

DYNAMICS OF DESERT-SHRUB POPULATIONS IN REGULATING SOIL
TRANSPORT BASED ON PLANT-SIZE AND BIOMASS SCALING RELEVANT TO
CLIMATE-CHANGE TIMESCALES

By

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To my family,

Friends,

And caffeine,

Without you this thesis certainly would not have been possible.

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MOTIVATION

Desert shrubs have a modulating effect on sediment transport on hillslopes [*Schlesinger and Pilmanis*, 1998; *Furbish et al.*, 2009a]. Shrub canopies provide sufficient protection from rainsplash transport, so that the inward flux of sediment grains toward the base of the shrub is greater than the outward flux of sediment grains [*Furbish et al.*, 2009a]. The result of this process is the formation of sediment mounds beneath the canopies of shrubs. The presence of these sediment mounds, acting as sediment ‘capacitors,’ decreases the flux on a hillslope, such that the sediment flux is less than similar hillslopes lacking vegetation [*Marston*, 2010; *Roering et al.*, 2010; *Worman*, 2010]. More generally, there is a growing interest in providing accurate descriptions of surface processes through the clarification and quantitative description of biotic and abiotic factors that contribute to landscape evolution [*NRC*, 2010; *Reinhardt et al.*, 2010]. The coupled behavior of sediment transport in combination with sediment ‘capacitor’ formation beneath desert shrubs provides an opportunity to characterize this complex system in a potentially changing climate. In particular, we are interested in the erosion of hillslopes in the sparsely vegetated Southwest United States desert, where rainsplash transport leads to the formation of mounds beneath shrub canopies.

To better understand this vegetation-modulated system of sediment transport, it is essential to fully and accurately characterize the shrub populations. Modeling and quantitative studies have shown that vegetation will lower the total sediment flux relative to unvegetated hillslopes [e.g., *Marston*, 2010; *Roering et al.*, 2010], yet to understand hillslope erosion and denudation it is necessary to model this system on climate change timescales (at minimum 100 - 200 years). Shrub population records for the Southwestern United States do not extend over these timescales and the future dynamics of shrub populations, given a changing climate, is

uncertain. Therefore, it is necessary to establish a biologically-informed characterization of shrub populations in order to develop predictions of sediment transport on hillslopes. We rely on a model created by Worman [2010] which implements a simple, probabilistic method to model the dynamics of a single-species population of shrubs. The model incorporates factors important to the survival of shrub populations, including: seasonal precipitation, age-based rooting depths, and unique, species-dependent sensitivity to arid conditions [Worman, 2010]. We couple the shrub population model with a model of hillslope erosion and shrub capacitance behavior [Stocky, 2012] to simulate this dynamic system and monitor variations in shrub populations, and thereby variations in sediment transport.

Water availability is the limiting growth factor for shrub populations in arid environments [Fischer and Turner, 1978; Comstock and Ehleringer, 1992]. Extreme drought could therefore result in fluctuations in a shrub population, and possibly include full population termination. When shrubs die, the underlying mounds are exposed to rainsplash transport and local sediment transport increases [Furbish *et al.*, 2009a]. Given the implication of increased shrub mortality under extreme arid conditions, we are particularly interested in climate predictions for North American deserts. There are two prevailing future climate predictions. The first predicts further aridification of the southwest United States, thereby lowering the available precipitation and ultimately the carrying capacity of the local area [National Assessment Synthesis Team, 2001]. Other models predict a climate of heightened extremes with periods of increased aridity and increased moisture, regulated by the El Niño Southern Oscillation (ENSO) [Yeh *et al.*, 2009; Lenart, 2006]. A goal of this study is to statistically characterize both the current and predicted precipitation scenarios, and evaluate likely associated changes in shrub populations and, consequently, changes in sediment transport within the context of our shrub dynamics model.

To better understand and describe the amount of vegetation on desert hillslopes, we turn

to allometric scaling in vascular plants [West *et al.*, 2008; Enquist *et al.*, 2000a; Niklas, 1992]. Allometric scaling provides a clear method to define relationships between structural and functional variables in plants [Enquist *et al.*, 2000a]. Scaling relationships hold over 12 orders of magnitude in vascular plants and provide a solid foundation for use in dynamic, biologically-informed, land surface evolution modelling. Our confidence in these scaling relationships provides us with a basis to estimate the total biomass of these shrub communities. Biomass measurements numerically describe the amount of vegetation present and serves as a common currency for comparing differing species and plant morphologies in a community. Furthermore, biomass acts as a proxy for other measurements, such as water availability. We apply biomass relationships to our model of coupled plant behaviour and sediment transport in order to quantitatively define transport rates in a changing climate.

Through this study, we use a dynamic, coupled model of shrub communities and the sediment flux on a hillslope. We use field-based measurements to gain confidence in allometric scaling relationships, which ultimately allows us to calculate biomass values. In turn, we use these biomass values to make comparisons between each shrub species, and furthermore, biomass values provide us with a foundation to make similar comparison to shrubs not included within this study. Additionally, we consider influences on the shrub communities related to climate change and discuss differences between modeled snakeweed and rabbitbrush shrubs in ENSO-modulated and aridification precipitation scenarios. Finally, we are able to make observations concerning biomass and the sediment flux, where we develop a relationship between the amount of vegetation on a hillslope and the resulting sediment flux.

CONCEPTUAL MODEL

Our work involves a biologically-informed dynamic model that tracks sediment transport over climate change timescales. In particular, we consider the influence of climate change associated with global warming trends on plant populations and, in turn, changes in the sediment flux. Our work focuses on two, interconnected questions. First, how will climate change affect desert-shrub populations? Secondly and consequentially, will climate change alter sediment transport on arid, vegetated hillslopes? To answer these questions we consider the nature of desert shrubs and rainsplash transport in these arid environments and consider biotic and abiotic factors essential to the working of our quantitative, probabilistic model. Specifically, we describe two desert shrubs native to the arid Southwestern United States and their strong dependence on water availability. In the next section, we explain how water, in the form of rainsplash, acts to modulate sediment transport which creates sediment ‘capacitor’ mounds beneath the same desert shrubs detailed in the previous section. In the final part of this chapter, we describe the significant connection between biomass and allometric scaling relationships that are essential to this study.

Desert Shrubs and Water Availability

In arid environments, water is the limiting growth factor of plant populations [*Fischer and Turner, 1978; Comstock and Ehleringer, 1992*]. We focus on environments dominated by precipitation as the source of water, rather than overland flow or groundwater sources. In particular we examine broom snakeweed (*Gutierrezia sarothrae*) and rabbitbrush (*Chrysothamnus viscidiflorus*) shrubs in New Mexico. Snakeweed is a relatively small, short-lived shrub with a maximum lifespan between 7 and 10 years. In comparison, rabbitbrush is a larger shrub with

a considerably longer maximum lifespan, between 30 and 40 years old. Desert environments in the western United States have a distinct seasonal precipitation pattern associated with two major air circulation systems, the North American monsoon and the Pacific frontal system [Rajagopalan and Lall, 1998; Adams and Comrie, 1997]. The monsoon affects summer precipitation and creates intense, brief, but frequent convective thunderstorm systems [Adams and



Figure 1: This conceptual model is used to visual describe differences in newly recruited shrub to mature member of the shrub population (left to right). The newly recruited members of the population do not have a visible ‘capacitor’ mound beneath the canopy, as the protection of the canopy is not sufficient to allow for the sediment accumulation. The upper rooting depth L_{UL} and the lower rooting depth L_{LL} , available to mature shrubs, are marked. Note that the winter precipitation P_W supplies the lower level, whereas the summer precipitation P_S supplies the upper level.

Comrie, 1997]. This precipitation is typically limited to the upper layer of the soil, because of the short duration of these storms and also due to the high evaporative demand during

the summer months, where much of the precipitation quickly evaporates after reaching the ground surface. The Pacific frontal system results in winter precipitation systems which are of longer duration, but lower intensity [Rajagopalan and Lall, 1998]. The cooler weather in the winter months decreases the evaporative demand and the longer duration weather systems yield precipitation that is able to penetrate and recharge the lower level of soil. We make use of Worman's [2010] conceptual model (Figure 1) which defines the upper level $L_{UL}[L]$ based on the juvenile rooting depths, and defines the lower level $L_{LL}[L]$ as the distance between the lower boundary of the upper layer and the maximum rooting depth of the shrub species.

The upper and lower soil layers, defined above, have important functional implications for desert shrubs [Schenk and Jackson, 2002; Fernandez and Caldwell, 1975; Ryel et al., 2008]. The upper soil layer is important for both shrub recruitment and juvenile mortality. Summer precipitation provides the necessary stimulus and nourishment for seeds to germinate and then establish a viable root system. Summer precipitation is therefore an essential part of juvenile shrub recruitment. Additionally, juvenile shrubs do not have access to the lower soil layer, as they lack extensive root systems and therefore rely on summer precipitation to become established adults.

If a shrub survives multiple growing seasons, it can then gain access to the lower soil level through the growth of an extensive root network, and in some shrub species, a long tap root. Adult shrubs tend to be unresponsive to summer rainfall events and rely on the uptake of winter precipitation for survival [Flanagan et al., 1992; Donovan and Ehleringer, 1994; Lin et al., 1996; Gebauer et al., 2002; Leffler et al., 2004]. In an effort to give a simple, yet defensible description of deeper moisture availability for mature plants, we consider the probability of adult shrub mortality to be a function of water availability provided during precipitation events in the winter months. Winter and summer precipitation support different parts of the shrub populations, and our dynamic model structures the probability of shrub

recruitment and mortality as functions of seasonal precipitation.

Sediment ‘Capacitor’ Formation

In arid environments, communities of a single species of shrubs modulate how sediment is transported [Furbish *et al.*, 2009a; Schlesinger and Pilmanis, 1998]. The process of rainsplash transport, where sediment grains are activated and set into motion by raindrop impacts, forms sediment ‘capacitor’ mounds beneath the canopies of desert shrubs [Furbish *et al.*, 2009a; Parsons *et al.*, 1992] (Figure 2). The formation of these mounds is attributed, in part, to the advective-dispersive process of rain splash transport [Furbish *et al.*, 2009b,a]. This process generates an inward flux of sediment grains toward the base of the plant which is greater than the outward flux of grains. This difference between the inward and outward flux is a result of the protection of the canopy that provides shelter from raindrop impacts [Parsons *et al.*, 1992]. Modeling and quantitative studies have shown that the presence of vegetation can affect the sediment flux on hillslopes, such that the annual sediment flux is less than similar hillslopes lacking vegetation [Worman, 2010; Roering *et al.*, 2010; Marston, 2010]. Detailed field measurements indicate that shrub canopy cover [L^2] (Snakeweed), on average, varies as a parabolic function with radial distance from the shrub center, declining radially outward [Childs, 2008; Furbish *et al.*, 2009a]. In turn, the mound approaches an approximately circular shape. Fundamentally, the presence of shrubs creates mound microtopography, which allows for temporary storage of sediment on vegetated hillslopes, an effect that is not present on similar, unvegetated hillslopes. Thus the presence of vegetation modulates sediment transport.

Biomass and Allometric Scaling

Our work seeks to relate biomass to sediment transport on arid hillslopes. We describe vegetation in terms of biomass for several reasons, but primarily because biomass provides



Figure 2: A mound beneath a Snakeweed plant, with a yellow tape highlighting the mound shape. For scale the arrow is 10 cm in length. Reprinted from the Master's thesis of E. M. Childs [Childs, 2008].

a simple unit of measure and is also a proxy for other processes. Biomass measurements numerically describe the amount of vegetation present at any given time, and is also an accepted unit of measurement in both ecological and geomorphological studies. Biomass measurements also allow for comparisons between different shrub species and shrub morphologies, which allows us to connect observations between plant communities.

Biomass is a useful proxy in evaluating water availability. In arid, resource-limited environments, total above-ground biomass positively correlates with water availability [Schlesinger and Gill; Stromberg et al., 1993; Seghieri and Simier, 2005]. Studies that test water potential in desert shrub communities show that water potential is a measure of soil moisture availability [Schlesinger and Gill]. When water is the limiting growth factor in these environments, we can assume that shrubs will fully utilize any available water. Therefore, the amount of

above ground biomass scales with moisture availability and essentially correlates with site productivity [Seghieri and Simier, 2005]. Furthermore, studies have shown that the structure of the shrub community is strongly related to water availability, where smaller shrubs are more sensitive to drought compared to older, established shrubs [Stromberg *et al.*, 1993; Schlesinger and Gill]. This is, in part, due to a water holding capacity of adult shrubs, in addition to a more extensive root network [Schlesinger and Gill].

