

High-Resolution Climatic Analysis and Southwest Biogeography

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Meteorologists and climatologists have produced significant new data on the fluid dynamics of the atmosphere, thus allowing biologists to examine more closely the cause-effect relation between the large-scale structure of the atmosphere and the dominant patterns of global biogeography. The inability to characterize the high-frequency variability of the weather has constrained such efforts. A method that allows year-to-year patterns of weather variability to be characterized in the contexts of global warming and cooling trends is applied in a combined analysis of long-term monthly weather records and data from an ecological monitoring project in southern New Mexico. The analysis suggests a cause-effect hypothesis of recent desertification in the North American Southwest. The links between the atmosphere and the biosphere are based on the fundamentally different responses to specific weather regimes of semidesert grasses with a C_4 photosynthetic pathway and desert shrubs with a C_3 photosynthetic pathway. The hypothesis appears to be of sufficient generality to explain the complex, but well-documented, floristic changes that have occurred in the same region since the last glacial maximum.

BIOLOGISTS HAVE LONG RECOGNIZED THAT THE GENERAL structure of the atmosphere is the dominant factor controlling the distribution of biomes on this planet. However, evidence of the causal links between the large-scale structure of the atmosphere and regional to local structure of vegetation has been elusive. The lack of a deterministic representation of weather patterns has forced most biologists to treat climatic variation as a random background, or, to ignore it altogether. Global climatic regimes have now been spatially defined within a complex, deterministically structured atmosphere and correlated with the general outlines of major floristic regions (1). The next step is to determine mechanistic cause-effect links between atmospheric dynamics and floristic distributions.

Neilson and Wullstein (2) described methods to produce a hypothesis of causal links between the atmosphere and the current and Holocene distributions of two southwestern oak species. The methods are extended here to an investigation of patterns of high-frequency weather variability within and between three temporally defined historical climatic regimes. A case study of regional floristic responses to these shifts in global climate is presented and placed in the context of glacial-interglacial cycles. The relation of these regional historic patterns to global biotic dynamics is also examined.

The regional focus is in the northern Chihuahuan desert in southern New Mexico, where a general shift from semidesert

grassland to desert shrubland has been well documented and attributed to climatic change, overgrazing, or both (3). These causal mechanisms are examined through the synthesis of several long-term data sets representing plant demography, climatology, and the Holocene fossil history of the region. The climatic forcing component of these floristic changes will be related to a frequently used index of global climatic patterns, North Pacific sea-surface temperature (SST) anomalies.

Background on the New Meteorology

Investigations into the temporal association of such diverse events as north Pacific SST anomalies, the failure of the east Pacific anchovy fishery (El Niño), the Sahelian and Indian droughts, and many other climatic and oceanographic anomalies have led to the consensus that they are each related to specific perturbations in the coupled ocean-atmosphere flow structure (4). The association of these events, through the flow structure of the atmosphere, has been termed "teleconnection." These teleconnections are brought about by the behavior of the long-wave patterns of the jet streams, that is the Rossby waves. When the pole-tropic temperature gradient is relatively steep (presumably during global cool periods, cooling trends, or both), these form high amplitude, north-south (meridional) loops which tend to resonate (that is, form standing waves) with surface features of SST anomalies, continental margins, and mountain ranges (5). When the pole-tropic temperature gradient is relatively shallow (presumably during warm periods, or warming trends, or both), wave amplitude and wavelength decrease and the entire, nonresonant wave train travels from west to east (zonal).

Different weather systems are associated with specific air masses that are separated by jet streams and large-scale surface topography. Cyclonic systems tend to originate in and travel along jet stream paths. Therefore, under meridional (resonant) flow, storm tracks frequently travel along consistent paths, producing chronically wet or cold regions immediately adjacent to chronically dry or warm regions. Under zonal (nonresonant) flow, storm tracks are temporally and spatially more random, since the entire wave train is moving. Thus, during zonal flow, wet and dry regions are more diffuse relative to each other and through time. Similar patterns prevail for convective type storms. Examples of these different atmospheric flow patterns can be found in (at least) three distinct global climatic regimes that have occurred since the mid-19th

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century. Each produced a distinct spatial and temporal pattern of weather variability which lasted for several decades (6, 7).

Plant Life Histories and Meteorological Events

Geographic expansions and contractions of species' ranges include processes of both dispersal and mortality. For most higher land plants the dispersal processes require the successful completion of every stage in the life history, each of which is sensitive to different frequencies of meteorological variability. These stages include flowering, pollination, seed development and dispersal, seedling establishment, juvenile growth to the age of first reproduction, and at least one repetition of this cycle before the plant dies. Successful dispersal will be truncated by the interruption of any one of these stages. Mortality can be produced by single catastrophic events at certain (usually early) stages in the life cycle, but might require complex sequences of sub-lethal events to produce mortality at other (usually later) stages in the life cycle (2). Asexual reproduction allows some plants to persist in regions virtually unfavorable to sexual reproduction, effectively uncoupling them from events which influence highly sensitive (early) stages in the life cycle. However, such truncation of the dispersal phase severely limits range extensions (excepting apomixis and other asexual dispersal mechanisms). Frequently these plants continue to produce abundant, viable seed with little to no successful new establishment (8).

There are important parallels between the lengths and annual timing of different stages of plant life histories and the lengths and annual timing of different climatic regimes [suggestive of an evolutionary relation, an approach more familiar to the Russian school of plant ecology (9)].

