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A Seed Demography Model for Finding Optimal Strategies for Desert Annuals

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A SEED DEMOGRAPHY MODEL FOR FINDING OPTIMAL STRATEGIES FOR DESERT ANNUALS

by

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ABSTRACT

A Seed Demography Model for Finding Optimal Strategies
for Desert Annuals
by
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A theoretical investigation of the factors that affect the population dynamics of annual plants growing in deserts was conducted through the use of computer modeling techniques. A series of three models of the yearly life cycle of desert annuals was constructed and their behavior examined. The dissertation centers around the third and most complex model, a computer simulation model with distinguishable seed cohorts in a randomly varying rainfall environment. A typical simulation run was for 80 years and cost $1.00.

The five plant functions were (1) seed losses (mainly predation) as a function of seed age, (2) seed dormancy as a function of seed age, (3) percent germination of the non-dormant seeds in response to germinating rainfall, (4) percent survival from the seedling stage to maturity as a function of total rainfall over the growing season and seedling density, and (5) seeds

produced per plant as a function of total rainfall over the growing season and density of mature plants. The stochasitc rainfall generator used historical rainfall probabilities from US Weather Bureau stations at Las Vegas, Nevada and Tucson, Arizona.

The literature on desert annuals was carefully searched to provide supporting data for the plant functions used in the simulation model. Most of the data is for winter annuals growing on the Nevada Test Site near Las Vegas. Single species data are rare, so the model functions reflected the average plant responses for winter annuals as a group. This base run set of functions reproduced the observed data quite well.

Sensitivity analysis of the simulation model indicated that in order to persist in the Las Vegas area, the seeds of annuals should have at least a one-year period of dormancy and a minimum threshold of about 15 mm of germinating rainfall. The age distribution of the seed reserves in the soil and the percent germinable is strongly influenced by the recent rainfall history of the site and the seed loss rate. The optimum balance is when the losses of older seeds from the seed reserves due to germination is the same size as the sum of the non-productive losses (e.g., predation).

Several experiments are suggested -- some to cover gaps in the published data and some that became evident through the sensitivity analysis of the model itself. (148 pages)

INTRODUCTION

Most observers of desert plant communities agree that the physical environment that these plants must cope with is harsh and unpredictable. Many of these same observers also believe that desert plants are decendants of more mesic species that have invaded deserts. If true, these invaders most certainly had to make some adaptive changes in their life cycle strategies in order to persist in their new environment. Regardless of their ultimate origins, however, the question still remains: How do they do it? What factor or factors are most critical in their life cycle?

My research objective is to give some tentative answers to these questions through the use of computer modeling techniques. My initial approach was conditioned by some earlier simulation modeling work that I had done with the US/IBP Desert Biome research program. I had written a rather simple computer model called ANNUALS[1] that simulated the germination, growth, and seed set of desert annuals. The model operated on a weekly time increment and a typical run was for 5-10 years. Weekly rainfall and temperatures were generated stochastically in a simple fashion.

The output of this model was not particularly informative. However, there were several obvious areas of improvement in the model that I felt would make it into a meaningfull dissertation. In particular, the following modifications were attempted:

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[1]Modeling Report Number 14, US/IBP Desert Biome, Utah State University, Logan, Utah.

(1) The stochastic rainfall and temperature generator was improved by carefully analyzing over twenty years of climatological data from four different US Weather Bureau stations (El Paso, Tucson, Las Vegas, and Elko) to obtain representative distributions of the rainfall and temperature probabilities for these sites. The resulting probability distributions were used as input data to the model.

(2) The simple soil moisture calculation was expanded to simulate changes in soil moisture for several soil depths.

(3) Vegetative growth parameters describing the root/shoot ratio and the root growth rate were included. Coupled with the soil moisture calculations, these parameters would allow for the testing of the effects of different rooting strategies.

(4) The improved model would keep track of seed cohorts, rather than just the total density of seeds in the soil. The model could then simulate the effects of changes in seed dormancy on the population dynamics of the plant.

In retrospect, the above procedures were much too ambitious, both in terms of computer costs and the data requirements. After working on just the soil moisture portion of the model for several weeks, I had a program that was over 200 statements long, cost $2.00 per year of simulation and still did not adequately predict soil moisture levels at different depths. In addition, the plant portion of the model had a number of functional responses that were simply "best guesses", with little or no hard data for a basis.

It soon became apparent that I had reached an impasse with this approach. (The soil moisture model was becoming a dissertation in itself!)

After some deliberation I realized that a weekly simulation model was working at a level that was unnessarily detailed and mechanistic for my stated objective: to determine what adaptive strategies are most suitable for annuals growing in deserts. For example, the weekly model might indicate the mechanism(s) whereby a plant could increase its survival probability from the seedling stage to maturity, but there were simply too many parameters to answer the larger question: Is an increased plant survival of more adaptive advantage than, say, a change in the pattern of seed dormancy?

I then decided to describe the population dynamics of a desert annual on a yearly basis (or, at most, on the basis of a whole growing season). There are several advantages for doing so: (1) the number of parameters needed to characterize the whole life cycle is considerable smaller than that needed for a weekly description, (2) because the parameters are few, the relative importance of very different aspects of the life cycle can be readily ascertained, and (3) most of the published data for desert annuals are based on at least a complete growing season.