Allometric scaling relationships in vascular plants provide a quantitative connection between structural and functional variables in plants, such as biomass and resource uptake, and hold over 12 orders of magnitude (Figure 3) [Enquist *et al.*, 2000a; Niklas, 1992; West *et al.*, 1997]. The dependence of a variable Y on the biomass M is characterized by the general form

$$Y = Y_0 M^b \tag{2.1}$$

where Y_0 is the normalization constant characteristic of the organism and b is a scaling exponent. Researchers have found that various variables scale to multiples of the quarter power of M when using annualized measurements [Enquist *et al.*, 2000b; West *et al.*, 1997]. For example, in samples over several orders of magnitude, the following relationships exist within vascular plants: $G \propto M^{\frac{3}{4}}$, $L \propto M^{\frac{1}{4}}$, and $N_0 \propto M^{\frac{3}{4}}$, where G is the biomass production or growth rate, L is the body length, and N_0 is the number of branches found within a plant [Enquist *et al.*, 2000b].

Allometric scaling laws illuminate simple relationships within complex organisms, such as the desert shrubs that are central to this study. For simplicity, several assumptions are made for vascular plants. Most importantly, an area and volume conserving, fractal-like structure is assumed [Enquist *et al.*, 2000a, p. 172-173]. The fractal-like system provides a fundamental basis for derivation of the quarter power scaling exponent [West *et al.*, 1999, p.1677]. Other assumptions include that (1) the branching network is space filling, and (2) the final or terminal

branch of the network is size invariant, for example, the size of the capillaries in the vascular system of a given plant is approximately equivalent in different species. Furthermore, (3) the energy required to transport and distribute resources throughout the network is minimized and uniform, and (4) the hydrodynamic resistance is minimized through the system to facilitate transport of water and nutrients [Enquist *et al.*, 2000b, p. 91]. This set of assumptions allows scaling laws to be readily applied to vascular plants which have conductive tissues for circulation and transport of resources throughout the organism.

In addition to individual plant characterization, this scaling model also can be applied on the community level. In diverse forests, individual scaling relationships are scaled up to the community level to include population dynamics, resource flux rates, canopy configurations, and mortality rates [Enquist *et al.*, 2008]. These scaling relationships are incorporated into our plant model and allow for quick conversion between varying plant characteristics.

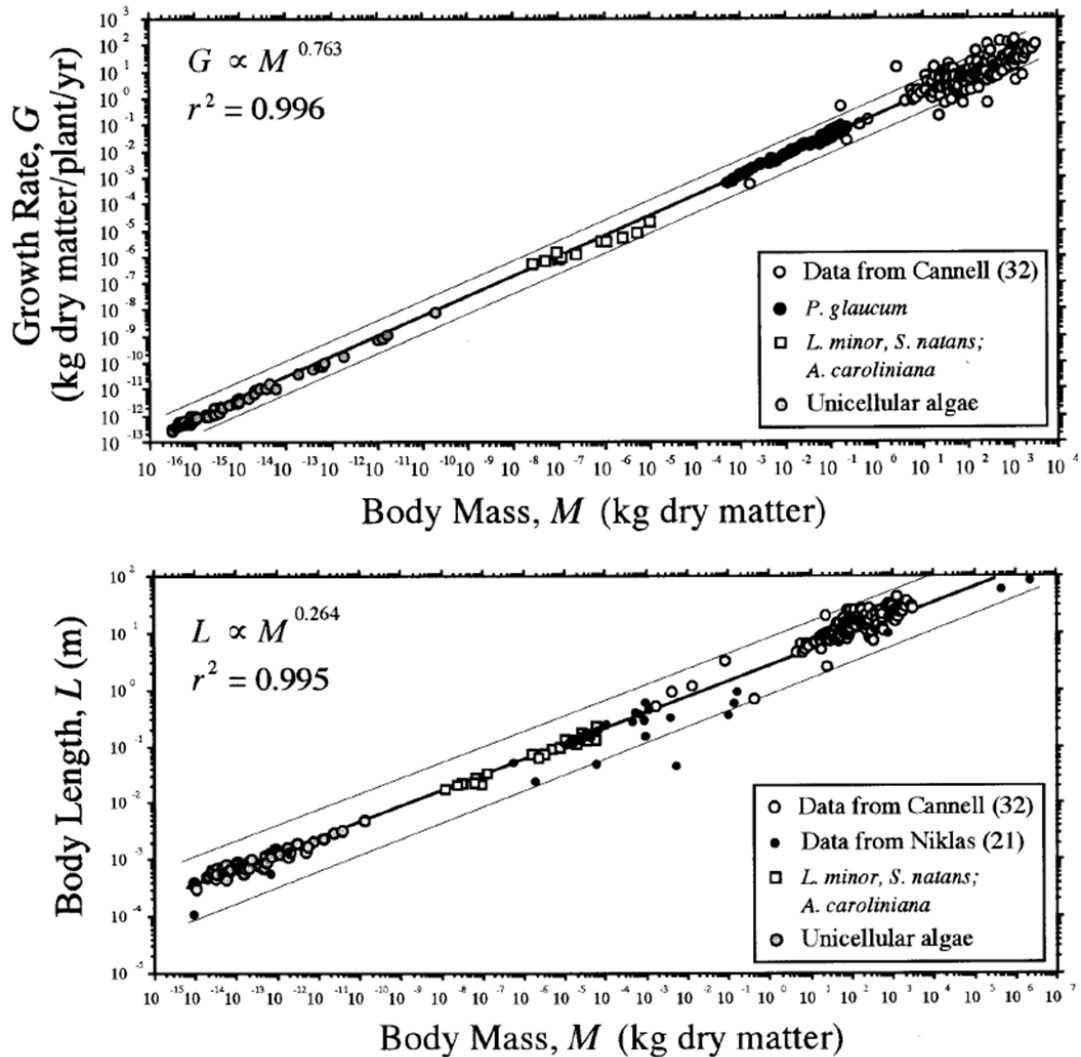


Figure 3: This figure depicts the scaling relationship between the annualized biomass production or growth rate G (upper graph) and the total body length or in the case of upright vascular plants, the aboveground body height. The lower graph displays L against the biomass M . These relationships in these graphs span multiple scales of magnitude in unicellular and multicellular plant species. The scaling relationship and the r-squared values are labelled on each graph. Reprinted from “Invariant scaling relationships for interspecific biomass production rates and body size,” K. J. Niklas and B. J. Enquist, *PNAS*, 98:5, 2001.

FIELD METHODS**Field Sites**

Data collected in the field were used to inform and constrain a dynamic sediment transport model in Matlab. This study is focused on two shrub species found in cold, arid steppe environments [Kottek *et al.*, 2006] in New Mexico, namely, broom snakeweed (*Gutierrezia sarothrae*) and rabbitbrush (*Chrysothamnus viscidiflorus*). Two previously established field sites were used to obtain measurements. Both these sites are characterized by the Köppen-Geiger climate index as arid steppe [Kottek *et al.*, 2006]. The first field site, Arrowhead Well, is southwest of Albuquerque in the Cibola National Forest, New Mexico (Figure 4). The second site, Placitas, is just north of Albuquerque, also within Cibola National Forest at the foot of the Sandia Mountains. We repeated similar surveys which were performed in these locations by Roberts [2010]. Specific field plots at each location were chosen based on several criteria, which include: the dominant presence of snakeweed, rabbitbrush, or both, the presence of relatively high shrub population densities, and the absence of significant disturbance associated with grazing or other land-use practices.

Individual and Shrub Population Data Collection

Measurements of desert shrubs were performed on individual shrubs and shrub populations. These measurements are designed to inform the scaling and population dynamic components of this study. At Arrowhead Well, measurements of both snakeweed and rabbitbrush were conducted. Three different 20 m \times 20 m areas were marked off with a tape measure and further divided into two meter intervals. Within each plot and subplot, counts of living rabbitbrush and snakeweed shrubs were recorded. Juveniles, measuring less than 13 cm in height were

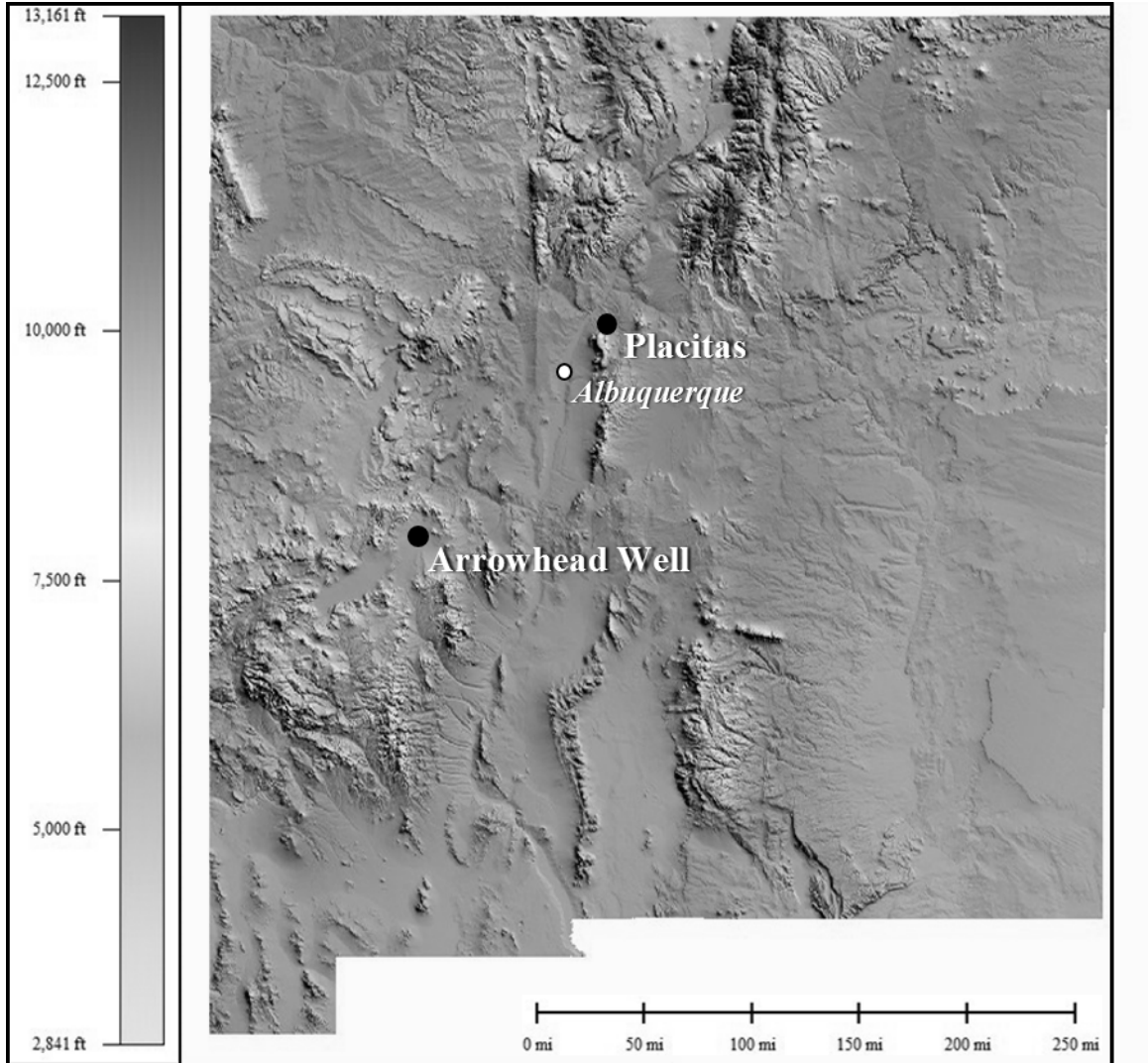


Figure 4: Our two field sampling locations, Arrowhead Well and Placitas, are marked on this digital elevation map (adapted from TopoCreator.com).

not counted, as sediment mounds were not found under the plant canopies of young shrubs. Within the first of the three plots, we recorded measurements of maximum height and plant width for each individual shrub. Two measurements of breadth were taken across the shrub at a 90 degree angle. Furthermore, base stem measurements were recorded for rabbitbrush shrubs which met breadth-based specifications. Ten shrubs were chosen for each size category if both breadth measurements satisfied the specifications of the category. Categories based on plant width are as follows: 25 cm and below, 26 cm - 50 cm, 51 cm - 101 cm, and 102 cm and above. To understand the general distribution of juvenile shrubs in the population, we performed a quick count of both snakeweed and rabbitbrush juveniles in a 6 m \times 20 m portion of the first plot.

The Placitas field site plots consisted of only snakeweed shrubs. In effort to choose snakeweed-dominant field plots, we chose sites which were less than 20 m \times 20 m in size. The first plot measured 14 m \times 14 m and the second measured 8 m \times 15 m. In addition to plant counts within each plot, the height and breadth of all shrubs within the plots were measured and recorded. Base stem measurements were taken for a mix of 38 small to large snakeweed shrubs within the plots. Large shrubs outside of plots also were sampled to obtain a range of sizes that were not present in the plots.

