A SIMPLE PROBABILISTIC, BIOLOGICALLY INFORMED MODEL OF THE POPULATION DYNAMICS OF DESERT SHRUBS

By

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For all the medium sized particles,
in my favorite mountain stream!

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CHAPTER I

MOTIVATION

In arid environments, desert vegetation directly and circuitously influences where and how sediment is transported by wind, surface-water flow, and rain splash. For example, the size, shape, and spacing of plants influence near surface wind speeds and turbulence structure, affecting the likelihood and location of aeolian entrainment and deposition [*Gillette et al., 2006; Bowker et al., 2008; Okin, 2008*]. By contributing to the development of surface roughness [*Bochet et al., 2000*] and to variations in soil infiltration rates [*Dunkerley, 2002*], plants influence the surface and subsurface partitioning of storm water and locally steer overland flows [*Dunne et al., 1991; Parsons and Abrahams, 1992*]. And, by intercepting rainfall, plant canopies and litter alter the rate of detachment of soil grains by raindrop impacts [*Gabet and Dunne, 2003*] where variations in canopy cover lead to spatial variations in grain detachment [*Parsons and Abrahams, 1992; Wainwright et al., 2000; Furbish et al., 2009*]. Spatiotemporal variations in the processes of erosion and deposition in desert regions are therefore strongly coupled with the structure and dynamics of plant communities as well as the specific life behavior of individual plants.

By altering grain activity, the canopy of a shrub creates a net inward sediment flux and passively harvests soil towards its base [*Childs, 2008*]. Accumulating and then releasing soil upon their death, desert shrubs function as sediment capacitors that locally regulate the overall rate of sediment transport down a hillslope [*Furbish et al., 2009*]. *Roberts* [2010] studied the development of these soil mounds in conjunction with shrub canopy growth across natural and theoretical hillslopes, finding that species, position, and areal density are important plant variables impacting downslope sediment flux rates. Addressing next, how mound building at the shrub-scale modulates the evolution of the land surface on geomorphic time-scales, necessitates spanning multiple shrub lifetimes and accounting for how processes affecting plant dynamics on these longer time-scales (i.e. the stresses associated with fire, grazing, drought, and climate change) may in turn impact this process. It is this need, to link this sediment transport process with the unfolding ‘biological play’ on a hillslope, which motivates the development of this desert shrub population dynamics model [*Furbish, 2009*].

Given our interest in shrubs as sediment capacitors, our objective is to create a model that can mimic the spatiotemporal behavior of a single species population. However, due to the fact that perennial desert shrubs can live for years, decades, or even centuries [*Christensen and Brown, 1963; Vasek, 1980; Goldberg and Turner, 1986; Ehrlén and Lehtilä, 2002*], we currently lack a comprehensive understanding of how these populations change over long-time periods. Field studies nonetheless help us unravel the underlying complexity of these systems, for example, by pointing to the key internal and external drivers of their dynamics. We therefore use biological insights from the literature, as well as information gathered in the field by our research group [*Roberts, 2010*], to help inform the development of this model as well as ensure that it leads to outputs which are consistent with the general trends that empirical work has noted.

Although this model is intended for subsequent coupling with a hillslope sediment transport model, herein it stands alone. Using the Master Equation to conserve shrub age, we develop probabilistic and biologically informed mathematical expressions for shrub recruitment and mortality to respectively function as our source and sink terms. This simple accounting framework, by tracking the number of individuals entering and leaving our modeled population, captures the changes in shrub count that we can expect to observe in time as the key variables driving the dynamics of these plant communities (i.e. precipitation) also change in time. The result is a tool through which it is possible to statistically describe the aggregate behavior of different shrub populations, with their own characteristic life-cycles and physical dimensions, under different external forcing scenarios. It offers plant population biologists as well as researchers working at the interface between ecological systems and earth-surface processes a biophysically based, quantitative framework through which the population dynamics of desert shrubs resulting from past climatic histories as well as predicted future scenarios can be mimicked and assessed. This has relevance, for example, to the stewardship of the U.S. nuclear waste legacy: This model could be used to build confidence in the design and long-term performance of the evapotranspiration landfill covers employed in arid regions, as alternatives to resistive barrier technologies, to isolate uranium mill tailings from the environment [*Clarke et al., 2004*].

CHAPTER II

CONCEPTUAL MODEL

Plants respond to a myriad of biotic and abiotic signals [*Trewavas, 2003*] but this research isolates the spatiotemporal distribution of water as the key governing variable and the one of particular interest. Since the hydrology and ecology of dryland environments are tightly coupled, this ecohydrological perspective provides an integrated and comprehensive conceptual framework through which to approach these complex environmental systems [*Rodriquez-Iturbe, 2000; Porporato et al., 2001; Ludwig et al*., *2005*]. And it will allow future research with this model to consider how climate induced changes in the hydrological cycle may impact these communities. Instead of a detailed water balance, however, our model is based on two distinct soil compartments (Figure 2.1) differentiated by the duration and source of their stored moisture [*Noy-Meir, 1973*]. This in turn informs our understanding of desert shrub ecology: As the water storing substrate, the hydrology of the desert-soil influences recruitment and mortality, and therefore, the dynamics of a population.

Desert-soil hydrology

Precipitation is our exclusive input, making this model not applicable to locations where groundwater and overland flow (i.e. arroyos) represent important sources of plant-available water [*Fonteyn and Mahall, 1981; Schlesinger and Jones, 1984; Ludwig et al., 2005*]. The uppermost region of the soil interacts with all precipitation events and due to the high evaporative demand in the desert, readily returns delivered moisture back into the atmosphere. As a consequence, soil moisture near the lithosphere-atmosphere boundary is characteristically low but fluctuates markedly in response to individual events [*Noy-Meir, 1973*]. This is dampened deeper in the soil profile: Wetting fronts penetrate only when the upper layers are near field capacity, an event exceeds a certain size, or surface evaporation is suppressed. This leads to more stable water-contents at depth that vary instead on a seasonal time scale [*Noy-Meir, 1973*].

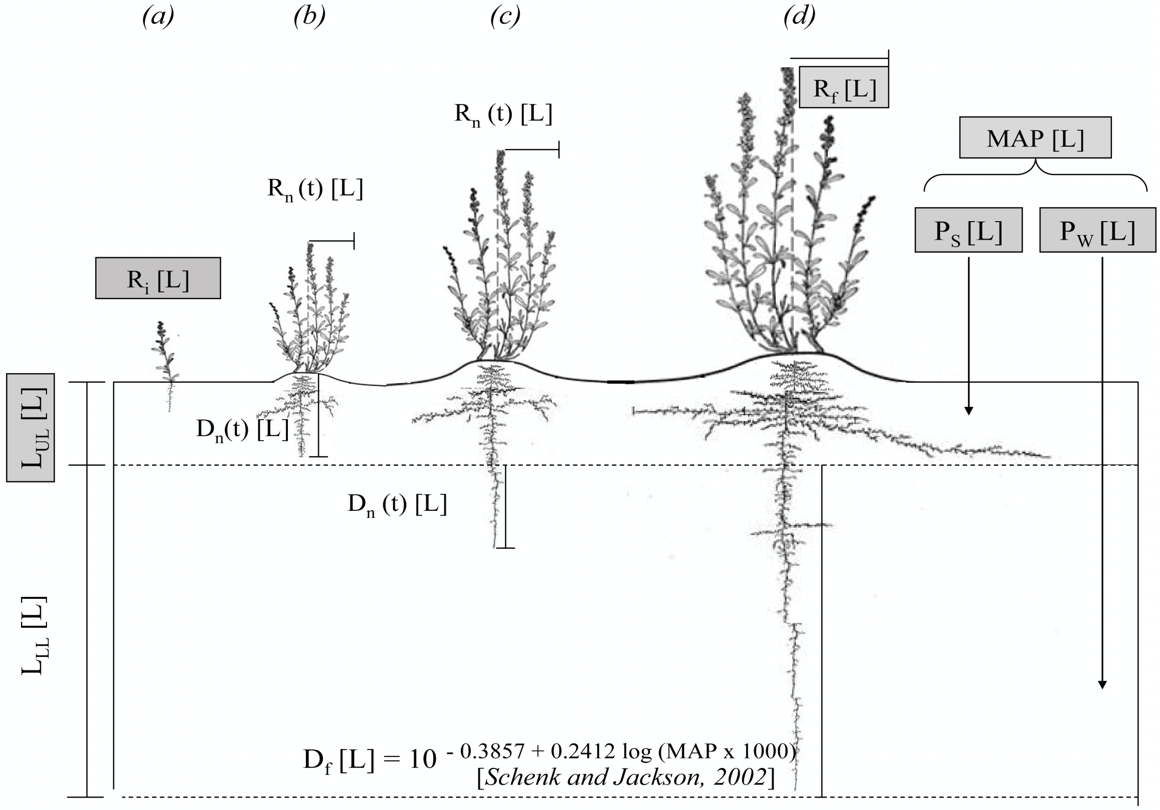

Figure 2.1. Conceptual model of desert soil hydrology and ecology throughout shrub ontogeny. *(a)* Successfully recruited individual, *(b)* juvenile with root access to the upper soil layer and winter precipitation, *(c)* adult with root access to the lower soil layer and winter precipitation, and *(d)* maximum or final size that can potentially be achieved by an adult in the population. The darkened boxes represent model inputs whereas all other notation represents calculated values.

Whereas some deserts have erratic precipitation regimes, those of the western U.S. have distinct seasonal patterns associated with two major air circulations [*Rajagopalan and Lall, 1998*]. The North American monsoon gives rise to brief but frequent convective summer thunderstorms which are characteristically small and coincident with peak evaporative demand [*Adams and Comrie, 1997*]. We therefore define an upper soil layer, L_{UL} [L], and confine all summer precipitation, P_s [L], to this compartment. Winter precipitation, P_w [L], in contrast, is carried by the Pacific frontal system and results in storms that are of longer duration and lower intensity [*Rajagopalan and Lall, 1998*]. Falling when evaporative demand is suppressed, this precipitation recharges our lower soil layer, L_{LL} [L] [*Sala et al., 1992; Scott et al., 2000*]. We define this compartment as the depth below the upper soil compartment and above the final or maximum rooting depth of a shrub, D_f[L], which we estimate *a priori* from the Mean Annual Precipitation (MAP) of a site according to a regression relationship for woody-plants in a water limited environment [*Schenck and Jackson, 2002*].

Note that the vertical variation in the water supply is our chief concern and we do not explicitly address any of the horizontal heterogeneities which may be ecologically significant [*Breshears et al. 1997; Loik et al., 2004; Breshears et al., 2009*]. For example, our model does not account for persistent spatial differences in water availability that arise in arid environments due to subsurface stratigraphy [*Abrahams and Parson, 1991; Nobel et al., 1992; Sternberg et al., 1996*].

Desert-plant ecology

Xerophytes (from Greek *xero* for dry and *phyte* for plant) possess a diverse suite of physiological mechanisms to cope, on different spatial and temporal scales, with the relatively low precipitation levels in the desert. However the upper and lower soil layers, previously defined, are of generic and functional importance to desert shrubs [*Fernandez and Caldwell, 1975; Ryel et al., 2008*] particularly in locations where the *MAP* is less than 0.250 m/yr [*Schenk and Jackson, 2002*].

The Upper Soil Layer: Recruitment and Juvenile Mortality

Seeds land on the surface of the soil, need favorable temperatures and sufficient light to germinate, and until established, lack extensive and robust root systems. A decrease in the water-content of the upper soil layer leads to an elevated flux of sensible heat and during the growing season, these higher soil temperatures are increasingly detrimental to establishing seedlings [*Gill and Jackson, 2000*]. The delivery of summer precipitation to the upper soil layer is therefore pertinent to our formulation of shrub recruitment. Once a new individual is successfully added to our population, we refer to it as a juvenile and transition its survival dependency to the lower soil layer after it has gained physical access to it through the development of a sufficiently long tap root.

The Lower Soil Layer: Adult Mortality

Many adult shrubs are unresponsive to summer rainfall events [*Flanagan et al., 1992; Donovan and Ehleringer, 1994; Lin et al., 1996; Gebauer et al., 2002; Leffler, 2004; Ogle and Reynolds, 2004*] and being tapped into the lower soil compartment rely instead on winter precipitation. To circumvent the uncertainty surrounding how deep-rooted vegetation uptakes water [*Canadell et al., 1996*] and the innate complexity of plant-water absorption in general, we use the water content (our dependent variable) at the rooting depth of an individual shrub (our independent variable) as a benchmark for assigning it a survival probability. This makes our model more immediately applicable to shrubs that are not active along the entire length of their tap root. Further research is necessary to compare the validity of this simplification with other approaches, for example, with volumetric based arguments of metabolic demand and resource consumption that scale with size [*Allen et al., 2008*].

CHAPTER III

MATHEMATICAL MODEL

Description of Initial Population

Defining a population as a collection of same-species individuals living in the same location at time t [t], we can consider some square area A [L^2] containing $N(t)$ perennial shrubs (Figure 3.1). A defines the scale of our model and in our analysis and discussion, we address the importance and implications of different size choice (Figure 3.1). Note that the shrub areal density, $\rho(t)$, is then simply $N(t)/A$. The canopy radius, $R_n(t)$ [L], and rooting depth, $D_n(t)$ [L], of any individual shrub n enclosed within A are of interest and vary with the age of shrub n, $T_n(t)$ [t].

Since measuring $R_n(t)$ is straightforward in comparison to determining $T_n(t)$, we momentarily use canopy size as a proxy for shrub age to establish an initial demographic description of our population. While the plasticity of plant growth [*Bradshaw, 1965*] makes this an imperfect assumption, we consider it valid only in the general sense that smaller shrubs are younger than larger shrubs. Knowing $R_n(t)$ for all $N(t)$ shrubs, we can rearrange the logistic canopy growth model developed by *Furbish et al.* [2009],

$$R_n(t) = R_i + (R_f - R_i)\left[1 - e^{-T_n(t)/T_{90}}\right] \tag{G1}$$

to solve for $T_n(t)$,

$$T_n(t) = -T_{90}\ \ln\left[\frac{R_n(t) - R_f}{R_f - R_i}\right] \tag{G2}$$

where R_i [L] represents the average initial canopy radius of new recruits, R_f [L] is the final or maximum radius that our shrubs achieve, and T_{90} [t] is a characteristic growth rate constant whose value is calculated by selecting the age at which the canopy radius of a shrub is $0.90R_f$.

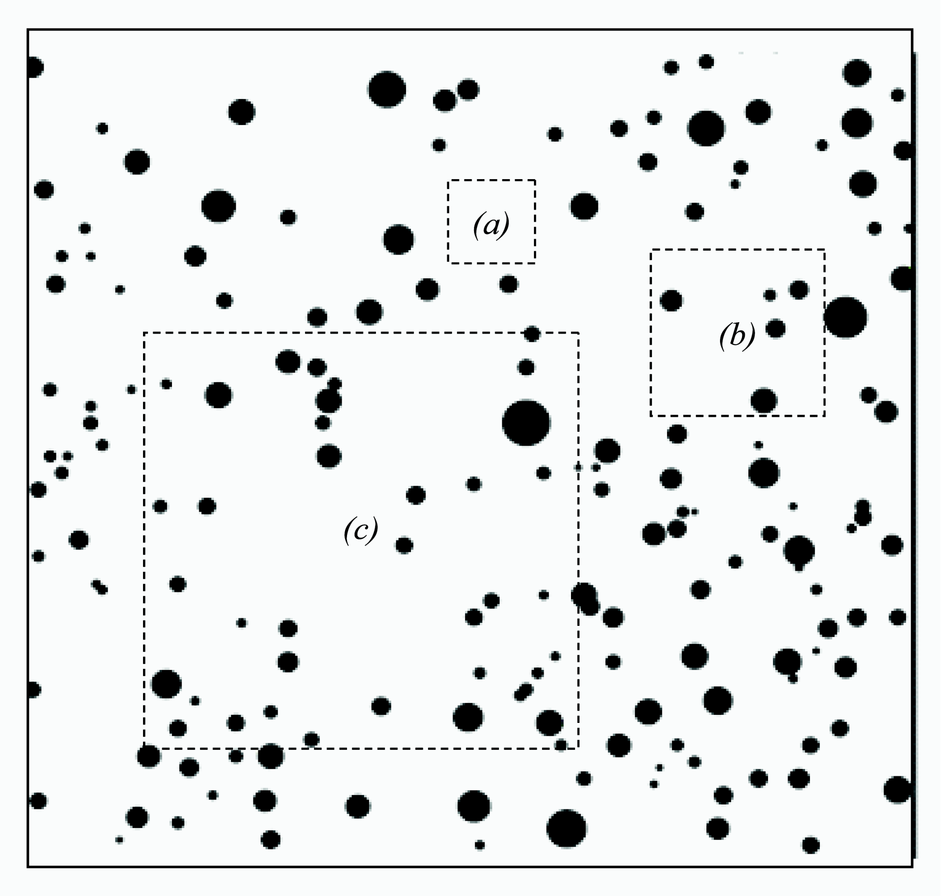

Figure 3.1. Aerial view of Rabbitbrush shrub population in Cibola National Forest, New Mexico. Field data collected during a 2009 vegetation survey depicting the locations and relative canopy sizes of shrub population in a 400 m^2 plot (Appendix D) [*Roberts, 2010*]. The dotted boxes demonstrate different possible size choices for the modeled area, A: (a) $1m^2$, (b) $4m^2$, and c) $100m^2$. Note the contrast in aeral shrub density, $\rho(t)$, between the different possible scales of observations; (a) 0 shrubs/m^2, (b) 1.25 shrubs/m^2, and c) 0.40 shrubs/m^2.

$D_n(t)$ is below-ground and therefore hard to observe. We can, however, estimate *a priori* the final rooting depth that our shrubs achieve, D_f [L], using a regression from *Schenk and Jackson* [2002] for woody-plants in water limited environments,

$$D_f = 10^{-0.3857 + 0.2412 \log(MAP \times 1000)}$$

where MAP [L] is the Mean Annual Precipitation of a site, reported in mm. Attributing D_f to the nth shrub having $R_n(t) = R_f$, a final or maximum canopy volume V_f [L^3] can be calculated from R_f assuming an ellipsoid shape, $V_f = (4/3)\,\pi R_f^3$. Likewise, the canopy volume of the nth shrub at time t, $V_n(t)$[L^3], is then $(4/3)\,\pi\,[R_n(t)]^3$. Assuming a constant rooting depth to canopy volume ratio, $\kappa =$

D_f / V_f [L^{-2}], we can relate $D_n(t)$ to its above-ground biomass by,

$$D_n(t) = \kappa V_n(t) \tag{G3}$$

Whereas the relationships in *Schenk and Jackson* [2002] were developed for gaining a global perspective and they capture systematic changes in rooting depth that go with changes in certain characteristics of a particular location (i.e. climate, soil texture, etc.), we use it for describing changes in rooting depth in one location throughout shrub ontogeny due to its conceptual simplicity. Further research is necessary to determine the merits and limitations of such an application. However this momentarily provides us with a generic isometric scaling rule that is specific to woody-plants in water limited environments to grow our shrubs, both above and below ground, in concert. In reality, growth is expected to deviate from the case of isometry and additional research into allometric relationships would strengthen the physical foundation of this model.