The responses of plants to specific sequences of meteorological events are, obviously, species specific. As will be discussed, there are frequencies of meteorological events on time scales ranging from days to decades. The inherent longevity of individual species and the lengths of the various life history stages will determine which frequencies of events might disrupt the life cycle of the plants. However, all plants are sensitive to high-frequency variability of weather at some stage in their life history. Meteorological events such as individual storms or days of extreme heat or drought tend to cluster into climatic regimes of 3 to 10 days (5). At specific times of the year these relatively high-frequency clusters of weather events can control the onset or release of dormancy and the success or failure of flowering, seed set, and germination. These relatively short-lived climatic regimes can alternate with other short-lived climatic regimes or can cluster into longer climatic regimes, which in turn can cluster into even longer climatic regimes, and so on. Such clusters, or weather regimes, can each be considered as an event with a specific temporal scale. Thus, high-frequency weather events are hierarchically nested within and controlled by a set of climatic regimes of about 30 days (1), 60 to 100 days (seasonal), and 1 year (annual). Likewise, similar years of weather can cluster into climatic regimes, which are characterized by distinct flow patterns of the atmosphere. Over the course of several years these flow patterns can oscillate from one to another, producing episodes of weather of varying lengths. Two dominant periodicities of this sort are 2 to 3 years (biennial oscillation) and 4 to 7 years (southern oscillation). These are the key climatic signals controlling the establishment processes of most perennial plants (or germination of ephemerals with long-lived seeds). However, once established, plants must reach the age of first reproduction and must successfully reproduce at least once before senescence, if colonization is to be considered successful. Climatic regimes of 10 to 12 years and 22 to 23 years (sunspot cycles) appear to coincide with either the entire life cycle of

some perennials or to the age of first reproduction (9). Climatic regimes of durations of about 50 years, 100 years, and 180 to 250 years (10) correspond to the life spans of most shrubs and trees (9). However, climatic regimes of about 800 years, 1700 to 2000, and 3500 years (1) appear to correspond to the maximum life span of trees that are limited to sexual reproduction (for example, *Pseudotsuga* sp. and *Juniperus* sp.). Bristlecone pines (*Pinus longaeva* and *P. aristata*) are among the longest lived, sexually reproducing organisms, living to about 6000 years.

Asexual reproduction releases the organism from the constraints of senescence and sexual reproduction and can extend the life span of genetic individuals beyond 6,000 years to 20,000 years or more, the time frame of glacial-interglacial cycles [for example, aspens, oaks, and creosote bush (8)]. Interestingly, the age of single stems within these long-lived, clonal organisms drops back to one or two centuries.

High-Resolution Climatic Analysis

Typically, bioclimatic regimes have been determined by temporally and spatially averaging weather patterns. However, sessile organisms respond to sequences of weather events at a point in space rather than to "average weather." Also, the use of standard normal statistics obscures the underlying fluid dynamic temporal determinism of the weather—that is, nonrandom clustering of weather events can not be resolved (for example, clusters of similar years). Thus, the elucidation of critical detail both within and between climatic regimes has remained elusive. Furthermore, the failure to explicitly recognize the physical basis of independence between intraannual time (circannual) and interannual time has obscured our perception of the signal-to-noise ratio in climatic data.

To appreciate my departure from previous analyses, it is useful to think of the earth as a gyroscope with (at least) two inertial periodicities, rotation and revolution. Uneven insolation, the distribution of landmasses, and the earth's rotation combine to produce the dominant patterns of circulation in the oceans and atmosphere, independent of the earth's revolution. In contrast, circannual time is a spatial, orbital metric indicating the position of the planet in its annual revolution around the sun. Deterministic patterns in the highly inertial, rotating, and revolving fluids of the earth should be most readily detected by comparing flow patterns at constant orbital positions. Considering the large inertia of these fluids, minor variations in the period and axis of rotation of the earth should produce large variations in the fluid circulation patterns on its surface (and in the core). Exchange of momentum between the atmosphere and the solid earth has been observed and related to climatic anomalies (11).

Variation in the behavior of the fluids on the earth is detectable by comparing the detailed weather patterns of each year to those of the previous and successive years, much as a stroboscope allows "stop-action" analysis of cyclic phenomena. Any climatic variable of interest can be graphed as a simultaneous function of circannual and interannual time, producing a two-dimensional "surface" (in three-dimensional space) which can be contoured for trend analysis (12). If seasonal climatic parameters were constant from year to year, the contour map would simply consist of parallel contours running straight through interannual time (the null hypothesis). To emphasize, this is not a statistical analysis, but one of pattern recognition.

Contour maps of monthly mean temperature and total monthly precipitation for each year of the meteorological record of Las Cruces, New Mexico, are shown in Fig. 1, A and B. To facilitate the observation and analysis of patterns through entire seasons, data for January of each year are preceded by data from October through

December of the preceding year. Thus, contours on the left side of Fig. 1 are identical to those on the right side of the graphs, but offset by 1 year.