In order to define the fractal-like structure of each species, we documented measurements of well-formed, healthy rabbitbrush and snakeweed branching structures. We used destructive methods to gain an understanding of the branching network. For both plant species, we chose small to large shrubs, and then dissected the shrubs in order to measure the branching network. We recorded measurements of branch segment lengths and branching angles, relative to the previous position of the branch, for every branching node level (Figure 5). For particularly large shrubs that had well developed branching systems from the main stem, measurements were taken from a single major limb due to time constraints. The measurements associated

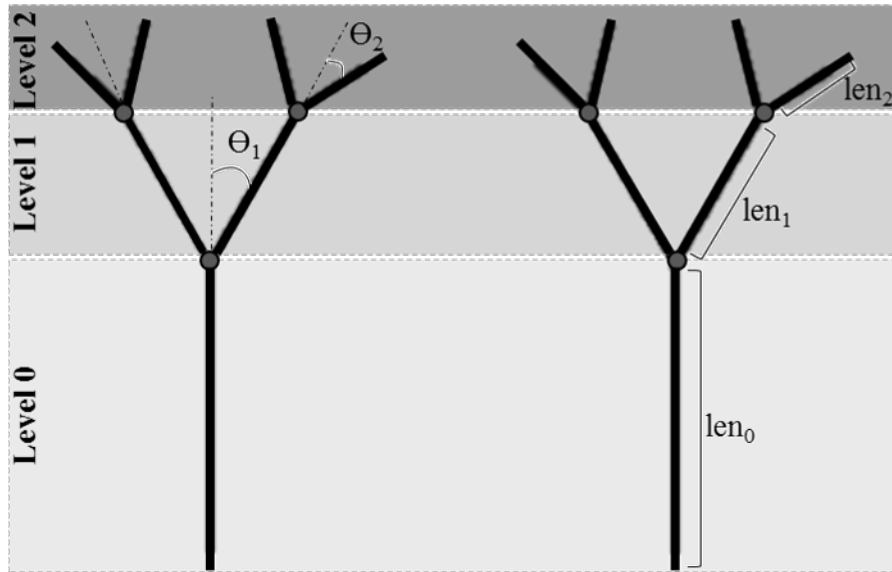


Figure 5: This figure diagrams simplified measurement locations taken in the field to characterize snakeweed and rabbitbrush shrubs. Each round circle separating levels in the branching network represents a node of bifurcation. The left plant structure depicts example locations within levels 1 and 2 where angles were measured relative to the position of the previous branch. The right plant structure indicates example locations where branch lengths were measured in all levels.

with this major limb are assumed to be characteristic for the shrub, so that we can make quick calculations for the entire plant. For example, when we calculate the biomass of a large shrub with several major limbs, we determine the biomass of the characteristic (measured) limb and multiply this value by the total number of major limbs. At Arrowhead Well, six rabbitbrush and nine snakeweed shrubs were surveyed using this method, and an additional three large snakeweed shrubs were measured at Placitas.

MODELING METHODS

We incorporate the measurements and observations made in the field into a coupled Matlab model of shrub population dynamics and associated sediment transport [*Worman*, 2010; *Stocky*, 2012] on desert hillslopes. Essentially there are two major components of this model: the dynamic plant populations and the hillslope response, where sediment transport is modulated by the vegetation present. This model acts as an interface which relates the response of plant populations, and therefore sediment transport, to a potentially changing climate.

Shrub Population Modelling

This portion tracks the number and age of individual shrubs which enter and leave the population at any given point in time. This allows us to vary key values within the model which drive plant population dynamics and capture changes in population size and structure (i.e. concentration of juveniles in the population). Detailed characterization of shrub populations allows us to view population dynamics on climate change time scales (100-200 years).

There are several components that are important in creating a dynamic shrub population that is consistent with populations measured in the field. These components include: specification of an initial shrub population, shrub growth, tracking the aging of shrubs throughout time, juvenile recruitment, and shrub mortality. These factors are grounded in field measurements and/or literature. The following is a brief description of both sections of the model; also additional commentary on the original model is provided by *Worman* [2010] and *Stocky* [2012].

Initial Population

The number of single-species, perennial shrubs $N(t)$ in a population is described at time t for a given square area A [L^2]. The minimum sample plot size, $10 \text{ m} \times 10 \text{ m}$, was determined based on field measurements to accurately capture the shrub density of the plot and also to maintain model stability [Roberts, 2010; Worman, 2010]. The initial population age demographics were provided using canopy size as a proxy for shrub age. Given that snakeweed shrubs grow approximately radially outward, then a shrub with a large canopy radius is, on average, older than a smaller shrub. Therefore, the initial population is defined using the distribution of canopy radii, the average shrub density in a given plot, and the minimum spacing between shrubs that was recorded within the field sites. Work done by Roberts [2010] indicates that the distribution of shrub canopies in a $20 \text{ m} \times 20 \text{ m}$ plot could be approximated by a gamma distribution $\Gamma(\alpha, \beta)$, where the two parameters which describe the size (and thereby age) of the population are defined. In addition, we provide estimates of initial canopy radius, R_i , and maximum canopy radius, R_f based on field measurements. This field-informed distribution of shrub sizes allows us to specify an initial population which is characteristic of shrub populations found at the field site in New Mexico.

Juvenile Recruitment

Mature shrubs have the ability to grow and disperse seeds which may then germinate and become established juvenile shrubs. We consider recruitment to be contingent on the successful completion of these events: seed production, dispersal, germination and seedling survival. Each of these factors for individual shrub species, as well as external factors (precipitation), are treated probabilistically.

We supply the model with an average seed production value for the number of mature shrubs $N_s(t)$. We note that there is inherent variability in seed production between individuals,

populations, and years for a single species [Kelly, 1994], but consider an average to sufficiently represent the shrub species over the desired time scales. Mature shrubs capable of producing seeds are identified based on access to water available in the lower soil level. Hence, we consider an ‘adult’ as any shrub that has a maximum rooting depth which surpasses the lower boundary of the maximum juvenile rooting depth zone ($D_N(t) > L_{UL}$). The model allows each of these shrubs to produce the average amount of seeds each summer growing season.

These seeds then must be dispersed far enough away from the canopy of the source shrub so that it may successfully germinate. From an areal perspective, we consider the minimum distance for effective germination to be the area outside of the canopy cover of the source shrub, and also not within the canopy cover of any other extant shrub. Therefore, the area available for seed dispersal is, in effect, unoccupied space. Germination, following dispersal, can then occur by the process of ‘heterogeneity’ [Baskin and Baskin, 1973]. Plants operating under this process produce seeds that are able to germinate under the varying prevailing environmental conditions, through the production of seeds with genetically different germination requirements [Baskin and Baskin, 1973]. Thus, we consider a proportion of the seed pool to germinate in any given year, as it is not unlikely that shrubs will produce seeds which are viable no matter the prevailing environmental conditions..

If a seed has successfully been produced, dispersed, and germinated, the seed becomes a seedling, and the final step to full juvenile recruitment is seedling survival. All of these steps occur during the summer months, as this is the growing season for most desert shrubs. Seedlings are particularly sensitive to precipitation deficiencies in the upper soil layer L_{UL} due to their limited rooting system. We consider the probability of seedling survival as a function of precipitation received in the growing season, where we calculate the water content θ_S present in the upper soil layer L_{UL} during the summer months in the model. If a seedling reaches its permanent wilting point, which is based on the water content available, it will not survive to

become a successfully recruited juvenile.

Each of these components of the recruitment process must be achieved to create new juveniles which are necessary to sustain the population. All parts of this process behave probabilistically, yet summer precipitation is the controlling factor in juvenile recruitment and could ultimately prevent seedling survival in dry seasons.

Shrub Mortality

Just as shrub recruitment is a critical part of a dynamic shrub population, shrub mortality is also essential to mimic this system. When considering shrub mortality we calculate the probability of shrub death in both juvenile and adult shrubs. Juvenile shrub mortality, much like seedling mortality, is a function of summer precipitation and the water content found in the upper soil layer, as these juvenile shrubs do not have an extensive root system and are not able to reach the lower soil layer. Therefore, adequate summer precipitation is needed to keep a juvenile shrub from reaching the permanent wilting point. In contrast, adult shrub mortality depends on winter precipitation which supplies moisture to the lower soil level L_{LL} [e.g., *Flanagan, 1992; Donovan, 1994*]. In this case, adult shrub mortality is inversely proportional to the volumetric water content of the lower level θ_W . Therefore, we assign a probability of shrub mortality that depends on summer or winter precipitation, accordingly.

Shrub Growth and Population Conservation

To further characterize a dynamic shrub system, we must grow our shrubs and conserve surviving shrubs in the model. For convenience, we adopt annual time steps Δt for shrub growth and conservation. This is done by convention and also to include annualized data sets. We include growth of above ground and below ground biomass each year. In this model, we represent growth in the above ground biomass as growth of the plant canopy. If canopy growth

is approximately radial and also a proxy for age, we allow the canopy to grow radially within the constraints of the shrub species. Below ground biomass is simplified into measurements of the maximum rooting depth D_N , which allows us to assess whether the shrub reaches the lower soil level.

The probability distribution of shrub ages is conserved for the number of surviving shrubs N_T , using the Master equation (4.1),

$$\frac{\partial N_T}{\partial t} = -\frac{\partial N_T}{\partial T} - M(T, t), \quad (4.1)$$

and is subject to the boundary condition that, $N_T(0, t) = R(t)$. Here $\partial N_T/\partial T$ is an “advective” term that describes the rate of change in N_T as shrubs age at the rate of $dT/dt = 1$, and $M(T, t)$ [t^{-1}] is a sink term, representing the local rate of shrub mortality which varies probabilistically with shrub age and time. The boundary condition is a source term which states that the recruitment rate $R(t)$ [t^{-1}] adds new individuals per unit time.

Sediment Transport Modelling

Work performed by Furbish et al. [2007, 2009] indicates that rain splash transport is an advection-dispersion process at the grain scale. To wit, the Exner equation gives us

$$\frac{\partial \zeta}{\partial t} = -\nabla \cdot \mathbf{q}, \quad (4.2)$$

where $\partial \zeta/\partial t$ denotes the rate of change in the land surface elevation ζ [L] with respect to time t [t], and ∇ is denoted by

$$\nabla = \left\langle \frac{\partial}{\partial x} \quad \frac{\partial}{\partial y} \right\rangle, \quad (4.3)$$

where x and y denote horizontal coordinates. The flux $\mathbf{q} = \mathbf{i}q_x + \mathbf{j}q_y$, where q_x and q_y denote the components of the flux in the x and y directions. The dot product in 4.2 thus takes the

form

$$\frac{\partial \zeta}{\partial t} = -\frac{\partial q_x}{\partial x} - \frac{\partial q_y}{\partial y} \quad (4.4)$$

[Parker *et al.*, 2000]. The components q_x and q_y can be further defined in terms of advective and diffusive parts involving the grain “activity” γ , or the volume of sediment in motion per unit area. Namely,

$$q_x = \gamma u - \frac{1}{2} \frac{\partial}{\partial x} (\gamma D_x), \quad (4.5)$$

where the mean grain drift velocity in the x -direction is given by u , and D_x represents the dispersion coefficient. Similarly,

$$q_y = \gamma v - \frac{1}{2} \frac{\partial}{\partial y} (\gamma D_y), \quad (4.6)$$

where the mean grain drift velocity in the y -direction is given by v , and D_y is the dispersion coefficient. These two equations may then be substituted into 4.4 giving,

$$\frac{\partial \zeta(x, y, t)}{\partial t} = -\frac{\partial}{\partial x} (\gamma u) - \frac{\partial}{\partial y} (\gamma v) + \frac{1}{2} \frac{\partial^2}{\partial x^2} (\gamma D_x) + \frac{1}{2} \frac{\partial^2}{\partial y^2} (\gamma D_y), \quad (4.7)$$

which is a Fokker-Planck-like equation.

To solve 4.7 we approximate ∂x and ∂y as finite, discrete values Δx and Δy due to the limitations of computational modelling. We numerically solve this equation using a mass-conserving finite-volume method [Stocky, 2012], but first we make two important assumptions. First, diffusion is isotropic ($D_x = D_y$), which allows us to reduce the diffusion coefficients into a single value D . Secondly, we approximate the mean grain drift velocities u and v as the product of a transport coefficient K [L t^{-1}] and the local land-surface slope in the x and y directions. Work done by Roberts [2010] provides us with calibrated values for the transport coefficient K and the diffusion coefficient term D , which produces results that are consistent

with field measurements, specifically mound volumes associated with varying aged shrubs. The simulation, involving sediment transport, assumes an average annual rate of transport, not linked to rainfall intensity and, transport is set on a symmetrical, parabolic profile with an average slope of 10.2° .