After a careful study of the literature, I became convinced that the key adaptation of desert annuals was the behavior of their seeds. The working hypothesis that I have chosen to test is: Seed dormancy and germination controls are the most important adaptive strategies of desert annuals. Since dormancy is described in terms of the age of the seed, this hypothesis requires that the model keep track of seed cohorts. In fact, I soon found that this approach centered around a dynamic life table for these seed cohorts.

The above hypothesis is certainly not original with me. However, hardly anyone seems to have attempted to test it, either experimentally or theoretically. The one exception is the work of Cohen (1966). Cohen's model (see Review of Literature, page 29) was borrowed from economic theory and applied to the problem of reproductive strategies for hypothetical desert annuals. The conclusions he reached have been quite helpful for me in the present study. However, Cohen did not distinguish between seed cohorts, nor did he allow for germination rates to be functions of rainfall -- a well-established phenomenon with desert annuals. Also, the relationships he used between rainfall and seed production had no apparent basis in hard data.

I constructed a sequence of three yearly models and examined the behavior of each in turn. The first model (Model 1) is quite simple and only incorporates the minimum set of assumptions necessary for describing the life cycle of an annual plant in a constant environment. Model 2 contains a dynamic life table for the seed cohorts, but the environment is still considered constant. Most of the dissertation deals with Model 3 -- a distinguishable cohort model with a randomly varying environment.

Model 3 has been tested with data for winter annuals growing in desert conditions. Single species data ~~is~~ are rare, so the model parameters have been chosen so as to reflect the mean plant responses of winter annuals as a group. Since water is the major limiting factor in deserts, rainfall is the only environmental variable that is considered. Temperature and/or length of the growing season could easily be added if the model were to be applied to annuals living in more mesic conditions.

The computer program that embodies the assumptions of Model 3 is written in PL/I and has been run on a Burroughs 6700. There are 502 source statements and the running cost is about $1.00 for an 80-year simulation.

REVIEW OF LITERATURE

The material that is reviewed here has been divided into five subject areas: climate, runoff, soil moisture, evapotranspiration, and desert annuals. Although the three subjects of runoff, soil moisture, and evapotranspiration are only relevant to the original weekly simulation model, I have retained this material for complete- padding?

e of the within-year variations that yearly

account for.

tions of the vegetation and climates of

the western United States can be found

Jaeger (1957). McDonald (1956) and

have done statistical analyses of the

atterns (both daily and seasonally) for

eson (1969) describe the winter-summer

a and surrounding states. Arizona tends

season, with roughly equal amounts in

the east of Arizona the summer rains

and west of Arizona the winter rains

udies of the spatial pattern of rainfall

ed meters was done by Humphrey (1933)

na. He found that no two of the 24

square tract read the same after any

particular storm. However, individual differences between gauges diminished during the course of the year. The greatest source of these variations was the spotted distribution of summer thunderstorms.

Runoff

Two papers that relate precipitation and runoff on a desert watershed are those of Tadmor and Shanan (1969) and Osborn and Lane (1969). Tadmor and Shanan found that the relation between daily precipitation and daily runoff for a naturally vegetated site in the Negev desert in Israel could be described by:

$$\text{Runoff} = 0.12(P - 2.9)$$

where Runoff and P are in millimeters per day. If the vegetation was removed from the site, the relationship changed to:

$$\text{Runoff} = 0.40(P - 1.8)$$

Their experiment demonstrated that vegetation removal decreases the runoff threshold (a decrease from 2.9 to 1.8 mm of rain) and increases the proportion of the rain above the threshold that goes to runoff (an increase from 12% to 40%).

Osborn and Lane (1969) obtained their data from several small (0.5 - 10 acre) semi-arid watersheds in southeastern Arizona. They found that 90% of the annual runoff occurs in July and August during the high intensity thunderstorms. Runoff correlated most significantly with total precipitation in each storm with an average relationship of:

$$\text{Runoff} = 0.32(P - 7.0)$$

where Runoff and P are in millimeters per storm.

Differences between the Tadmor and Shanan data and the Osborn and Lane data could be attributed to differences in slope of the watersheds, soil type, plant cover, and storm intensity. In fact, the Negev precipitation is almost entirely from relatively low intensity winter storms (Noy-Meir, private communication), whereas the Arizona runoff is from high intensity summer storms.

Soil Moisture

Soil moisture measurements in deserts have been reported rather infrequently. Rickard and Murdock (1963) measured tha field capacity and wilt point for several desert soils on the Nevada Test Site near Las Vegas for several depths, as well as the loss of soil moisture over a spring growing season. Rickard (1967) measured the seasonal pattern of soil moisture for two neighboring shrub communities in southeastern Washington at 10 depths over a 2-year period. A bare soil plot was also used as a comparison.

Cable (1969) made measurements of soil moisture changes in a desert grassland site in southern Arizona. His general observations on the seasonal pattern are (1) there are one or more recharges to field capacity in late July and early August to 3" and usually to 12", but only rarely to 24"; (2) there is rapid extraction to the wilt point in 3-6 weeks, depending on subsequent rain; (3) there is recharge at 3" and 12", and usually but not always at 24", sometime in late fall and early winter; (4) high soil moisture levels are maintained for 2-5 months during the winter rainy season; (5) extraction to wilt point occurs to at least the 24" depth by the end of April or early May.