Walter recognized that the temperature curve can be used to filter the precipitation curve (correcting for potential evapotranspiration) to assess "effective moisture" and "effective drought" (13). Walter's "climadiagram" approach has the effect of delineating two mutually exclusive kinds of time, wet time and dry time, as indicated by the intersection of the temperature and precipitation curves when overlain with appropriate scaling. This provides the means for quantifying the relative intensity of each kind of time by integration of the area between the two curves (Fig. 2). The ecological significance of this approach is that plants do not experience mean climate, but are exposed to alternating sequences of growth time and stress time (14). This is also consistent with a growing consensus among climatologists that the atmosphere abruptly "flips" between different, relatively stable, dynamic states (1). Thus, Walter's approach is ideally suited to the physical realities of the plant environment. By algebraically combining long-term temperature and precipitation data sets (Fig. 1, A and B), as just described, I extended the concept of the Walter climadiagram to examine within and between year variability of effective moisture at a single station in what I term a "running" Walter climadiagram (Fig. 1C). A second running climadiagram of effective drought has also been constructed, but for simplicity is represented as uncounted time in Fig. 1C.

Regional Background and Data

The Chihuahuan desert is located at the southern end of the Rocky Mountains, between the Sierra Madre Occidental and the Sierra Madre Oriental, and is bordered by the Great Plains grassland to the northeast and Sonoran desert scrub to the northwest. The present focus is on the northern Chihuahuan desert from about 31° to 35°N latitude. The vegetation is characterized by a mosaic of desert grassland dominated by black grama (*Bouteloua eriopoda*) (C_4 photosynthetic pathway) and desert scrub, primarily creosote bush (*Larrea tridentata*) and mesquite (*Prosopis glandulosa*) (C_3 photosynthetic pathway) (3). Black grama, being a C_4 grass, completes its flowering, seed maturation, dispersal, and early establishment processes during late summer and fall rains. Once established, an individual may survive through asexual reproduction up to several decades while continuously producing seed (15–17). Creosote bush and mesquite, being C_3 shrubs, flower in spring or summer and require several months to mature the seed, which will germinate in the following winter or spring (15–17). Once mature, these shrubs may live for at least several decades in a potentially reproductive state.

Phytogeographic change in the southwestern United States has long been a subject of controversy, fueled by regional desertification, a general shift from semidesert grassland to desert shrubland. This shift has been most remarkable in New Mexico and Arizona (northern Sonoran and Chihuahuan deserts) where desertification has been variously attributed to overgrazing, its attendant soil loss, and climatic change (3). Attempts to delineate causal factors of desertification in the Southwest are frustrated by a confusing superposition of shifts in climate and land use (1, 3). A marked shift in the climate at about 1900 (the end of the "little ice age") was coincident with a rapid and extreme rise in stocking rates. Grazing peaked by the 1920's, has been on the decline since then, and was accompanied by a shift from global warming to global cooling about 1940. Hence, much confusion remains as to the relative influences of climatic change and overgrazing in producing phytogeographic change in the southwestern deserts.

One long-term data set to be considered is from one of the longest continuous vegetation monitoring projects in the world. Since 1915 between 34 and 90 1-m² quadrats have been monitored annually on the Jornada Biosphere Reserve in the northern Chihuahuan desert [~25 km north of Las Cruces (17, 18)]. Demographic data for the dominant grasses of the region are available from this project (17).

Another long-term data set consists of 130 years of monthly weather records from Las Cruces, New Mexico (19). Las Cruces is located in the northern Chihuahuan Desert (32° 25' N, 106° 50' W) at the southern end of the Rocky Mountains, one of the most dominant modulators of upper atmospheric global circulation. The station comes under the influence of major air masses originating from the northwest and -east and southwest and -east of Las Cruces. The relative influence of any given air mass on Las Cruces' weather is determined by the positions of the polar front and subtropical jet streams in relation to the north-south Rocky Mountain axis (1, 20, 21). The jet streams may run tangentially to the mountain axis (polar front jet) or may obliquely transect the axis near Las Cruces (polar and subtropical jets), thus producing the four separate air mass gradients.

Las Cruces' Climate

The period before 1900 marked the end of the "little ice age" in the Southwest and was characterized by a predominantly meridional flow structure. From 1900 to 1940 the globe experienced the first major warming trend since the beginning of the "little ice age" in the 15th century. This warming trend was characterized by predominantly zonal flow. From 1940 to 1972 the globe was in a cooling trend with a moderate return to meridional flow. As will be discussed later, the two meridional periods were somewhat different from each other.

The contoured graph of average monthly temperature (Fig. 1A) presents several interesting patterns. Winter minima averaged <5°C in the 1890's, were warmer in the early years of this century with gradual cooling into the 1940's followed by warming in the late 1960's and early 1970's—the reverse of the 20th-century global temperature trend (also examine the slope of the 10°C November contour). The summer maximum temperatures were cooler in the 1890's than at any time in this century with only a few exceptional years. The annual timing of cooling in the fall is remarkably consistent between years (consistent with the null hypothesis). On the other hand, the timing of the spring warming is highly variable, with strong interannual trends persisting for 2 to 4 years. The year to year variability in spring warming before 1940 is more random (zonal flow) than that since 1940 (meridional flow). Both climatic regimes exhibit a periodicity in spring warming of about 3.08 years (based on the 10°C March contour). However, the variance-mean ratio of the wavelength is 31 percent greater (that is, more random) during the warming trend (0.34) compared to the cooling trend (0.26). This shift in the character of year to year variability in spring warming is consistent with a shift in the general circulation from relatively zonal (nonresonant) flow to relatively meridional (resonant) flow at about 1940.