The geomorphic aspect of this model acts on a short time step (7.3 days), whereas the shrub population portion of the model operates on an annual timescale. This difference in timescales is necessary to maintain model stability [Stocky, 2012]. We synchronize the geomorphic portion to 50 timesteps through the course of a year, before the biological portion of the model is able to alter shrub recruitment, deaths, and growth. Therefore, both portions of the model operate independently of one another, yet the model is coupled so that annual biological growth affects the magnitude of sediment transport over the area of the hillslope.

ANALYSIS AND RESULTS

Precipitation

Precipitation is essential to the survival and reproduction of shrub species in nature and in our model. Both adult and juvenile shrubs are sensitive to precipitation, such that lowered precipitation increases the probability of shrub mortality [Aldon and Pase, 1981; Comstock and Ehleringer, 1992; Donovan and Ehleringer, 1994]. To summarize the description provided in Chapter 4: in the model, we confine summer precipitation to the upper soil layer and allow winter precipitation to penetrate the lower soil layer. We therefore define two specific time periods to evaluate precipitation patterns: the summer season (June-September) and the winter season (October-May). As precipitation is imperative to the survival of the modelled shrub populations, we statistically analyzed precipitation data local to one of our field sites. We evaluated data from NOAA cooperative station, Augustine 2 E, which neighbors the first field site at Arrowhead Well. This precipitation record contains hourly precipitation measurements, which we aggregate into more manageable records. We take the hourly measurements and make monthly records, which we further separate into three records that accumulate precipitation into winter seasonal precipitation, summer seasonal precipitation, and an annual record. Each record extends from 1948 - 2010, but the length of this record is not sufficient to capture fluctuations inherent to climate change. Therefore, we produced a precipitation signal which statistically represents the precipitation data from Augustine, NM.

To generate a precipitation signal suitable for the timescales evaluated in our dynamic model, we evaluated the autocorrelation and partial autocorrelation as an indicator of an autoregressive (AR) model. AR modelling allows us to examine the precipitation signal at Augustine for persistent precipitation patterns. The rapid decay of the autocorrelation and

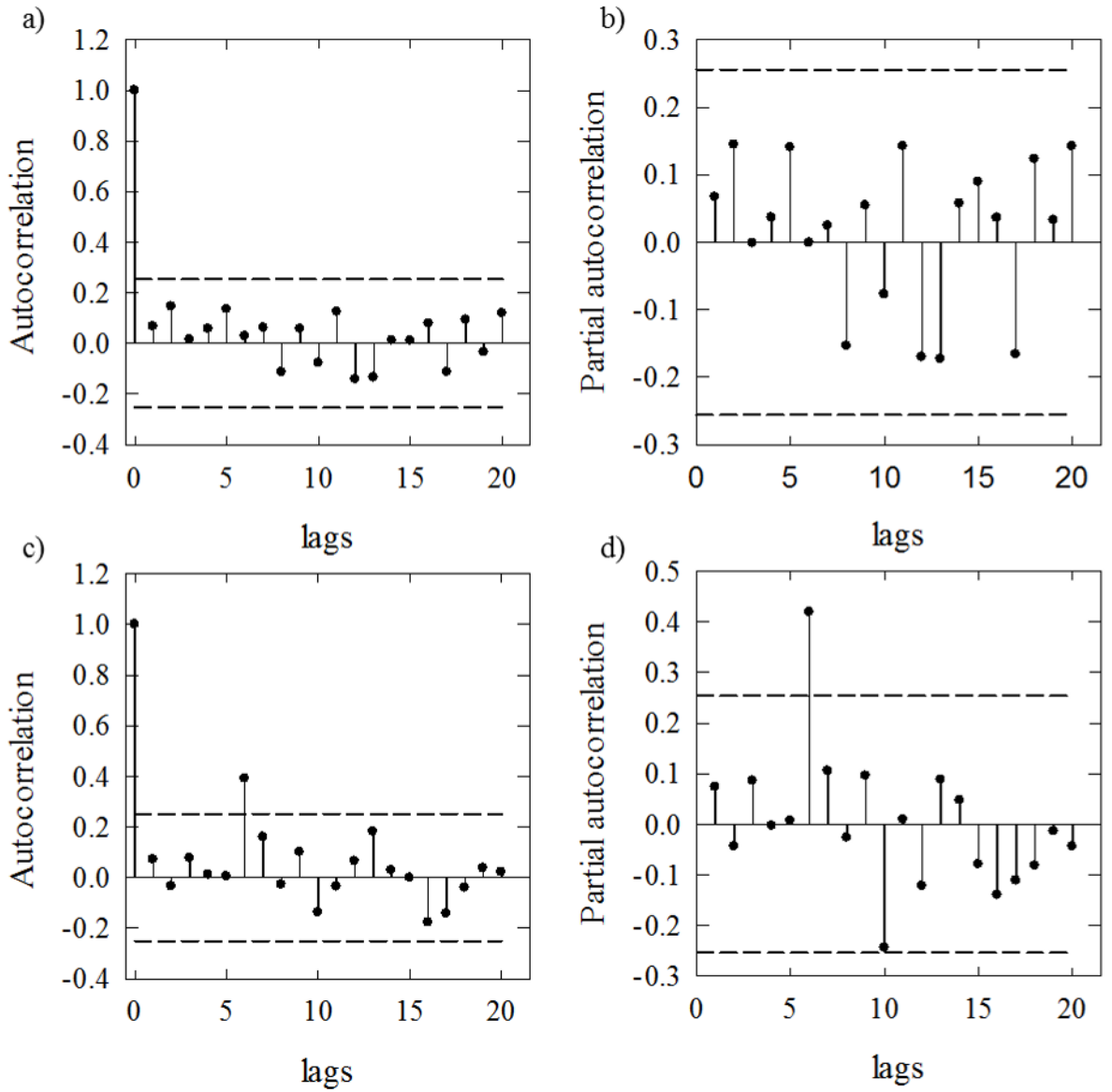


Figure 6: This figure depicts the autocorrelation and partial autocorrelation for winter (the upper two graphs) and summer (the lower two graphs) precipitation at Augustine, NM.

partial autocorrelation (Figure 6), of both the summer and winter precipitation, suggests an extremely weak first-order AR process which can be approximated as a white noise signal. To capture this precipitation signal, we generated white noise precipitation signals for the summer and winter months with a mean and variance consistent with the precipitation record. These signals act as baseline precipitation in the model, so that we can evaluate shrub population dynamics in a statistically consistent precipitation regime.

It is necessary to evaluate shrub dynamics in ‘normal’ precipitation conditions; however we are also interested in evaluating shrub population dynamics in a changing climate. So, we test two different possible scenarios of climate change, the first representing an increased magnitude of wet and dry periods, modulated by the El Niño Southern Oscillation (ENSO). The second scenario is a general trend of increasing aridity. We created precipitation signals that are meant to mimic these climate situations, and evaluated changes in our shrub population model as a result of precipitation.

ENSO Modulated Precipitation Signals

Research suggests that winters in the southwestern United States are currently influenced by the El Niño Southern Oscillation (ENSO), such that precipitation during El Niño winters is above normal and precipitation in La Niña winters is below normal [Bradley *et al.*, 1987; Mason and Goddard, 2001]. Climate change predictions suggest heightened extremes with periods of amplified aridity and moisture, regulated by ENSO [Yeh *et al.*, 2009; Lenart, 2006]. To modulate the winter precipitation signal for our model, we used the Southern Oscillation Index (SOI) which extends from 1866 - 2012 (146 years). The SOI is a standardized index which calculates the pressure differences between Tahiti and Darwin, Australia, using a scale which ranges from positive five to negative five. Extended periods of high magnitude, negative SOI values coincide with warm ocean waters and therefore El Niño conditions, whereas extended

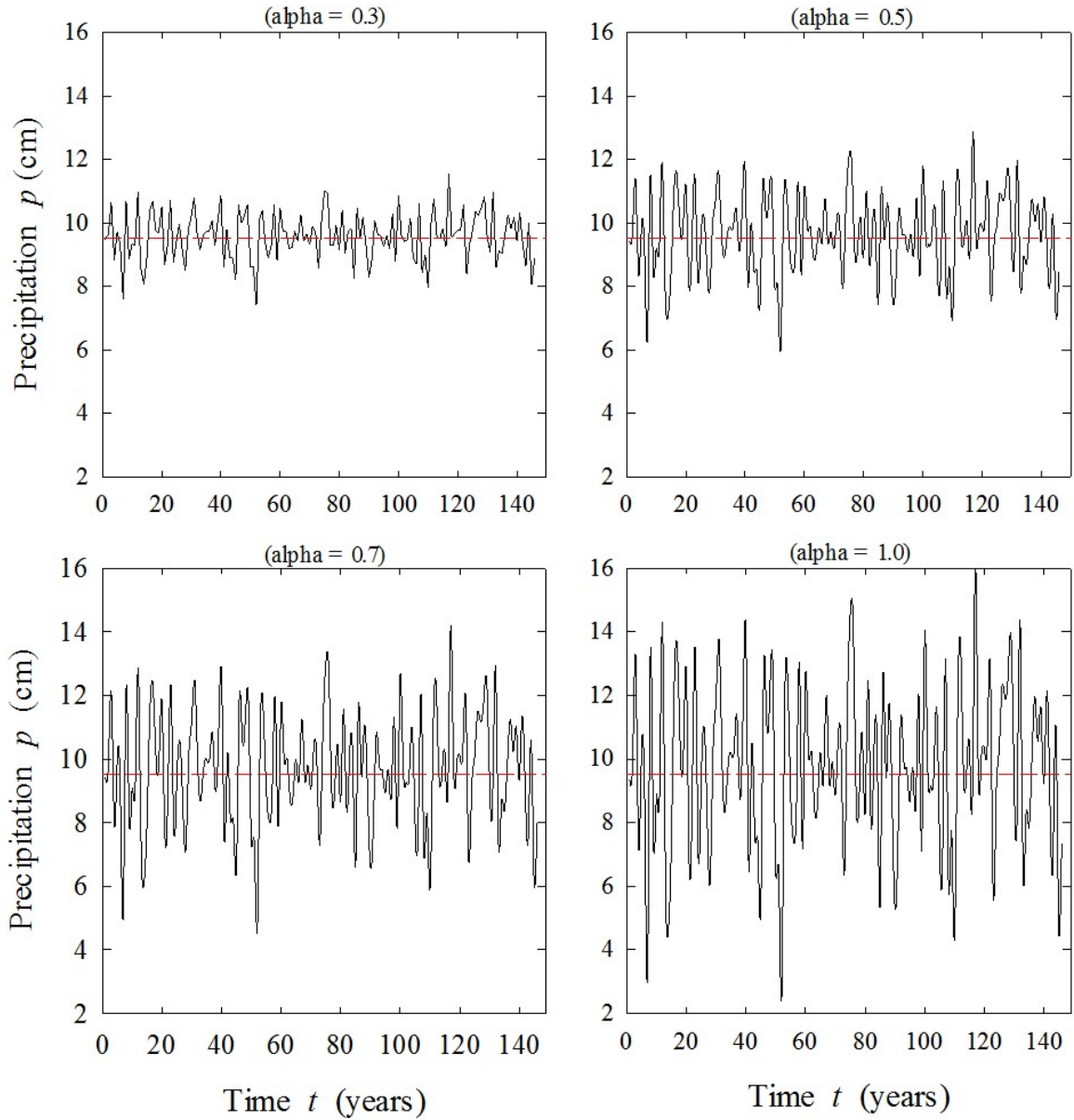


Figure 7: Each of these graphs plots fluctuations associated with ENSO, where each plot represents a different value of the factor α according to equation 5.1. This shows that higher α values increase the magnitude of fluctuations in the wet and dry periods, we use this to create a new ENSO-modulated signal, m_n . For reference, the mean precipitation is represented by the dashed red line.

periods with positive, high magnitude SOI values coincide with cool ocean waters and La Niña conditions [National Climate Data Center, 2013]. This index is therefore a proxy for El Niño and La Niña events [National Climate Data Center, 2013]. Since ENSO has the propensity to influence winter precipitation, we modulate the mean value of winter precipitation based on the magnitude of the SOI. To account for a potentially increasing influence of ENSO, we scale the impact of the SOI on the mean winter precipitation m by a factor α , where we generate an ENSO-modulated precipitation signal m_n as a result of a SOI index value,

$$m_n = m - (\alpha \times SOI). \quad (5.1)$$

We limit the length of this signal, based on the SOI record (146 years), and also vary α to increase the magnitude in which the SOI index modulates the precipitation value to create a new ENSO-modulated signal. We acknowledge that there are many methods to develop an ENSO-modulated precipitation signal, but to maintain parsimony, we used this simple, straightforward method. Four different signals were created using α values equal to 0.3, 0.5, 0.7, and 1.0 (Figure 7). This range of signals was created to test different magnitudes of ENSO-modulation, as climate prediction scenarios are unable to provide a confident estimate of the magnitude of modulation [Mason and Goddard, 2001; Yeh et al., 2009]. In each of these scenarios the ENSO-modulated precipitation m_n is then added to the our previously generated, weak, first-order AR signal. In creating these modulated signals, the inherent AR-structure may be lost; nevertheless we consider these signals to be an approximation of ENSO in combination with the underlying white-noise-like signals.

