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Modeling The Climatic Requirements For Southwestern Plant Species

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Abstract

Modeling the geographic relationships between climate and plant species distributions in the southwestern United States has been difficult because of the extreme topographic diversity and complex seasonal precipitation patterns. Species ranges may be restricted to isolated mountain peaks or deep canyons with climates unlike those of the surrounding region. Seasonal moisture extremes occur during different months across the region. In order to account for these complex relationships, we developed monthly climate surfaces for North America on a $\sim 1 \text{ km}^2$ grid from historical instrumental weather records. Because existing continental-scale species distribution maps were often completed prior to modern advances in georeferencing, we compiled existing state and regional geographic data for several species using GIS to further refine their range maps. Applying a new computer application (ClimLim), we evaluated the statistical relationships between monthly climate values and species geographic ranges in order to establish the most critical values limiting distribution. These methods are demonstrated using Utah Agave (*Agave utahensis*) and four needle morphological variants of pinyon pine: *Pinus monophylla*, *P. edulis*, and their varieties of ambiguous taxonomic status, the *californiarum* and *fallax* types. Utah Agave is primarily limited by winter minimum temperature and high monsoon precipitation. The four different needle types of pinyon pine are segregated principally by seasonality of precipitation and drought.

Introduction

Modeling the climate requirements of plants is necessary for the reconstruction of past climates from plant fossils, as well as projecting future potential plant species ranges. There have been many barriers to understanding the precise climatic tolerances of plants without detailed experimentation on each species. As climatic, informational, and geospatial technologies advance, these barriers are gradually being overcome.

Whereas previous studies of modeling the relationships between climatic parameters and plant species have been limited to coarse spatial resolutions ($\geq 25 \text{ km}^2$) and/or coarse climate variables (ie. January vs. July means), here we attempt to refine the spatial resolution to $\sim 1 \text{ km}^2$ and the climate variables to seasonal maxima and minima calculated from monthly values. The months incorporated into various seasons become flexible as climatic seasonality varies across regions. For example, the months of maximum or minimum moisture availability change as the synoptic climatology shifts across the sub-continental region.

Many efforts to model climatic requirements have ignored the observation that climate is only one of many components controlling a species' distribution. Some models simply assume that if the climate is within the species' tolerances, then the species must occur there. As Austin (1990) and Jackson and Overpeck (2000) and others have emphasized, populations only occur within a realized niche space, which only occupies a portion of their potential niche space, which, in turn, can be a smaller portion still of their fundamental niche space. That is, although a species may have a fairly wide tolerance for different climatic variables, its distribution is limited to those combinations which actually occur somewhere near its extant population. And within those limits, it is even further confined to only a portion of this potential climatic space by other factors, some of which are evident (ie. fire frequency, substrate), and others that are not evident. Thus, each species distribution is contained within a larger area of potential climatic space for which no climatic reason can be found for its exclusion, at least not in our Twentieth Century climatic records. The species could certainly still be limited by some historical climatic variable not represented within the dataset.

This discrimination between realized niche space and potential niche space becomes essential to modeling future species distributions. To assume that if a species *can* grow somewhere, it *will* grow there, is an ecological fallacy. Understanding the mechanisms, such as plant migration, causing the disparity between the realized and potential distributions will be an essential component to modeling future distributions.

Bartlein et al. (1986) and Thompson et al. (1999) pioneered the applications of probability response-surface techniques and bioclimatic variables to this type of modeling. These approaches could not be used because of the unavailability of bioclimatic variables in $\sim 1 \text{ km}^2$ grid surfaces, and the intractability of applying logistic regression with 20 or more simultaneous variables to tens of millions of grid points. However, the methods described here could be used to build more detailed spatial datasets of bioclimatic variables, and to prioritize the most important climatic variables for the construction of more relevant probability response-surfaces.

In this project, we have concentrated on the incorporation of much finer geographic resolution, monthly climatic extremes, and a longer historical climate record than used in any previous study. These improvements were required to address the effects of climate on the vegetation of the arid and semi-arid North American deserts where climates change radically over short distances due to the extreme topographic gradients. In addition, we have applied a technique (ClimLim) to distinguish between climatic variables statistically limiting a species boundary, and variables that seem merely coincidental to its geographic extent.