The period from 1850 to 1900 contained at least three winter droughts of duration 5 to 7 years (Fig. 1B), indicating a highly organized flow pattern (meridional and resonant). Although each drought was punctuated by an occasional heavy rain, comparison with the well-documented mid-1950's drought (20) indicates that these were intense winter droughts. From 1900 to 1940 no lengthy clusters of winter drought years occurred. Instead, winter precipitation was erratic, both within and between years, being characterized by short, isolated bursts of precipitation. Since 1940 winter precipi-

tation has again become considerably more organized in time with periods of high continuity within and between years. The result has been increased year to year persistence of both winter wet periods and winter dry periods. The most notable dry period since 1940 was the mid-1950's drought, the beginning and ending of which were also noted as climatic shifts in the Southern Hemisphere (22). Moreover, the episodes of winter precipitation at Las Cruces corresponded in time and relative intensity with an interannual, long-wave pattern in north Pacific SST anomalies (23). These clusters of years are remarkably synchronous with clusters described by Lamb for Great Britain (1), which he also related to observations of Pacific SST anomalies.

Although global temperature appears to have been increasing since about 1972 (24), the precipitation patterns have remained

highly organized in both winter and summer, consistent with the fact that global circulation patterns are still strongly meridional. Potential explanations for this apparent uncoupling of temperature and precipitation patterns might involve global pollution, but are beyond the scope of the present discussion.

Examination of the running Walter climadiagram (Fig. 1C) reveals that all droughts since 1892 are resolved as uncountoured time. To name just a few, there were droughts in 1908–1913, 1934–1935, 1951–1956, 1963–1965, 1971 (20), and 1976 (25). These severe droughts were generally dry in both winter and summer, as indicated by a lack of contours, but were occasionally punctuated by a short burst of intense summer rain. However, there were long periods during which one season (winter or summer) was dry, but not both. For

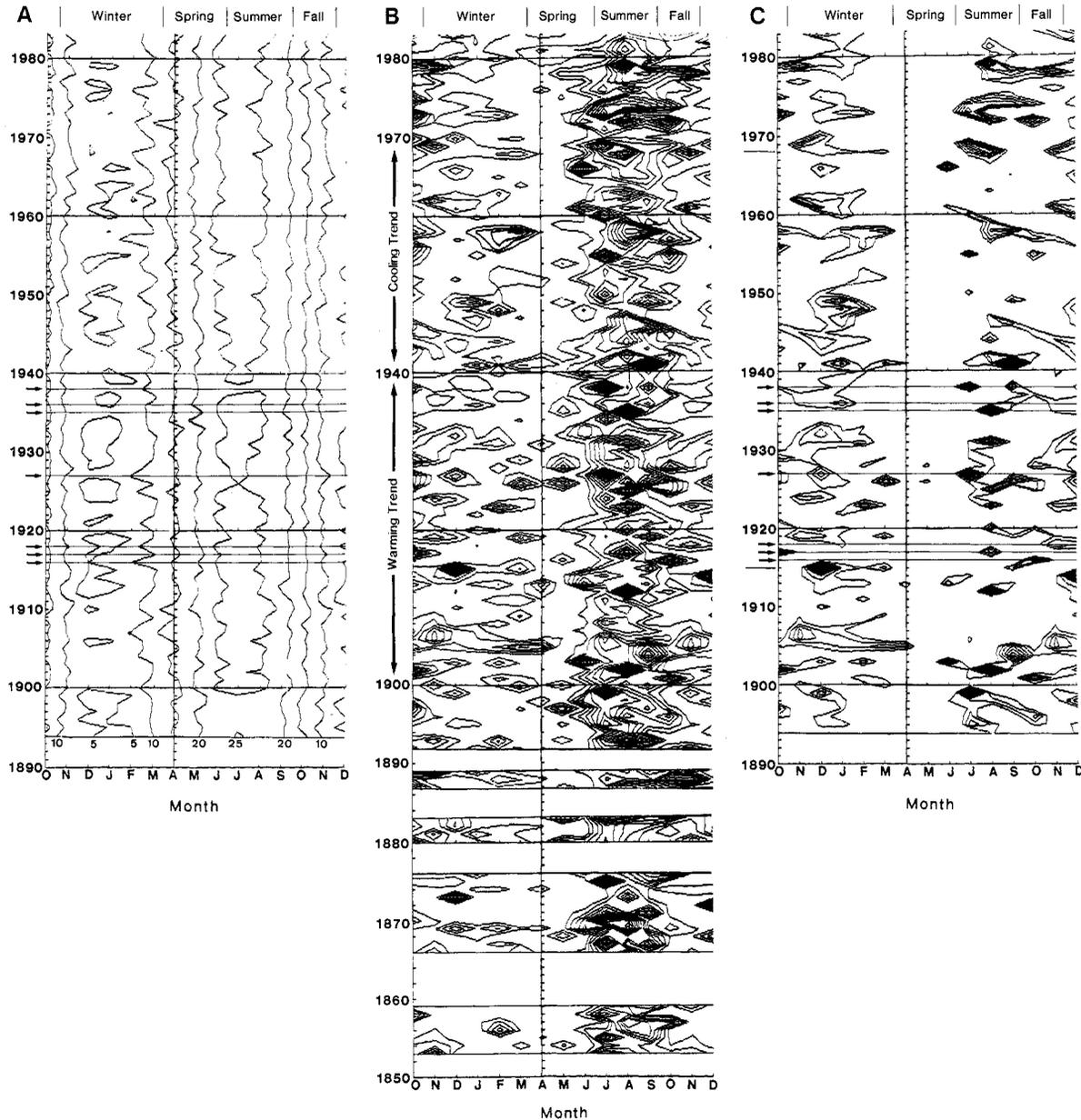


Fig. 1. (A) Contour map of average monthly temperature at Las Cruces, New Mexico (contour interval 5°C). (B) Contour map of total monthly precipitation at Las Cruces (contour interval 10 mm). (C) "Running" Walter climadiagram [combining (A) and (B) and portraying only the periods of total monthly "effective moisture," contour interval 10 mm (13)]. Arrows (followed by solid lines) in (A) and (C) indicate black grama seedling years; solid lines (in margin) above and below arrows in (C) bracket plant census period (17). Caution must be exercised in the interpretation of the contours.