Climate Aridification

In the past decade, record temperatures have been recorded in the southwestern United States, where temperatures in 2000-2010 were on average higher than temperatures from 1901

to 1999 [*Overpeck et al.*, 2012]. This warming was accompanied by unusually severe drought periods, which is supported by tree-ring derived climate records from the past ~ 600 years in the Southwest United States [*Overpeck et al.*, 2012]. Predictions from nineteen global climate change models suggest further aridification of the Southwest. Specifically, by the end of the twenty-first century, precipitation is expected to decline by an average value of 7 cm annually, as determined by the average of the nineteen models [*Seager et al.*, 2007; *Geophysical Fluid Dynamics Laboratory (GFDL)*, 2007]. We model warming trends by decreasing the mean precipitation, linearly, over a 100 year period by a factor β ,

$$m_d(i) = m_d(i - 1) - m(i)\beta, \quad (5.2)$$

where m_d represents the increasingly dry mean precipitation value, m is the original mean precipitation, and i is used as a time counter. Such that, with increasing time, denoted by i , there is a linear decrease in the annual precipitation. Similar to the ENSO-influenced signal, we superimpose the weak first-order AR signal (which is a approximately a white noise signal) to the decreasing mean m_d to create a new precipitation signal (Figure 8). When we change the value of β we can simulate aridification scenarios with varying severity.

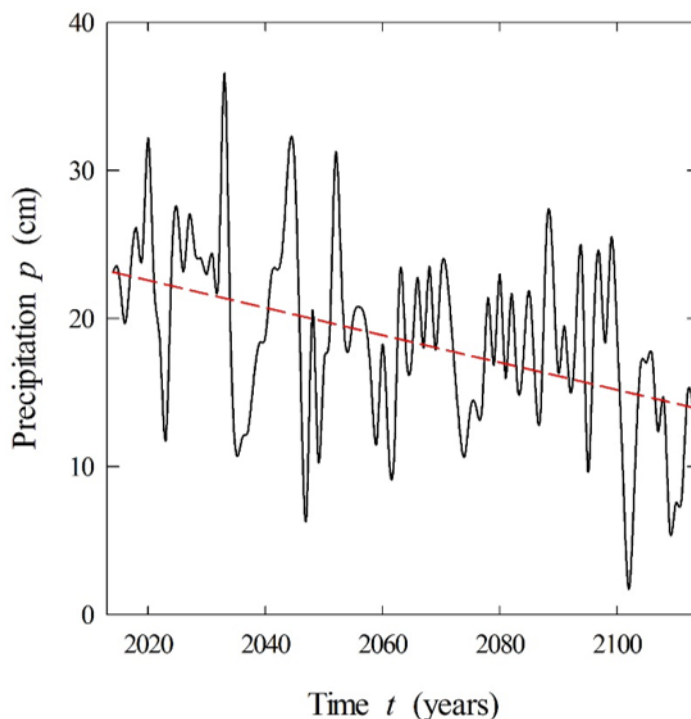


Figure 8: This figure depicts a sample annual precipitation signal which extends over a 100 year period (2013-2113), which adheres to climate predictions which state a 7.5 cm decrease in mean precipitation by then end of the 21st century. Here β is equal to .004 and the dashed red line indicates the mean annual precipitation and the black line is the precipitation signal when we add the random, white-noise-like signal to the decreasing mean.

Proof of Concept: Allometric Scaling in Desert Shrubs

Previous studies concerning allometric scaling in vascular plants focus on vegetation in environments which are not as resource-limited as the conditions found in the New Mexican desert [West *et al.*, 1999; Enquist *et al.*, 2000a, 2008]. As scaling research in arid or resource-limited environments is not typically done, we take time to test whether snakeweed and rabbitbrush adhere to the allometric scaling relationships described by West, Brown, and Enquist (2000). We used two methods to evaluate scaling relationships in these shrubs. First, we used field measurements of physical plant characteristics and plotted them in comparison to allometric scaling relationships. To perform the second test, we rely on a central tenet of allometric scaling that assumes a fractal-like plant structure [Enquist *et al.*, 2000a]. We create a model

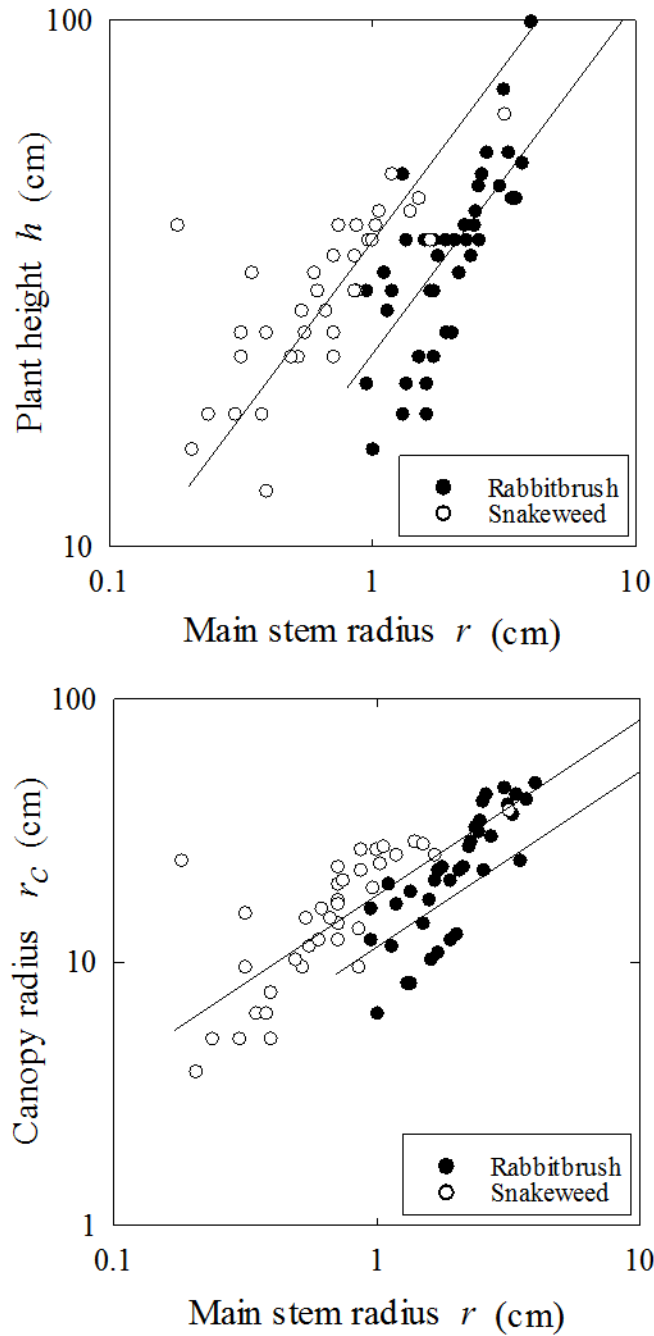


Figure 9: This figure contains two graphs which relates structural characteristics of snakeweed and rabbitbrush shrubs. The graph on the left relates plant height h to the main stem radius r and the graph on the right displays the relationship between the canopy radius r_c and r . The solid black lines were added for reference and each have a slope of $2/3$, by plotting two point with the appropriate slope.

of plant structure based on field measurements to ascertain whether or not we could create relevant scaling relationships, using plant height and canopy radius, in model space.

Researchers define allometric scaling relationships between certain physical parameters in various plant species [Enquist *et al.*, 2000a]. Two scaling relationships are: $r_c \propto r^{2/3}$ and $h \propto r^{2/3}$, where r_c is the plant canopy radius, h is the plant height, and r is the main or base stem radius. We plotted field measurements of these characteristics for both snakeweed and rabbitbrush species (Figure 9). The first graph in Figure 9 relates r to h and the second graph presents the second relationship involving r and r_c . The solid black lines in both graphs are reference lines which have a slope equal to $2/3$. The separation between the snakeweed and rabbitbrush populations is expected, and could be normalized by determining the normalization constant Y_0 (Equation 2.1). Snakeweed better fits the reference lines than rabbitbrush in Figure 9. We surmise that rabbitbrush may not fit the scaling relationships as closely due to differences in its morphology. In the field, we noticed rabbitbrush tends to branch from the base as it matures and allows the center of the shrub to die as the new, outer branches prosper, whereas snakeweed tends to grow from a single base stem and does not exhibit failing inner limbs. We believe that this difference in mature rabbitbrush morphology accounts for its deviation from scaling relationships. This is because we see that the breadth of the shrub does not reflect the amount of living branches in these large mature shrubs, as some of the interior branches have died. Nonetheless, based on the qualitative relationships evident in each of the graphs in Figure 9, we are confident that the relationships between the structural properties in snakeweed and rabbitbrush are not inconsistent with allometric scaling relationships.

To further evaluate allometric scaling in these shrubs, we also developed a model which mimics the branching structure of the snakeweed and rabbitbrush shrubs. To characterize the branching network of both shrubs, we compared the branch length and angles in neighboring branching levels. Given the size of our data set, we used the non-parametric Mann-Whitney

Plant species	Levels	Branch Length	Angles
Snakeweed	L1:L2	0.931	0.006
	L2:L3	0.311	0.279
	L3:L4	0.483	0.748
	L4:L5	0.958	0.229
Rabbitbrush	L1:L2	0.010	0.140
	L2:L3	0.511	0.307
	L3:L4	0.717	0.558

Table 5.1: Results of the non-parametric Mann-Whitney test for statistical significance in branch lengths and angles in adjacent branching levels. Bold numbers indicate statistically significant p value based on $\alpha = 0.05$.

test to assess whether branch lengths and angles in adjacent levels are from the same population (Table 5.1). Of all the tests, there is a statistically significant difference in the branch lengths between the first and second branching levels in snakeweed, and in rabbitbrush, and there is a statistically significant difference in the angle size between the first and second branching levels. Otherwise, we do not see statistically significant differences between neighboring levels in either category. We use these data to construct a two-dimensional model which mimics the plant structure of each shrub, using the mean and variance of the angles and branch length values that we measured in the field. Within this model we can specify the branching level, so that older shrubs have a greater number of branching levels in comparison to younger shrubs. Figure 10 provides a visual comparison of the fractal model output of snakeweed and rabbitbrush shrubs compared to photos taken in the field. We used these models as a test to recreate scaling relationships evident within vascular plants. We can readily query the model for maximum plant height and plant radius. Based on scaling relationships, we expect a linear relationship between the canopy radius and the plant height ($r_c \propto h$). When we plot model results for these physical characteristics for increasing branching levels, we do indeed see a linear relationship between the variables (for example, Figure 11). When we consider our field