Population Dynamics: Shrub Conservation

Considering our previously described $N(t)$ perennial shrubs, let $f_T(T, t)$ [t^{-1}] denote the probability density function of shrub ages T. Then, $N_T(T, t) = N(t) f_T(T, t)$ [t^{-1}] is the distribution of the number of shrubs per unit age, where we note that

$$\int_0^\infty f_T(T,t)\,\mathrm{d}T = 1$$

and

$$\int_0^\infty N_T(T,t)\,\mathrm{d}T = N(t)$$

We may write $N_T[T(t),t]$. Then the substantive derivative of N_T is $\mathrm{D}N_T/\mathrm{D}t = (\partial N_T/\partial T)\mathrm{d}T/\mathrm{d}t + \partial N_T/\partial T = 0$ where $\mathrm{d}T/\mathrm{d}t = 1$. Conservation thus requires (Appendix A)

$$\frac{\partial N_T}{\partial t} = -\frac{\partial N_T}{\partial T} - M(T,t) \tag{PD1}$$

subject to the boundary condition that,

$$N_T(0,t) = R(t)$$

where $\partial N_T / \partial T$ is an "advective" term that describes the rate of change in N_T as shrubs age at the rate dT /dt = 1 and $M(T, t)$ [t^{-1}] is a sink term, representing the local rate of shrub mortality which varies with both shrub age and time. In turn, R(t) [t^{-1}] is a source term, the rate of recruitment of new individuals per unit time which may vary with time. We choose an annualized time step, dt = 1, to be consistent with plant phenology and enable the incorporation of annualized data sets.

Shrub Recruitment (Source Term)

We approach recruitment phenomenologically and conceptualize it is an event contingent upon a successful procession of preceding events (seed production, dispersal, germination, and seedling survival) whose independent probabilities each depend on characteristics specific to the shrub species as well as the external forcing of the environment.

Seed Production

Conspecific perennial shrubs can exhibit several mechanisms of reproduction. However in reflection of the high degree of genetic diversity found in deserts [*Nevo and Belies, 1989*] and to exclude the possibility of resource sharing or habitat selection [*Salzman, 1985*], we assume our entire population is composed of gamets (derived from seed). We let $s(t)$ denote the average number of seeds produced per shrub per year while noting that seed production varies between individuals, populations, and years [*Kelly, 1994; Herrera et al., 1998*]. Idiosyncratic variability typically arises from size or age discrepancies [*Bonser and Aarssen, 2009; Weiner et al., 2009*] and is, by definition, embedded within $s(t)$. Variability between different geographical locations is a caveat of the site characterization process and to account for interannual variability, we treat $s(t)$ as a stochastic variable drawn from a normal distribution with mean, μ_s, and standard deviation, σ_s.

We then use $N_s(t)$ to denote the number of seed-producing shrubs. Since allocating energy to reproduction diverts resources away from other critical functions like growth and maintenance, plants produce seeds only after reaching a certain point of maturity [*Weiner et al., 2009*]. We therefore exclude all juveniles ($D_n(t) \leq L_{UL}$) and include all adults ($D_n(t) > L_{UL}$) in our count of $N_s(t)$. Eliminating the possibility of plant senescence, the total number of seeds produced during a given year t, $s_p(t)$, becomes,

$$s_p(t) = s(t)\, N_s(t) \tag{R1}$$

Since desert perennials typically have transient seed banks [*Guo, 1998*], we assume that any seed produced during t but which may remain in the soil at the onset of $t + 1$ (i.e. because it never germinated) is non-viable during $t + 1$. (R1) now represents the total number of potential recruits during dt from which all realized recruits must be drawn as well as the pool of seeds that will undergo dispersal during dt.

Seed Dispersal

Despite the apparent sparseness of the desert landscape, space influences recruitment through the dispersal process [*Chambers and MacMahon, 1994; Schupp and Fuentes, 1995*]. We begin by defining the effective area of the nth shrub, $a_n(t)$ [L^2], as the extent to which this extant shrub usurps space and precludes the addition of new individuals. From an aerial view, we recognize the footprint of the nth shrub as the ground directly beneath the outer circumference of its canopy. Assuming seedlings cannot establish in this area for shading, soil-moisture, allopathic, etc. reasons [*Osman et al., 1987*] and approximating the footprint of a shrub as a circle, we can estimate the minimum effective area of n as $\pi[R_n(t)]^2$ (Figure 3.2) and summing up over all $N(t)$ individuals, the minimum effective area occupied by the extant population at time t is then,

$$a_{\min}(t) = \sum_{n=1}^{n=N(t)} \pi [R_n(t)]^2$$

Below ground, desert shrubs forage for essential but sparse resources resulting in root systems which typically extend far beyond their above ground canopies. While root excavations reveal irregularly shaped polygons [*Brisson and Reynolds, 1994*], the lateral roots of neighboring shrubs frequently overlap signifying that the physical presence of roots is inadequate for characterizing below ground effective areas [*Casper et al., 2003*]. We therefore, for simplicity, use the above ground position of the nth shrub and equate its maximum effective area with the area enclosed by its Thiessen polygon (Figure 3.2). As before, if we sum up over all $N(t)$ individuals, the maximum amount of space usurped by the entire population, $a_{max}(t)$, is then physically constrained at A.

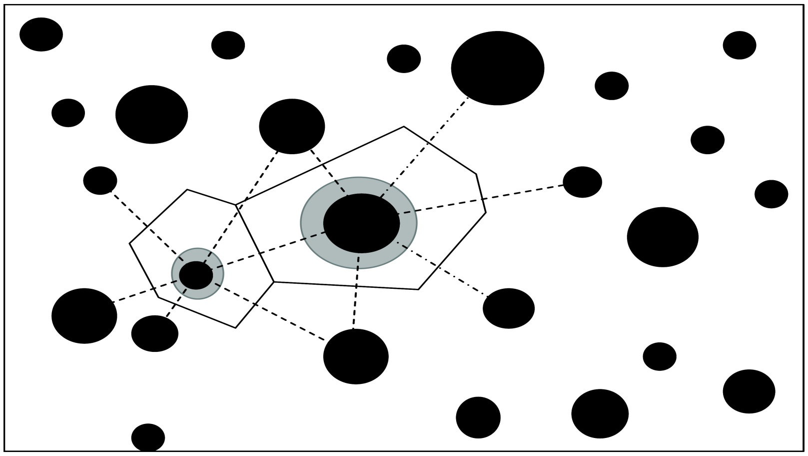

Figure 3.2. Estimating the average effective area of the *n*th shrub, $a_n(t)$. The black circles represent the canopy area of individual shrubs and collectively provide an estimate of the minimum amount of space the extant population occupies at time t, $a_{min}(t)$. Example dotted lines connect the center point of the nth shrub with the center points of their neighbors. The solid lines are perpendicular bisectors which enclose the Thessien polygons of the nth shrubs and provide an estimate of their maximum possible effective area. These two extremes are used to establish the potential range for $a_n(t)$, the effective area occupied by shrub n, with an example of $a_n(t)$ depicted by the gray circles with $a_n(t) \approx \pi[1.5\ R_n(t)]^2$.

The likelihood that a dispersed seed lands somewhere in A that is unoccupied by the $N(t)$ extant shrubs is then $[A - a(t)]/A$ where $a_n(t)$ is inferred from field data and must satisfy $a_{min}(t) \leq a(t) \leq A$. Examples of relevant field data may include the average distance between emerged seedlings or juveniles to their nearest adult [*Hamill and Wright, 1986*] or a spatial analysis of the structure of the population through a nearest-neighbor test (Appendix C). Our final expression for the number of successfully dispersed seeds, $s_d(t)$, defined as the number of seeds that land in “available” sites is then,

$$s_d(t) = s_p(t)\,\frac{A - a(t)}{A} \qquad \text{(R2)}$$

Note that the direct proportionality to the relative sizes of the two potential landing sites implies that seed dispersal is random. While a complete depiction of dispersal is beyond the scope of this model, the observation and modeling of phase I dispersal (the initial movement of a seed from its parent plant to any surface) suggests otherwise [*Chambers and MacMahon, 1994*]. However phase II dispersal (all subsequent seed movements including both horizontal and vertical redistributions) determines the ultimate location where a seed will be when it germinates. Given the diverse array of physical and biological agents involved (i.e. wind, surface flows, rain splash, harvester ants, birds, rodents, etc.), this highly dynamic process is intractable [*Chambers and MacMahon, 1994*]. Instead, we can simply anticipate spatial heterogeneities in seed densities [*Parmenter and MacMahon, 1983; Reichman, 1984*], and incorporate any preference seeds may exhibit between "available" and "unoccupied" sites below in our rate constant.

Seed Germination

Plants inhabiting deserts typically exhibit one of two distinct germination strategies: heterogeneity or selectivity [*Baskin and Baskin, 1973; Gutterman, 1994*]. Heterogeneity occurs when an individual plant produces seeds with genetically different germination requirements while selectivity refers to the coordinated emergence of a species in response to a specific suite of environmental conditions. Heterogeneity is a form of "bet-hedging" and ensures that some fraction, g, of the seed pool germinates independent of the prevailing environmental conditions during a given year t [*Simons and Johnston, 2006; Simons, 2009*]. Under this scenario, our formulation for the number of seeds which germinate is simply,

$$s_g(t) = g\, s_d(t) \qquad\qquad 0 < g < 1 \tag{R3}$$

In contrast, a selective germination strategy applies to species whose germination is observed to either be episodic or else confined to favorable years, regardless of their occurrence frequency. While we do not explicitly describe such species (i.e. *Larrea Tridentata*), our model can be modified by assuming that all $s_d(t)$ are quiescent: They are simply awaiting the arrival of the appropriate environmental cues. The probability that any given year t will be hospitable towards germination can then be calculated based on the frequency with which those necessary conditions are observed.

Seedling Survival

Following germination, a seed becomes a seedling. Lacking an established root system and sensitive to water deficiencies in the upper soil zone, we let $f_{PT*}(P,T^*)$ denote the joint probability distribution of a daily precipitation event of size P [L] given an average daily temperature of T^* [°C]. If T_C [°C] is the critical temperature demarcating the summer from the winter season, then the probability that a daily precipitation event occurs in the summer season, $p_{\Delta ts,}$ can be expressed as,

$$p_{\Delta t_S} = \int_0^\infty \int_{T_c}^\infty f_{PT^*} \, \mathrm{d}T \mathrm{d}P \tag{R4}$$

And in turn, the number of days comprising the summer season, Δt_S [t], can then be expressed by,

$$\Delta t_S = d_Y p_{\Delta t_S}$$

where d_Y [t] denotes the number of days in a year. Independently, if $P(t)$ [L] represents the annual daily precipitation record, then the total summer precipitation in a given year t, $P_S(t)$ [L] is,

$$P_S(t) = \int_{\Delta t_S} P(t) \, \mathrm{d}t \tag{R5}$$

If Ω denotes the proportion of summer rainfall that is not lost to the atmosphere, then the effective precipitation in year t, $P_e(t)$ [L], can be expressed as,

$$P_e(t) = \Omega P_S(t) \qquad 0 \leq \Omega \leq 1$$

Assuming that $P_e(t)$ infiltrates uniformly over the depth of the upper soil layer, L_{UL} [L], the average volumetric water-content of the upper soil zone during the year t, $\theta_S(t)$ [L^3/L^3], is then,

$$\theta_S(t) = \frac{P_e(t)}{L_{UL}} + \theta_{PWP} \tag{R6}$$

As a general rule which neglects any osmotic effects, the permanent wilting point, θ_{PWP}, can be treated as the minimum water-content necessary for shrub survival. Coinciding with the lowest water-content achievable by a specific soil type, it therefore also represents a baseline water-content to which our volumetric input of summer precipitation, $P_e(t)/L_{UL}$, is added. If we consider the adequacy of $\theta_S(t)$ for seedling survival, and eliminate the possibility of adverse effects associated with a water surplus, the seedling survival count, $\mathrm{d}n_R$, then becomes

$$\mathrm{d}n_R = s_g(t) \frac{\theta_S(t) - \theta_{PWP}}{\theta_S(t)} \qquad \theta_{PWP} \leq \theta_S(t) \leq \theta_{FC} \tag{R7}$$

$\theta_S(t)$ is constrained between θ_{PWP} and the field capacity of the soil, θ_{FC} [L^3/L^3], to represent plant available water, which is moisture retained in the soil profile between the field capacity and the permanent wilting point.

Recruitment Rate

Our expression of dn_R (R7) represents the number of seedlings that are successfully recruited during dt. Combing (R1), (R2) and (R3) with (R7), the probability of recruitment during dt (or the probability that any seed produced during dt is successful in all phase of the recruitment processes and will then be added to our population) is proportional to the product of the probabilities associated with dispersal, germination, and seedling survival;

$$\frac{\mathrm{d}n_R}{sN_S} \sim \left(\frac{A - a(t)}{A}\right) g \left(\frac{\theta_S(t) - \theta_{PWP}}{\theta_S(t)}\right)$$

And the rate of recruitment, $R(0, t) = \mathrm{d}n_R/\mathrm{d}t$ [Nt^{-1}], is formally expressed with the final statement,

$$R(0,t) = \alpha\left(\frac{A - a(t)}{A}\right)\left(\frac{\theta_S(t) - \theta_{PWP}}{\theta_S(t)}\right) s(t)\, N_S(t) \tag{R8}$$

where g is absorbed into α [t^{-1}], an empirically observed rate constant. We have already alluded to a number of factors important to the recruitment process and any variable not explicitly incorporated above but functions to remove seeds or seedlings from our potential pool of progeny is embedded within α. A comprehensive but not exhaustive list includes: Pre-dispersal seed predation [*Louda, 1983; Hanley, 1998*], granivory [*Brown et al., 1979*], crowding [*Ross and Harper, 1972; Turkington et al., 2005*], seeds buried by soil movements [*Ren et al., 2002; Tobe et al., 2005*], salinity induced stress or ion toxicity [*Khan and Ungar, 1997; Dodd and Donovan, 1999*], intraseasonal precipitation patterns [*Fay et al., 2000*], soil compaction, and for nutrient poor soils, an inability to form mycorrhizae [*Fenner, 1987; Stahl et al., 1998*]. In effect, decreasing the value of α represents conditions that are increasingly hostile.

Shrub Mortality (Sink Term)

Juvenile Mortality

We consider the *n*th shrub a juvenile, n_J, if its rooting depth $D_n(t)$ is within L_{UL} (if $D_n(t) \leq L_{UL}$) during the year *t*. Similar to seedling survival (R7), we then assign it a probability of mortality proportional to the probability that $\theta_S(t)$ (R6) is inadequate for survival,

$$\frac{\mathrm{d}n_J}{N_J} \sim 1 - \frac{\theta_S(t) - \theta_{PWP}}{\theta_S(t)} = \frac{\theta_{PWP}}{\theta_S(t)}$$

where $\mathrm{d}n_J$ denotes the number of juvenile deaths during d*t* and $N_J(t)$ denotes the total number of juveniles in our population. The rate of juvenile mortality, $\mathrm{d}n_J/\mathrm{d}t = M_J(t)$, can be expressed,

$$M_J(t) = \frac{\mathrm{d}n_J}{\mathrm{d}t} = \beta_J\left(\frac{\theta_{PWP}}{\theta_S(t)}\right)^m N_J(t) \qquad \text{(M1)}$$

where β_J [t^{-1}] is a juvenile mortality rate constant and *m* is a parameter representing how tolerant the modeled species is to changes in the water-content of the soil.

Adult Mortality

If, on the other hand, $D_n(t)$ extends into the lower soil layer, L_{LL} [L] (if $D_n(t) > L_{UL}$), we consider the *n*th shrub an adult, n_A, with access to moisture supplied by winter precipitation. We coincide the beginning of year *t* with the onset of the summer season so that soil-moisture throughout the L_{LL} is at its yearly maximum; suppressed transpiration during the cooler, preceding months enabled all precipitation falling during the winter of *t*-1, $P_W(t-1)$ [L], to recharge the L_{LL}, where the form of precipitation (i.e. rain, snow, etc.) bears no special consideration. Analogous to our formulation of summer precipitation (R4), the probability that a daily precipitation event will occur in the winter season, $p_{\Delta tw}$, can be expressed as,

$$p_{\Delta t_W} = \int_0^\infty \int_{-273^\circ}^{T_c} f_{PT*}\, \mathrm{d}T^*\, \mathrm{d}P$$

where the lower limit of -273 °C corresponds to absolute zero and the number of winter precipitation days, Δt_W [t], is then simply,

$$\Delta t_W = d_Y p_{\Delta t_W}$$

Independently, if $P(t\text{-}1)$ [L] represents the annual daily precipitation record, then $P_W(t\text{-}1)$ is,

$$P_W(t-1) = \int_{\Delta t_W} P(t-1)\,\mathrm{d}t$$

Assuming a first order autoregressive process, we can conceptualize the total amount of water added to the L_{LL} in year t, $P^*_W(t)$ [L], as,

$$P_W^*(t) = \varphi\, P_W(t-2) + P_W(t-1) \qquad\qquad 0 \le \varphi \le 1$$

where φ represents the propensity of the soil to retain moisture from year to year. Note that when $\varphi = 0$ our expression reduces to $P^*_W(t) = P_W(t\text{-}1)$. In other cases, the inclusion of antecedent moisture conditions, $\varphi P_W(t\text{-}2)$, enables our model to consider possible population consequences associated with interseasonal precipitation trends like a noted tendency for abundant rainfall years to fall in succession. Assuming that $P_W(t)$ infiltrates over the entire L_{LL} (where from before, $L_{LL} = D_f - L_{UL}$) and redistributions below Df are negligible, the water input per unit volume deep soil, $\theta_W(t)$ [L^3/L^3], is,

$$\theta_W(t) = \frac{P_W^*(t)}{L_{LL}} \tag{M2}$$

If moisture is distributed uniformly with depth, then $\theta_W(t) + \theta_{PWP}$ represents the soil-water content experienced by an adult shrub, independent of its rooting depth. More generally, $\theta_W(t)$ will be distributed non-uniformly with depth [*Schwinning et al., 2005*] depending on the amount and timing of precipitation and on both soil (i.e. permeability, texture, horizons, biotic crusts, etc.) and plant (i.e. canopy architecture with impacts on throughfall and stem flow) properties that influence infiltration, redistribution, and uptake [*Navar and Bryan, 1990; McAuliffe, 1994; Gile et al., 1998; Devitt and Smith, 2002*]. Letting $\gamma(t) = (1/\theta_W(t))(\partial\theta_W/\partial z)$ [L^{-1}] denote a normalized first-order variation in the average soil moisture per unit volume soil, the soil-water content observed by adult shrub n during t, $\theta_n(T,t)$, can be obtained from a first-order Taylor series expansion assuming that $\theta_W(t)$ occurs at D_f,

$$\theta_n(T,t) = \theta_W(t)\left[1 + \gamma(D_n(t) - D_f)\right] + \theta_{PWP} \qquad\qquad \theta_{PWP} \le \theta_W(t) \le \theta_{FC} \tag{M3}$$

where the same condition from (R7) ensures consistency with the principles of soil physics. Note that when $\gamma = 0$, (M3) reduces to $\theta_W(t) + \theta_{PWP}$. Assuming a smooth transition in water-content between the upper and lower soil layer, that is when $D_n(t) = L_{UL}$, $\theta_n(t) = \theta_S(t)$, suggests that,

$$\gamma(t) = \frac{\theta_W(t) - \theta_S(t) + \theta_{PWP}}{L_{LL}\,\theta_W(t)}$$

