285-308.

May, L. H., and J. L. Davidson. 1958. The role of carbohydrate reserves in regeneration of plants. Australian J. Agr. Res. 9:767-777.

México. Servicio Meteorológico. 1939. Atlas climatological de México. Talleres gráficos de la dirección de geografía, meteorología, e hidrología, Tacubaya, Distrito Federal. 158 p.

Miller, R. V., Jr. 1967. Ecotypic variation in *Andropogon scoparius* and *Bouteloua gracilis*. Ph.D. Diss. Colorado State Univ., Fort Collins. 154 p.

Olmsted, C. E. 1944. Growth and development in range grasses. IV. Photoperiodic responses in twelve geographic strains of sideoats grama. Bot. Gaz. 106:46-74.

Paulsen, H. A., Jr., and F. N. Ares. 1962. Grazing values and management of black grama and tobosa grasslands and associated shrub ranges of the southwest. U.S. Dep. Agr. Tech. Bull. 1270. 56 p.

Rauzi, F., R. L. Lang, and L. I. Painter. 1968. Effects of nitrogen fertilization on native rangeland. J. Range Manage. 21:287-291.

Rauzi, F., L. I. Painter, and A. K. Dobrenz. 1969. Mineral and protein contents of blue grama and western wheatgrass. J. Range Manage. 22: 47-49.

Rauzi, F., and A. K. Dobrenz. 1970. Seasonal variation of chlorophyll in western wheatgrass and blue grama. J. Range Manage. 23:372-373.

Reynolds, H. G., and S. C. Martin. 1968. Managing grass-shrub cattle ranges in the southwest. U.S. Dep. Agr., Agr. Handbook No. 162. 44 p.

Riegel, A. 1940. A study of the variations in the growth of blue grama grass from seed produced in various sections of the Great Plains region. Kansas Acad. Sci., Trans. 43:155-171.

Risser, P. G. 1969. Competitive relationships among herbaceous plants and their influences on the ecosystem function in grasslands, p. 153-182. *In* R. L. Dix and R. G. Beidleman [ed.] The grassland ecosystem: A preliminary synthesis. Range Sci. Dep. Sci. Ser. No. 2. Colorado State Univ., Fort Collins.

Sariahmed, A., and C. C. Kisiel. 1968. Synthesis of sequences of summer thunderstorms volumes for the Atterbury watershed in the Tucson area, p. 439-447. *In* Use of analog digital computers in hydrology. Vol. 2, Proc. IASH Symp.

Shantz, H. L., and R. Zon. 1924. The natural vegetation of the United States. *In* Atlas of American agriculture, Section 7. U.S. Dep. Agr., Washington, D.C.

Shreve, F. 1939. Observations on the vegetation of Chihuahua. Madroño 5(1):1-13.

Shreve, F. 1942. Grassland and related vegetation in northern Mexico. Madroño 6:190-198.

Shreve, F. 1944. Rainfall of northern Mexico. Ecology 25:105-111.

Sims, P. L., G. R. Lovell, and D. F. Hervey. 1971. Seasonal trends in herbage and nutrient production of important sandhill grasses. J. Range Manage. 24:55-69.

Smith, D. 1964. Freezing injury of forage plants, p. 32-56. *In* Forage plant physiology and soil-range relationships. Amer. Soc. Agron. Spec. Pub. No. 5. Madison, Wisconsin.

Smoliak, S. 1956. Influence of climatic conditions on forage production of shortgrass range. J. Range Manage. 9:89-91.

Striffler, W. D. 1969. The grassland hydrologic cycle, p. 101-116. *In* R. L. Dix and R. G. Beidleman [ed.] The grassland ecosystem: A preliminary synthesis. Range Sci. Dep. Sci. Ser. No. 2. Colorado State Univ., Fort Collins.

Stubbendieck, J., and D. F. Burzlaff. 1970. Nature of phytomer growth in *Bouteloua gracilis* (H.B.K.) Lag. Presented at Annu. Meeting Amer. Soc. Range Manage., Denver, Colorado.

Turner, G. T., and G. E. Klipple. 1952. Growth characteristics of blue grama in northeastern Colorado. J. Range Manage. 5:22-28.

Tysdal, H. M. 1933. Influence of light, temperature, and soil moisture on the hardening process in alfalfa. J. Agr. Res. 46:483-515.

U.S. Department of Commerce. 1949. The thunderstorm. Report of the thunderstorm project. A joint project of four U.S. government agencies: Air Force, Navy, National Advisory Committee for Aeronautics, and Weather Bureau. U.S.Government Printing Office, Washington, D.C. 287 p.

U.S. Department of Commerce and U.S. War Department. 1947. Thunderstorm rainfall. Part 1, text. Hydrometeorol. Rep. No. 5. Waterways Exp. Sta., Vicksburg, Mississippi. 331 p.

Wardlaw, I. F. 1968. The control and pattern movement of carbohydrates in plants. Bot. Rev. 34:79-105.

Weaver, J. E., and F. W. Albertson. 1956. Grasslands of the Great Plains. Johnson Publ. Co., Lincoln, Nebraska. 395 p.

Williams, R. D. 1964. Assimilation and translocation in perennial grasses. Ann. Bot., N.S. 28(111):419-426.

Wolff, S. E. 1951. Harvesting and cleaning grass and legume seed in the western gulf region. U.S. Dep. Agr., Agr. Handbook No. 24.