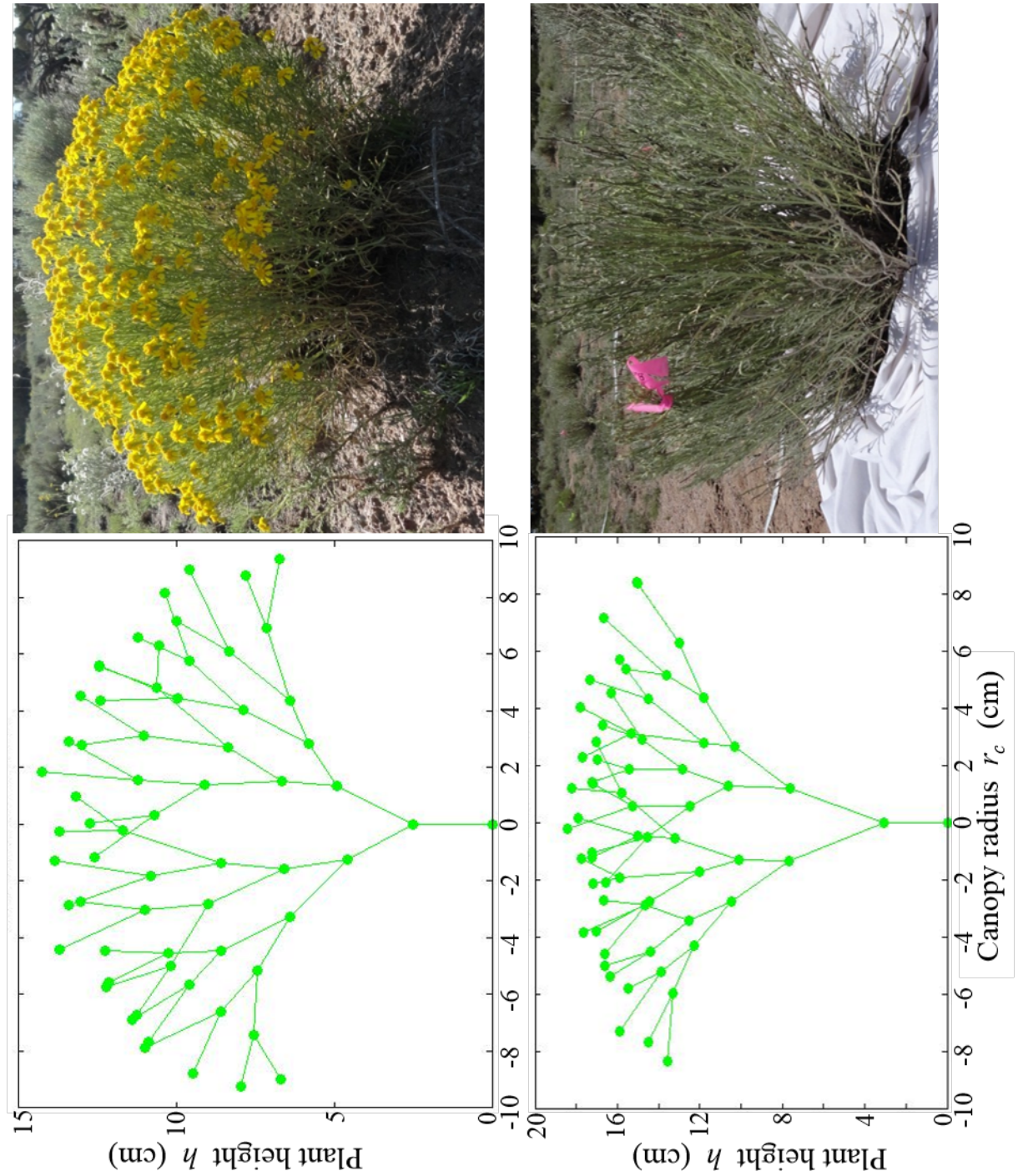


Figure 10: This figure provides a visual comparison between the statistically accurate, two-dimensional fractal model and field photos of the modeled shrub. The upper area of this figure depicts a snakeweed model compared to a photo of a blooming snakeweed shrub in the field and the lower graphic contains a modeled rabbitbrush shrub compared to a rabbitbrush shrub taken in the field.

measurements and the results of the fractal-like model, we are confident that the desert shrubs adhere to allometric scaling laws. This allows us to confidently use scaling relationships to estimate other plant characteristics, specifically biomass, which we did not measure in the field.

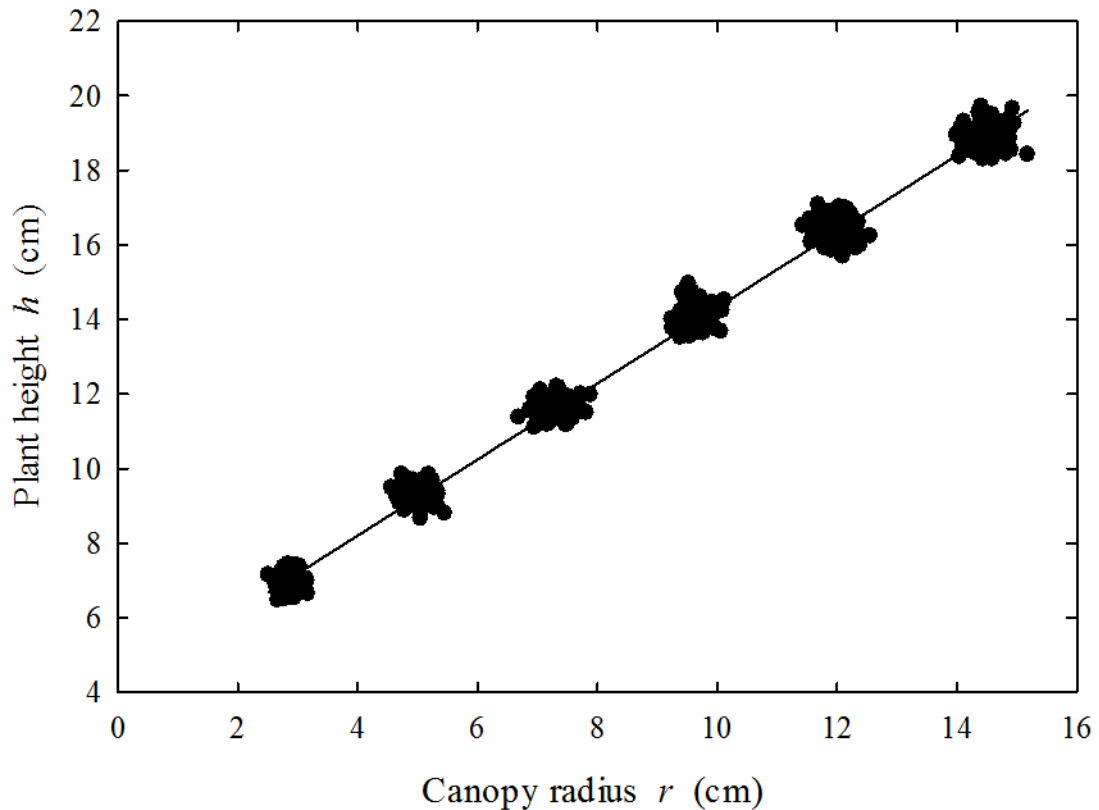


Figure 11: This figure utilizes data from the fractal-like model of a snakeweed shrub. The relationship plotted in this figure is plant canopy radius versus plant height. Each cluster of points represents a different branching level, so that each collection of points represents a larger (older) shrub. A trend line was added to this graph to highlight the linear relationship.

Biomass and Sediment Transport

We know that the presence of shrubs on desert hillslopes modulates the sediment flux [Furbish *et al.*, 2009a; Schlesinger and Pilmanis, 1998], such that the sediment flux on vegetated hillslopes is less than the flux on similar, unvegetated hillslopes [Marston, 2010; Roering *et al.*, 2010; Roberts, 2010]. We have also suggested that biomass can be used as a common currency between different types of shrubs. Given this information, we explore the extent to which

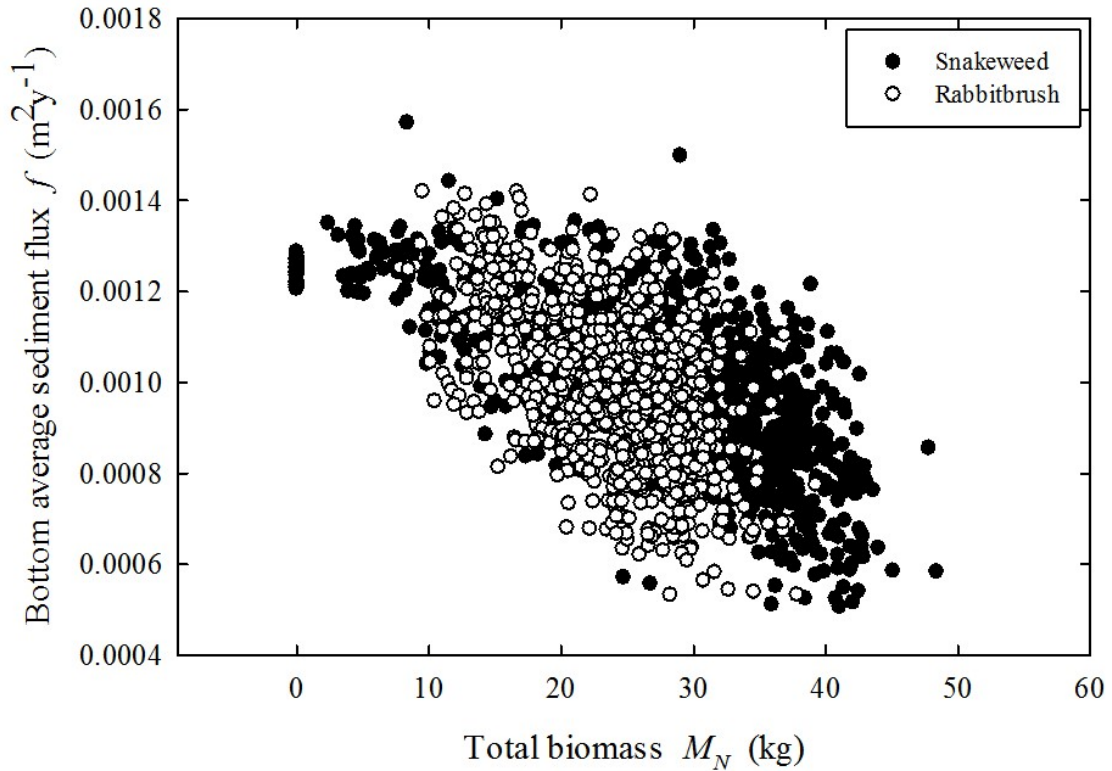


Figure 12: This plot depicts the relationship between biomass and the sediment flux across the bottom of the hillslope in our model for snakeweed and rabbitbrush shrubs. We see a clear inverse relationship, where higher biomass values result in smaller fluxes and vice versa.

snakeweed and rabbitbrush biomass data share relationships corresponding to the sediment flux as a result of the relationship between shrub canopy cover and sediment ‘capacitor’ behavior. If we can indeed use biomass as a common currency, we expect to see an overlapping trend in

the biomass and associated sediment flux values.

Biomass is calculated within the model using the allometric scaling relationship $r_c \propto M^{3/4}$ [West *et al.*, 2008]. This is a general proportionality, but we do not calculate ‘true’ biomass values as we have not derived the normalization constant Y_0 for either snakeweed or rabbitbrush. Rather, we set Y_0 equal to one for all biomass calculations. This scaling relationship is then applied to all shrubs at any given time t , so that a biomass value is associated with each shrub present on the hillslope. To further simplify, we also calculate the total biomass M_N on the modeled hillslope for each time interval. We compare calculated biomass values to corresponding, modeled average annual sediment flux values. Flux values are calculated as the mean sediment flux across the bottom of the hillslope for a given time interval. For each tested precipitation scenario (normal, ENSO-modulated, and increased aridification), we plot the annual biomass values and the average sediment flux values for both shrub species (Figure 12). Even though there is evident scatter, we can see a clear inverse relationship between the sediment flux and the biomass present on the hillslope, where higher biomass values are correlated with smaller sediment flux values. This result was expected, given previous observations, but we also see a significant amount of overlap in the snakeweed and rabbitbrush values. This overlap in values is consistent with our hypothesis, in that biomass, whether it be snake-weed or rabbitbrush, is inversely related to the sediment flux in a similar relationship. This compelling correlation opens an opportunity to use biomass as a common currency between different species of shrubs to describe the sediment flux on a hillslope, inasmuch as biomass can be estimated remotely over large areas using satellite imagery [Jensen, 1983; Muldavin *et al.*, 2001].