For example, some peaks in the graphs, indicated by diamond-shaped contours, appear to possess some within or between year persistence. However, unless the contours extend beyond one time interval from the peak, the apparent persistence is artificial and the peak represents an event at one point in time without intra- or interannual persistence. Any deviation from the diamond shape demonstrates clustering of two or more data points and does indicate temporal persistence (continuity).

example, the extreme drought of the early 1950's (during the recent cooling trend) was preceded by nearly a decade of summer drought. Examination of Fig. 1B reveals the opposite pattern before 1900, when winters were dry and summers were wet.

Conditions for Black Grama Establishment

Only 7 years between 1915 and 1968 produced black grama seedlings (as distinct from asexual sets), all during the 20th century global warming trend. These 7 years (indicated by arrows in Fig. 1, A and C) were 1916, 1917, 1918, 1927, 1935, 1936, and 1938 (17). They were compared as a set (26) to each of three subsets of the meteorological record, defined on the basis of the major global climatic regimes.

Statistical comparisons between subsets of years in these records are based on seasons, defined as winter (November to March), spring (April to June), summer (July to September), and fall (October to November). These definitions roughly coincide with seasonal shifts in the general circulation of the atmosphere (1). Recognizing the overlap in phenology of winter and summer season plants (primarily C₃ and C₄, respectively) (15), November has been used twice in this definition of seasons. Late fall, extending into November, usually coincides with the mature stages of the life cycle of C₄ grasses, which have set seed and perhaps established seedlings by this time, but are generally inactive during the winter. By contrast, C₃ ephemerals and shrubs may be dependent (in part) on November soil moisture recharge to carry new germinants through the winter drought periods.

Walter climadiagrams for each of the three climatic regimes and for the seven black grama years are in Fig. 2, A-C. On average, the winters were drier and the summers were wetter before 1900 than during either climatic regime of the 20th century. The average

weather patterns of the latter two climatic regimes do not differ greatly from each other. However, the similarity of average weather patterns stands in contrast to the quite distinct temporal patterns of interannual variability of these three periods (Fig. 1, A-C).

The seven black grama seedling years (all within the warming trend) occurred during periods of winter drought, sandwiched between periods of winter wet, but only when the dry winter was followed by high summer rainfall (Figs. 1C and 2B). Usually a single burst (1-month resolution) of summer rainfall was sufficient. Although there was less effective winter moisture (wet time) during the seven black grama years (Fig. 2B) (1.50 mm for 26 non-black grama years, 0.7 mm for the 7 years; difference, 0.76 ± 0.47 mm), this is not a statistically strong pattern ($P = 0.06$). Yet, these winters were statistically drier (dry time) ($P = 0.01$; 57.2 mm for non-black grama years, 39.7 mm for black grama years; difference, 17.5 ± 7.5 mm). That is, the amount of precipitation that fell during wet times in these winters was not remarkably less than average (Fig. 2, A-C). But, in the same winters the dry times were considerably more drought stressful, a function of warmer winter temperatures produced by northward incursions of tropical air. This underscores the value of Walter's delineation of two distinct kinds of time. A few of the seven black grama years do indicate some level of effective winter moisture (Fig. 1C). However, these moist periods were always early in the winter and were associated with warm temperatures producing long desiccating spring intervals (Fig. 1, A and C). It is for this reason that the statistically significant difference in black grama winters is primarily one of increased drought through evaporative demand and only secondarily a difference in rainfall input. However, this index of drought intensity is conservative (13). Actual differences in winter-spring drought between grama and non-grama years were likely much greater than indicated.

The reverse pattern occurred during the black grama summers (Fig. 2, A-C). That is, the amount of effective summer rainfall (wet