As in juvenile mortality, the probability that an adult shrub with age T, n_{AT}, perishes is then proportional to the probability that the water content will be inadequate for shrub survival,

$$\frac{\mathrm{d}n_{AT}}{N_{AT}} \sim \frac{\theta_{PWP}}{\theta_n(T,t)}$$

where $\mathrm{d}n_{AT}(T,t)$ denotes the number of adults of age T that die during year t and $N_{AT}(T,t)$ denotes the total number of adult shrubs of age T. The age specific or local rate of adult mortality, $M_A(T,t)$ [t^{-1}], is then,

$$M_A(T,t) = \frac{\mathrm{d}n_{AT}(T,t)}{\mathrm{d}t} = \beta_A \left(\frac{\theta_{PWP}}{\theta_n(T,t)} \right)^m N_{AT}(T,t) \qquad \text{(M4)}$$

where as in (M1), m is a parameter reflecting the ability of the shrub species to tolerate changes in the water-content of the soil and β_A [t^{-1}] is an adult mortality rate constant. Letting T_A denote the age at which a shrub becomes an adult, the total rate of adult mortality, $\mathrm{d}n_A/\mathrm{d}t$, is then,

$$\frac{\mathrm{d}n_A}{\mathrm{d}t} = \int_{T_A}^{\infty} M_A(T,t)\,\mathrm{d}T$$

Total Rate of Shrub Mortality

Combining juvenile and adult mortality, our final expression for the mortality rate of the population at time t must be solved for numerically but conceptually, is simply,

$$M(T,t) = \frac{\mathrm{d}n_J(t) + \mathrm{d}n_A(T,t)}{N(t)}$$

Shrub Growth

For all shrubs surviving t, we grow their canopy radii according to (G1) where its time derivative yields the average age-specific annual radial growth rate, $\mu_{\mathrm{d}R_n}(T)$ [L],

$$\mu_{dR_n}(T) = \frac{\mathrm{d}R_n(T)}{\mathrm{d}t} = \frac{e^{-T_n(t)/T_{90}}}{T_{90}} (R_f - R_i) \tag{G2}$$

As previously discussed, the plasticity of plant growth and development results in a loose correlation between size and age [*Bradshaw, 1965; Novoplansky, 2002*]. We describe this apparent variation and collectively incorporate the different drivers of this phenomenon (i.e. developmental instability [*Sachs, 2002*], genetic differentiations [*Linhart and Grant, 1996; Alpert and Simms, 2002*], stress induced dormancy, adaptive phenotypic responses [*Via, 1993*], etc.) by drawing the realized radial growth rate of an individual shrub, $\mathrm{d}R_n(T)$ [L], from a normal distribution with a mean given by (G2) and a standard deviation, $\sigma_{\mathrm{d}R_n}(T)$ [L],

$$\sigma_{\mathrm{d}R_n}(T) = \frac{\mathrm{d}R_n(T)}{p} \qquad 0 \le p \le 1$$

where p is a parameter that characterizes the degree of plasticity that our modeled species is known to exhibit with $p = 0$ corresponding to deterministic and $p = 1$ to highly plastic growth. Since the diversion of resources away from resource-acquiring functions towards mechanisms enhancing defense, storage, or maintenance suppresses growth and may enhance survivorship [*Mooney and Gulmon, 1982*], the applicability of logistic growth to desert shrubs may need to be reexamined. Nonetheless, plants inhabiting harsh environments have comparatively slow growth rates [*Chapin, 1991; Chapin et al., 1993*] which are sustained during periods of relative resource abundance [*Woodell et al.,1969; Leffler et al., 2004*]. For these reasons, our annual above-ground growth rate is independent of precipitation [*Padilla et al., 2009*]. While evidence suggests a stronger connection between rainfall and root growth [*Padilla et al., 2009*], the specifics are not currently well understood. So we stay consistent with our previously discussed isometric scaling rule (G3) and calculate the new rooting depth of all surviving shrubs at $t + 1$ from their new canopy volumes at $t + 1$ assuming that $R_n(t+1)/V_n(t+1) = \kappa$. Note that through this relationship, our treatment of canopy growth simultaneously translates into plasticity in rooting depth.

CHAPTER IV

ANALYSIS AND RESULTS

All cases except the steady-state require numerical solutions. The governing equations of our model are coded in MATLAB (Appendix B) allowing the spatiotemporal behavior of a population to be simulated for a specified number of time steps. For the population in Table 4.1 (Appendix C), our statements of recruitment and mortality are individually analyzed for one time step. Example simulations (with deviations noted) are then run in order to demonstrate the functioning of key variables and parameters.

Site Specific Parameters	Climate	Mean Annual Precipitation (MAP [L])	0.250 m
	Soil	Length of Upper Soil Compartment (L_{UL} [L])	0.20 m
		Permanent Wilting Point (Θ_{PWP} [L^3/L^3])	0.06
		Field Capacity (Θ_{PWP} [L^3/L^3])	0.14
		Propensity of Soil to Retain Moisture from Year to Year (φ)	0
Shrub Specific Parameters	Initial Conditions	Modeled Area (A [L^2])	400 m^{2*}
		Shrub Areal Density (ρ [N/L^2])	0.675 N/m^{2*}
		Age/Size Structure ($\Gamma(A,B)$)	$\Gamma(5, 0.04)$*
		Spatial Pattern	Random*
	Logistic Growth	Initial Canopy Radius (R_0 [L])	0.05 m*
		Final Canopy Radius (R_f [L])	0.60 m*
		Age when Canopy is 0.90 R_f (T_{90} [t])	10 yr
	Recruitment	Rate Constant (α)	0.0055
		Average Effective Area of shrub n (a_n [L^2/N])	$1.5\pi[R_n(t)]^2$
		Average Number of Seeds Produced per Shrub (s [seeds/N])	10,000 seeds/N
	Mortality	Juvenile Rate Constant (β_J)	0.40
		Adult Rate Constant (β_A)	0.30

Table 4.1 Site and shrub-specific parameters used in analysis of model behavior. *Appendix C

Recruitment

Our final statement of recruitment (R8) contains four variables and for one time step (dt = 1 year), Figure 4.1.a-d displays the systematic variation of (a) the total effective area occupied by the population, $a(t)$, (b) the amount of summer precipitation, $P_S(t)$, (c) the number of seeds produced per shrub, $s(t)$, and (d) the number of seed producing shrubs, $N_S(t)$. While the recruitment rate must be an integer to reflect whole shrubs, the step functions overlap at low values so for illustrative purposes, rounding is momentarily forgone. A comparison between Figure 4.1.e. and Figure 4.1.f then demonstrates the functioning of α, our recruitment rate constant, where both $P_s(t)$ and $s(t)$ are treated as stochastic variables drawn randomly from normal distributions. The importance of our other key parameter, the permanent wilting point, θ_{PWP}, is demonstrated by running each above analysis for two different soil types (a loamy sand, $\theta_{PWP} = 0.06$ [L^3/L^3] and a sandy clay loam, $\theta_{PWP} = 0.15$ [L^3/L^3]) (Figure 4.1.a-f).

Mortality

Due to their analogous nature, our analysis of the juvenile mortality rate (M1) and the local rate of adult mortality (M4) are similar. In Figure 4.2 and Figure 4.3, summer and winter precipitation are increased systematically and respectively. For juveniles, Figures 4.2.a-c depict differences in mortality rates between two populations differing in their soil type. A comparison between Figure 4.2.a and Figure 4.2.b demonstrates the responsiveness of two species which exhibit different sensitivities to changes in the water supply (m = 1/4 and m = 4). Figures 4.2.a-b also capture the influence that the juvenile mortality rate constant ($\beta_J = 0.95$ yr^{-1} and $\beta_J = 0.45$ yr^{-1}) imparts on a population. Moving to adult mortality, Figures 4.3a-b likewise examines the relative behavior of two species with different sensitivities to changes in the water supply (m = 1/4 and m = 4), noting the average age of the dying individuals as well as the comparative probability of death for two shrubs of the same species differing only in their rooting depth.

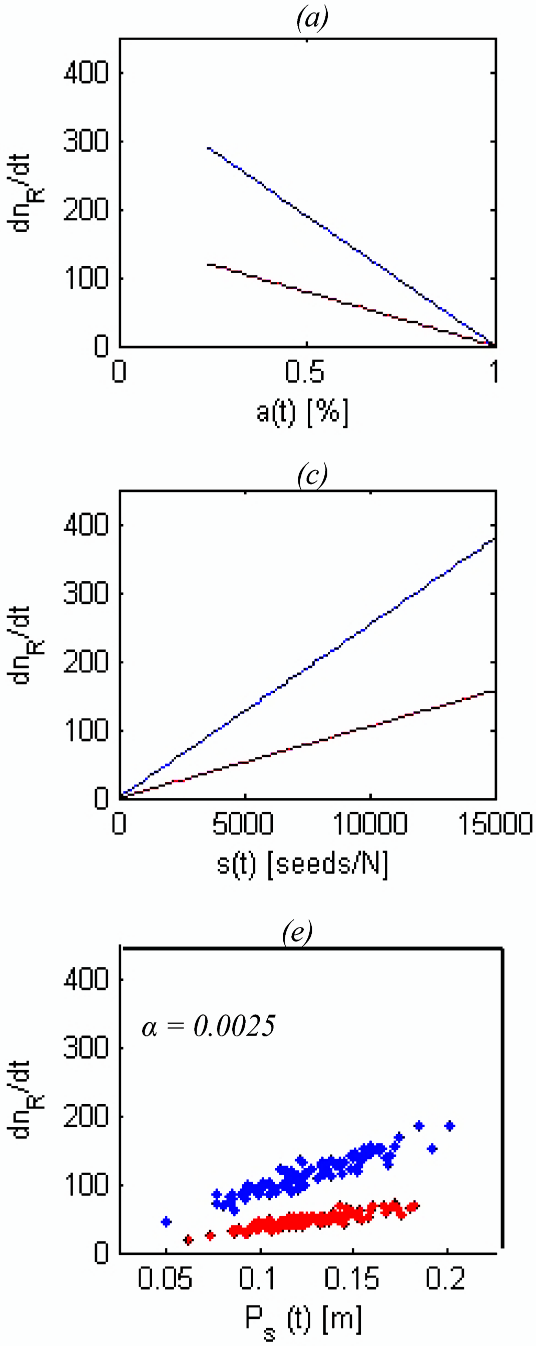

Figure 4.1. Influence of the recruitment variables on the recruitment rate for two different soil types. Blue results represent a loamy sand ($\theta_{PWP} = 0.06$ [L^3/L^3]) whereas the red results reflect a sandy clay loam ($\theta_{PWP} = 0.15$ [L^3/L^3]) for the response of recruitment to increases in (a) the effective area occupied by the extant population, *a(t)*, *(b)* summer precipitation, $P_s(t)$, *(c)* the number of seeds produced per shrub, *s(t)*, and *(d)* the number of seed producing shrubs, $N_s(t)$. Treating $P_s(t)$ and *s(t)* as stochastic variables, two recruitment rate constants are then compared in *(e)* and *(f)*.

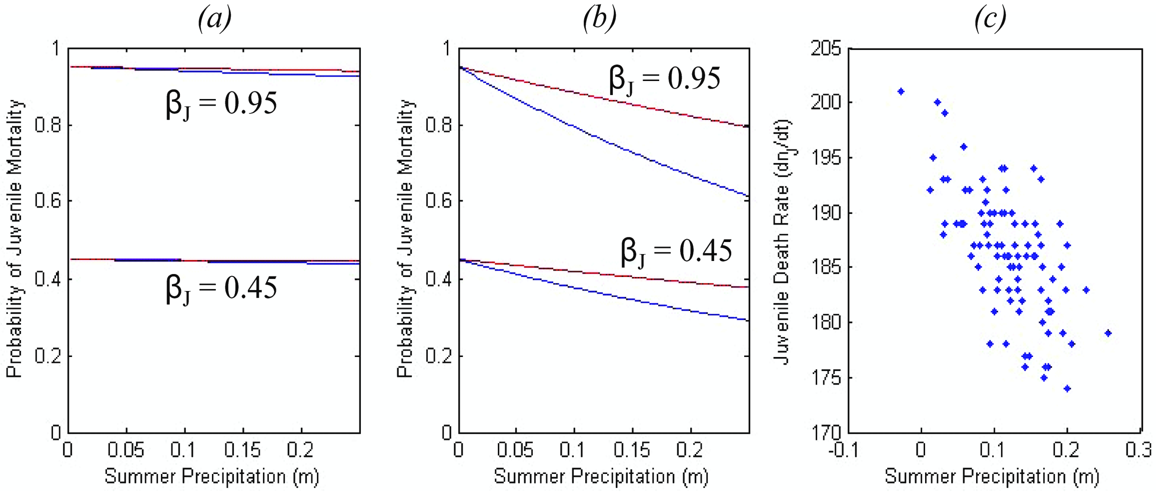

Figure 4.2. Results depicting the influence of summer precipitation, the sensitivity of a shrub species to changes in water supply, the soil type of a site, and the rate constant on juvenile mortality. For two shrubs species with different sensitivities to changes in the water supply, *(a)* $m = 1/4$ and *(b)* $m = 4$, the blue results reflect the probability of mortality for a juvenile on a loamy sand ($\theta_{PWP} = 0.06$ [L^3/L^3]) and the red results for a juvenile on a sand clay loam soil ($\theta_{PWP} = 0.15$ [L^3/L^3]). In *(c)* $m = 1$ and the observed juvenile death rate during dt is reported as a function of summer precipitation.

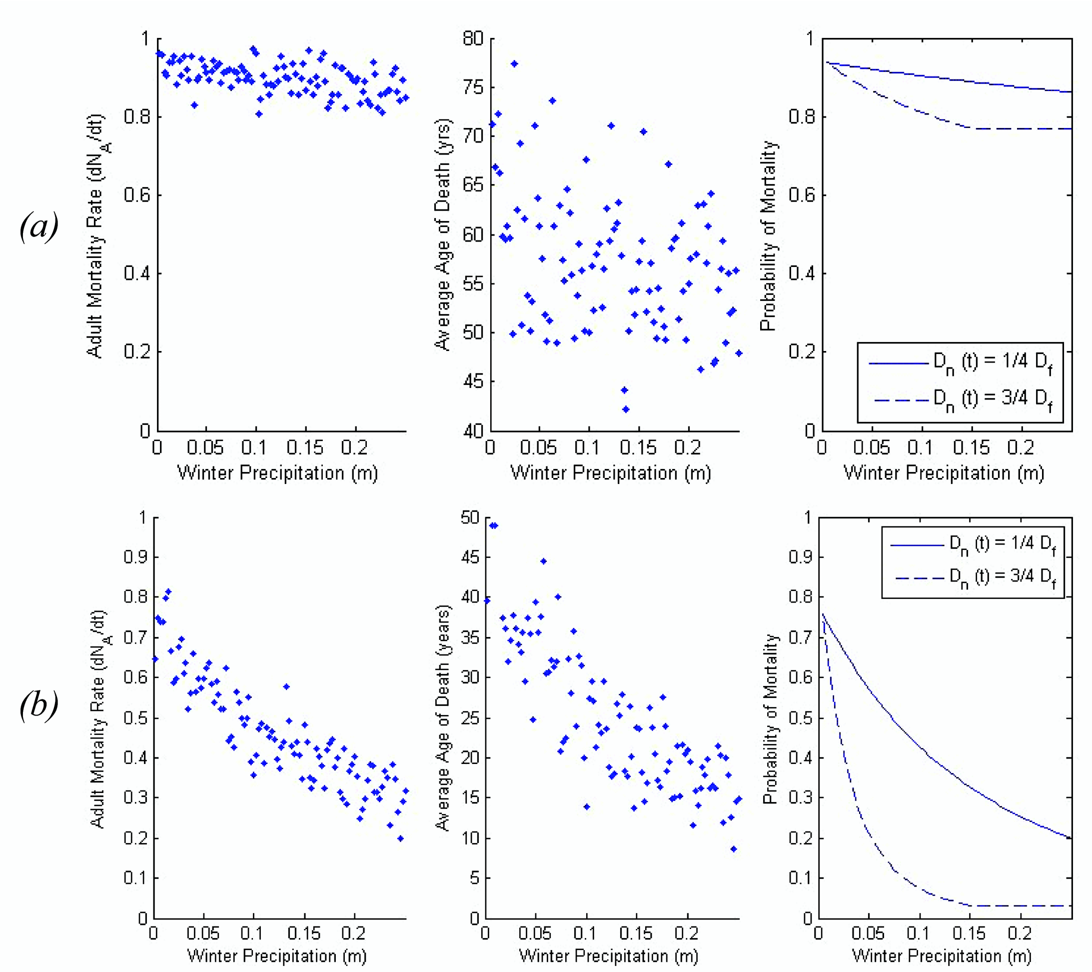

Figure 4.3. The influence of winter precipitation on adult mortality for different shrub species and for two shrubs of the same species differing only in their rooting depth, $D_n(t)$. The responsiveness of adults, including the total rate of adult mortality as well as the average age of the dying individuals, is calculated for two shrub species which display different sensitivities to changes in the water supply, *(a)* $m = 1/4$ and *(b)* $m = 4$. For these two shrub species, the probability of death for two individuals with different rooting depths, $D_n(t) = 1/4D_f$ and $D_n(t) = 3/4D_f$, is then calculated and compared.

Simulation of Population Dynamics

Focusing on depicting changes in shrub count, we probe two variables and two parameters to explore their influence: $P_s(t)$, $P_w(t)$, m, and A. Our manipulation of $P_s(t)$ and $P_w(t)$ reflect the widely recognized, and previously discussed, importance of water in arid ecology. Figure 4.4 investigates different precipitation regimes and captures the results when both summer and winter precipitation inputs are constants, when one is a constant and the other fluctuates stochastically, and when both are stochastic inputs that differ only in the magnitude of their standard deviation. Figure 4.5 depicts the difference between the same population inhabiting sites with different levels of mean annual precipitation (*MAP*) where $P_s(t)$ and $P_w(t)$ are both constant inputs. Figure 4.6 then compares these rainfall scenarios for two species differing only in their sensitivity to changes in the water supply ($m = 1/4$ and $m = 4$). We end with Figure 4.7 which forecasts further into the future and offers 500-year projections of these two species to demonstrate how longer-term climatic trends can be embedded within our model and also compares the results arising from different sizes of the modeled area, A.