Ackerman and Bamberg (1972) have measured the phenological stages of the major shrubs on the Nevada Test Site, along with soil temperature, soil moisture (2 depths), and rainfall for several years.

relevance?

Evapotranspiration

The problem of predicting the rates of soil moisture loss due to evaporation from the soil surface and to transpiration by the plants has been studied by a multitude of workers in many fields. The literature on the subject is voluminous and only a few citations which are of direct relevance to a weekly simulation model will be mentioned here.

The primary measure of the rate of water loss from crop-covered soil is called potential transpiration. Penman (1956) defines it as "the amount of water transpired in unit time by a short green crop, completely shading the ground, of uniform height and never short of water".

The difficulty with this definition is that few situations in the field (cropland or natural vegetation) meet these conditions. Either the vegetation does not "completely shade the ground" or the soil does not meet the "never short of water" condition. To be useful in cases where the plant cover is not 100%, the term is usually lengthened to potential evapotranspiration. This allows for evaporation directly from the soil surface. All potential evapotranspiration equations thus have a "crop coefficient" included in them which is usually less than 1.0 and varies seasonally.

There have traditionally been two alternate ways of calculating potential evapotranspiration (hereafter abbreviated as PET), the aerodynamic approach and the energy balance approach. Excellent reviews of the advantages and limitations of each approach may be found in Penman (1956), Tanner and Pelton (1960), and Van Bavel (1966a).

The aerodynamic approach uses basic physical principles of turbulent air flow to arrive at a measure of the "drying power" of the air mass flowing over the soil and plant surfaces. This approach is of limited practical application because of the many difficult-to-measure parameters, particularly the soil surface temperature.

The energy balance approach computes PET from the energy input (initially solar radiation) that is needed to change water from a liquid to a vapor. The two most well-known methods in this country are those of Thornthwaite (1948) and Blaney and Criddle (1950). To make this approach quite practical for agricultural needs, very simple indicators of the energy input are used. For example, the Blainey-Criddle formula for the PET for a particular time interval (usually a month) is:

$PET = kFT$, where PET is in inches per time interval,

k is the crop coefficient (dimensionless),

F is the fraction of annual daylight hours occuring in the time interval, and

T is the mean air temperature in °F

Blaney (1952) found crop coefficients for his formula (based on native phreatophyte vegetation in California and New Mexico) to range between 0.5 and 1.2, depending on site, plant species, and season.

Penman (1948) derived a "combination" method which uses the advantages of the simple data requirements of the energy balance approach and the theoretical soundness of the aerodynamic approach. The quantities required by his method are mean air temperature, mean relative humidity, mean wind velocity, and mean daily duration of sunshine. Penman found that for southern England, the crop coefficient was 0.6 in winter, 0.7 in spring and autumn, and 0.8 in summer.

Pelton and Korven (1969) made an experimental test of the Penman, Thornthwaite, and Blainey-Criddle methods on an irrigated alfalfa field in Canada. They found that the latter two methods predicted weekly water requirements with reasonable accuracy, but described daily values inadequately. The Penman equation did fairly well in predicting daily PET.

Van Bavel (1966a) has derived an improved version of Penman's formula and has found that it predicts both daily and hourly PET under a variety of conditions.

As noted above, a further difficulty with applying PET calculations to field situations is that the only time the soil is not "short of water" is immediately after irrigating or rain. Hence, a distinction is usually made between potential evapotranspiration (PET) and <u>actual</u> evapotranspiration (AET).

The relationship between PET and AET is a confused one. Some investigators say that AET decreases significantly from PET as soon as the soil begins drying out. Others say that AET remains close to PET until the soil has been dried to almost the wilt point. An example of the former is found in Slatyer (1956) and the latter in Veihmeyer and Hendrickson (1955). The debate still continues and has been further confused by the data of Denmead and Shaw (1962). They show curves of the AET/PET ratio as functions of soil water potential and PET. At high PET values, the ratio falls below 1.0 at relatively moist soils. At low PET values, the ratio remains near 1.0 until the soil has dried significantly. These curves were obtained from growing corn plants in 20-gallon cans buried in the field. Hanks (private communication) questions the validity of their measurements for naturally growing plants where the root systems have access to widely differing soil water potentials at different depths.

Grigal and Hubbard (1971) have used the Denmead and Shaw curves in a soil moisture model for a deciduous forest and find reasonable agreement with measured values for AET on an annual basis.

Mathemetical models of soil water movements have been developed by Gardner (1958, 1960, 1964), Hanks _et al_ (1962, 1969), Molz and Remson (1970), and Nimah (1972). They all use the one-dimensional soil moisture flow equation (the Darcy equation) as the central relationship. Molz and Remson (1970) and Nimah (1972) have a root extraction term to account for water uptake by plants.

Desert Annuals

One of the earliest series of studies of the life cycle of desert annuals was that of Went (1948, 1949), Went and Westergaard (1949), and Juhren, Went, and Phillips (1956). These papers describe field studies conducted at two Mojave desert sites, Joshua Tree National Monument and Death Valley National Monument, both in California. In addition, laboratory studies of the germination of desert annual seeds and competition experiments were conducted. The general conclusions of these papers are:

(1) There is great variation in the spatial and temporal patterns of annual vegetation in deserts due to the spatial and temporal patterns of rainfall and its effect on germination.