Methods and Results

Modern Species Range Maps

The first requirement for high resolution modeling of species' climatic requirements is better distribution maps of their current ranges. Compiling these detailed maps has proven to be a major hurdle to this research, often taking years. Existing paper distribution maps for most species have errors of 10 to 50 km for many well documented locations. These errors can be reduced to less than 5 km through extensive georeferencing, editing, and compilation of all

existing data with specific geographical references. For example, about half of all herbarium records contain spatial data allowing them to be located within a km of the collection site. A few of the distribution maps completed using these techniques are posted on the project's web site at: http://www.usgs.nau.edu/global_change/

Widespread species usually have varieties or ecotypes that have modified anatomy, especially of leaves or needles, reflecting different sub-regional climates. Where possible, species range maps can be not only improved to finer spatial accuracy, but simultaneously to finer taxonomic detail. In this paper we discriminate between four morpho-types of pinyon pine, all distinguished by their needle anatomy: Colorado Pinyon, Single-Needle Pinyon, Arizona Singleleaf Pinyon, and California Singleleaf Pinyon. Their geographic distributions are shown in Figure 1. For additional discussion and a key to their anatomical differences see the document at: (http://www.usgs.nau.edu/global_change/RangeMaps/PinyonMapSources.pdf). Different plant taxonomists have classified these as four separate species, as variants of a single species, and many combinations in between. While taxonomists endlessly debate the proper taxonomic ranks and relationships for these plants, their distributions can be mapped and climatic requirements modeled.

High Resolution Climate Surfaces

Twentieth Century monthly temperature extremes and precipitation means were interpolated to a grid scale of $\sim 1 \text{ km}^2$ using an ANUSPLINE technique (Hutchinson, 1989) using data from the Global Historical Climatology Network (<http://cdiac.esd.ornl.gov/ghcn/ghcn.html>).

ANUSPLINE generates excellent results in the topographically diverse, arid to semi-arid habitats of the southwestern deserts (Figure 2). These 36 monthly climate surfaces cover most of North America and can be downloaded from the project's web site. These surfaces consist of monthly values for mean precipitation, monthly maximum mean temperatures, and monthly minimum mean temperatures.