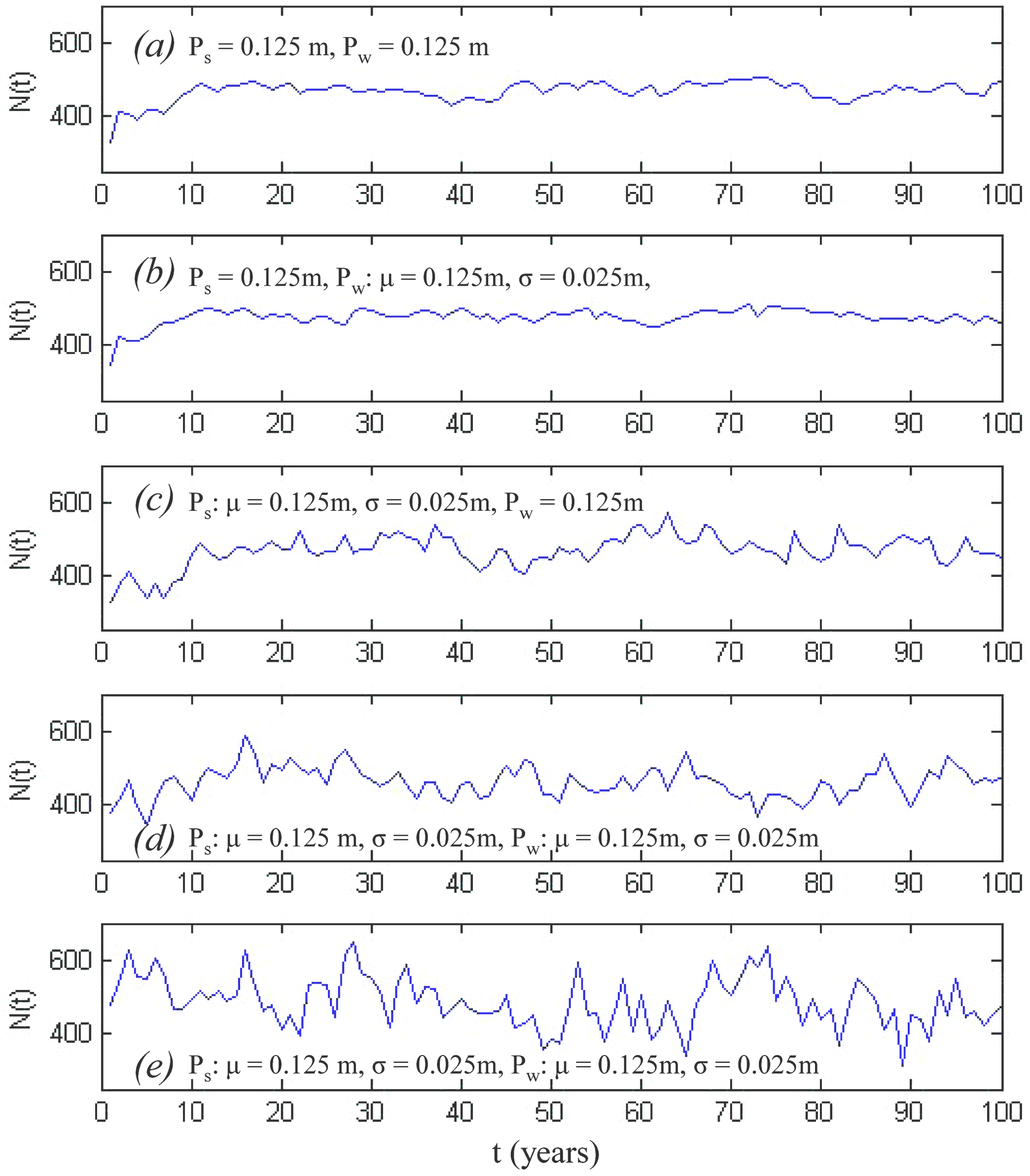

Figure 4.4. 100-year simulation of the influence of different precipitation regimes on changes in shrub count. *(a)* Constant summer and winter precipitation, *(b)* constant summer and stochastic winter precipitation, *(c)* stochastic summer and constant winter precipitation, *(d)* stochastic summer and winter precipitation with moderate interannual variability, and *(e)* stochastic summer and winter precipitation with higher interannual variability.

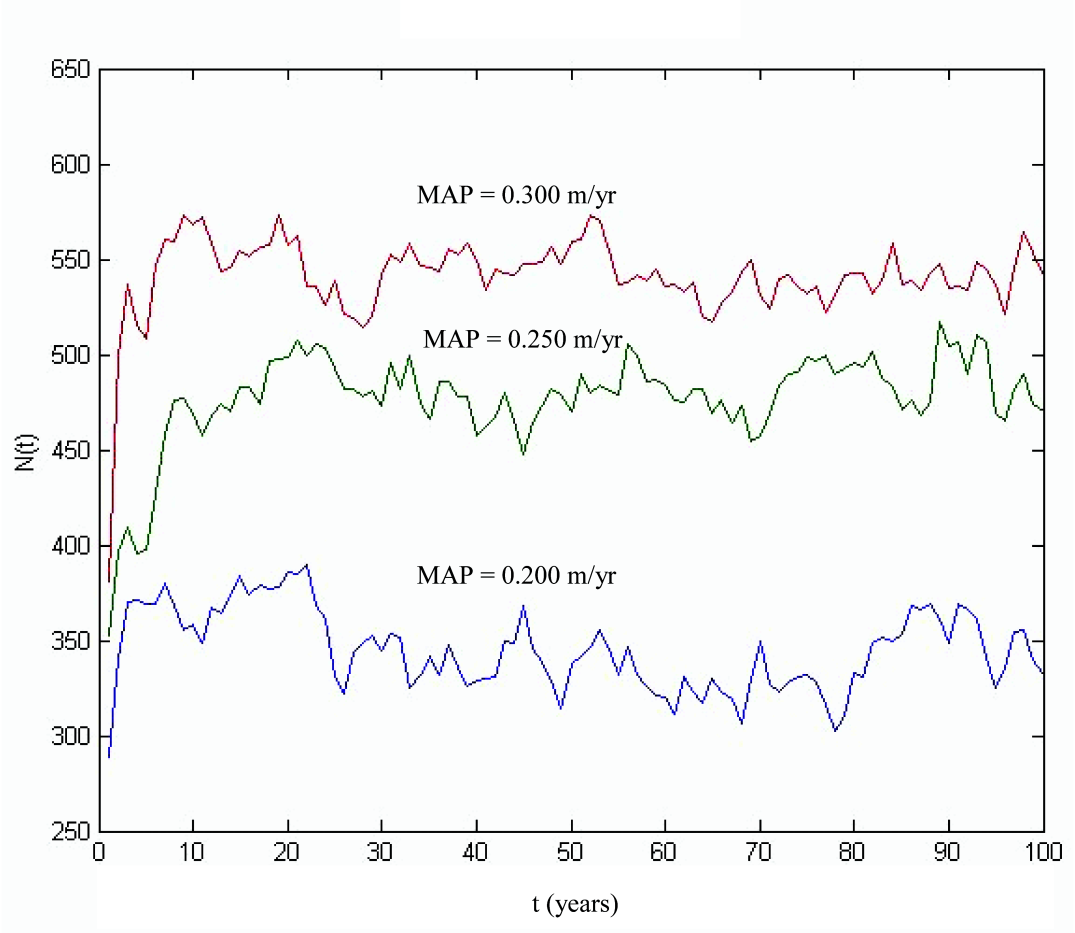

Figure 4.5. 100-year simulation depicting fluctuations in shrub count at sites with different Mean Annual Precipitation *(MAP)*.

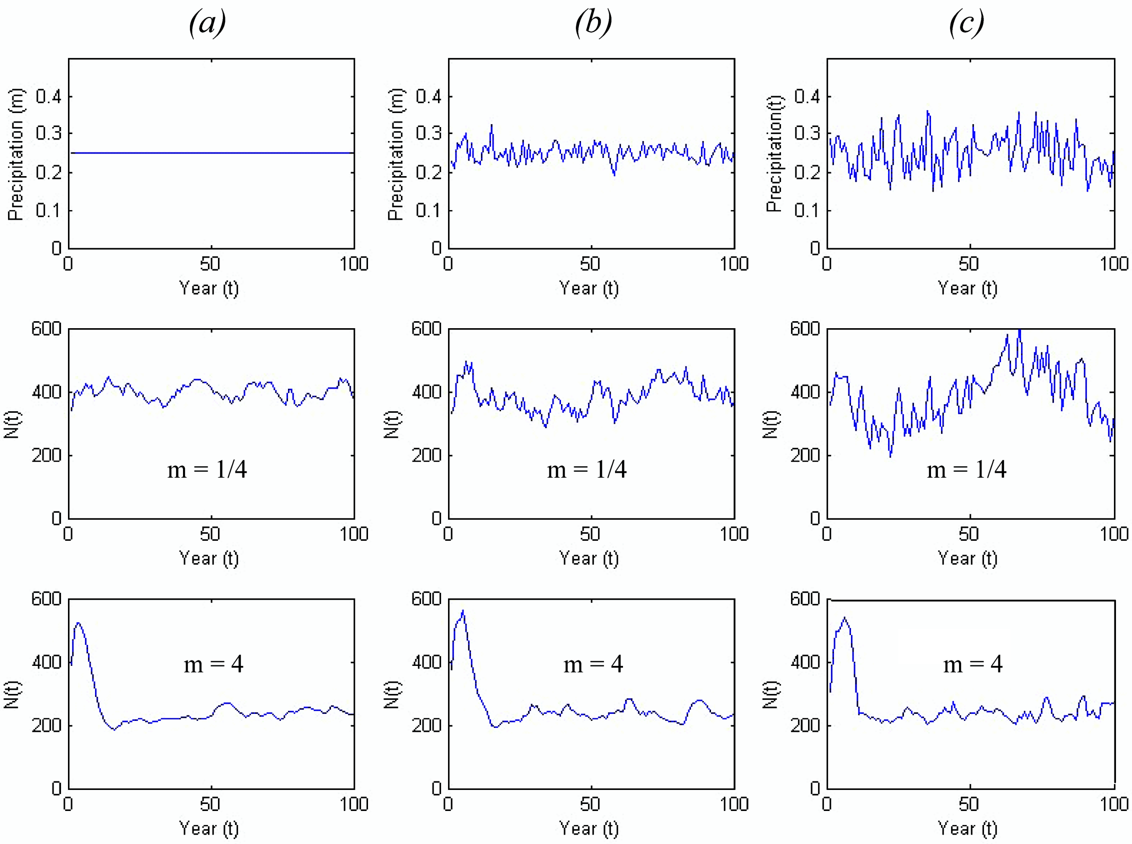

Figure 4.6.a. 100-year simulation depicting fluctuations in shrub count resulting from different precipitation regimes for two shrubs with different sensitivities to changes in the water supply. *(a)* Constant winter and summer precipitation ($P_w(t) = 0.125$ m and $P_s(t) = 0.125$ m), *(b)* constant winter ($P_w(t) = 0.125$ m) and stochastic summer ($P_s(t)$: $\mu = 0.125$ m, $\sigma = 0.025$ m) precipitation, and *(c)* constant winter ($P_w(t) = 0.125$ m) and stochastic summer precipitation with higher interannual variability ($P_s(t)$: $\mu = 0.125$ m, $\sigma = 0.050$ m).

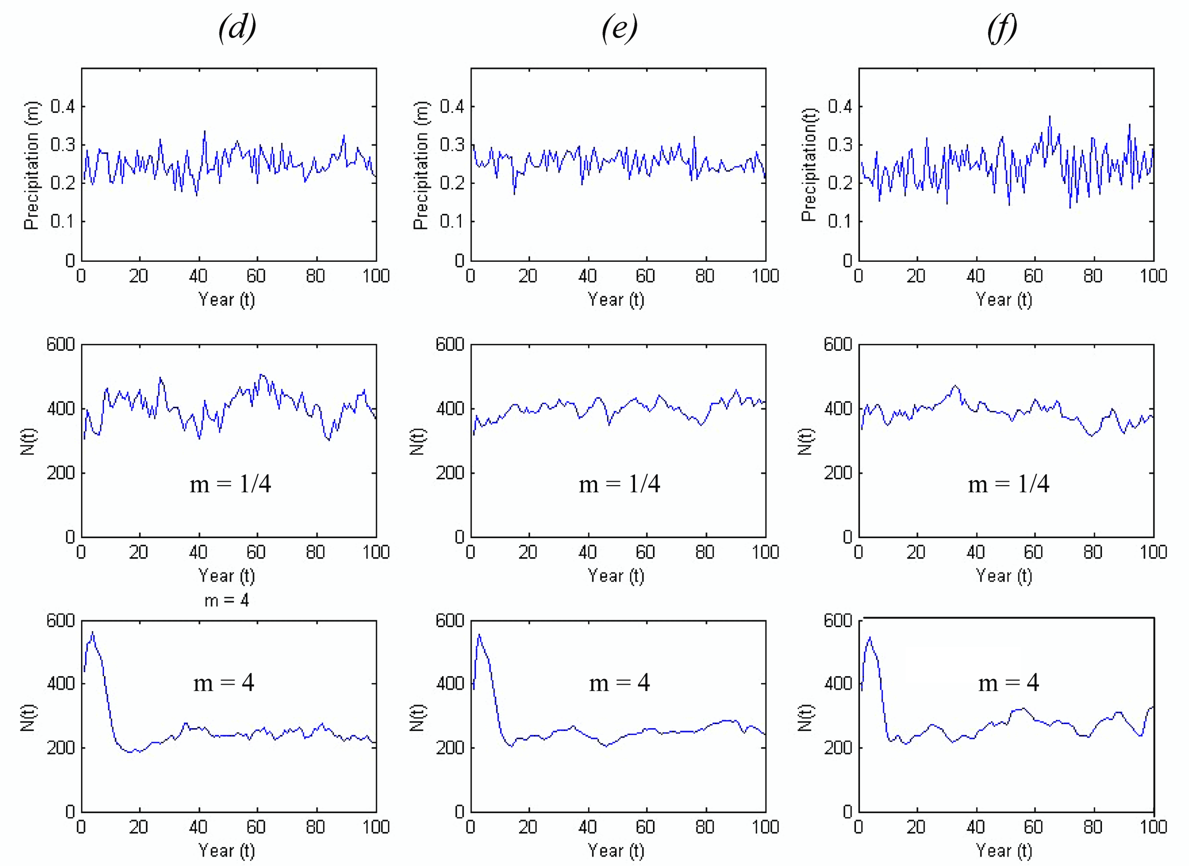

Figure 4.6.b. 100-year simulation depicting fluctuations in shrub count resulting from different precipitation regimes for two shrubs with different sensitivities to changes in the water supply. *(d)* Stochastic winter ($P_w(t)$: $\mu = 0.125$ m, $\sigma = 0.025$ m) and stochastic summer ($P_s(t)$: $\mu = 0.125$ m, $\sigma = 0.025$ m) precipitation, *(e)* stochastic winter ($P_w(t)$: $\mu = 0.125$ m, $\sigma = 0.025$ m) and constant summer ($P_s(t) = 0.125$ m) precipitation, and *(f)* stochastic winter precipitation with higher interannual variability ($P_w(t)$: $\mu = 0.125$ m, $\sigma = 0.050$ m) and constant summer ($P_s(t) = 0.125$ m) precipitation.

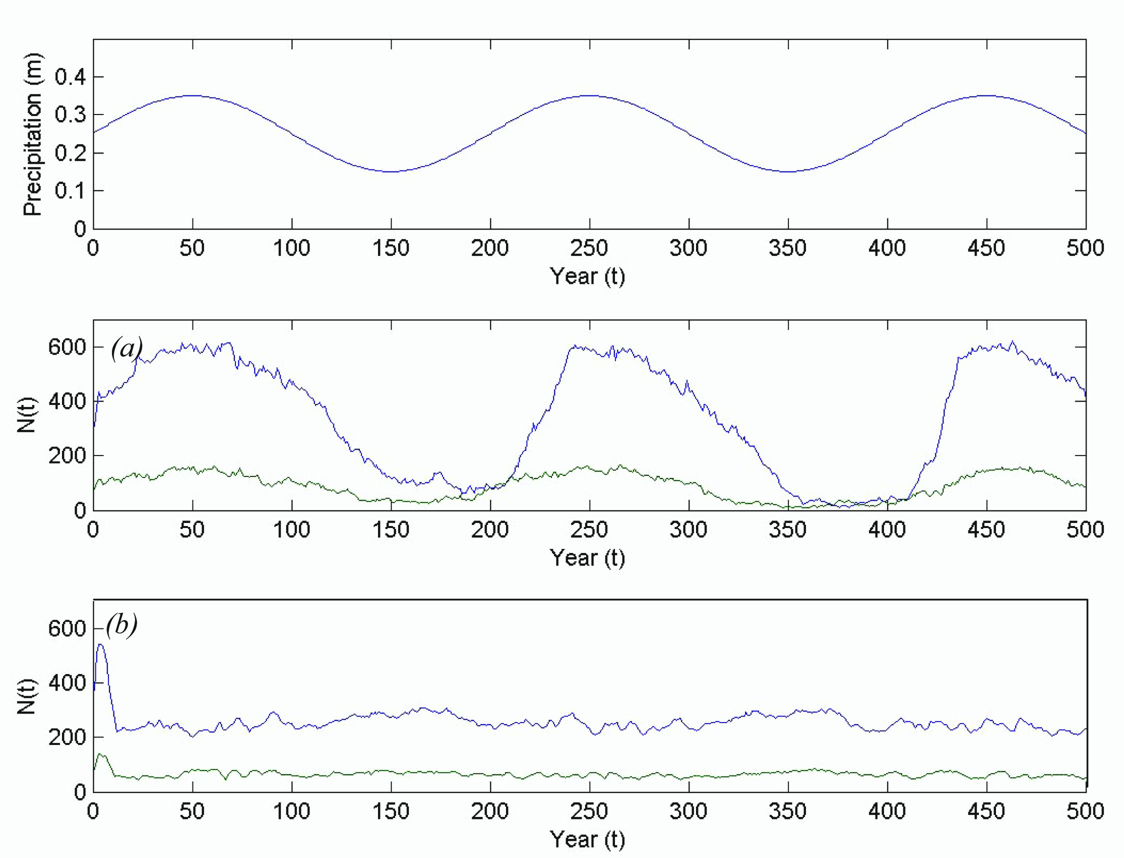

Figure 4.7. 500-year simulation of the influence of a long-term oscillating precipitation pattern on changes in shrub population count. In each graph, the changes in shrub count observed for a species with less [*(a) m* = 1/4] and greater [*(b) m* = 4] sensitivity to changes in the water supply are depicted for two model area sizes, A = 100 m^2 (green) and A = 400 m^2 (blue).