(2) On the Joshua Tree sites there are two sets of annuals, winter and summer. The winter annuals usually germinate in late fall or early winter, undergo rapid growth in early spring, and set seed in April or May. The summer annuals germinate in mid-summer and grow from 3-8 weeks before setting seed in late summer or early fall. There are no summer annuals in Death Valley because of almost total absence of summer rainfall.

(3) Regardless of the season or the species, germination of annuals only occurs after rains of 25 mm or more.

(4) If the rains which trigger germination are large, the plants will grow relatively large before flowering and setting seed. If rains are just barely sufficient for some germination, little growth occurs before the plants switch over into the reproductive

stage. A large proportion of the plants reach maturity and produce at least one seed per plant.

(5) The germination controls are more important than competition between the growing plants. When moisture stress begins, the plants set seed regardless of their size.

(6) In laboratory experiments, summer annuals germinated best when the air temperature was around 26°C. Winter annuals germinated best when the temperature was about 15°C.

(7) Following a rain of 25 mm or more, 10-25% of the total viable seeds in the soil germinated.

(8) Germination densities at Joshua Tree ranged between 200-2000 seedlings per square meter. In Death Valley the densities were 40-100 seedlings per square meter on the valley floor and as much as 5000 seedlings per square meter at higher (and wetter) sites.

(9) Total seed reserves of annuals in the soil at Joshua Tree was 25,000 per square meter.[2] Reserves of viable seed at Death Valley (as determined by forced germination in the lab) was estimated at only 500 per square meter.[3]

(10) Overall survival from germination to seed set of winter annuals at Joshua Tree ranged between 9-71%, with a mean of 46%.

In another classic study of desert annuals, Tevis (1958 a, b, c) induced germination of annuals on a Mojave site near Indio, California

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[2]It is not mentioned how this value was obtained.

[3]A dubious procedure where seed dormancy is involved.

by watering several plots with an irrigation sprinkler once a month over a period from July to December in 1956. He made careful studies of the two distinct populations of annuals (summer and winter) which resulted from this sprinkling and a summary of his findings are as follows:

(1) Both groups of annuals required at least 25 mm of simulated rain to initiate germination. Summer annuals germinated in July and August when the mean air temperature was near 30°C. Winter annuals germinated in October and November when the mean air temperatures were 12-18°C. Real rainfall was several times more effective in initiating germination in both groups of annuals.

(2) Summer annuals had an average survival of 45% and set seed in late September. Winter annuals had an average survival of 35%, with the greatest mortality occuring when rapid spring growth brought on moisture stress in March and April.

(3) Of the two cohorts of winter annuals, the October germinating plants were 5 times the size of the November germinating plants when they all reached maturity in March. The October group had 2000 flowers per plant compared to only 25 flowers per plant for the November group.

(4) Plant densities at seed set in April were about 400 per square meter. Total seed production was greater than 300,000 seeds per square meter.[4] The bulk of the winter annual biomass and seed crop was contributed by one species.

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[4]It is not clear whether this figure is only for the watered plots or includes the adjoining areas which received no supplemental water.

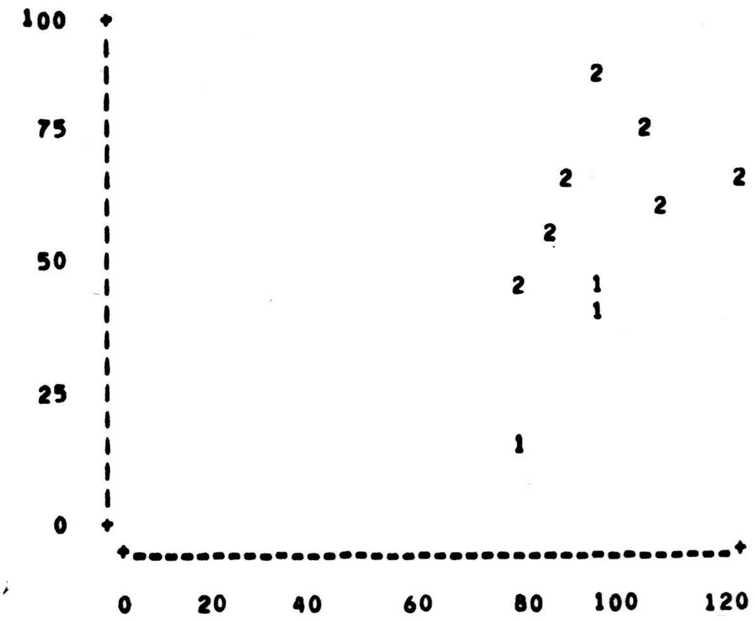
(5) A census of granivorous ant colonies near the sites and estimates of foraging rates indicate that ants are collecting less than 0.1% of the seeds produced by the annuals.

recent Bio Science paper by Went and Wheeler

The most recent series of papers on desert annuals are those of Beatley (1967, 1969a, 1969b, 1972a). Her findings are based on many years of field work on the Nevada Test Site near Las Vegas.