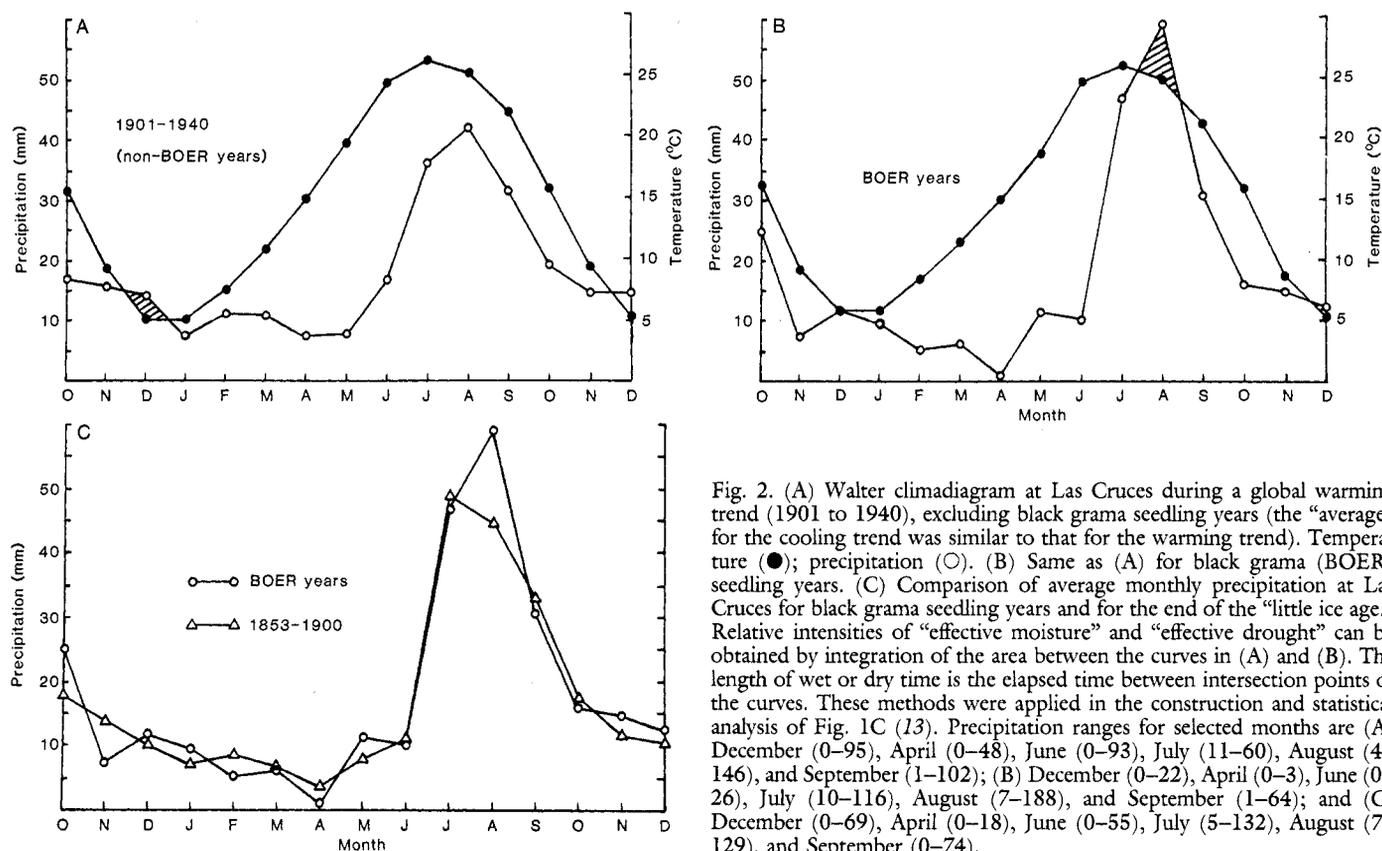


Fig. 2. (A) Walter climadiagram at Las Cruces during a global warming trend (1901 to 1940), excluding black grama seedling years (the "average" for the cooling trend was similar to that for the warming trend). Temperature (●); precipitation (○). (B) Same as (A) for black grama (BOER) seedling years. (C) Comparison of average monthly precipitation at Las Cruces for black grama seedling years and for the end of the "little ice age." Relative intensities of "effective moisture" and "effective drought" can be obtained by integration of the area between the curves in (A) and (B). The length of wet or dry time is the elapsed time between intersection points of the curves. These methods were applied in the construction and statistical analysis of Fig. 1C (13). Precipitation ranges for selected months are (A) December (0-95), April (0-48), June (0-93), July (11-60), August (4-146), and September (1-102); (B) December (0-22), April (0-3), June (0-26), July (10-116), August (7-188), and September (1-64); and (C) December (0-69), April (0-18), June (0-55), July (5-132), August (7-129), and September (0-74).

time) was higher during the black grama years ($P = 0.04$; non-black grama years, 12.3 ± 31.6 mm, range 0 to 157 mm; black grama years, 26.5 ± 38.5 mm, range 0 to 111 mm), while the summer dry times (that is, temperatures) were not statistically different from non-black grama years. The relationship to "wet time" is strengthened in a combined summer-fall analysis ($P < 0.01$; non-black grama years, 17.4 ± 32 mm, range 0 to 157 mm, compared to 34.5 ± 37.3 mm and range 14 to 119 mm). This is in agreement with findings by Kemp (15) that C_4 grasses in this region are, in general, responsive to late summer-fall rainfall. Examination of Fig. 1C reveals that the black grama years were associated with specific summer events, all of which occurred in late summer or early fall. (One apparently marginal year, 1918, was wet all summer with over 40 mm rain in August; Fig. 1B). Examination of Fig. 2B indicates that the seven black grama seedling years are quite different from the average climate of the global warming trend (non-grama years) within which they were embedded. They were more similar to the 1941–1970 global cooling trend and most similar to the pre-1900 tail end of the "little ice age" (Fig. 2C).