CHAPTER V

DISCUSSION AND CONCLUSIONS

Recruitment

Our model predicts higher recruitment with increasing summer precipitation, seed production, and the number of seed producing shrubs (Figure 4.1.b-d). Conversely, lower recruitment is encountered if the population occupies a higher effective area and there is therefore less space available for new recruits (Figure 4.1.a). Note that these results are reflected analytically in (R8); as any of the terms independently approach zero, the overall recruitment rate does as well. The formulation leaves open the possibility that, in any given year, recruitment can be limited either because of a shortage of seeds or seed producing shrubs, as well as due to a dearth of space or water. Furthermore, recruitment is always favored on the loamy sand as opposed to the sandy clay loam suggesting that soil texture has a significant impact on shrub regeneration (Figure 4.1.a-f). This is consistent with field observations as well as controlled greenhouse studies [*Mayeux, 1983; Young et al., 1990; Lauenroth, 1994; Bowers, 2004; Tobe et al., 2005*] and this result is elaborated on in our discussion of shrub mortality.

In the biological and ecological literature, studies pay individualized attention to the different phases of recruitment outlined here, with insights into these underlying processes and mechanisms gained through controlled experiment. However as recruitment plays out in the real-world, it is possible to imagine a large set of extraneous factors which may interfere with what might otherwise be a deducible, *a priori*, outcome. Insomuch as any statement of recruitment must ultimately reflect *a posteriori* successes and failures, our probabilistic approach furnishes results that align well with empirical findings. For instance, our results are consistent with studies which report higher recruitment in years with higher moisture availability [*Ackerman, 1979; Kruse, 1979; Thomas and Davis, 1989; Harrington, 1991; Lamont, 1993; Donovan and Ehleringer, 1994; Bowers, 1994; deVillalobos and Pelaez, 2001; Loik et al., 2004; Padilla and Pugnaire, 2007*] as well as ones that report a correlation with basal area [*Ross and Harper, 1972; Owens and Norton, 1987*] and also has the capacity to mimic instances of either “safe-site” (i.e. no “available” space) or “seed” limited recruitment [*Eriksson and Ehrlen, 1992; Turnbull et al., 2000*].

This suggests that (R8) captures the innate complexity of the recruitment process, a common shortfall of most simple recruitment models which only manage to tenuously, on a case by case basis, link seeds with their seedlings [*Houle, 1995*]. In contrast, our model may be applicable across a wide-range of species and environmental conditions since its framework allows for similar outcomes (i.e. $dn_R(t)$ counts) to result from different specified combinations of known influential factors. It could therefore be used in regeneration research where much attention has focused on discerning the bottlenecking step in the recruitment process by helping to clarify the specific conditions under which one stage of the procession (seed production, dispersal, germination, or seedling survival) becomes relatively more important than the others. For example, the slopes in Figures 4.1.a-d reflect how the recruitment rate changes with changes in one of our four variables with the relative steepness of Figure 4.1.a suggesting that summer precipitation may have the strongest influence on the overall recruitment rate of our shrub population. However field applications of our model would require determining realistic estimates for the encountered ranges of each of our variables. For example, a population might experience a less dramatic summer precipitation range (Figure 4.1.a) while the number of seed producing shrubs may in fact be much greater than we have explicitly allowed for (Figure 4.1.d). Such considerations might revel which recruitment variable is relatively more important for a particular population in a particular location. Such a perspective would provide complimentary insights into what is, at present, strictly theoretical.

The recruitment rate constant, α, directly impacts our recruitment count and the population with the higher α is more sensitive to changes in $P_s(t)$ (Figure 4.1.f). In contrast, a lower α results in recruitment which appears largely unresponsive to fluctuations in the summer water supply (Figure 4.1.e). This is consistent with field research which has demonstrated that, although summer precipitation broadly increases recruitment, the actual magnitude of the response is species-specific [*Frazer and Davis, 1988; Thomas and Davis, 1989; Harrington, 1991; Richards and Lamont, 1996; Wilson and Witkowski, 1998; Gillespie and Loik, 2004*]. Furthermore, it suggests how short-term, fitted field data can provide estimates of the parameters needed for modeling the long-term population trends of that specific species.

Mortality

Juvenile Mortality

Increasing summer precipitation translates into a decreasing probability of juvenile mortality (Figures 4.2.a-c), with m being a parameter that is adjusted to reflect the responsiveness of a species to changes in the water supply. A species relatively insensitive to changes in precipitation ($m < 1$), perhaps because it is highly adaptable [*Bradshaw and McNeilly, 1991*], unintegrated physiologically (i.e. via axis splitting [*Schenk, 1991*]) and can therefore undergo partial-canopy mortality, or has water-use patterns that are consistently low, exhibits mortality rates that appear independent of summer precipitation (Figure 4.2.a). Conversely, if the mortality of a species is more strongly related to summer water availability ($m > 1$), the probability of juvenile mortality decreases more drastically as the amount of summer precipitation is increased (Figure 4.2.b). Since the number of adults comprising a population hinges on the survival of juveniles, these results may help explain how pioneer species which tend to be more robust (i.e. weed-like) throughout their infancy (i.e. $m < 1$), manage to maintain their numbers even when subjected to disturbances or extreme fluctuations in their external conditions. As indicated by the relative steepness of slopes, higher values of the juvenile mortality rate constant, β_J, lead to marginal changes in summer precipitation having a proportionally larger impact on the juvenile mortality rate (Figure 4.2.b). β_J also sets the minimum and maximum probability mortality range (Figures 4.2.a-b) which is also captured analytically in (M1); in the absence of summer precipitation, $\theta_S(t) = 0.0$ m, (M1) suggests that mortality is not guaranteed but rather approaches its maximum value, $M_J(t) = \beta_J N_J$. For field applications, observations detailing the percentage of a population dying in an extreme drought, for instance, might provide a starting point for estimating β_J.

Note that the transition between the upper and lower soil compartment is set at 0.20 m. Since this parameter distinguishes juveniles from adults, as well as the source of water to which the survival of each is coupled to, further research is necessary to determine whether this is physically appropriate as well as whether or not our canopy volumes properly scale with rooting depths. In addition to its importance for juvenile mortality, the depth of the upper soil compartment, L_{UL}, sets the number of seed producing shrubs so these clarifications also have consequences directly related to our formulation of shrub recruitment.

And lastly, note the difference between populations differing only by soil type: The probability of juvenile mortality is always higher on the sandy clay loam site. This aligns with studies which provide evidence that the responsiveness of plants to drought varies considerably as a function of soil texture [*Alizai and Hulbert, 1970; Fernandez-Illescas et al., 2001; Hamerlynch and McAuliffe, 2008*]. In humid climates, where the largest loss of the water balance is deep drainage, sandy soils have poor moisture retention and therefore tend to be less vegetated. In water limited environments, however, sandy soils support higher vegetation densities: Allowing rapid infiltration, they remove the majority of the delivered water from the soil-atmosphere boundary, saving it from evaporative loss and thus sequestering it for later plant consumption [*Noy-Meir, 1973*]. Whether this result emerges as a coincidence or due to the physical foundation underpinning our model warrants closer examination.

Adult Mortality

The dependence of the moisture supply of an adult shrub, $\theta_n(T,t)$, on t captures the external forcing of the unsteady environment while its dependence on T mimics maturation; the vertical extension of a tap root grants a shrub physical access to deeper, and progressively moister, regions of the soil profile. In addition to the general trend that adult survival increases with increasingly wet conditions, our model predicts that for a given species, a deeper rooted individual has a higher probability of surviving across all levels of rainfall (Figure 4.3). The magnitude of this comparative advantage, however, does reach a maximum with the ensuing probability of mortality remaining constant after the deepest part of our lower soil layer has reached its field capacity, $\theta_{FC.}$. Note that when a species is more responsive to changes in moisture (i.e. $m > 1$), these relationship become more pronounced and their associated impacts on the mortality rate becomes more significant (Figure 4.3.b). Aside from suggesting that winter precipitation can be a key driver of desert plant dynamics [*La March and Fritts, 1971; Brown et al., 1997; Reynolds et al., 2004; Bowers, 2005; Hereford et al., 2006; Miriti, 2007; Miriti et al., 2007*], this result reflects selective mortality since there is an observed correlation between death events and a specific characteristic of the dying individuals, $R_n(t)$. When winter moisture is relatively abundant, our model preferentially kills younger shrubs (with shorter tap roots) with increasingly severe drought conditions prompting the death of older shrubs (with longer tap roots) (Figure 4.3). Since this graph is composed of only adult shrubs, this trend is apt to become more pronounced with the inclusion of the juvenile death count, a result reflecting what ecologists and biologists refer to as type III survivorship. Taken together, these results suggest that our model may provide a biophysical basis for a phenomenon which has been observed [*Toft, 1995; Bowers and Turner, 2001; Miriti et al., 2007; Hamerlynch and McAuliffe, 2008*] but at current, has only empirical descriptions [*Lauenroth, 2008*].

Further research also needs to examine potential shortcomings which may arise as artifacts of parmeterization or due to small number statistics. Before application and utilization, for example, it is imperative to understand how difference choices of the modeled area *A* (discussed in the next section) affect the statistical defensibility of these results. Because drought is often an indirect cause of shrub death [*Mattson and Haack, 1987; Chapin, 1991*] our model may be providing conservative estimates of mortality. If ecological forecasting is one objective of the potential application of this model, understanding how to account for these other stress factors (i.e. pest outbreaks [*Mattson and Haack, 1987*]), which are induced by water-stress, is another potential area for future research.

Simulations of Population Dynamics

Over the time frame of 100 years, our shrub population exhibits a degree of indifference towards the different precipitation regimes that we present it with (Figure 4.4). For example, when winter precipitation is treated as a stochastic input (Figure 4.4b), the results are indistinguishable from the case when the input of water is held constant at the mean annual precipitation (*MAP*) of a site (Figure 4.4.a). While fluctuations in shrub count do become slightly more pronounced when summer precipitation is treated stochastically (Figure 4.4c), they represent only a small percentage of the total number of shrubs in our population and it is therefore uncertain whether or not significance can be assigned to this outcome. The random fluctuations observed when precipitation is constant (Figure 4.4.a) suggests that the dynamics are internal to the system as opposed to externally forced. This result is intriguing in light of an on-going debate in the Soil-Plant-Atmosphere Continuum (SPAC) community: The apparent complexity of biology leaves scientists conflicted on the appropriate level of detail to incorporate in the modeling effort with concerns over tractability often pitted against concerns that the results will be too general to be useful [*Jeltsch et al., 2008*]. Further experimentation with our model might help resolve, for example, site and species specific circumstances under which a stochastic formulation of precipitation is warranted and when a simplification such as using only *MAP* is instead sufficient [*Schwinning et al., 2004; Jeltsch et al., 2008*]. Because shrub count alone offers an incomplete description of a population, further research should consider how other characteristics relevant to the dynamics of this population might be changing in response to these different precipitation regimes. For example, an inquiry into the changing demographic structure of this population could be conducted and is possible with our model as it is currently structured.

Despite the apparent indifference of shrub count to interannual differences in precipitation quantities, the total shrub count is directly related to the *MAP* of a site (Figure 4.5). This general trend, suggesting that biological productivity increases with increasing precipitation, is consistent with basic ecological knowledge. The higher shrub counts observed at sites with higher *MAP*s implies that the resources delivered to a site are determining the resulting number of shrubs. This result provides an alternative paradigm to theories based on the idea that the environment regulates population counts which must not exceed some upper limit [*White, 2001*]. Note too that because we use the site-specific rooting depth relationship in *Schenck and Jackon* [2002]*,* this result incorporates any changes in rooting depth (and therefore adjustment in the dimensions of our lower soil compartment) that may occur due to these different climates. Further attention is warranted since we do not specify the carrying capacity of a site as a model input, but rather, one appears to emerge as one of our model outputs.

When interannual precipitation has a higher standard deviation, fluctuations in shrub count become more pronounced (Figure 4.4.e) suggesting that our model might be useful to those studying how a changing climate may impact desert shrub communities. While there is uncertainty surrounding magnitudes, global climate models (GCM) do agree that the interannual variability in precipitation is apt to increase and be season specific [*Weltzin et al., 2003*]. Research at the climate change and desert ecology interface is motivated by the presupposition that these systems will be those most effected by such changes due to the central role that water plays in the functioning of these ecosystems [*LeHouerou, 1984; Weltzin et al., 2003*]. Since our model provides a platform for exploring the range of variability (i.e. both magnitude and net per season) that has been projected, it may help advance the conceptual understanding of the dynamics of these systems. For example, one could posit that having evolved in the face of low and stochastic water supply conditions, desert shrubs may actually instead thrive under numerous future climate change scenarios as long as the anticipated variations in precipitation stay within the envelope of known historic variations.

Different underlying drivers can give rise to resultant dynamics that are indistinguishable, signifying that caution must be employed when assigning causality to empirical observations (Figure 4.6). This result highlights the criticality of accurate ecological insight; understanding how a particular species responds to short-term water deficits has profound and counter-intuitive implications on discerning their longer-term dynamics. In our mortality analysis for one time step, the theoretical species which was insensitive to a water-deficit ($m < 1$) appeared to be relatively insensitive to changes in the water supply (Figure 4.3.a). However a different longer-term picture emerges when recruitment and mortality are considered together; this species tracks the cyclical precipitation pattern while the one more sensitive to the water-supply ($m > 1$) is instead out of phase with the prevailing precipitation regime as its numbers are highest when the precipitation levels are the lowest (Figure 4.3.b). This lag results from the coupled relationship between our recruitment and mortality arguments; when adults of the sensitive species die due to a lack of water, the recruitment rate cannot recover immediately upon the return of elevated precipitation levels due to a lack in seed producing shrubs.

Therefore field studies which try to extrapolate long-term trends from short-term observations of either recruitment or mortality alone may mistakenly interpret their observations, suggesting that our model may help provide complimentary information that will help scientists place snapshots into their large context. Although our model suggests a numeric recovery in the abundance, in both species where the population count follows and lags behind these longer-term precipitation trends (Figure 4.7), such results may not be actualized for other reasons. For example, the physical space relinquished upon the widespread mortality of longer-lived species often primes sites for invasions. In the field, this could result in either slowed recolonization or opportunistic ‘pioneer’ species could alter the biogeochemistry of the soil enough to irreversibly prohibit the recuperation of our modeled species (i.e. *Bromus Tectorum*) [*Evans et al., 2001*].

Lastly, additional exploration into the appropriate spatial scale of this model is essential [*Levin, 1992*]: Correlations absent when A = 100 m become observable when A = 400 m (Figure 4.7). Future research should determine the minimum plot size at which population level trends become noticeable and the outputs of this model, with consideration paid to small number statistics, become defensible. Modeling an area that is large enough to be reliable, but not too large to the point where the results become redundant, would simultaneously minimize data requirements and computational time. This would help clarify the circumstances under which this model could be applied and might lead to insights regarding how field studies and other technologies (i.e. satellite imagery) might play complimentary roles in understanding the long-term dynamics of these complex biological and ecological systems.

CHAPTER VI

IMPLICATIONS FOR FUTURE RESEARCH

The subsequent coupling of this model with a sediment transport model [*Roberts, 2010*] will advance our understanding of how shrubs modulate overall erosion rates in the desert. Whereas this is the immediate application, its simplistic nature and biologically informed underpinning means it is apt to find applications in other research communities also working at the interface between ecological systems and earth surface processes. For those working exclusively with plant communities, this research contributes a novel methodology that, with appropriate modification, might lead to valuable quantitative descriptions of the population dynamics of other plants in other environments. Our simple probabilistic approach appears to balance the uncertainty of the underlying complexity of our modeled populations while still retaining the essential influences on their behavior. Our model features inputs that have a solid biophysical basis and insofar as it has the capacity to mimic key features of real processes, leads to outputs which appear consistent with findings reported in the literature. It therefore contributes a promising framework through which to analyze how different shrub populations may change with time and could help clarify our mechanistic understanding of such systems, for instance, by providing a lense through which to examine both internal and external drivers or by helping in the preliminary determination of the appropriate level of detail needed for addressing specific research questions. In addition, for scientists studying the responsiveness of desert vegetation to variations in the water supply and those interested in the consequences associated with climate induced variations in the hydrological cycle, this model provides a means through which anticipated future changes, as projected by Global Climate Models (GCM), can be explored. It may also help identify sites and species that warrant particular concern, including those with vulnerabilities on human time-scales. Insomuch as this is relevant to the wealth-fare of future society (i.e. erosion, water-quality, grazing, property value), gaining such a perspective has relevance to the current decision making process. For example, by helping scientists place short-term results from field studies in proper context with the longer-term dynamics of a population, this research hold promise of complementing our empirical capacity and extending the current scope of our knowledge.

APPENDIX A

THE MASTER EQUATION AND THE CONSERVATION OF SHRUB AGE

The statement of conservation of shrub age, (PD1), can be formally obtained from the Master Equation. Momentarily neglecting sources and sinks, and letting τ [t] denote a small interval of time, the Master Equation may be written in classic form as

$$f_T(T,t+\tau) - f_T(T,t) = \int_0^\infty f_T(T',t)\,W(T,t+\tau|T',t)\,\mathrm{d}T' - \int_0^\infty f_T(T,t)\,W(T',t+\tau|T,t)\,\mathrm{d}T' \qquad \text{(A1)}$$

Here, $W(T, t + \tau \mid T', t)\mathrm{d}T'$ is the probability that a shrub will be of the age T at time $t + \tau$ given that it had an age T' at time t, and $W(T', t + \tau \mid T, t)\mathrm{d}T'$ is the probability that a shrub will be of the age T' at time $t + \tau$ given that it had an age T at time t. The first integral in (A1) represents the aging of shrubs from all possible ages T' to the age T during τ, and the second intregral quantity represents the aging of shrubs with age T at time t to all possible ages T' during τ. Note, however, that because shrubs age at precisely the rate $\mathrm{d}T/\mathrm{d}t = 1$, a shrub of the age T at time $t + \tau$ by definition had an age $T' = T - \tau$ at time t; and a shrub of the age T' at time $t + \tau$ by definition had an age $T = T' - \tau$ at time t. This means that $W(T, t + \tau \mid T', t) \equiv \delta\,(T - \tau - T', t)\mathrm{d}T'$ and $W(T', t + \tau \mid T, t) \equiv \delta\,(T' - \tau - T, t)$, where the Dirace delta function δ [t^{-1}] is fundamentally a probability density function. Substituting W and T′ in (A1) with $\mathrm{d}T' = \mathrm{d}\tau$ then gives,

$$f_T(T,t+\tau) - f_T(T,t) = \int_0^\infty f_T(T-\tau,t)\,\delta(0,t)\,\mathrm{d}\tau - \int_0^\infty f_T(T,t)\,\delta(0,t)\,\mathrm{d}\tau \qquad \text{(A2)}$$

By definition of the Dirac function, this simplifies to,

$$f_T(T-\tau,t) - f_T(T,t) = f_T(T-\tau,t) - f_T(T,t) \qquad \text{(A3)}$$

We now expand $f_T(T - \tau, t)$ as a Taylor series to give,

$$f_T(T-\tau,t) = f_T(T,t) - \frac{\partial f_T}{\partial T} + \frac{1}{2}\frac{\partial^2 f_T}{\partial T^2}\tau^2 - \ldots \qquad \text{(A4)}$$

Substituting (A4) into (A3), diving by dt, noting that $\tau = \mathrm{d}t$, and taking the limit as $\mathrm{d}t \to 0$ gives

$$\frac{\partial f_T(T,t)}{\partial t} = -\frac{\partial f_T}{\partial T}$$

which represents an “advection” of shrub age.