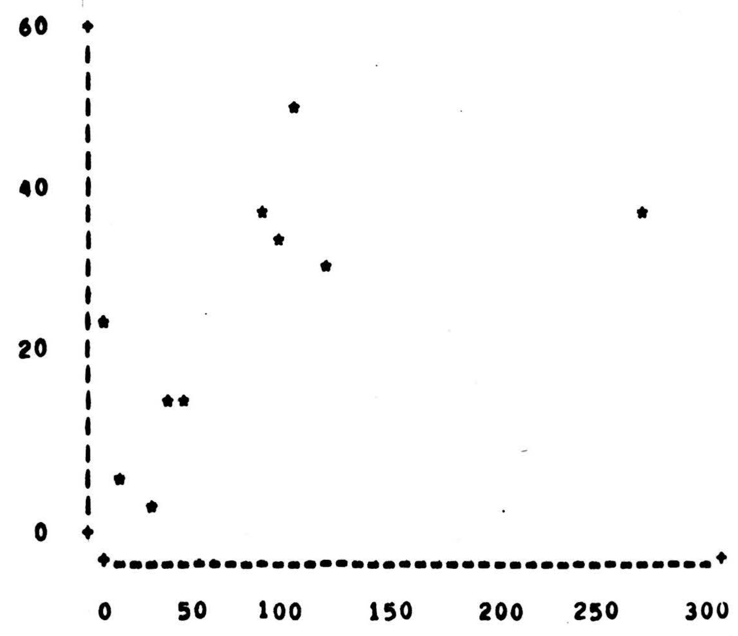
Beatley (1967) discusses the survival of winter annuals over two consecutive growing seasons. In 1963-64, autumn rains initiated good germination and the annuals enjoyed a 7-8 month growing season. There was 38% survival to maturity. Following a dry autumn in 1964, heavy rains in March, 1965 initiated some germination, with a resulting growing season of only 6-10 weeks. Survival rates averaged 60%. Both of these sets of data (from several different sites) are shown in Figure 1, with the 1963-64 data points denoted with '1' and the 1964-65 data points denoted with '2'. There is a definite increase in survival with increasing rain (and a shorter growing season!). In both seasons the greatest mortality occurred in March and April when there is rapid stem elongation. Evidently soil moisture is limiting at this time, although no wilting of plants was ever observed.

The relation between winter annuals and seed-eating rodents (principally kangaroo rats and pocket mice) was reported in Beatley (1969a). She has recorded the amount of germinating rainfall, density of annuals in May, and rodent densities the following summer for the years 1963-1968. Average plant densities varied from a low of 10 per square meter to a high of 110 per square meter, depending



PLANT SURVIVAL (%) OVER GROWING SEASON (Y-AXIS)
VS RAINFALL (MM) OVER GROWING SEASON (X-AXIS)
(DATA SOURCE: BEATLEY 1967)

Figure 1.



RODENT DENSITY (#/HECTARE) IN SUMMER (Y-AXIS) VS
PLANT DENSITY (#/SQ METER) THE PRECEEDING SPRING (X-AXIS)
(DATA SOURCE: BEATLEY 1969A)

Figure 2.

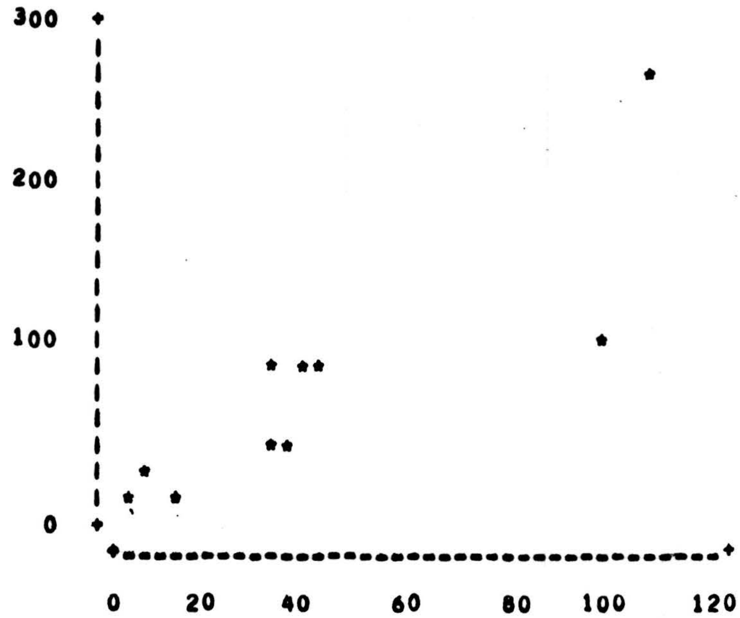
on rainfall. Average rodent densities (all species) ranged from 3-38 per hectare. These data are shown in Figure 2. The correlation between plant densities and rodent densities appears quite good. Except for the single point on the far right, it seems that the rodents follow the ups and downs of their "prey" quite well. Beatley conjectures that the rodents are dependent on the green vegetation in the spring for dietary water and/or vitamins to initiate their reproduction. She further says that it does not appear "that food resources (fruits and seeds) available beyond the spring season are a potential critical factor in reproductive activity of the rodents the next season".

Figure 3 shows the relation between the density of mature annuals in the spring and the amount of germinating rainfall the preceding autumn (generally the rain occurring from late September to early December). Figure 4 shows the same set of spring densities as a function of the total rainfall over the growing season (from the beginning of autumn germination until late April or early May). Note that for the Nevada Test Site a minimum of 60 mm of total rain is required to insure any production of winter annuals.