Jet Stream Patterns and Biotic Regionalization

There is a continuum from zonal (west-east) to meridional (north-south) flow, most readily recognized by the number of wave modes in the Rossby waves around the globe. These may range from greater than ten (highly zonal) to one (strongly meridional). Resonance tends not to occur until the wave number drops to three or less, which can result in several distinct resonant patterns (1, 5). Two of these are typified by (i) the winter of 1976–77, which produced extreme drought in the Southwest (in concert with a negative sea-surface or SST anomaly) and (ii) the winter of 1977–78, which produced excessive rain in the Southwest (in concert with an increase in SST, although still a negative anomaly) (23). During the 1976–77 winter the polar front jet stream was in a resonant position traveling down the Rocky Mountains, deflecting storms away from the West and into the Midwest. During the 1977–78 winter the jet stream shifted to the West Coast, driving storms into southern California. Thus, there are at least two distinct meridional flow patterns, both of which might be symptomatic of global cooling or cool periods and which produce opposite winter precipitation patterns in the Southwest (27). Each of these flow patterns should favor the establishment of quite distinct floras in the Southwest. The long droughts of the late 1800's suggest a strong meridional flow, more characteristic of a winter dry type of flow in the Southwest, whereas the more recent cooling trend seems to indicate an oscillation between winter wet and winter dry flow patterns every 2 to 5 years. Of the three distinct climatic regimes, McGuirk (6) found that the two strongly meridional periods produced much higher variance in precipitation patterns along the West Coast of the United States than did the zonal flow period. I suggest this may have resulted from the two extreme, resonant positions of the jet stream which result in extreme drought or wet cycles, respectively.

These observations suggest a hypothesis predicting the kind of vegetation that should be favored for establishment under the different climatic regimes. I argue that some degree of year to year persistence of summer rainfall is necessary for the establishment of any perennial vegetation in the southwestern deserts (north of about 31°N). This is because the winters are, in general, too cold to be an effective growing season and the summers are too hot for plants to remain active without rainfall. Although the amount of summer rainfall at Las Cruces is quite variable (Fig. 1C), the occurrence of summer rainfall is quite consistent (Fig. 1B). Thus, given summer

precipitation, the pattern of winter precipitation becomes crucial to the establishment of different perennial life forms. Warm season species (usually C_4) are favored if winters are dry. Cool season species (usually C_3) are favored if winters are wet. In effect, the pattern of seasonal precipitation determines which group of plants is favored for establishment. If winter season species (C_3) become established, they appear to present a competitive background, through soil water and nutrient depletion, thus producing an environment unfavorable to the establishment of summer season species (C_4) (28). Once established, C_3 shrubs can become photosynthetically active in warm winters and in spring, essentially shut down during dry summers, and may again fix carbon in the fall if moisture arrives. By contrast, established C_4 grasses are much more dependent on summer moisture because the photosynthetic apparatus is relatively inefficient during winter and spring (15).

Before 1900, cool season species would have had difficulty in establishment during the persistent winter drought periods. Soil nutrients should have been more available to summer season species (that is, not sequestered in standing biomass or soil detritivores (28), thus favoring the seedling establishment of warm season black grama grass. The increased, but erratic, winter precipitation during the global warming of 1901–1940 should have favored winter season desert annuals or biennials, which alone might have diminished critical nutrients to the extent of hindering the development of summer adapted species, even when summer rains were abundant. There was a short period of persistent interannual winter rainfall about 1930, which coincided with a large increase of desert perennial shrubs, specifically creosote bush (3). After 1940, winter rainfall became even more organized exhibiting many periods of considerable interannual continuity and should have favored establishment of perennial desert shrubs. The lengthy summer drought of the 1940's should have been more detrimental to C_4 grasses than to C_3 shrubs, whereas consistent winter rains during this period (with some summer rain) should have favored the establishment of C_3 shrubs. Although all vegetation suffered during the 1950's drought, this is noted as a period of shrub expansion (3).

Overgrazing would have acted synergistically with climatic change to enhance desertification through accelerated soil erosion and the truncation of asexual reproduction (3). Without overgrazing, asexual reproduction might have maintained the grassland in a condition sufficient to resist invasion by shrubs ["biological inertia" (9)]. Numerous enclosure experiments have demonstrated both the deleterious effects of grazing on grassland maintenance and the difficulty (but not impossibility) for reestablishment of grasses under the current climate when protected from grazing (29). These studies have also noted the deleterious effects of hard winter freezes associated with the 1977–78 flow pattern on both grasses and shrubs.

Prehistoric and Global Perspectives

On the basis of the atmospheric flow patterns, the three historic climatic regimes have been used as analogs of the late Pleistocene glacial maximum, the early Holocene warming, and the late Holocene cooling, respectively (7).

In the Southwest during the last 130 years, there were a series of climatic and biotic changes of smaller magnitude, but qualitatively similar to, those described for the last 20,000 years. The late Pleistocene–Holocene floristic changes of the Southwest were roughly as follows (30). At the peak of the glacial maximum (about 20,000 years ago) the current piedmont grassland regions in Arizona and New Mexico were dominated by a mixed-woodland assemblage of piñon (*Pinus* sp.), or juniper (*Juniperus* sp.), or both,

with a predominantly C_4 perennial grass understory (south of about 36°N). During the early Holocene warming trend, the woodland retreated, while the grassland apparently attained its peak dominance in the mid-Holocene thermal maximum. The late Holocene cooling trend saw the expansion of desert shrubland, first mesquite, followed by creosote bush, thus producing the present mosaic of grassland and desert shrubland. Several specific questions arise from this brief encapsulation. (i) If C_4 grassland is characteristic of relatively hot climates (15, 16), then how did it become juxtaposed with C_3 , perennial woodland in the glacial maximum? (ii) What eliminated the woodland while favoring the grassland in mid-Holocene? (iii) What produced the late Holocene expansion of desert shrubland? Climatic change was obviously the primary forcing function for these late Pleistocene–Holocene changes, but we do not understand what specific aspects of climatic change produced this vegetation change, nor do we understand the synergism between climatic forcing and biotic interactions. (iv) Finally, do these patterns bear any relation to the vegetation changes of the last century?