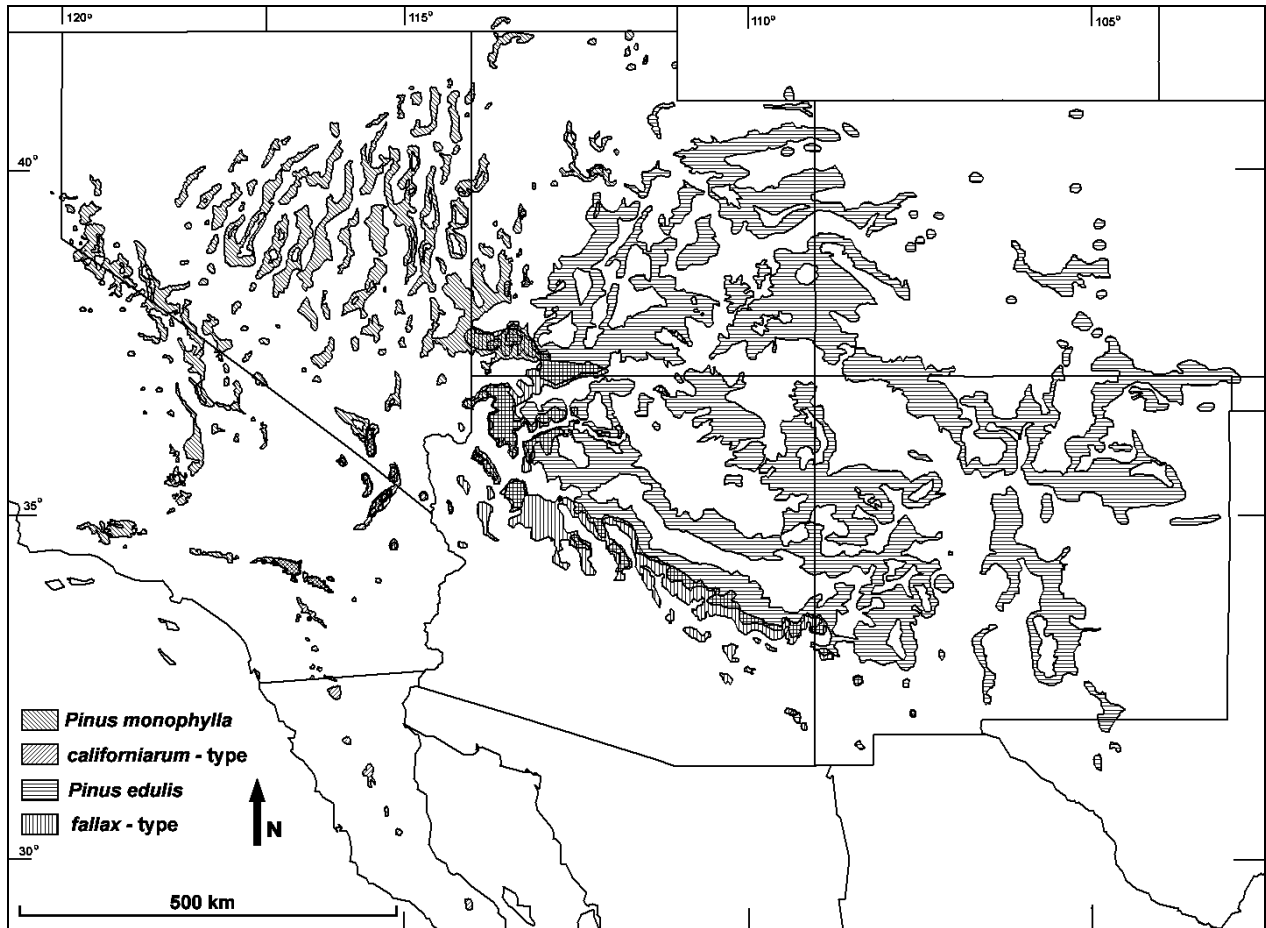


Figure 1. Distribution map of one and two-needled pinyon pines in western North America.

Tailored Seasons and Climatic Limiters

During the early stages of this research, it became evident that a traditional approach of representing summer climates with July values would not be appropriate for the region. Over much of the western North American deserts, July represents a transitional month between a dry early summer and a wet late summer (monsoon) season. As a result, the summer period was subdivided into two different seasons: early summer (May and June), and the Monsoon period (July, August, September). The five precipitation seasons are illustrated in Figure 3 using values extracted from the range of Arizona Singleleaf Pinyon (*fallax*-type).