Beatley (1969b) has extensive peak biomass data on winter annuals from 68 sites for the springs of 1964, 1965, and 1966, as well as the total precipitation over each growing season for each site. Figure 5 shows these data graphically. Her observations for these annuals may be summarized as follows:

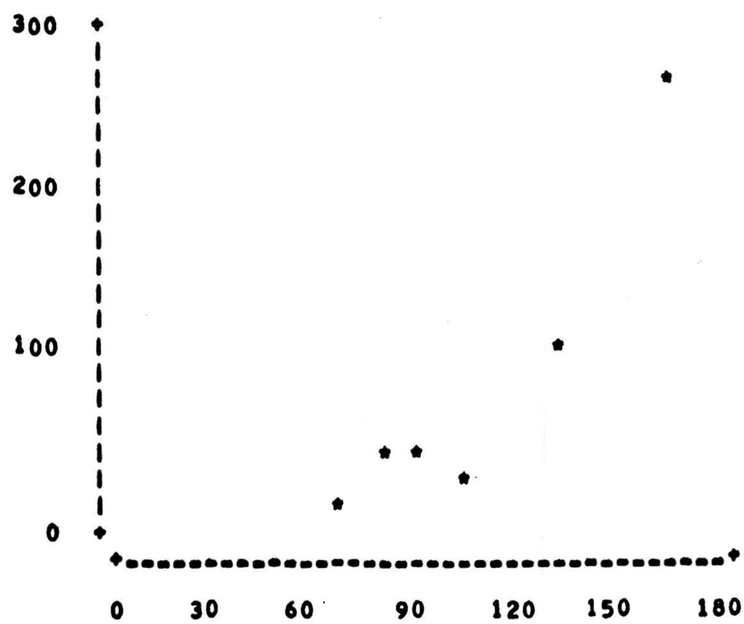
(1) Plant height ranges between 3-20 cm.

(2) Rooting depth ranges between 1-20 cm.



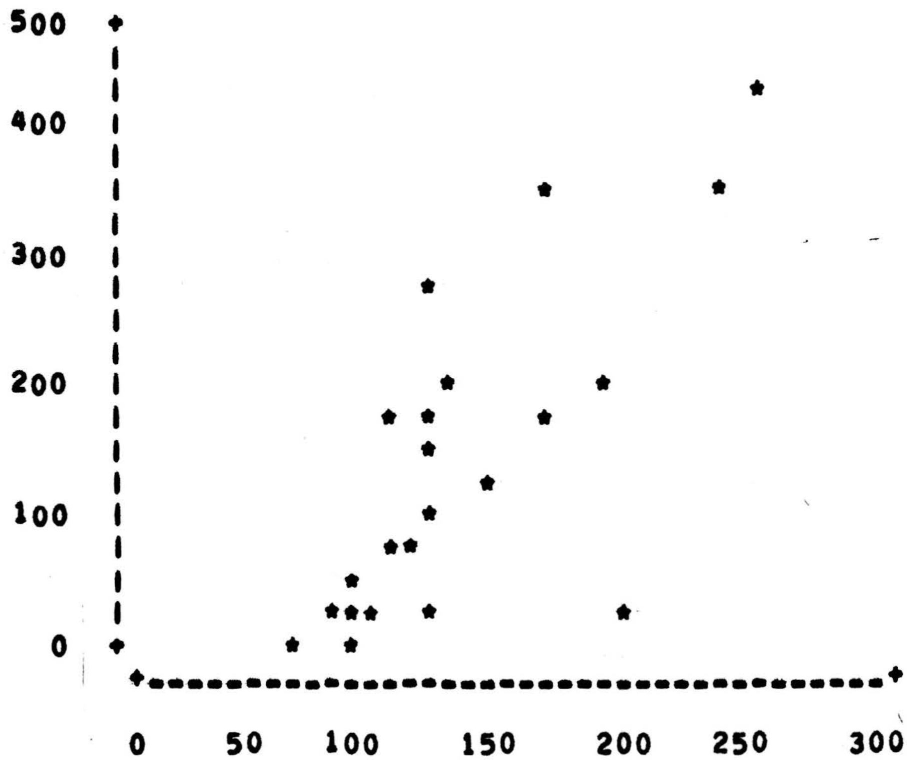
PLANT DENSITY (#/SQ METER) IN SPRING (Y-AXIS)
VS AUTUMN RAINFALL IN MM (X-AXIS)
(DATA SOURCE: BEATLEY 1969A)

Figure 3.



PLANT DENSITY (#/SQ METER) IN SPRING (Y-AXIS)
VS RAINFALL (MM) OVER GROWING SEASON (X-AXIS)
(DATA SOURCE: BEATLEY 1969A, 1969B)

Figure 4.



PLANT BIOMASS (KGM/HECTARE) IN SPRING (Y-AXIS)
VS RAINFALL (MM) OVER GROWING SEASON (X-AXIS)
(DATA SOURCE: BEATLEY 1969B)

Figure 5.

(3) Plant densities range between 0-975 per square meter.

(4) Plant cover has a range of 0-30%.