Furthermore, we strive to create a realistic distribution of biomass within the model space. We use field measurements of shrub canopy radii for both rabbitbrush and snakeweed within a field plot at Arrowhead Well, where we consider canopy radius r_c to be a simple proxy

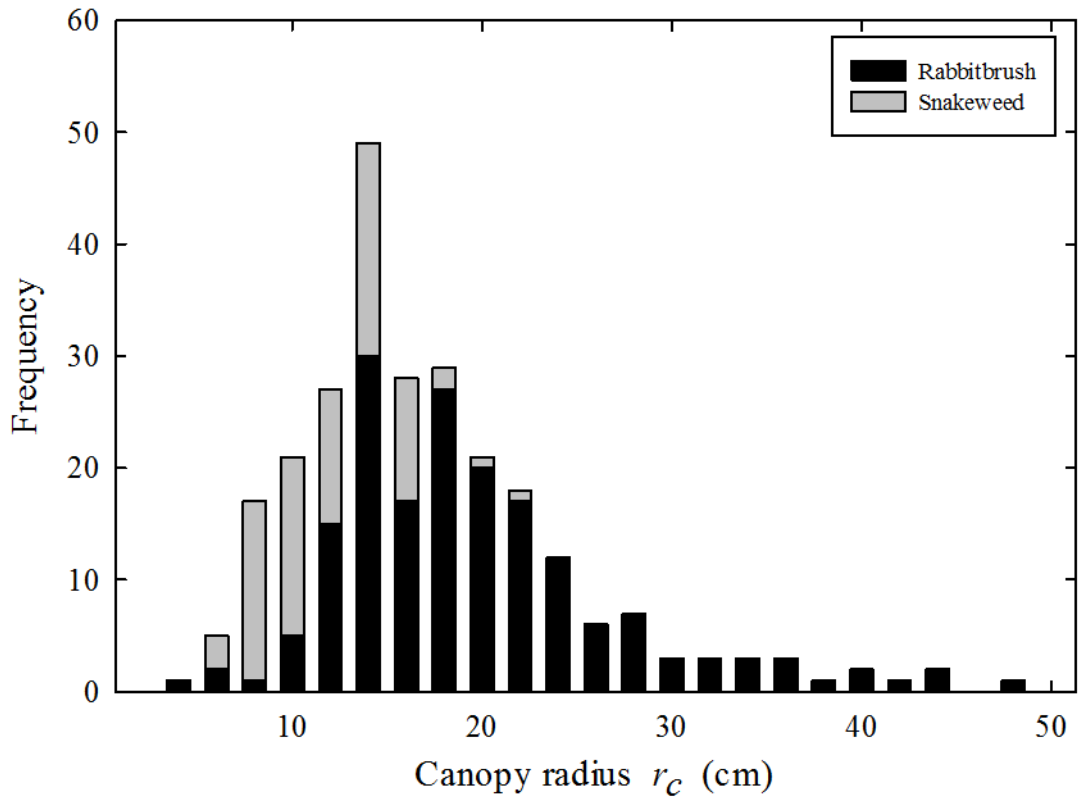


Figure 13: This figure displays the distribution of shrub canopy radii for snakeweed and rabbitbrush shrub in a field plot at Arrowhead Well.

for shrub age (Figure 13). These data are from a $20 \text{ m} \times 20 \text{ m}$ mixed plot of both shrub species. Figure 13 contains data from shrubs which are greater than 13 cm in height; any shrub less than this height was considered to be a juvenile. These juveniles generally did not have a sizeable mound beneath these sparse canopies, and therefore were not included in the histogram of the canopy radii. Given this information, we do note that on average we counted 2.17 juvenile shrubs per square meter (of either snakeweed or rabbitbrush) within a $4 \text{ m} \times 20 \text{ m}$ area of the plot. If we multiply this average amount of juvenile shrubs throughout the plot, we would find more than 800 juveniles within the entire plot. This would change the shape of the distribution of sizes to an exponential-like distribution. We use the parameters of this distribution to inform the initial population of shrubs in the model. Furthermore, we qualitatively monitor the shrub size distribution throughout each model run to be sure that it mimics this general exponential-like shape, albeit fluctuating from year to year. As the model

does recreate this distribution of canopy sizes, we are reassured that the calculated biomass is reasonable for size distributions found in the field.

ENSO-Modulated Precipitation Scenarios

To gauge the influence of varying ENSO-modulated precipitation regimes, we recorded changes in snakeweed and rabbitbrush populations under five different precipitation scenarios in our model. These scenarios are: unmodulated, or ‘normal’, precipitation and four different ENSO-modulated scenarios, in which increasing α values modulate winter precipitation based on the Southern Oscillation Index. We hypothesize that when shrubs receive increased or decreased winter precipitation, there may be differences in population size. In particular, we expect larger fluctuations in older, mature members of the population, rather than in younger shrubs, as the mature members are altogether dependent on winter precipitation for survival. We expect that the scenario with the greatest magnitude of ENSO modulation ($\alpha = 1$) will exhibit similar extremes in the population, where strong El Niño events would result in larger populations in following years, and strong La Niña events would lower the population in subsequent years. Furthermore, we assume that juvenile recruitment proceeds “normally” during the summer season as we do not expect or model ENSO-modulated fluctuations in the summer precipitation.

To evaluate changes in shrub populations we use ‘crossing theory’ methods [*Nordin and Rosbjerg, 1970*], in which we record instances in which the number of shrubs in a population crosses a certain threshold. In particular, we document two different types of data. First, we record the number of years a population falls below a lower threshold or surpasses an upper threshold. Furthermore, we calculate the ‘area’ of a particular excursion, where we record the number of shrubs which surpasses an upper or lower threshold. For example, if snakeweed has an upper threshold set at 225 shrubs and the population count for a particular year is

235 shrubs, then we record that the population is 10 shrubs above the threshold. Each of these measurements was recorded for snakeweed and rabbitbrush shrubs for the five different precipitation scenarios in 50 different model runs, each of which is 146 years long.

The upper and lower thresholds vary based on the shrub species. The upper threshold for snakeweed is set at 225 shrubs and the lower threshold is set at 125 shrubs, and the upper threshold for rabbitbrush shrubs is set at 125 shrubs and the lower threshold is set at 75 shrubs. Unique plant morphologies account for differences in population sizes between these shrub species. Mature snakeweed shrubs, on average, are significantly smaller than mature rabbitbrush shrubs, which allows many more snakeweed shrubs to survive in the same area within our model. To account for these differences in population size, we choose population thresholds specific to each shrub species.

Table 5.2: Results of comparison tests in snakeweed and rabbitbrush populations in the number of years which exceed or fall below certain thresholds, as listed in table 5.3. Once again, this table compares results in ‘normal’ conditions versus ENSO-modulated conditions, as indicated by alpha values (0.30, 0.50, 0.70, and 1.00). Bold values indicate statistical significance based on $\alpha = 0.05$.

	Precip. Regime	Snakeweed	Rabbitbrush
Number of years above threshold	AR:0.30	0.762	< 0.001
	AR:0.50	0.453	0.152
	AR:0.70	0.487	0.034
	AR:1.00	0.245	< 0.001
Number of years below threshold	AR:0.30	0.498	0.352
	AR:0.50	0.898	0.359
	AR:0.70	0.934	0.112
	AR:1.00	0.138	0.083

We statistically compare the number of years in which snakeweed and rabbitbrush cross their upper or lower thresholds using a t-test using simulated values from 100 runs of each precipitation scenario (Table 5.2). In each test, we compare data from a ‘normal’ precipitation scenario and an ENSO-modulated scenario. We find that there is not a statistically significant difference between the number of years in which snakeweed crosses the upper or lower threshold

in each of the tested precipitation scenarios. Similarly, the number of years in which rabbitbrush shrubs fall below the lower threshold is statistically indistinguishable when comparing normal precipitation patterns and a modulated signal. Aside from these results, however, we do see a statistically significant relationship in three of the four tests when we evaluate the number of years when rabbitbrush population counts surpass the upper threshold. Cautiously,

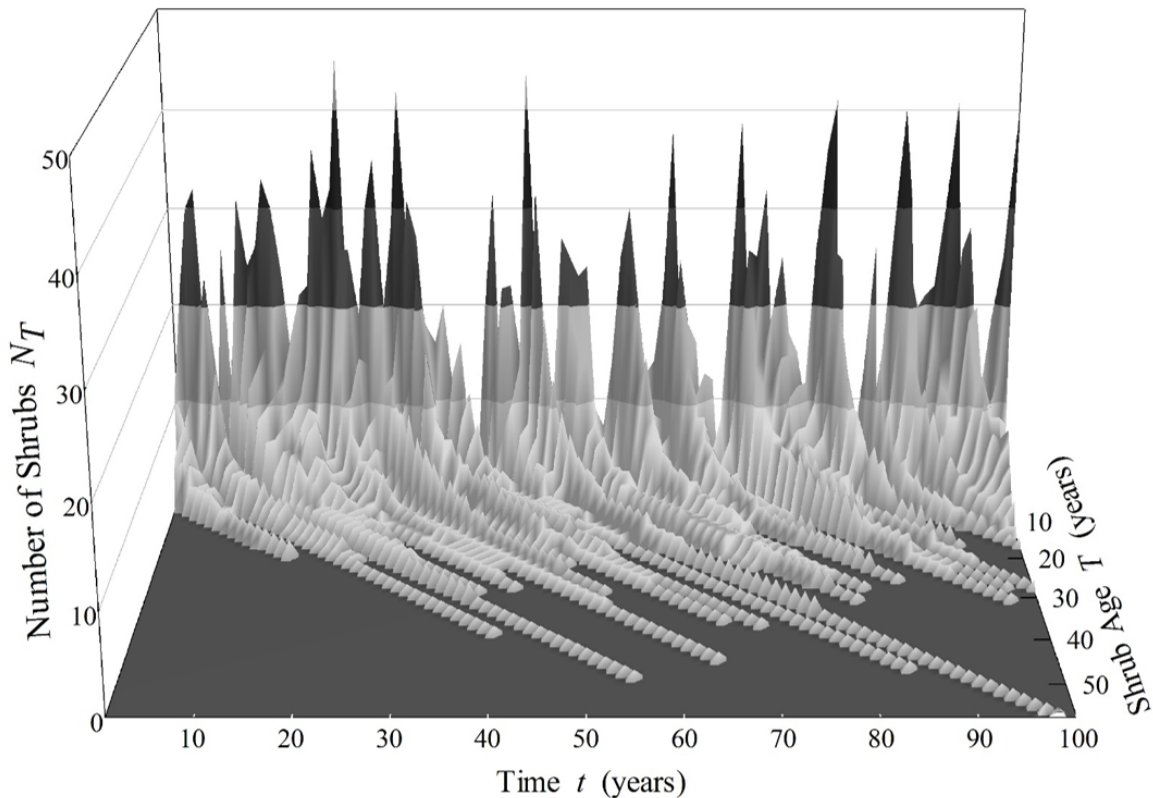


Figure 14: This 3D histogram plots the number of rabbitbrush shrubs, of a particular age, throughout 100 year run of our model.

we interpret that rabbitbrush shrubs may be more difficult to kill during La Niña dry periods, as they are notably resilient to drought and disturbed conditions [Aldon and Pase, 1981]. Even if a small number of rabbitbrush shrubs survive during arid periods, they can provide a large seed bank for juvenile recruitment in the summer season. Figure 14 provides an example of a 100 year long, ENSO-modulated precipitation scenario model ($\alpha = 0.30$), where we track

the number of shrubs of a given age over the course of the model. Interestingly, we see long diagonal ‘trails’ of mature rabbitbrush shrubs through time. Often, just a small number of shrubs survive beyond 20 years of age, but these shrubs which provide a sufficient seed bank for juvenile recruitment. Upon the death of these large, mature shrubs, we tend to see an immediate decline in recruitment the following year. These long lived shrubs may provide a more resilient seed bank than the short-lived snakeweed shrubs, so that rabbitbrush may be more resistant to changes in precipitation. Therefore, we may see a small amount of shrub mortality in La Niña periods, and in wetter El Niño periods we see a higher amount of shrubs present. Even though we do see statistically significant results, we acknowledge that these results do not hold for one of the four tests, and cautiously present this relationship which tends to show a greater number of years with large rabbitbrush populations.

As a second comparative measure, we evaluate the amount or number of shrubs which surpass the upper and lower threshold in normal and ENSO-modulated precipitation conditions using a Mann-Whitney non-parametric test again using modeled values from 100 runs of each simulation (Table 5.3). For each excursion, we record the magnitude or number of shrubs which pass the upper or lower threshold. We find that the data are consistently statistically insignificant, meaning that the number of shrubs which surpass either the lower or upper threshold are likely from the same population. The majority of tests suggest statistical insignificance, but there is one significant value in the lower threshold of snakeweed between normal precipitation conditions and an ENSO signal modulated by an alpha value of 0.30. Given the non-parametric nature of these values and the relatively high p-value, we do not wish to over-interpret this value and choose to focus on the greater correlation found in these data, which suggests that the number of shrubs crossing each threshold is statistically indistinguishable in normal precipitation conditions versus ENSO-modulated conditions.

Based on comparative tests which evaluate differences in the population size in normal

Table 5.3: This table compares the size of shrub populations in ‘normal’ precipitation conditions (AR) compared to populations in varying ENSO-modulated precipitation regimes, denoted by corresponding α values. Results of the Mann-Whitney non-parametric test results for snakeweed (SW) and rabbitbrush (RB) populations are listed under categories, for the total amount of shrubs less than a certain threshold and for the total amount of shrubs under a designated threshold. Bold values indicate statistical significance based on $\alpha = 0.05$.

	Precip. Regimes	p Value
Amount of SW shrubs < 125	AR:0.30	0.024
	AR:0.50	0.065
	AR:0.70	0.695
	AR:1.00	0.345
Amount of SW shrubs > 200	AR:0.30	0.832
	AR:0.50	0.430
	AR:0.70	0.669
	AR:1.00	0.376
Amount of RB shrubs < 75	AR:0.30	0.390
	AR:0.50	0.407
	AR:0.70	0.135
	AR:1.00	0.284
Amount of RB shrubs > 125	AR:0.30	0.179
	AR:0.50	0.664
	AR:0.70	0.119
	AR:1.00	0.856

precipitation scenarios versus ENSO-modulated precipitation scenarios in our biologically-informed, dynamic model, we cannot definitively state that ENSO has a strong influence on shrub mortality. We tested increasing magnitudes of an ENSO signal to capture a possible future climate scenario, but did not see a significant change in either the snakeweed or rabbitbrush shrub populations. These simulated data suggest that our hypothesis is incorrect and, rather, these shrubs are actually relatively insensitive to the El Niño Southern Oscillation. Furthermore, based on these data, we would not expect to find large fluctuations in shrub populations, and thereby sediment transport, as a result of increased extremes of ENSO in the Southwest United States.