APPENDIX B

MATLAB CODE FOR NUMERICAL SOLUTIONS

```
%Lasted Updated 6/9/2010
tic
clear all;

%Basic Model Parameters
dt = 1; % time step (yr)
tmax = 500; % simulation run time (yr)
kmax = tmax/dt;
nframes = 100;
framespacing = kmax/nframes;

%Physical Dimensions of Modeled Area
X = 20; % downslope length (m)
Y = 20; % cross-slope length (m)
Area = X*Y; % Total area (m^2)

%Site specific climatic parameters
WPmu = 0.125; %Long-term average annual winter precipitation (m/yr)
WPsigma = 0.025; %Standard deviation of WPmu (m/yr)
phi = 0.15; %Constant describing the soil's propensity to retain moisture from
year to year, 0<phi<1
SPmu = 0.125; %Long-term average annual summer precipitation (m/yr)
SPsigma = 0.025; %Standard deviation of Spmu (m/yr)
OMEGA = 0.50; %Proportion of SP not lost to atmosphere
MAP = WPmu + SPmu; %Mean Annual Precipitation (m/yr)

%Model estimating shrub rooting depth (Schenk and Jackson 2002)
RDMax = 10^(-0.3857 + 0.2412*log10(MAP*1000)); %Max rooting depth (m)

%Soil profile differentiation and parameters
UL = 0.20; %Depth of upper soil layer (m), pertinent to recruitment and juvenile
mortality
LL = RDMax - UL; %Depth of lower soil layer (m), pertinent to adult mortality

%Description of initial population and population specific parameters
```

```
shrubdensitymu  =  0.675;  %  Average  areal  density  of  individuals  (N/m^2)
minshrubspacing = 0.20; %Minimum distance between extant shrubs (m)

%Parameters for characterizing shrubs comprising the initial population

    %Assuming a gamma distribution, parameters used to assign radius'
    A = 5; %Shape Parameter
    B = 0.04; %Scale Parameter
    %Canopy dimensions and parameters for Furbish 2009 logistic growth model
    R0 = 0.05; %Initial Radius (m) assigned to shrubs with age = 0 yr
    Rf = 0.60; %"Final" Radius (m) achieved by a shrub
    t90 = 10; %Age when a shrub reaches 90% of Rf (yr)
    T = (-t90)/log(1-((0.90*Rf - R0)/(Rf - R0))); % Characteristic growth
    rate constant
    RDCVRatio = RDMax/((4/3)*pi*(Rf)^3); %Rooting depth to canopy volume
    ratio (m^-2), where it is assumed that RD/CV is constant throughout
    shrub ontogeny

%Mortality Parameters
FC = 0.14; %Soil’s field capacity (m^3/m^3)
PWP = 0.06; %Soil’s permanent wilting point (m^3/m^3)
m = 2; %Parameter describing the species' sensitivity to water deficits
betaJ = 0.40; %Juvenile mortality rate constant, where 0 < betaJ < 1
betaA = 0.30; %Adult mortality rate constant, where 0 < betaA < 1

%Recruitment Parameters
smu = 10000; %Average seed production (Seeds/N)
ssigma = 0; %Interannual variability in smu (Seeds/N)
alpha = 0.0055; %Recruitment rate constant

%% Description of Initial Population
shrubdensity = shrubdensitymu;
N0 = round(Area * shrubdensity); % initial number of shrubs (N)

for n=1:N0;

    %Shrub attributes
    status(n) = 1; % 1 = live, 0 = dead
    radius(n) = gamrnd(A,B); % Assigns each shrub a radius from known/fitted
    gamma distribution of the population's radius (m)
```

```
    canopyvolume(n) = (4/3)*pi*(radius(n))^3; %Assigns canopy volume based
    on radius(n) assuming the shrub has a spherical shape (m^3)
    RD(n) = canopyvolume(n)*RDCVRatio;  %Assigns the shrub a rooting depth a
    based on its canopy volume and assuming isometric scaling
    age(n) = round(log(1-((radius(n) - R0)/(Rf - R0)))*(-T));  %Estimates
    the shrub’s age using the logistic growth function

    %Positions the shrub
    xc(n) = random('unif',0,X); % x-coordinate of shrub center (m)
    yc(n) = random('unif',0,Y); % y-coordinate of shrub center (m)
    temp = n;
    if temp > 1; %Tests the shrub’s position with respect to previously
    planted shrubs
       b = 1;
       attempt = 1;
       while b <= n - 1;
             flag = 1;
             d = sqrt((xc(n)-xc(b))^2 + (yc(n)-yc(b))^2)- radius(n) -
           radius(b);
             if d <= minshrubspacing; %Repositions the shrub if it is too
             close to an extant shrub
                xc(n) = random('unif',0,X); % new x-coordinate (m)
                yc(n) = random('unif',0,Y); % new y-coordinate (m)
                flag = 0;
             end
             b = b + 1;
             if flag == 0;
                b = 1;
                attempt = attempt + 1;
                if attempt > 1000;
                   error('cannot position shrub')
                end
             end
       end
    end
end

N = N0; %Initial population count
V = 0; %Movie frame counter
```

```
for k=1:kmax
    time(k) = k*dt;

    %Recruitment/Juvenile Mortality Variables
      %Different Summer Precipitation Scenarios (Turn on/of as desired)
      SP(k)= SPmu; %Constant
      %SP(k) = normrnd(SPmu,SPsigma); %Stochastic
      %SP(k) = 0.05*sin((pi()/100)*k)+ SPmu; %Cyclical

      ULthetaave = (SP(k)*OMEGA)/UL + PWP; %Average daily water content of upper
      soil layer assuming water is distributed uniformly with depth of the
      compartment (m/m)
    if SP(k) < 0; %Corrects for any negative random numbers that are drawn
       SP(k) = 0;
    end

    %Adult Mortality Variables

    %Different Winter Precipitation Scenarios (Turn on/off as desired)
    WP(k) = WPmu; % Constant
    %WP(k) = normrnd(WPmu,WPsigma); %Stochastic
    %WP(k) = 0.05*sin((pi()/100)*k)+WPmu; %Cyclical
    %WP(k) = phi*WP(k-1) + normrnd(WPmu,WPsigma); % Winter precipitation in
     lower soil layer in year k assuming a first-order auto-regressive
     process:  some fraction "phi" of k-1's precipitation + average WP + some
     random shock
    if WP(k) < 0;
       WP(k) = 0;
    end
    LLthetaave = WP(k)/LL; %Average water content of lower soil layer if
    water is distributed uniformly with depth (m/m)

            %Boundary Conditions:
            if LLthetaave < 0; %Precipitation cannot be a negative value
               LLthetaave = 0;
            end
            if LLthetaave > FC - PWP; %Precipitation cannot contribute more
          water than the soil's water holding capacity
               LLthetaave = FC - PWP; %Maximum plant available water
            end
```

```
gamma = (((ULthetaave - PWP)/LLthetaave)-1)*(-1/LL); %Description of how
LLthetaave varies with depth (m^-1)

%% Juvenile and Adult Mortality
PJM = betaJ*(PWP/(ULthetaave))^m; %Probability of Juvenile Mortality in
the year k is proportional to the adequacy of the upper soil layer's
water content 0 < PJM < 1

for n=1:N;

  %For "juvenile" shrubs, dependent on upper level moisture/summer
  precipitation
  if RD(n) <= UL; %If n's rooting depth is within the confines of the
     upper soil layer
       Death = rand();
       if Death <= PJM;
          status(n) = 0; %Shrub dies
       end
       if Death > PJM;
          status(n) = 1; %Shrub lives
       end
  end

  %For "adult" shrubs, dependent on lower level moisture/winter
   precipitation
    if RD(n) > UL; %If n has a root system long enough to access the
     lower soil layer
       theta(n) = LLthetaave*(1 + gamma*((RD(n)-UL) - LL)) + PWP; %This
       is the water content at n's rooting depth, adjusted for the fact
       that water is not distributed uniformly with depth
       PMA(n) = betaA*(PWP/theta(n))^m; %Probability of adult mortality
       is related to soil’s water content at the shrub’s rooting depth
       Death = rand();
       if Death <= PMA(n);
          status(n) = 0; %Shrub dies
       end
       if Death > PMA(n);
          status(n) = 1; %Shrub lives
       end
```

```
    end
end

%% Population count: Renumbering and aging all survivors
count = 0;
for n=1:N;
    temp = status(n);
    if temp == 1 %If n was a survivor
       count = count + 1; %Count it
       xc(count) = xc(n); %The x-position of the surviving shrub is
       simply its original position
       yc(count) = yc(n); %The y-position of the surviving shrub is
       simply its original position
       age(count) = age(n) + dt; %The age of this aged shrub is simply
       its old age plus the elapsed time step
       dRdtmu = (exp(1)^(-age(count)/T))/T*(Rf-R0); %Average age
       specific annual growth rate (m/yr);
       dRdtsigma = 0.15 * dRdtmu; %Standard deviation in dRdtmu
       reflecting the species' plasticity (m/yr)
       dRdt = normrnd(dRdtmu,dRdtsigma); %Actualized growth drawn from
       normal distribution (m/yr)
       radius(count) = radius(n) + dRdt*dt; %new radius (m)
       canopyvolume(count) = (4/3)*pi*(radius(count))^3; %new canopy
       volume (m)
       RD(count) = canopyvolume(count)*RDCVRatio; %new rooting depth (m)
    end
end
Nsurvivors = count; %Number of Survivors

%% Recruitment Variables
%Calculates the number of seed producing shrubs ("Adults")
Nseed = 0;
for n = 1:Nsurvivors;
    if RD(n) > UL; %Shrubs with access to LL moisture produce seeds
       Nseed = Nseed + 1;
    end
end
s = round(normrnd(smu,ssigma)); %Number of seeds produced per shrub
%Proportion of area occupied by extant population; "effective area" (EA)
precludes the addition of new individuals (m^2)
```

```
EAPop = 0;
for n = 1:Nsurvivors;
    EA(n) = 1.5 * pi()*(radius(n))^2; %Effective area of shrub n (m^2)
    EAPop = EAPop + EA(n);
end
SPACE = (Area - EAPop)/Area; %Area available for new recruits
WATER = (ULthetaave-PWP)/ULthetaave; %Water available to seedlings;

%% Final Statement of the Number of Recruited Shrubs
Nrecruited = round(alpha * WATER * SPACE * Nseed* s);

%Assigns New Recruits Physical Dimensions
for n = Nsurvivors + 1:Nsurvivors + Nrecruited;
       status(n) = 1;
       age(n) = 0;
       radius(n) = R0;
       canopyvolume(n) = (4/3)*pi*(radius(n))^3;
       RD(n) = canopyvolume(n)*RDCVRatio;
       %Positioning of new recruit
       xc(n) = random('unif',0,X);
       yc(n) = random('unif', 0,Y);
       temp = n;
       b = 1;
       attempt = 1;
       while b <= n-1; %Tests positioning with respect to other shrubs
             flag = 1;
             d = sqrt((xc(n)-xc(b))^2 + (yc(n)-yc(b))^2)- radius(n) -
                 radius(b);
             if d <= minshrubspacing; %Repositions if too close
                xc(n) = random('unif',0,X);
                yc(n) = random('unif',0,Y);
                flag = 0;
             end
             b = b + 1;
             if flag == 0;
                b = 1;
                attempt = attempt + 1;
             end
             if attempt > 1000000;
                error ('cannot position shrub')
```

```
                break
            end
        end
end

N = Nsurvivors + Nrecruited; %Shrub count at time k
Nplot(k) = N;

%Preallocation of matrices
x = zeros(N,1);
y = zeros(N,1);
r = zeros(N,1);
g = zeros(N,1);

%Collects demographic information of the shrub population at time k
AgeCount = 0;
for n = 1:N;
    x(n) = xc(n);
    y(n) = yc(n);
    r(n) = radius(n);
    g(n) = age(n);
    AgeCount = AgeCount + g(n);
end
AverageAge(k) = AgeCount/N;
agemax = 100;
for w = 1:agemax;
    AGE = w;
    agecount = 0;
    for n = 1:N;
        if g(n) == AGE;
           agecount = agecount + 1;
        end
    end
    finalagecount(w) = agecount;
end


%Graphs of results
clf('reset')
Vtemp = mod(k,1);
```

```
    if Vtemp == 0
        V = V + 1;
        subplot(2,2,[1 3]); %Bird’s eye view of population dynamics
        scatter(x,y,round(r*100),'markerfacecolor','g');
        axis equal;
        axis([0,10,0,10]);
        subplot(2,2,2); %Change in Shrub Count with time
        plot(time, Nplot);
        axis([1,tmax,0,750]);
        xlabel('Year')
        ylabel('shrub count')
        subplot (2,2,4); %Demographics of shrub population at time k
        bar(1:agemax,finalagecount);
        xlabel('age')
        ylabel('shrub count')
        axis([0 50 0 500]);
        Mov(V) = getframe(gcf);
    end

end
%movie2avi(Mov,'PopDemo','fps',2) %Turn on to create a movie

toc
```

APPENDIX C

PARAMETER VALUES AS INFORMED BY FIELD DATA

A vegetation survey of a Rabbitbrush population, conducted in May 2009 in a 20 m x 20 m plot in Cibola National Forest (Figure C.1), helped inform the parameter values that are used in our modeled shrub population. Data collected by *Roberts* [2010] included shrub position, canopy breadth, and height. The distribution of canopy radii was fit using a gamma distribution, leading to the two parameters describing the age/size structure, $\Gamma(\alpha,\beta)$, of the population as well as our estimates for the initial canopy radius, R_i, and the final or maximum canopy radius, R_f (Figure C.2).

Figure C.1. Vegetation survey conducted in May 2009 on a Rabbitbrush population in Cibola National Forest, NM.

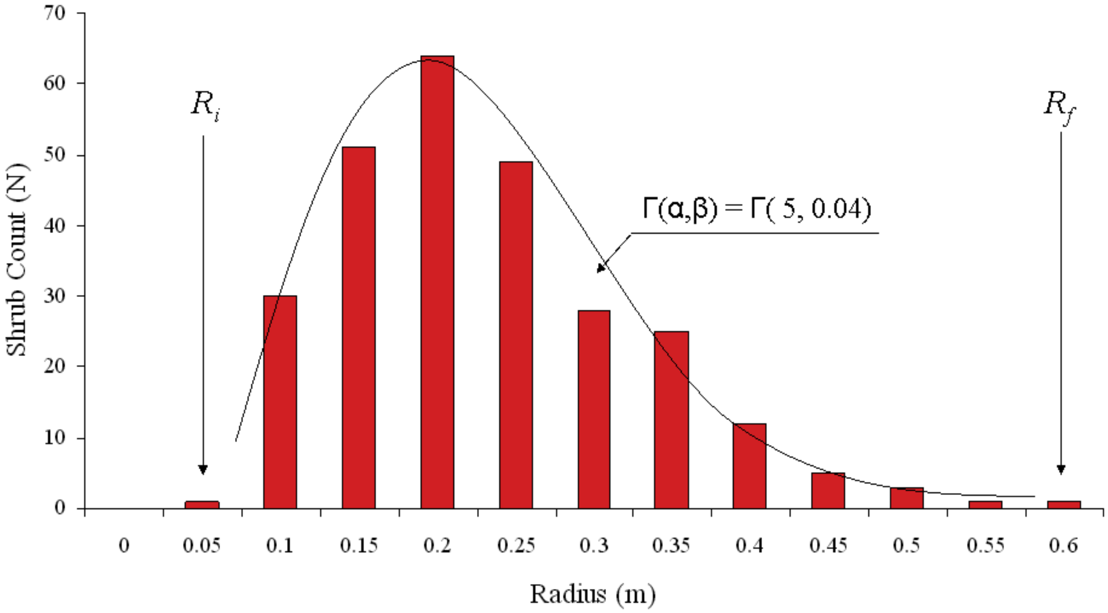

Figure C.2. Parameters from a gamma distribution fit of Rabbitbrush canopy radii data.

Spatial Pattern

To ecologists, dispersion refers to the spatial arrangement which results from the dispersal, or movement, of individual organisms [*Pielou, 1977*]. The dispersion of a population, or the physical spacing of individuals across a given plane, can be classified on a continuum ranging from highly aggregated to random to regular or hyper-dispersed. To classify the spatial pattern of our surveyed population, we use the nearest neighbor test as outlined in *Clarke and Evans* [1954] (Figure C.3).

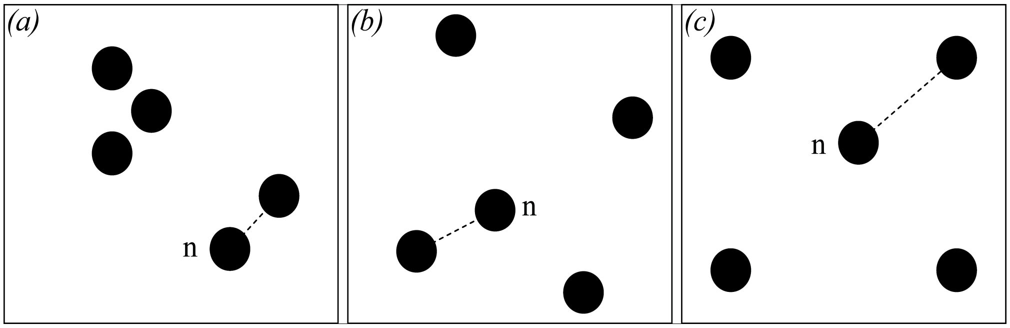

Figure C.3. Example spatial arrangements (or dispersions) of individuals located in a plane. *(a)* Aggregated, *(b)* random, and *(c)* regular spatial pattern with the distance to the nearest neighbor, represented by the dashed line, drawn for shrub *n*.

Under the null hypothesis, we assume our population has a random dispersion where the locations of all individuals are independent of one another and each site within our modeled area A has the same probability of occupancy as all others. The actual average distance to the nearest neighbor of the surveyed population, r_A, is then given by,

$$r_A = \frac{\sum_{n=1}^{n=N(t)} r_n}{N(t)}$$

where r_n is the distance between the nth shrub and its nearest neighbor (Appendix D). We can then calculate the mean distance that would be expected, r_E, if a theoretical population of the same density, $\rho = N(\mathrm{t})/A$, were distributed at random, r_E, by,

$$r_E = \frac{1}{2\sqrt{\rho}}$$

The degree to which our surveyed population departs from the case of randomness is then determined by the ratio of these two values or the nearest-neighbor statistic, $R = r_A / r_E$. R ranges from 0.0 for a spatial distribution where all the points are aggregated, to 1.0 for a random spatial distribution, to a maximum value of 2.15 where the population is hyper-dispersed. The values needed for testing the null hypothesis can be found in Table C.1 and allow us to conclude that individuals located within our field population are randomly positioned.

r_A	0.6556
r_E	0.6086
R	1.0077

Table C.1. Values used to test the null hypothesis that the surveyed Rabbitbrush population has a random spatial distribution.