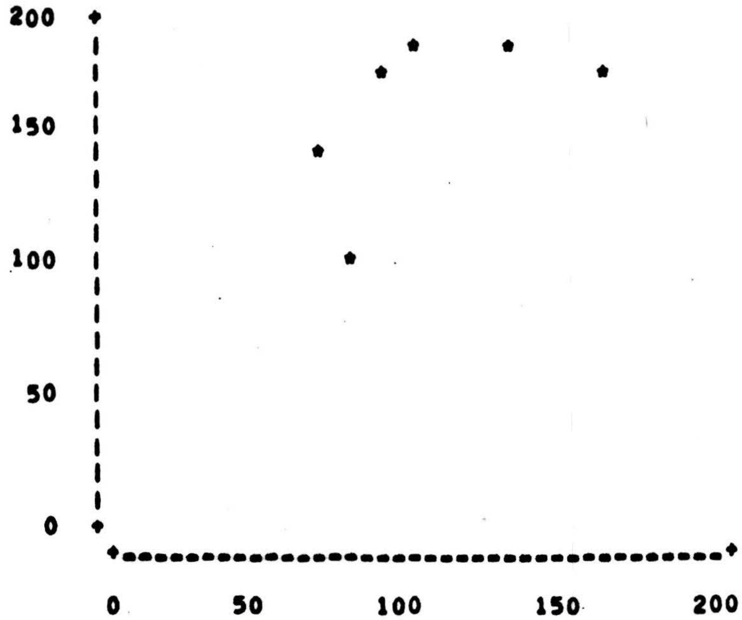
(5) Peak biomass values range between 0-62 grams per square meter.

(6) Average biomass was 6.0 grams per square meter in 1964 (an average rainfall year), 1.9 grams per square meter in 1965 (a poor rainfall year), and 16.0 grams per square meter in 1966 (a good rainfall year).

Using the few data in common in Beatley (1967) and Beatley (1969b), I have calculated the mean plant weight (all species combined) for two growing seasons. Figure 6 shows these mean weights as a function of total rainfall over the growing season. Figure 7 shows mean weight as a function of plant density at maturity. There is no discernable pattern with these few points, even when considering mean plant weight as a function of both variables simultaneously.

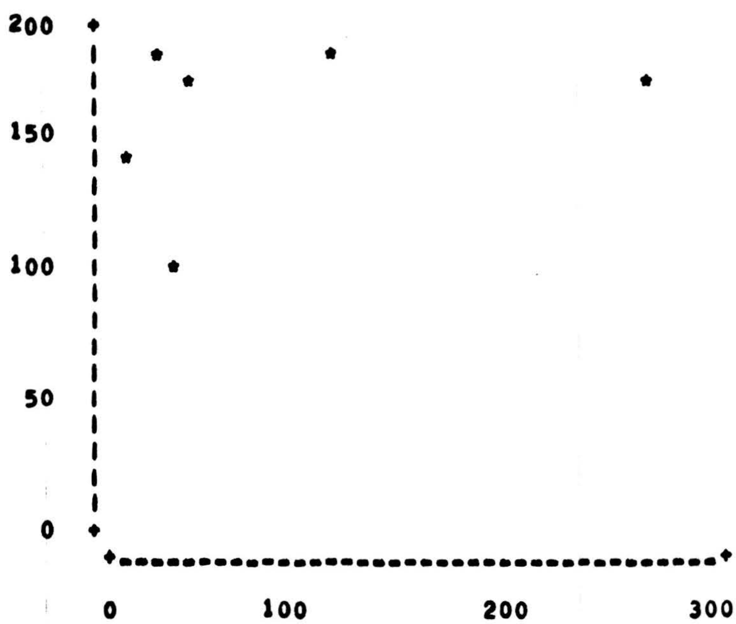
A summing up of her observations on both shrubs and annuals in the Mojave desert is found in Beatley (1972a). This paper is a very detailed word model of the way the vegetation responds to the yearly rainfall and temperature pattern of the region. It is a collection of causal relationships of the form: if climatic condition _A_ occurs within a time period _T_, then species _S_ will respond in manner _X_; however, if condition _B_ occurs in that time period, then the response will be _Y_.

A classic study of the seed-producing ability of plants is that of Salisbury (1942). He made extensive collections of plants



MEAN PLANT WEIGHT (MILLIGRAMS) AT MATURITY (Y-AXIS)
VS RAINFALL (MM) OVER THE GROWING SEASON (X-AXIS)
(DATA SOURCES: BEATLEY 1967, 1969B)

Figure 6.