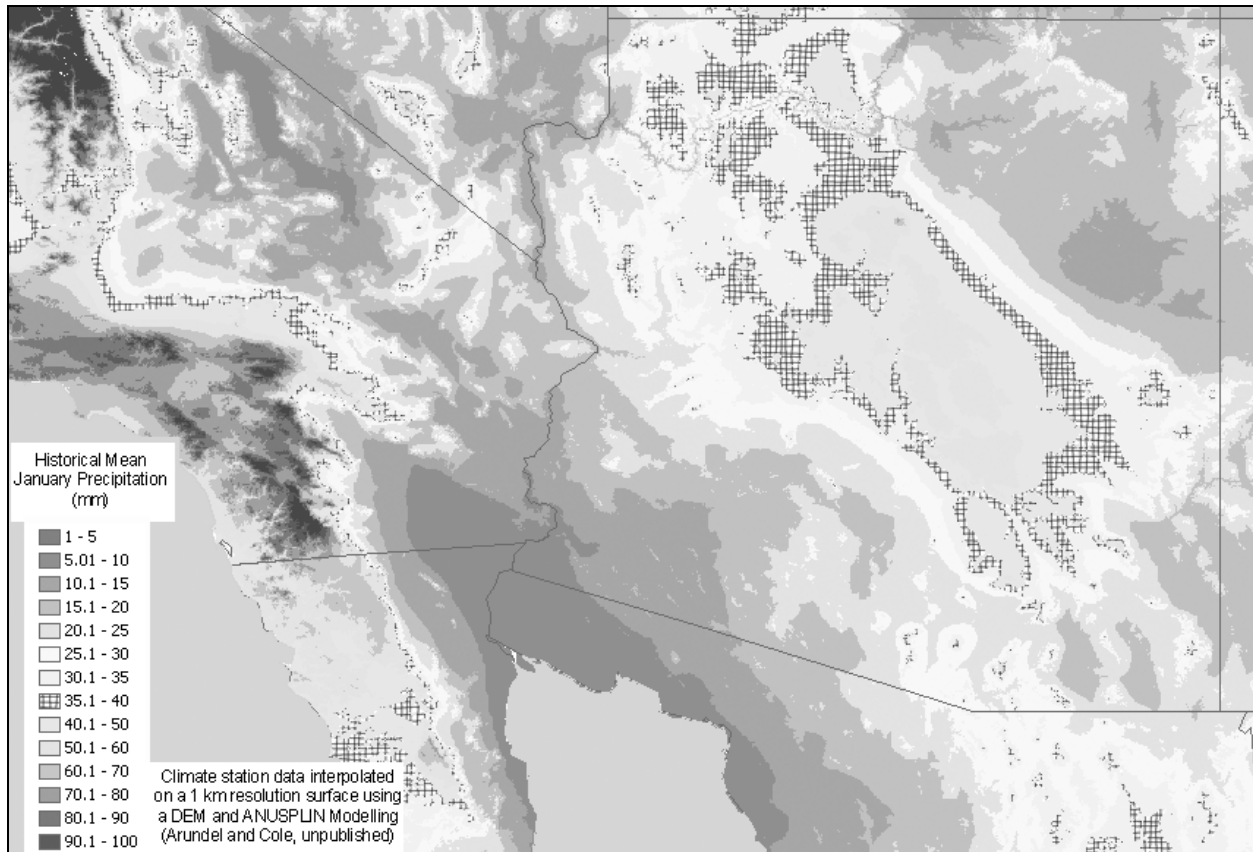


Figure 2. Mean January precipitation in the Southwestern U. S. as modeled using ANUSPLINE. Values are shown in mm. Map shows detail from one of the 36 1 km² North American climate surfaces available at: http://www.geog.nau.edu/global_change/climate_surfaces.html

A second innovation applied in this study is the statistical evaluation of the spatial influence of individual climate variables to each plant type's range using a geospatial application called ClimLim. This approach to evaluating limiting climate variables was originally suggested by Warren (1979). But, the rigorous application of this concept was delayed until geospatial technologies had developed sufficiently to assist in its application by Arundel (2002; In Press).