APPENDIX D

SPATIAL DATA AND NEAREST NEIGHBOR ALGORITHM

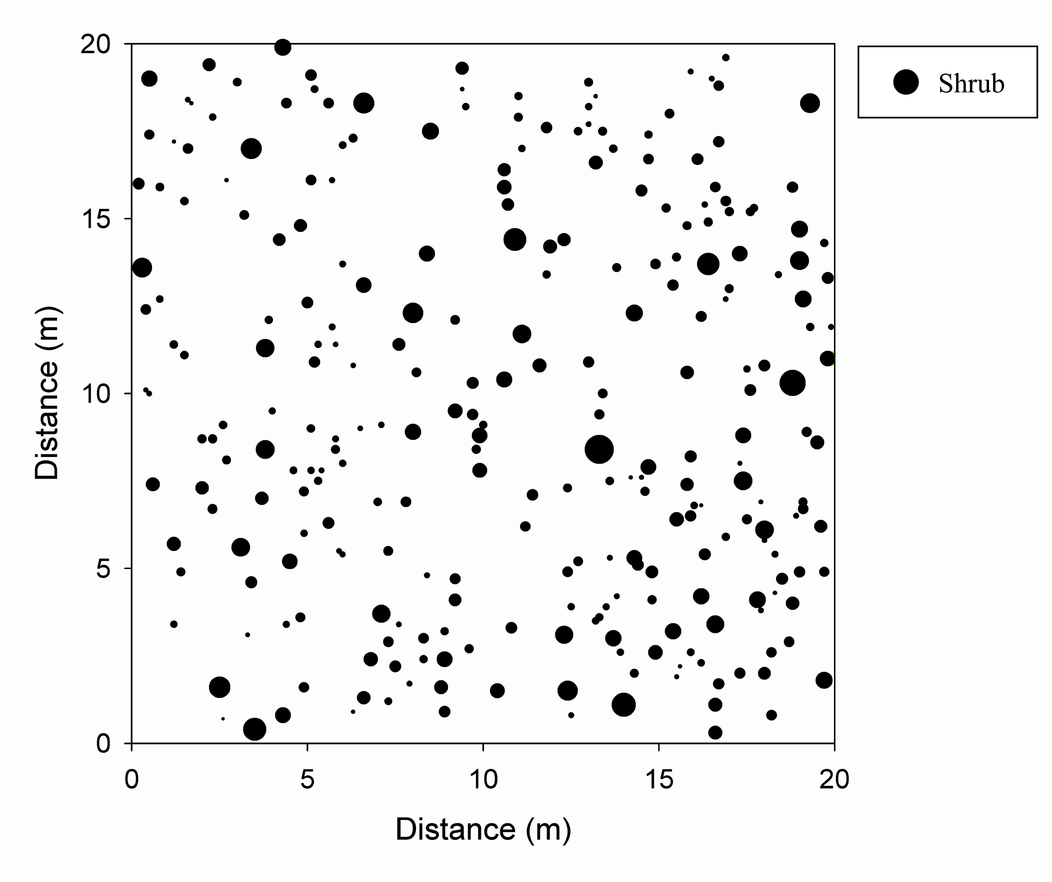

Figure D.1. Map depicting the location and relative canopy size of individuals comprising a May 2009 surveyed Rabbitbrush shrub population in Cibola National forest, New Mexico [*Roberts, 2010*].

```
%MATLAB Code Calculates the Observed Average Distance to the Nearest Neighbor
from surveyed field data

%Survey
X = 20; % Length of X transect (m)
Y = 20; % Length of Y transect (m)
A = 20; % Total Surveyed Area (m^2)
N = 270; % Number of shrubs observed
rho = N/A; %Shrub areal density (N/m^2)

%Coordinates of all individuals within the surveyed area
```

```
for n = 1:N;

%x position
x = [1.2 2.6 14.2 16.2 6.3 1.7 18.3 15.6 15.6 17.9 13.2 0.4 3.3 2.7 6.5 6.3 9.4
17.3 8.4 15.5 7.6 14.5 1.6 13.6 16.9 5.8 18 0.5 12.5 5.4 17.9 13.8 16.5 5.7 19.9
13 7.9 5.9 7.1 10 15.9 16.3 6 18.3 18.9 5.8 5.7 2.3 5.3 13.3 6 8.3 1.2 4.9 4.4
13.5 1.2 16.9 6 13 9.5 17.5 18.4 0.8 7.3 12.5 13.9 4 16.2 4.6 5.3 15.9 5.1 11
13.2 16 8.9 5.2 11 3.9 19.3 6 1.5 6.3 16.9 19.2 14.7 1.5 11.1 7 2.3 5.8 11.8 17.7
13.6 12.7 13 0.8 15.5 5.1 2.6 19.7 13.4 13.8 1.4 12.4 14.3 2.7 13.7 17 17.6 3
14.6 17 9.2 3.2 8.1 12.7 16.7 15.8 0.4 7.3 13.3 17.5 9.6 14.8 19.1 9.8 4.9 2.3
2 0.5 16.4 11.2 8.3 4.8 15.2 1.6 13.4 4.4 18.2 5.6 0.2 18.5 9.7 16.7 2 7.8 16.2
14.9 15.3 19.1 18.2 13 7.3 4.9 16.6 12.4 3.4 17.3 5.1 9.2 11.4 15.9 5.1 16.7 5
16.3 18.8 19.7 8.9 15.4 9.7 16.9 18.7 14.4 10.8 14.7 9.2 5.2 16.7 14.5 4.2 18 6.6
15.9 10.7 2.2 19.8 17.6 19 7.6 5.6 7.5 16.6 11.8 3.7 14.8 18 0.6 15.8 10.6 13.2
17.3 16.1 1.2 15.8 4.8 12.3 19.5 6.8 8.8 9.4 19.6 10.6 6.6 10.4 14.7 18.8 15.5
17.4 9.2 11.9 9.9 16.6 11.6 14.9 14.3 4.5 7.1 8.4 9.9 16.2 15.4 19.8 13.7 10.6
4.3 4.3 0.5 17.8 8 19 19 19.7 14.3 8.9 19.1 11.1 16.6 12.3 3.8 3.1 2.5 0.3 12.4
17.4 8.5 18 19.3 3.4 3.8 6.6 8 3.5 16.4 14 10.9 18.8 13.3];

%Y Position
y = [17.2 0.7 7.6 6.8 0.9 18.3 4.3 2.2 2.2 6.9 18.5 10.1 3.1 16.1 9 10.8 18.7 8
4.8 1.9 3.4 7.6 18.4 5.3 12.7 11.4 5.8 10 0.8 7.8 3.8 4.2 19 16.1 11.9 17.7 1.7
5.5 9.1 9.1 19.2 15.4 13.7 5.4 6.5 8.7 11.9 17.9 11.4 3.6 5.4 2.4 11.4 6 3.4 3.9
3.4 19.6 8 18.2 18.2 10.7 13.4 12.7 1.2 3.9 2.6 9.5 2.3 7.8 7.5 2.6 7.8 18.5 3.5
6.8 3.2 18.7 17.9 12.1 11.9 17.1 15.5 17.3 5.9 8.9 17.4 11.1 17 6.9 8.7 8.4 13.4
15.3 7.5 17.5 18.9 15.9 13.9 9 9.1 14.3 17.5 13.6 4.9 7.3 2 8.1 17 13 15.2 18.9
7.2 15.2 12.1 15.1 10.6 5.2 1.7 14.8 12.4 5.5 9.4 6.4 2.7 4.1 6.9 8.4 7.2 6.7 7.3
17.4 14.9 6.2 3 3.6 15.3 17 10 18.3 2.6 18.3 16 4.7 9.4 17.2 8.7 6.9 12.2 13.7
18 6.7 0.8 10.9 2.9 1.6 15.9 4.9 4.6 2 19.1 4.7 7.1 6.5 16.1 18.8 12.6 5.4 15.9
4.9 0.9 13.1 10.3 15.5 2.9 5.1 3.3 16.7 4.1 10.9 1.7 15.8 14.4 10.8 1.3 8.2 15.4
19.4 13.3 10.1 4.9 11.4 6.3 2.2 0.3 17.6 7 4.9 2 7.4 7.4 16.4 16.6 14 16.7 5.7
10.6 14.8 14.4 8.6 2.4 1.6 19.3 6.2 15.9 13.1 1.5 7.9 4 6.4 8.8 9.5 14.2 7.8 1.1
10.8 2.6 5.3 5.2 3.7 14 8.8 4.2 3.2 11 3 10.4 0.8 19.9 19 4.1 8.9 14.7 13.8 1.8
12.3 2.4 12.7 11.7 3.4 3.1 8.4 5.6 1.6 13.6 1.5 7.5 17.5 6.1 18.3 17 11.3 18.3
12.3 0.4 13.7 1.1 14.4 10.3 8.4];

end


%This loop calculates the nearest neighbor for the first shrub
```

```
for n = 1;
       a = n;
       Neighbor(a) = 100;
            for n = 2:N;
                d(n) = sqrt((x(n)-x(a))^2+(y(n)-y(a))^2);
                if d(n) < Neighbor(a);
                   Neighbor(a) = d(n);
                end
            end
end

%This loop calculates the nearest neighbor for the last shrub
for n = 270;
       a = n;
       Neighbor(a) = 100;
            for n = 1:N-1;
                d(n) = sqrt((x(n)-x(a))^2+(y(n)-y(a))^2);
                if d(n) < Neighbor(a);
                   Neighbor(a) = d(n);
                end
            end
end

%This loop calculates the nearest neighbor for all other shrubs
for n = 2:N-1;
    a = n;
    Neighbor(a) = 100;
            for n = 1:a-1;
                d(n) = sqrt((x(n)-x(a))^2+(y(n)-y(a))^2);
                if d(n) < Neighbor(a);
                   Neighbor(a) = d(n);
                end
            end
            for n = a+1:N;
                d(n) = sqrt((x(n)-x(a))^2+(y(n)-y(a))^2);
                if d(n) < Neighbor(a);
                   Neighbor(a) = d(n);
                end
            end
```

```
end

ActualANN = mean(Neighbor) %Actual average distance to nearest neighbor


ExpectedANN = 1/(2*(rho)^(0.5)) %Expected average distance to nearest
                         neighbor
R = ActualANN/ExpectedANN
```

REFERENCES

Abrahams, A.D. and A.J. Parsons (1991), Relation between infiltration and stone cover on a semiarid hillslopes, southern Arizona, *Journal of Hydrology, 122*, 49-59.

Ackerman, T.L. (1979), Germination and survival of perennial plant species in the Mojave Desert, *The Southwestern Naturalist, 24*, 399-408.

Adams, D.K. and A.C. Comrie (1997), The North American monsoon, *Bulletin of the American Meteorological Society, 78*, 2197-2213.

Alizai, H.A. and L.C. Hulbert (1970), Effects of soil texture on evaporative loss and available water in semi-arid climates, *Soil Science, 110,* 328-332.

Allen, A.P., W.T. Pockman, C. Restrepo, and B.T. Milne (2008), Allometry, growth, and population regulation of the desert shrub Larrea tridentata, *Functional Ecology, 22,* 197-204.

Alpert, P. and E.L. Simms (2002), The relative advantages of plasticity and fixity in different environments; when is it good for a plant to adjust? *Evolutionary Ecology, 16,* 285-297.

Baskin, Jerry M. and Carol C. Baskin (1973), Plant Population Differences in Dormancy and Germination Characteristics of Seeds: Heredity or Environment? *American Midland Naturalist, 90,* 493-498.

Bochet, E., J. Poesen, and J.L. Rubio (2000), Mound development as an interaction of individual plants with soil, water erosion and sedimentation processes on slopes, *Earth Surface Processes and Landforms, 25,* 847-867.

Bonser, S.P. and L.W. Aarssen (2009), Interpreting reproductive allometry: Individual strategies of allocation explain size-dependent reproduction in plant populations, *Perspectives in Plant Ecology, Evolution and Systematics, 11,* 31-40.

Bowers, J.E. (1994), Natural conditions for seedling emergence of three woody species in the northern Sonoran Desert, *Madrono, 41,* 73-84.

Bowers, J.E. (2005), Effects of drought on shrub survival and longevity in the northern Sonoran Desert, *Journal of the Torrey Botanical Society, 132,* 421-431.

Bowers, J.E. and R.M. Turner (2001), Dieback and episodic mortality of *Cercidium microphyllum* (foothill paloverde), a dominant Sonoran Desert tree, *Journal of the Torrey Botanical Society, 128*, 128-140.

Bowers, J.E., R.M. Turner, and T.L. Burgess (2004), Temporal and spatial patterns in emergence and early survival of perennial plants in the Sonoran Desert, *Plant Ecology*, 172, 107-119.

Bowker, G.E., D.A. Gillette, G. Bergametti, B. Marticorena, and D.K. Heist (2008), Fine-scale simulations of Aeolian sediment dispersion in a small area in the northern Chihuanhuan Desert, *Journal of Geophysical Research-Earth Surface,* 113(F2).

Bradshaw, A.D. (1965), Evolutionary significance of phenotypic plasticity in plants, *Advances in Genetics, 13,* 115-155.

Bradshaw, A.D. and T. McNeilly (1991), Evolutionary response to global climatic-change, *Annals of Botany, 67,* 5-14.

Breshears, D.D., O.B. Myers, and F.J. Barnes (2009), Horizontal heterogeneity in the frequency of plant-available water with woodland intercanopy-canopy vegetation patch type rivals that occurring vertically by soil depth, *Ecohydrology, 2,* 503-519.

Bresearch, D.D., P.M. Rich, F.J. Barnes, and K. Campbell (1997), Overstory-imposed heterogeneity in solar radiation and soil moisture in a semiarid woodland, *Ecological Adaptations, 7,* 1201-1215.

Brisson, J. and J.F. Reynolds (1994), The effect of neighbors on root distribution in a creosotebush (Larrea tridentata) population, *Ecology, 75,* 1693-1702.

Brown, J.H., O.J. Reichman, and D.W. Davidson (1979), Granivory in desert ecosystems, *Annual Review of Ecology and Systematics, 10,* 201-227.

Brown, J.H., T.J. Valone, and C.G. Curtin (1997), Reorganization of an arid ecosystem in response to recent climate change, *Proceedings of the National Academy of Sciences of the Unites States of America, 94,* 9729-9733.

Canadell, J., R.B. Jackson, J.R. Ehleringer, H.A. Mooney, O.E. Sala, and E.D. Schulz (1996), Maximum rooting depth of vegetation types at the global scale, *Oecologia, 108,* 583-595.

Casper, B.B., H.J. Schenk, and R.B. Jackson (2003), Defining a plant's belowground zone of influence, *Ecology, 84,* 2312-2321.

Chambers, J.C. and MacMahon, J.A. (1994), A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems*, Annual Review of Ecology and Systematics,* 25, 263-292.

Chapin, F.S. (1991), Integrated response of plants to stress, *Bioscience, 41,* 29-36.

Chapin, F.S., K. Autumn, and F. Pugnaire (1993), Evolution of suites of traits in response to environmental stress, *The American Naturalist, 142,* 78-92.

Childs, E.M. (2008), Rain splash as an advection-dispersion process, with implications for plant-soil interactions in arid environments, M.S. thesis, Vanderbilt University, Nashville.

Christensen, E.M. and R.C. Brown (1963), A blackbrush over 400 years old, *Journal of Range Management, 16,* 118.

Clark, P.J. and F.C. Evans (1954), Distance to nearest neighbor as a measure of spatial relationships in populations, *Ecology, 35,* 445-453.

Clarke, J.H, M.M. MacDonell, E.D. Smith, R.J. Dunn, and W.J. Waugh (2004), Engineered containment and control systems: Nurturing nature, *Risk Analysis, 24*, 771-779.

Czaran, T. and S. Bartha (1992), Spatiotemporal dynamic models of plant populations and communities, *Trends in Ecology and Evolution, 7,* 38-42.

de Villalobos, A.E. and D.V. Pelaez (2001), Influences of temperature and water stress on germination and establishment of Prosopis caldenia burk, *Journal of Arid Environment, 49,* 321-328.

Devitt, D.A. and S.D. Smith (2002), Root channel macropores enhance downward movement of water in a Mojave Desert ecosystem, *Journal of Arid Environments, 50,* 99-108.

Dodd, G.L. and L.A. Donovan (1999), Water potential and ionic effects on germination and seedling growth of two cold desert shrubs, *American Journal of Botany, 86,* 1146-1153.

Donovan L.A. and Ehleringer J.R. (1994), Water stress and use of summer precipitation in a Great Basin shrub community, *Functional Ecology, 8,* 289-297.

Dunkerley, D. (2002), Systematic variation of soil infiltration rates within and between the components of the vegetation mosaic in an Australian desert landscape, *Hydrological Processes, 16*, 119-131.

Dunne, T., W.H. Zhang, and B.F. Aubry (1991), Effects of rainfall, vegetation, and microtopography on infiltration and runoff, *Water Resources Research, 27,* 2271-2285.

Ehrlén, J. and K. Lehtilä (2002), How perennial are perennial plants? *Oikos, 98,* 308-322.

Evans, R.D., R. Rimer, L. Sperry, and J. Belnap (2001), Exotic plant invasion alters nitrogen dynamics in an arid grassland, *Ecological Applications, 11,* 1301-1310.

Eriksson, O. and J. Ehrlen (1992), Seed and microsite limitation of recruitment in plant populations, *Oecologia, 91,* 360-364.

Fay, P.A., J.D. Carlisle, A.K. Knapp, J.M. Blair, and S.L. Collins (2000), Altering rainfall timing and quantity in a mesic grassland ecosystem: Design and performance of rainfall manipulation shelters, *Ecosystems, 3,* 308-319.

Fenner, M. (1987), Seedlings, *New Phytologist, 106,* 35-37.

Fernandez, O.A. and M.M. Caldwell (1975), Phenology and Dynamics of root growth of three cool semi-desert shrubs under field conditions, *Journal of Ecology, 63,* 703-714.

Fernandez-Illescas, C.P., A. Porporato, F. Laio, and I. Rodriquez-Iturbe (2001), The ecohydrological role of soil texture in a water-limited ecosystem, *Water Resources Research, 37,* 2863-2872.

Flanagan, L.B., J.R. Ehleringer, and J.R. Marshall (1992), Differential uptake of summer precipitation among co-occurring trees and shrubs in a pinyon-juniper woodland, *Plant Cell and Environment, 15,* 831-836.

Fonteyn, P.J. and B.E. Mahall (1981), An experimental analysis of structure in a desert plant community, *Journal of Ecology, 69,* 883-896.

Frazer, J.M. and S.D. Davis (1988), Differential survival of chaparral seedlings during the first summer drought after wildfire, *Oecologia, 76,* 215-221.

Furbish, D.J., E.M. Childs, P.K. Haff, and M.W. Schmeeckle (2009), Rain splash of soil grains as a stochastic advection-dispersion process, with implications for desert plant-soil interactions and land-surface evolution, *Journal of Geophysical Research- Earth Surface, 114,* F00A03.

Gabet, E.J. and T. Dunne (2003), Sediment detachment by rain power, *Water Resources Research, 39,* 1002.

Gebauer, R.L.E., S. Schwinning, and J.R. Ehleringer (2002), Interspecific competition and resource pulse utilization in a cold desert community, *Ecology, 83,* 2602-2616.