If the glacial maximum was indeed characterized by meridional flow, it might then as now have oscillated between periods of different kinds of meridional flow, each favoring a different biota on a regional scale. The late Pleistocene perennial woodland could have become established under several decades of flow similar to the 1977–78 pattern (or an oscillatory pattern similar to the recent cooling trend), while the C_4 grassland might have become established under a 1976–77 type of flow pattern (or similar to the end of the “little ice age”). Each flora would have enough “biological inertia” (9) through adult longevity and asexual reproduction to withstand several decades of unfavorable establishment conditions. During the mid-Holocene a weakening of the polar front and an expansion of the Bermuda High (2, 30) possibly reduced winter precipitation while enhancing summer precipitation in the region. Even though the temporal and spatial distribution of the precipitation would have been more random (zonal flow), the overall pattern of variability should have been favorable to the establishment of C_4 , perennial grassland (to the detriment of the Pleistocene woodland, which dispersed up and north) and unfavorable to the establishment of perennial shrubland. Not until the late Holocene cooling, presumably with a moderate return to meridional flow, did desert shrubland (C_3) arrive in the region, producing the modern “mosaic.” I propose that the “pristine” vegetation of the northern Chihuahuan desert, recorded 100 years ago, was a vegetation established under and adapted to 300 years of “little ice age” and is only marginally supported under the present climate.

The recent dynamics of Southwest vegetation and climate have occurred in some synchronicity with spatially distant biotic and climatic phenomena. A relation between the annual growth rate of trees in the Southwest and the latitudinal distribution of albacore tuna in the Pacific Ocean has been described along with simultaneous disruptions in other deep-sea fisheries, offshore kelp communities, Gulf of California starfish populations, and seabird communities (31). These oceanic disturbances appear to be temporally associated both with the establishment of desert perennials and with the widespread mortality of western shrubs through atmospheric teleconnections (32). Sea-surface temperature anomalies have also been related to corn yields and Great Plains droughts in the United States (33). Similar “coincidences” may be drawn from around the globe (4, 22), including an apparent asynchrony in the fossil and current meteorological records of wet-dry cycles between the American Southwest and the Sahara Desert (34).

In conclusion, climatic regimes of different temporal scales ranging from days to decades can be systematically detected and characterized from historic meteorological records. These different

scales of variability can be related to the establishment and mortality processes of terrestrial plants with known life history characteristics to produce testable hypotheses of floristic distributions. These hypotheses, if robust, should provide explanatory power for vegetation dynamics as recorded in the fossil record. These and other recent advances in our understanding of atmospheric dynamics provide ecologists with the means to test one of the dominant assumptions of our science, that the earth’s atmosphere is the primary controlling factor in the distribution and abundance of the biota on this planet.

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A Receptor-Mediated Pathway for Cholesterol Homeostasis

MICHAEL S. BROWN AND JOSEPH L. GOLDSTEIN

IN 1901, AFTER STUDYING A PATIENT WITH BLACK URINE, A physician named Archibald Garrod suggested that a single mutant gene can produce a discrete block in a biochemical pathway, which he called an “inborn error of metabolism.” Garrod’s brilliant insight anticipated by 40 years the one gene–one enzyme concept of Beadle and Tatum. Similarly, the chemist Linus Pauling and the physician Vernon Ingram, through study of patients with sickle cell anemia, showed that mutant genes alter the amino acid sequences of proteins. Clearly, many fundamental advances in biology were spawned by perceptive studies of human genetic diseases (1).

We began our work in 1972 in an attempt to understand a human genetic disease, familial hypercholesterolemia (FH). In patients with this disease, the concentration of cholesterol in the blood is elevated many times above normal and heart attacks occur early in life. We postulated that this dominantly inherited disease results from a failure of end-product repression of cholesterol synthesis. The possibility fascinated us because genetic defects in feedback regulation had not been observed previously in humans or animals, and we hoped that study of this disease might throw light on fundamental regulatory mechanisms.

Our approach was to apply the techniques of cell culture to

unravel the postulated regulatory defect in FH. These studies led to the discovery of a cell surface receptor for a plasma cholesterol transport protein called low density lipoprotein (LDL) and to the elucidation of the mechanism by which this receptor mediates feedback control of cholesterol synthesis (2, 3). FH was shown to be caused by inherited defects in the gene encoding the LDL receptor; these defects disrupt the normal control of cholesterol metabolism. Study of the LDL receptor in turn led to an understanding of receptor-mediated endocytosis, a general process by which cells communicate with each other through internalization of regulatory and nutritional molecules (4). Receptor-mediated endocytosis differs from previously described biochemical pathways because it depends on the continuous and highly controlled movement of membrane-embedded proteins from one cell organelle to another in a process termed receptor recycling (4). Many of the mutations in the LDL receptor that occur in FH patients disrupt the movement of the receptor between organelles. These mutations define a new type of cellular defect that has broad implications for normal and deranged human physiology.

The Problem of Cholesterol Transport

Cholesterol is the most highly decorated small molecule in biology. Thirteen Nobel Prizes have been awarded to scientists who devoted major parts of their careers to cholesterol (5). Ever since it was first isolated from gallstones in 1784, cholesterol has exerted an almost hypnotic fascination for scientists from the most diverse areas of science and medicine. Its complex four-ring structure and its

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