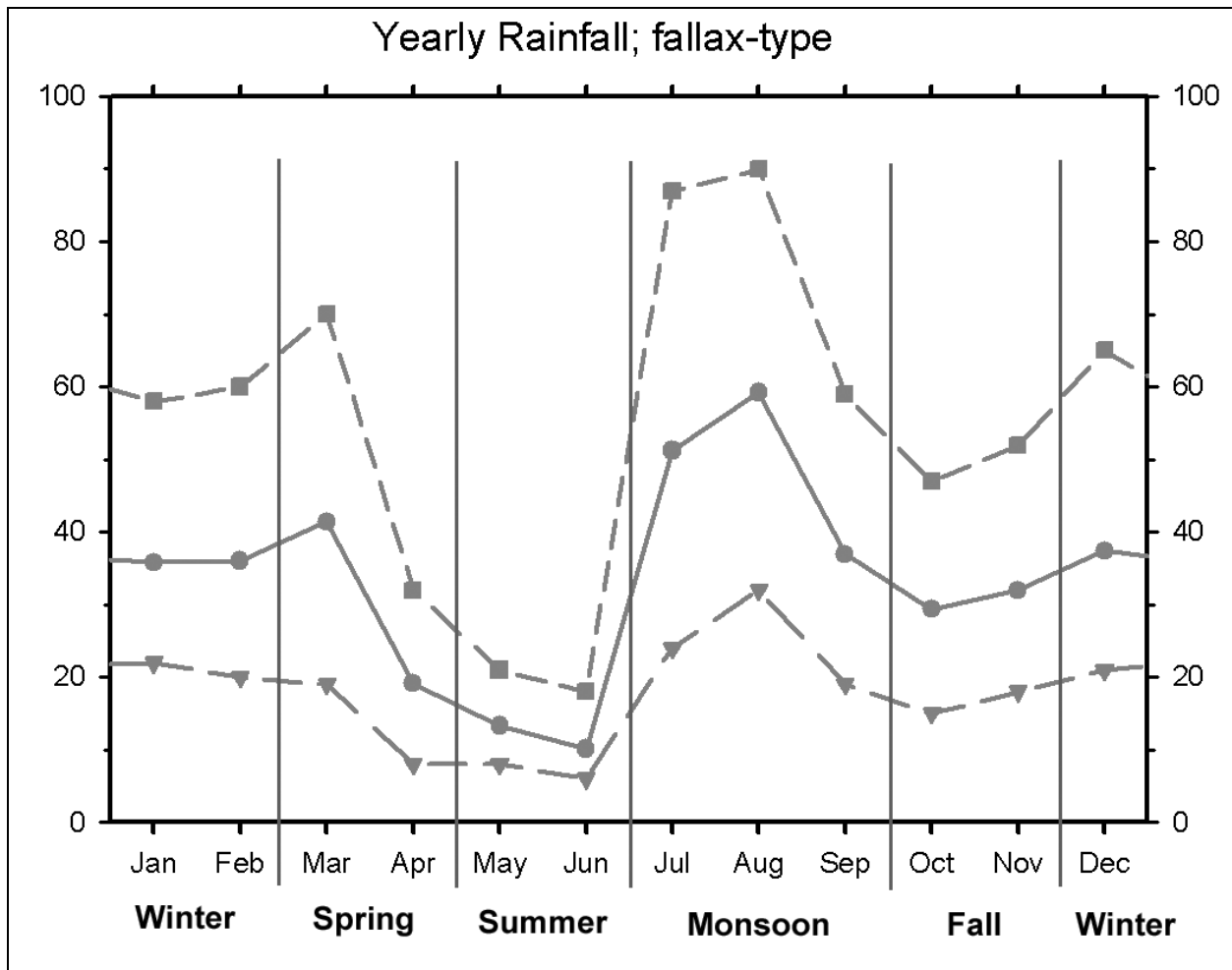


Figure 3. Graph summarizing the historical mean monthly precipitation values at all 37,350 km² grid squares within the range of Arizona Singleleaf Pinyon (*fallax* - type). The three lines connect the 95th percentile (short dash with boxes), the mean (solid line with circles), and the 5th percentile (long dash with triangles) values for each month. Note the extreme shift contrasting the early summer drought with late summer monsoon.

Since all geographic ranges must have boundaries, some boundaries must by chance be located at specific values along the climatic gradient. Many of these values have no effect on the plant's distribution; they are merely coincidental to the range boundary. The influence of each climatic variable in "pinning in" a spatial limit can be evaluated by "releasing" the distribution from the control of that variable. That is, after the limits of each climate variable surrounding a plant

range are determined, each variable can be eliminated one at a time. The plant range is then allowed to spatially expand, ignoring that released variable, until it encounters other limiting variables. The release of climate variables significantly controlling the range boundary should result in a substantial spatial expansion while irrelevant variables should result in less change. The relative scale of the range expansion resulting from the release of a single variable can then be evaluated by applying a chi-square statistic:

$$\chi^2 = \frac{(N_{sp} - N_{tp})^2}{N_{tp}}$$

where:

sp = sample population (potential distribution)

tp = total population (release distribution)

An Example of ClimLim Modeling using Utah Agave

The results from an application of these techniques is shown in Figure 4 and Table 1 using Utah Agave (*Agave utahensis*). Utah Agave is a medium sized succulent species endemic to the eastern Mojave Desert of eastern California, southern Nevada, and the Grand Canyon of Arizona. Its modern distribution is very well documented due primarily to an extensive series of vegetation plots within the Grand Canyon (Cole and Cannella, In Press).