Aridification Precipitation Scenarios

To test the second climate change prediction, increased aridification, we evaluate the response of snakeweed and rabbitbrush populations to various aridification scenarios. We look at changes in shrub populations in two different ways: (1) we record changes in the number of shrubs present and (2) we track changes in total biomass M_N .

To test the influence of generated, aridification precipitation scenarios, we use a Monte Carlo technique and run our dynamic shrub population model 100 times for the length of the precipitation signal for both snakeweed and rabbitbrush populations for a 100 year long time period. In this simulation, we record the number of shrubs on the hillslope in each annual time step and plot these data as box plots (Figure 15). In each simulation, drying or otherwise, we notice quick population growth in the first 5-10 years as the model equilibrates from the assigned initial population to maximum carrying capacity given space constraints. This response is not a result of these particular scenarios, but rather, the response is a product of the model. Beyond this immediate growth, we observe differences in how snakeweed and rabbitbrush respond to increasingly limited precipitation. First, we highlight the drying scenario predicted by global climate change models, which predict a 7.5 cm decrease in precipitation by the year 2100 in the Southwestern United States [*National Assessment Synthesis Team, 2001*]. Plots a) and c) in Figure 15 present data for the predicted climate scenario ($\beta = 0.004$) for snake-weed and rabbitbrush populations, respectively. We can readily see a significant difference in the trend of these plots. It is clear that the snakeweed population rapidly decays, almost to complete mortality in the 100 year period, whereas rabbitbrush experiences significantly less population decay.

To make comparisons between these shrub populations and further define the difference between responses in snakeweed and rabbitbrush populations, we also evaluate changes in biomass for the same data (Table 5.4). In particular, we compare the biomass on the hillslope

at the start of the model to the end of the drying trend. To correct for the initial population growth and variations in biomass values, we calculate the mean biomass in the first ten years (i.e., mean biomass of years 0-10) and the last ten years (i.e., mean biomass of years 90-100) of our 100 year long Monte Carlo simulation for each shrub species. We find that rabbitbrush biomass drops by 14.4% in the predicted climate scenarios from the first ten years to the last ten years, whereas snakeweed biomass drops by a considerable 64.4% when comparing the same time periods. This disparity in the response of the shrubs species indicates that rabbitbrush is more resilient to aridification whereas snakeweed is far more sensitive to similar conditions. This is not inconsistent with other research which suggests that rabbitbrush is highly resilient [Aldon and Pase, 1981] and is supported by observations regarding Figure 14. Again we assert that because rabbitbrush has a longer lifespan than snakeweed, and can grow roots to deeper depths, it is better adapted to low precipitation periods.

To further highlight the difference in responses between snakeweed and rabbitbrush shrubs, we present a comparative scenario in which snakeweed and rabbitbrush exhibit approximately the same loss in biomass over the 100 year drying period, but are placed in scenarios with different magnitudes of aridification. For Rabbitbrush and Snakeweed to experience approximately a 40% decline in biomass in the course of 100 runs of a Monte Carlo simulation, there must be a significant difference in the magnitude of each drying scenario. In particular, see that Rabbitbrush experiences a 42.1% loss in biomass and snakeweed loses 41.3% of its biomass in the course of Monte Carlo simulations under significantly different precipitation scenarios (Table 5.4 and Figure 15). To achieve an approximately 40% loss in biomass, rabbitbrush populations are evaluated in a drying scenario where $\beta = 0.006$ and snakeweed is evaluated in a $\beta = 0.003$ scenario. For perspective, both of these scenarios start with a mean precipitation value of ~ 23 cm, but in the $\beta = 0.003$ scenario the mean precipitation drops by ~ 6.8 cm or approximately 30%, whereas in the $\beta = 0.006$ scenario the mean precipitation drops by ~ 13.7

cm or approximately 60%.

This wide difference between the responses of snakeweed and rabbitbrush populations suggests a significant difference in the sensitivity of each species to arid conditions. The snakeweed, a short-lived shrub with shallow rooting depth is far more sensitive to dry weather conditions. In contrast, rabbitbrush, a larger, long-lived shrub with a relatively deep rooting depth, is able to persevere through increasingly arid conditions and provide a seedbank for continued juvenile recruitment.

Table 5.4: This table presents the average biomass (kg) in the first and last ten years of each model run. The bottom row shows the percent change in biomass from the first to last ten years. Note that the 0.004 model approximates the predicted decrease in precipitation as presented in global climate change data [*National Assessment Synthesis Team, 2001*].

	SW 0.004	RB 0.004	SW 0.003	RB 0.006
average first 10 years	13.1	18.7	12.6	18.4
average last 10 years	4.6	16.0	7.4	10.6
% difference	-64.6	-14.4	-41.3	-42.1

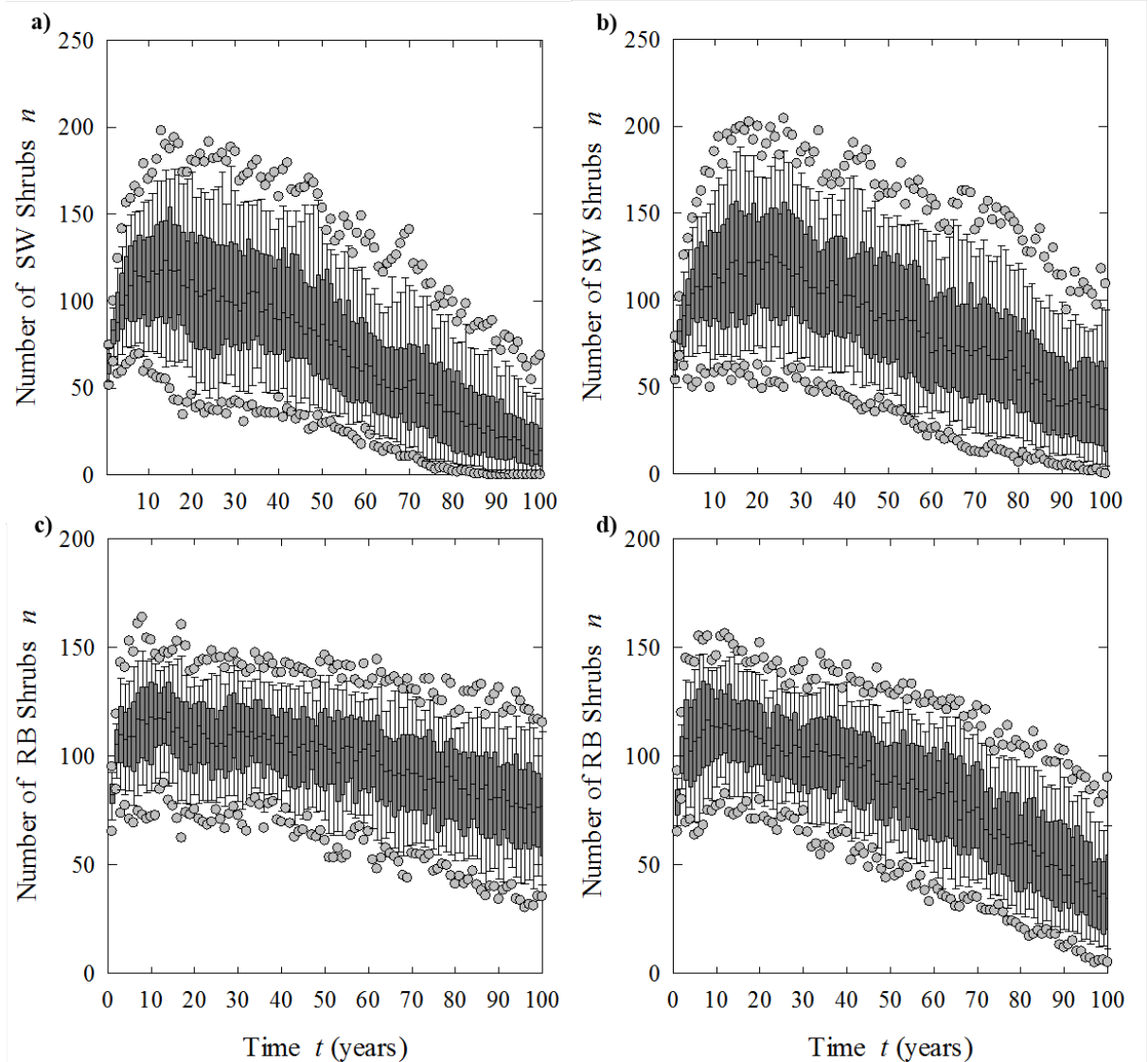


Figure 15: This figure show population counts for each year in a given drying precipitation scenario for model runs done 100 times over a 100 year period. Each shaded bar in the box plot represents the upper to lower quartile of data points, the tails of the “whiskers” indicate the maximum and maximum values, and the dots indicate any outliers. Plot a) shows data for snakeweed shrubs under $\beta = 0.004$, predicted aridification scenario, b) also plots snakeweed population data under a less extreme, $\beta = 0.003$ scenario, c) plots rabbitbrush shrub population data in the predicted climate change scenario and d) plots rabbitbrush data under a more extreme, $\beta = 0.006$ aridification scenario.

CONCLUSIONS

Data presented herein suggest that allometric scaling relationships presented by Enquist et al. [2000a] do indeed hold for snakeweed and rabbitbrush shrubs, even though these shrubs inhabit a highly resource-limited environment. Specifically, our data are consistent with the idea that shrub height and breadth each scale with the basal root radius to the two-thirds power. Adherence to these scaling laws allows us to make connections to biomass (and other measurements) which we did not measure in the field. Furthermore, we have suggested that biomass could be used as a common currency between different shrubs. This idea is supported by the trend seen between modeled shrub biomass and sediment transport by rain splash. Specifically, we have shown that both rabbitbrush and snakeweed have a similar influence on the sediment flux in model space, wherein the annually averaged flux varies inversely with population biomass due to the connection between biomass and canopy size, which modulates the influence of rain splash transport (Figure 12).

We have tested several precipitation regimes in our model which approximate predicted climate change scenarios. Here, we see varying influences, depending on the precipitation scenario and the shrub species. First, in the ENSO-modulated precipitation scenarios, shrubs are generally insensitive to fluctuations in winter precipitation as a result of a more intense ENSO signal. Yet, we do notice a slight difference within rabbitbrush shrubs, where a few large shrubs survive during drier periods associated with ENSO and are able to sustain a slightly larger population in more years than in a scenario unmodulated by ENSO.

In contrast, simple aridification scenarios, wherein average annual precipitation steadily declines with time, reveal strong differences in how snakeweed and rabbitbrush respond to increasingly limited precipitation. In predicted aridification scenarios associated with climate

change, we see snakeweed biomass decrease by 65% in a 100 year period, whereas rabbitbrush biomass decreases by 15% under the same conditions. Here, we note the resilience of rabbitbrush in increased aridification scenarios. We attribute this difference to the size and morphology of rabbitbrush, which is able to grow larger, with a longer taproot, in comparison to snakeweed. Also, this result is consistent with research indicating that rabbitbrush is longer lived and more resistant to fluctuations in precipitation than the short-lived snakeweed [*Aldon and Pase, 1981*].

Furthermore, we see an inverse relationship between sediment transport and the amount of vegetation present on a hillslope. We see that larger amounts of vegetation, which we calculate in the form of biomass, correlate to smaller magnitudes in sediment flux in both shrub species. If during the next century Southwestern deserts experience an increased influence from ENSO-modulated precipitation, then we predict limited influence on shrub population biomass and changes in sediment transport. If, however, deserts experience approximately a 10 cm average decrease in annual precipitation in the next century, then we predict a systematic decline in shrub populations leading to increased sediment transport, especially in short-lived, smaller shrubs like snakeweed. Moreover, this opens the possibility of large-scale monitoring, if not prediction, of likely changes in shrub population health and associated sediment transport in hillslopes in the Southwest desert, potentially through the use of satellite imagery in combination with climate prediction data. Additionally, we suggest that allometric scaling relationships could be applied to calculate other plant characteristics, like metabolic rate, for individual shrubs and plant communities in these environments. This work therefore provides a valuable tool for estimating shrub biomass and related quantities in a resource-limited environment, in response to climate change, including changing sediment transport rates.

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