Gile, L.H., R.P. Gibbens, and J.M. Lenz (1998), Soil-induced variability in root systems of creosotebush (Larrea tridentata) and tarbush (Flourensia cernua), *Journal of Arid Environments, 39,* 57-78.

Gill, R.A. and R.B. Jackson (2000), Global patterns of root turnover for terrestrial ecosystems, *New Phytologist, 147*, 13-31.

Gillespie, I.G. and M.E. Loik (2004), Pulse events in Great Basin Desert shrublands: physiological responses of Artemisia tridentate and Purshia tridentata seedlings to increased summer precipitation, *Journal of Arid Environments, 59,* 41-57.

Gillette D.A., J.E. Herrick, and G.A. Herbert (2006), Wind characteristics of mesquite streets in the northern Chihuahuan Desert, New Mexico, USA, *Environmental Fluid Mechanics, 6,* 241-275.

Goldberg, D.E. and R.M. Turner (1986), Vegetation Change and Plant Demography in Permanent Plots in the Sonoran Desert, *Ecology, 67,* 695-712

Guo, Q., PW Rundel, and D.W. Goodall (1998), Horizontal and vertical distribution of desert seed banks: patterns, causes and implications, *Journal of Arid Environments, 38,* 465-478.

Gutterman, Y. (1994), Strategies of Seed Dispersal and Germination in Plants Inhabiting Deserts, *Botanical Review, 60,* 373-425.

Greene, D.F. and E.A. Johnson (1993), Seed mass and dispersal capacity in wind-dispersed diaspores, *Oikos, 67,* 69-74.

Hamerlynck, E.P. and J.R. McAuliffe (2008), Soil-dependent canopy die-back and plant mortality in two Mojave Desert Shrubs, *Journal of Arid Environments, 72,* 1793-1802.

Hamill, D.N. and S.J. Wright (1986), Testing the dispersion of juveniles relative to adults: a new analytic method, *Ecology, 67,* 952-957.

Hanley, M.E. (1998), Seedling herbivory, community composition and plant life history traits, *Perspectives in Plant Ecology, Evolution, and Systematics, 1,* 191-205.

Harrington, G.N. (1991), Effects of soil moisture on shrub seedling survival in a semi-arid grassland, *Ecology, 72,* 1138-1149.

Hereford, R., R.H. Webb, C.I. Longpré (2006), Precipitation history and ecosystem response to multidecadal precipitation variability in the Mojave desert region, 1893-2001, *Journal of Arid Environments, 67,* 13-34.

Herrera, C.M., P. Jordano, J. Guitian, and A. Traveset (1998), Annual variability in seed production by woody plants and the masting concept: Reassessment of principles and relationship to pollination and seed dispersal, *The American Naturalist, 152,* 576-594.

Houle, G. (1995), Seed Dispersal and Seedling Recruitment: The Missing Link(s), *Ecoscience, 2,* 238-244.

Jeltsch, F., K.A. Moloney, F.M. Schurr, M. Köchy, and M. Schwager (2008), The state of plant population modeling in light of environmental change, *Perspectives in Plant Ecology, Evolution, and Systematics, 9,* 171-189.

Kelly, D. (1994), The evolutionary ecology of mast seeding, *Trends in Ecology and Evolution, 9,* 465-470.

Khan, M.A. and I.A.Ungar (1997), Effects of light, salinity, and thermoperiod on the seed germination of halophytes, *Canadian Journal of Botany, 75,* 835-841.

Kruse, W.H. (1979), Temperature and moisture stress effect germination of Gutierrezia sarothrae, *Journal of Range Management, 23,* 143-145.

LaMarch, V.C. and H.C. Fritts (1971), Anomaly patterns of climate over western united states, 1700-1930, derived from principle component analysis of tree-ring data, *Monthly Weather Review, 99,* 138.

Lamont, B.B., E.T.F. Witkowski, N.J. Enright (1993), Post-fire litter microsites: safe sites for seeds, unsafe for seedlings, *Ecology, 74,* 501-512.

Lauenroth, W.K., O.E. Sala, D.P. Coffin, and T.B. Kirchner (1994), The importance of soil-water in the recruitment of bouteloua-gracilis in the shortgrass steppe, *Ecological Applications, 4,* 741-749.

Lauenroth, W. K. and P.B. Adler (2008), Demography of perennial grassland plants: survival, life expectancy and life space, *Journal of Ecology, 96,* 1023-1032.

Leffler, A.J., C.Y. Ivans, R.J. Ryel, and M.M. Caldwell (2004), Gas exchange and growth responses of the desert shrubs Artemisia Tridentata and Chrysothamnus Nauseous to shallow- vs. deep-soil water in a glasshouse experiments, *Environmental and Experimental Botany, 51,* 9-19.

Le Houerou, H.N. (1984), Rain use efficiency: a unifying concept in arid-land ecology, *Journal of Arid Environments, 7,* 213-247.

Levin, S.L. (1992), The problem of pattern and scale in ecology, *Ecology, 73,* 1943-1967.

Lin, G., S.L. Phillips, and J.R. Ehleringer (1996), Monsoonal precipitation responses of shrubs in a cold desert community on the Colorado Plateau, *Oecologia, 106,* 8-17.

Linhart, Y.B. and M.C. Grant (1996), Evolutionary significance of local genetic differentiation in plants, *Annual Review of Ecology and Systematics, 27,* 237-277.

Loik, M.E., D.D. Breshears, W.K. Lauenroth, and J. Belnap (2004), A multi-scale perspective of water pulses in dryland ecosystems: climatology and ecohydrology of the western USA. Special section: Precipitation pulses in Arid Ecosystems, *Oecologia, 141,* 269-281.

Louda, S.M. (1983), Seed predation and seedling mortality in the recruitment of a shrub, haplopappus-venetus (Asteraceae), along a climatic gradient, *Ecology, 64,* 511-521.

Ludwig, J.A., B.P. Wilcox, D.D. Breshears, D.J. Tongway, and A.C. Imeson (2005), Vegetation Patches and Runoff-Erosion as Interacting Ecohydrological Processes in Semiarid Landscapes, *Ecology, 86,* 288-297.

Mattson, W.J. and R.A. Haack (1987), The role of drought in outbreaks of plant-eating insects, *BioScience, 37,* 110-118.

Mayeux, H.S., Jr. (1983), Effect of soil texture and seed placement on emergence of four subshrubs, *Weed Science, 31,* 380-384.

McAuliffe, J.R. (1994), Landscape evolution, soil formation, and ecological patterns and processes in Sonoran Desert Bajadas, *Ecological Monographs, 64,* 112-148.

Mooney, H.A. and S.L. Gulmon (1982), Constraints on leaf structure and function in reference to herbivory, *Bioscience, 32,* 198.

Miriti, M.N. (2007), Twenty years of changes in spatial associations and community structure among desert perennials, *Ecology, 88,* 1177-1190.

Miriti, M.N., S. Rodriquez-Buritica, S.J. Wright, H.F. Howe (2007), Episodic death across species of desert shrubs, *Ecology, 88,* 32-36.

Navar, J. and R. Bryan (1990), Interception loss and rainfall redistribution by three semiarid growing shrubs in northeastern Mexico, *Journal of Hydrology, 115,* 51-63.

Nevo, E. and A. Belies (1989), Genetic diversity in the desert - patterns and testable hypotheses, *Journal of Arid Environments, 17,* 241-244.

Nobel, P.S., P.M. Miller, and E.A. Graham (1992), Influence of rocks on soil-temperature, soil-water potential, and rooting patterns for desert succulents, *Oecologia, 92,* 90-96.

Novoplansky, A. (2002), Developmental plasticity in plants: implications of non-cognitive behavior, *Evolutionary Ecology, 16,* 177-188.

Noy-Meir, I. (1973), Desert ecosystems: environment and producers, *Annual Review of Ecology and Systematics, 4,* 25-51.

Okin, G.S. (2008), A new model of wind erosion in the presence of vegetation, *Journal of Geophysical Research-Earth Surface, 113(F2).*

Osman, A., R.D. Pieper, and K.C. McDaniel (1987), Soil seed banks associated with individual broom snakeweed plants, *Journal of Range Management, 40,* 441-443.

Owens, M.K. and B.E. Norton (1989), The impact of ‘available area’ on Artemisia Tridentata seedling dynamics, *Vegetatio, 82,* 155-162.

Padilla, F.M. and F.I. Pugnaire (2007), Rooting depth and soil moisture control Mediterranean woody seedling survival during drought, *Functional Ecology, 21,* 489-495.

Padilla, F.M., J.D. Miranda, M.J. Jorquera, and F.I. Pungaire (2009), Variability in amount and frequency of water supply affects roots but not growth of arid shrubs, *Plant Ecology, 204,* 261-270.

Parmenter, R.R. and J.A. MacMahon (1983), Factors determining the abundance and distribution of rodents in a shrub-steppe ecosystem – the role of shrubs, *Oecologia, 59,* 145-156.

Parsons, A.J. and A.D. Abrahams (1992), Controls on sediment removal by interrill overland flow on semi-arid hillslopes, *Israel Journal of Earth Sciences, 41*, 177-188.

Pielou, E.C. (1962), The use of plant-to-neighbor distances for the detection of competition, *Journal of Ecology, 50,* 357-367.

Porporato, A., F. Laio, L. Ridolfi, and I. Rodriguez-Iturbe (2001), Plants in water-controlled ecosystems: active role in hydrologic processes and response to water stress III. Vegetation water stress, *Advances in Water Resources, 24,* 725-744.

Rajagopalan, B. and U. Lall (1998), Interannual variability in western U.S. precipitation, *Journal of Hydrology,* 210, 51-67.

Rees, M. and M.J. Crawley (1989), Growth, Reproduction, and Population Dynamics, *Functional Ecology, 3*, 645-653.

Reichman, O.J. (1984), Spatial and temporal variation of seed distributions in Sonoran Desert soils, *J. Biogeog,* 11, 1-11.

Ren, J., L. Tao, and X.M. Liu (2002), Effect of sand burial depth on seed germination and seedling emergence of Calligonum L. species, *Journal of Arid Environments, 51*, 603-611.

Reynolds, J.F. (2004), Modifying the 'pulse-reserve' paradigm for deserts of North America: precipitation pulses, soil water, and plant responses, *Oecologia, 141*, 194-210.

Richards, M.B. and B.B. Lamont (1996), Post-fire mortality and water relations of three congeneric shrub species under extreme water stress – a tradeoff with fecundity? *Oecologia, 107,* 53-60.

Roberts, A.S. (2010), Rainsplash induced mound development beneath desert shrubs: Modulation of sediment transport and storage with implications for hillslope evolution. M.S. Thesis, Vanderbilt University, Nashville.

Rodriquez-Iturbe, I. (2000), Ecohydrology: A hydrologic perspective of climate-soil-vegetation dynamics, *Water Resource Research, 36,* 3-9.

Ross, M.A. and J.L. Harper (1972), Occupation of biological space during seedling establishment, *Journal of Ecology, 60,* 77-88.

Ryel, R.J., C.Y. Ivans, M.S. Peek, and A.J. Leffler (2008), Functional differences in soil water pools: a new perspective on plant water use in water-limited ecosystems, *Progress in Botany, 69,* 397-422.

Sachs, T. (2002), Consequences of the inherent developmental plasticity of organ and tissue relations, *Evolutionary Ecology, 16,* 243-265.

Sala, O.E., W.K. Lauenroth, and W.J. Parton (1992), Long-term soil-water dynamics in the short grass steppe, *Ecology, 73,* 1175-1181.

Salzman, A.G. (1985), Habitat selection in a clonal plant, *Science*, 228, 603-306.

Schenk, 1991. Clonal splitting in desert shrubs, *Plant Ecology, 141*, 41-52.

Schenk, H.J. and R.B. Jackson (2002), Rooting depths, lateral root spreads, and below-ground/above-ground allometries of plants in water-limited ecosystems, *Journal of Ecology, 90,* 480-494.

Schlesinger, W.H. and C.S. Jones (1984), The comparative importance of overland runoff and mean annual rainfall to shrub communities in the Mojave desert, *Botanical Gazette, 145*, 116-124.

Schupp, E.W. and M. Fuentes (1995), Spatial patterns of seed dispersal and the unification of plant-population ecology, *Ecoscience, 2,* 267-275.

Schwinning, S., O.E. Sala, M.E. Loik, J.R. Ehleringer (2004), Thresholds, memory, and seasonality: understanding pulse dynamics in arid/semi-arid ecosystems, *Oecologia, 141,* 191-193.

Schwinning S, BI Starr, and J.R. Ehleringer (2005), Summer and winter drought in a cold desert ecosystem (Colorado Plateau) part I: effects on soil water and plant water uptake, *Journal of Arid Environments, 60,* 547-566.

Schwinning S, BI Starr, and J.R. Ehleringer (2005), Summer and winter drought in a cold desert ecosystem (Colorado Plateau) part II: effects on plant carbon assimilation and growth, *Journal of Arid Environments, 61*, 61-78.

Scott, R.L., W.J. Shuttleworth, T.O. Keefer, and A.W. Warrick (2000), Modeling multiyear observations of soil moisture recharge in the semiarid American Southwest, *Water Resources Research, 36*, 2233-2247.

Simons, A.M. and M.O. Johnston (2006), Environmental and genetic sources of diversification in the timing of seed germination: implications for the evolution of bet hedging, *Evolution, 60*, 2280-2292.

Simons, A. M. (2009), Fluctuating natural selection accounts for the evolution of diversification bet hedging, *Proceedings of the Royal Society B*, 276.

Stahl, P.D., G.E. Schuman, S.M. Frost, and S.E. Williams (1998), Arbuscular mycorrhizae and water stress tolerance of Wyoming big sagebrush seedlings, *Soil Science Society of American Journal, 62*, 1309-1313.

Sternberg, P.D., M.A. Anderson, R.C. Graham, J.L. Beyers, and K.R. Tice (1996), Root distribution and seasonal water status in weathered granitic bedrock under chaparral, *Geoderma, 72*, 89-98.

Thomas, C.M. and S.D. Davis (1989), Recovery patterns of three chaparral shrub species after wildfire, *Oecologia, 80*, 309-320.

Tobe, K., L. Xiaoming, and K. Omasa (2005), Effects of irrigation on seedling emergence and seedling survival of a desert shrub Haloxylon ammodendron (Chenopodiaceae), *Australian Journal of Botany, 53*, 529-534.

Toft, C.A. (1995), A 10-year demographic study of Rabbitbrush (Chrysothamnus-Nauseosus) - growth, survival, and water limitation, *Oecologia, 101*, 1-12.

Trewavas, A. (2003), Aspects of plant intelligence, *Annals of Botany, 92*, 1-20.

Turkington, R., D.E. Goldbery, L. Olsvig-Whittaker, and A.R. Dyer (2005), Effects of density on timing of emergence and its consequences for survival and growth in two communities of annual plants, *Journal of Arid Environments, 61,* 377-396.

Turnbull, L.A., M.J. Crawley, and M. Rees (2000), Are plant populations seed-limited? A review of seed sowing experiments, *Oikos, 88,* 225-238.

Vasek, F.C. (1980), Creosote Bush – Long-lived clones in the Mojave Desert, *American Journal of Botany, 67,* 246-255.

Via, S. (1993), Adaptive phenotypic plasticity: target or by-product of selection in a variable environment? *American Naturalist, 142*, 352-365.

Wainwright, J., A.J. Parsons, and A.D. Abrahams (2000), Plot-scale studies of vegetation, overland flow and erosion interactions: case studies from Arizona and New Mexico, *Hydrological Processes, 14*, 2921-2943.

Weiner, J., L.G. Campbell, J. Pino, and L. Echarte (2009), The allometry of reproduction within plant populations, *Journal of Ecology, 97*, 1220-1233.

Weltzin, J.F., M.E. Loik, S. Schwinning, D.G. Williams, P.A. Fay, B.M. Haddad, J. Harte, T.E. Huxman, A.K. Knapp, G.H. Lin, W.T. Pockman, M.R. Shaw, E.E. Small, M.D. Smith, S.D. Smith, D.T. Tissue, and J.C. Zak.(2003), Assessing the response of terrestrial ecosystems to potential changes in precipitation, *Bioscience, 53*, 941-952.

White, T.C.R. (2001), Opposing paradigms: regulation of limitation of populations? *Oikos, 93*, 148-152.

Wilson, T.B., and E.T.F. Witkowski (1998), Water requirements for germination and early seedling establishment in four African savanna woody plant species. *Journal of Arid Environments, 38*, 541-550.

Woodell, S.R.J., H.A. Mooney, and A.J. Hill (1969), The behavior of Larrea divaricata (Creosote bush) in response to rainfall in California, *Journal of Ecology, 57*, 37-44.

Young, J.A., R.A. Evans, and D. Palmquist (1990), Soil surface characteristics and emergence of big sagebrush seedlings, *Journal of Range management, 43*, 358-67.

BIOGRAPHICAL SKETCH

Stacey was raised in New Canaan, CT and spent her childhood perpetually covered with boo-boos, refusing to eat any sandwich which was cut in half the wrong way, and assembling the most viscerally offensive outfits. She was the quintessential middle child and attributes being ignored with the early development of her tremendous capacity to self-entertain... as demonstrated by the fact that her parents often found her putting together and pulling apart the same 10-piece puzzle...over and over... without any signs of fatigue... for uninterrupted hours. She also embodied all the classic characteristics of a Leo. For example, for her first communion she stubbornly refused to wear a dress and emerged as victor in the argument with her parents by accidentally (?) falling out of her favorite tree and ending up in the ER. Throughout high school, Stacey was a track & field athlete and an instructor for the Walter Schalk School of Dance. Her senior year she placed second in high-jump at states... and after a weird twist of events... ended up running the dancing school with her two best friends. When her mother told her she could not go to college anywhere further than a six-hour drive, she obeyed by only submitting applications to schools below the Mason Dixon line. She flocked south to Nashville and... because of her high school teacher Mr. Spooner... arrived knowing that she was going to study Chemistry. She ended up double majoring in Economics, after discovering that the subject – with brilliant concepts like diminishing marginal returns and opportunity costs – enabled her to rationalize taking a more balanced approach to life. As a Wilskills instructor, she spent her free time exploring – and helping others explore – the caves, crags, rivers, and hills throughout the Southeast. Upon graduating, she was selected as the 2006 Keegan Traveling Fellow and spent over a year directing her own self-designed... around the world... wild goose chase. Endeavoring to better understand the nuances of conservation, she adventured to some of our planets most breathtaking ecosystems to explore diverse cultural (from scientific to indigenous) conceptions of the "environment". After being a nomadic gypsy who circumnavigated the globe with a 7-lb backpack and a coconut doll named Brenda, she returned to Vandy...kookie and mal-adjusted.... to begin graduate school. She eventually realized that smell-testing her clothes was no longer an appropriate way to make friends and settled into what proved to be every bit as much of an adventure. After her thesis was finally signed, sealed, and delivered... she reached for the doorknob at the end of the hall... and got on her way, having reconfirmed that this world is an incredibly beautiful place and having learned that her mind is... perhaps... the best vessel to be able to travel it with.