Note that in this example (Table 1) the seasonal distribution of variables was slightly different for temperature and precipitation. This is because annual temperatures have a bimodal pattern, with intermediate temperatures in the fall and late spring, while the seasonality of precipitation is more complex, as shown on Figure 3. ClimLim allows for different seasonal definitions (by month) in order to determine which monthly combinations are the most relevant for a plant species. This allows ClimLim to be flexibly applied to different sub-regions or species types which are controlled by different aspects of the annual climate cycle.

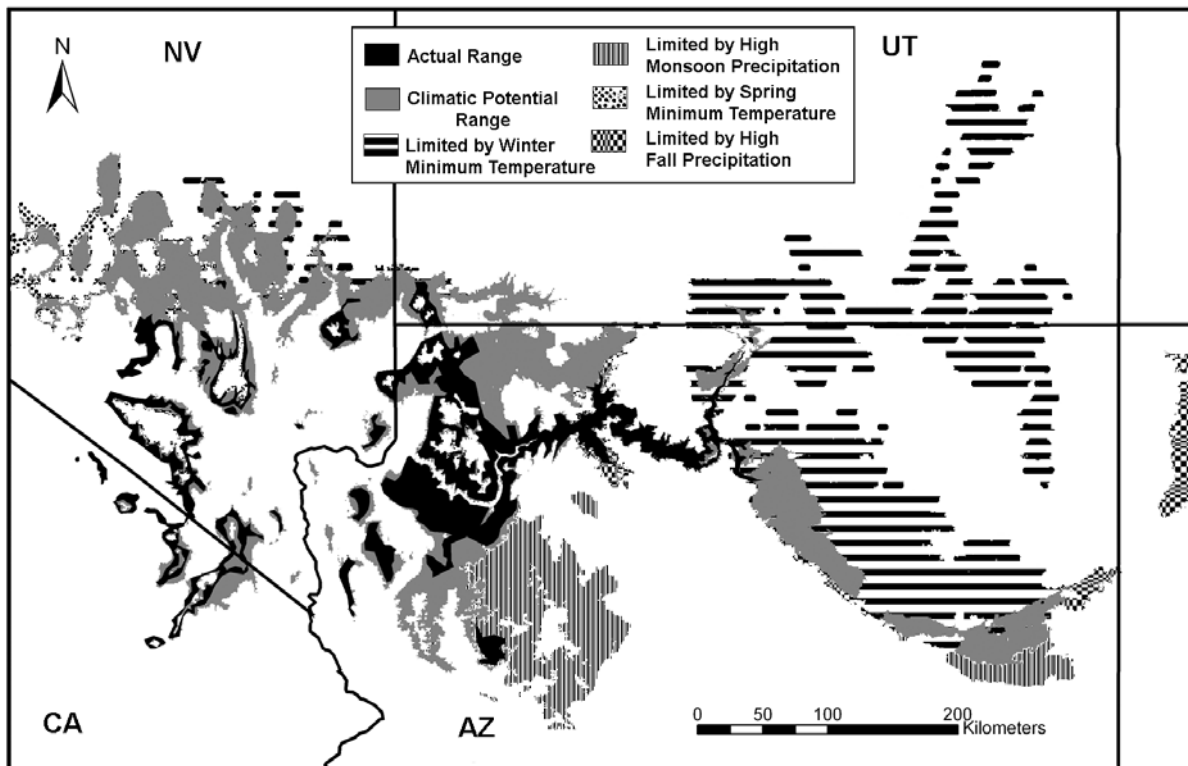


Figure 4. The modern range of Utah Agave (black), the range of its potential climate space (gray), and areas where it is excluded by its four principal climate limiters. White regions denote areas where two or more climate variables restrict the species.

This analysis demonstrates that the climate variable limiting this species the most is winter minimum temperature. When Utah Agave’s potential climatic range is released from the control of this variable, it expands much further up both the Colorado River and Little Colorado River drainages (Figure 4; horizontal striped pattern). Note that its potential climate space (gray) also extends far up the Little Colorado River drainage across east-central Arizona. The exclusion of Utah Agave from this part of its potential climate space could easily be the result of colder years that occurred prior to the instrumental climate record. The plant would probably not have had time to reclaim this part of its range if it were excluded by a climatic event of the Nineteenth or early Twentieth Centuries.

Table 1: Constraining modern climate variables for *Agave utahensis*. Climate variables are ranked by significance in constraining the modern limits for Utah Agave using a Chi-Square test. *Extreme outlier values usually result from small mapping and georeferencing errors along the range's perimeter. These have been removed, and the limiting values listed are the climatic extremes of the range at the 97.5 and 2.5 percentile values.

Climate Variable	Limiting Value*	Chi-Square Statistic	Location of Influence on Modern Boundary of Utah Agave
December to March Monthly Mean Minimum Temperature	-8.0 °C	22079	Higher elevations in eastern Grand Canyon and upstream along the Colorado River and Little Colorado Rivers
Maximum July to September Monthly Precipitation	50 mm	3717	Higher elevations and along the Mogollon Rim in western Yavapai Co., AZ
Maximum October to November Monthly Precipitation	25 mm	264	Eastern extremes of range into New Mexico
October & April to May Monthly Mean Minimum Temperature	4.9 °C	121	Higher elevations and north-western boundary in Mojave Desert
Minimum December to January Monthly Precipitation	13 mm	68	Low elevations near Page, Arizona, and northeastern Mojave Desert
Minimum July to September Monthly Precipitation	9 mm	53	Low elevations in northwestern Mojave Desert
Minimum May to June Monthly Precipitation	3 mm	52	Low elevations in southwestern Mojave Desert

The second most important climate variable is high monsoon precipitation limiting the plant from the Mogollon Rim area of western Arizona (Figure 4; vertical stripped area). This result may seem counter-intuitive, that a desert species would be limited by too much rain; never the less, it is a frequent result of these analyses. Although many species are attacked by mold or

fungus under moist conditions, the more likely limiting factors could be related to the high fire frequency in the chaparral plant communities of this area, and possibly to the infrequency of the steep rocky substrates that the species dominates throughout the rest of its range.

Results from Pinyon Analyses

Similar analyses for the pinyon needle types have shown their distributions (Figure 1) are primarily controlled by seasonality of precipitation and drought. Their three most important limiting variables are listed in order of significance ($p < 0.05$ for all).

Pinus edulis (Colorado Pinyon): Maximum May-June Precipitation, Minimum July-September Precipitation, Maximum October-November Precipitation.

Pinus monophylla (Single-Needle Pinyon): Maximum July-September Precipitation, Maximum May-June Precipitation, Maximum October-November Precipitation.

fallax-type (Arizona Singleleaf Pinyon): Minimum December-February Precipitation, Minimum March-April Precipitation, Minimum July-September Precipitation.

californiarum-type (California Singleleaf Pinyon): Maximum July-September Precipitation, Minimum July-September Precipitation, Minimum December-February Temperature.

The results show that these four different pinyon needle types are geographically partitioned by precipitation seasonality. *Pinus edulis* and the *fallax*-type grow only in areas with both winter and summer precipitation. The expansion of *Pinus edulis* northeastward onto the Great Plains (fire-prone prairie habitat) is prevented by too much early summer precipitation, and northwestward into the Great Basin (*P. monophylla* habitat) by too little monsoon precipitation. The growth of the *fallax*-type in the four corners region (*P. edulis* habitat) is prevented by too little winter precipitation. Both *Pinus monophylla* and the *californiarum*-type grow only in areas with significant winter precipitation. *Pinus monophylla* is excluded from areas with high monsoon precipitation (*P. edulis* habitat). The *californiarum*-type is restricted from the Mogollon Rim (*fallax* habitat) by too much monsoon precipitation, and from the central Valley of California by too little monsoon precipitation. The extensive hybridization between these pine varieties makes taxonomic classification difficult; but it seems that all four needle types are

either differentiated by their climatic tolerances, or that pinyon trees grow different needle types in different climate regimes.

Acknowledgments

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