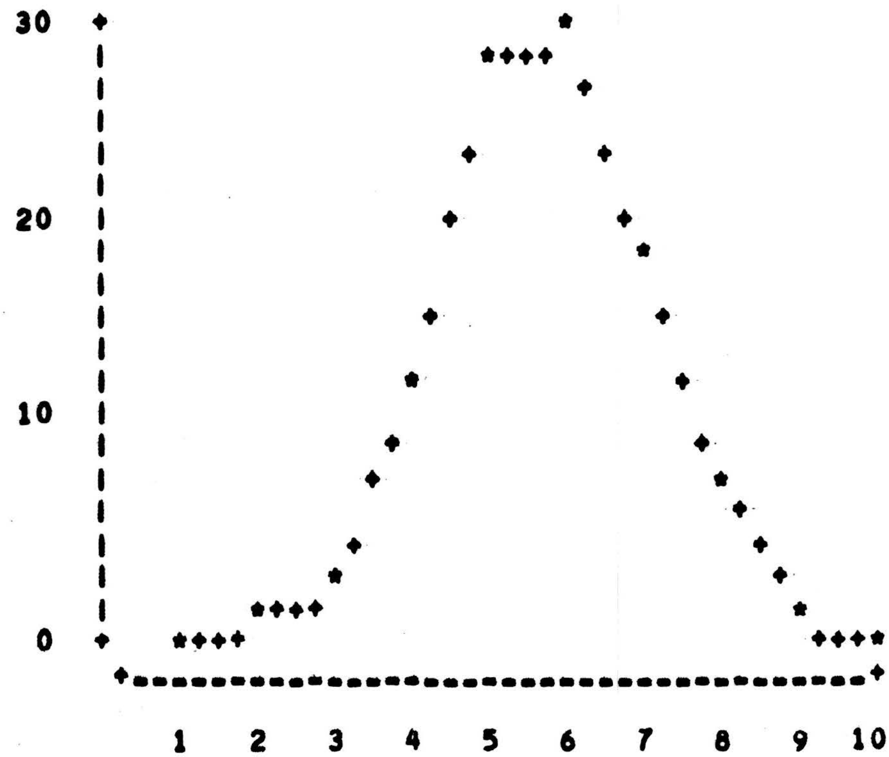
MEAN PLANT WEIGHT (MILLIGRAMS) AT MATURITY (Y-AXIS)
VS PLANT DENSITY (#/SQ METER) AT MATURITY (X-AXIS)
(DATA SOURCES: BEATLEY 1967, 1969B)

Figure 7.

and seeds from a wide range of habitats in England. His general conclusions are: (1) species whose seedlings become established in the shade have heavier seeds than those whose germination occurs in full light, (2) species that grow in more advanced stages of a sere have heavier seeds than do the earlier successional ones, (3) average seed output (seeds per plant) are higher for species growing in open habitats than for species of closed communities, and (4) percent germination is markedly lower for open habitat species (about 50%) than for closed habitat species (75-80%). His data for open habitat species may be relevant to desert annuals: mean seed weight is .001 gram and seeds per plant range between 40-23,000 with an arithmetic mean of 3,000.

A very recent study by Baker (1972) on the seed weight of annual plants of semi-arid regions of California is in agreement with Salisbury's data. Baker found that seed weight is lognormally distributed about a modal value of .001 gram, with approximately half of the species having seed weights between .0001-.003 gram. Figure 8 shows the distribution of seed weights for several hundred species of semi-arid annuals of California. The modal value (class 6) represents a seed weight of .001 gram. Successive seed weight classes differ by a factor of 3 (e.g., class 5 is .0003 gram and class 7 is .003 gram).

Taylor and Rossiter (1967) have discovered the presence of a germination inhibitor in the seed coats of the seeds of some plant species. It appears that this substance must be leached out of the seed coat by water infiltrating into the soil before the seed can



% FREQUENCY OF SEED WEIGHT CLASS (Y-AXIS)
VS SEED WEIGHT CLASS (X-AXIS, LOG SCALE)
(DATA SOURCE: BAKER 1972)

Figure 8.

germinate. The action of this inhibitor would explain the widely observed phenomenon of seed dormancy, particularly evident in many species of desert annuals.

A set of three Masters theses that deal with desert annuals on sites near Las Cruces, New Mexico are those of Dye (1969), Hettinger (1969), and Shiffler (1968).

Dye measured the densities of annual seeds in the soil and found them to be 13,000-22,000 per square meter. Microscopic inspection determined that only one third of them were potentially viable. He also conducted germination experiments in the laboratory with samples of seeds and soil collected from different depths. Only 2% of the seeds could be induced to germinate, regardless of the treatment. The greatest germination rate was from seeds found at 1.5 cm depths. These seeds were presumably older than the majority of the seeds, 80% of which were in the top 0.5 cm of soil. The emergence of seedlings in the lab experiments corresponded to the same densities found in the field: 100-200 seedlings per square meter. Annual grasses constituted 40% of the seed reserves and 40% of the greenhouse seedlings. The dominant species of annual forb constituted 50% of the seed reserve, but only 5% of the seedling population.

Hettinger (1969) made measurements of the total production of annuals by species over one growing season. He found that, depending on species, mature plant densities ranged between 1-70 plants per square meter and plant weight was between .03-5.7 grams. A mean plant weight for all species of annuals (weighted by their relative abundance) was 0.5 gram. Total production of annuals was 200 grams per square meter over a growing season of 180 days. His only reference to seeds was that "a large portion of the energy (of production) is assimilated into fruiting structures and seeds".

Shiffler (1968) conducted phenology observations on populations of summer annuals on the Las Cruces sites (a summer rainfall region). He found that the plants germinated after rains of 0.5 inch or more, grew rapidly, and set seed after a growing season as short as 4-5 weeks. There were several overlapping cohorts throughout the summer, each cohort having been germinated by a different storm. All of the summer annuals had set seed by mid-September.

The most recent reports dealing with seed reserves of desert annuals are the US/IBP studies of Goodall et al (1972) and Balda et al (1972). Goodall et al have preliminary indications that the densities of annual seeds on Great Basin sites a few miles north of the Great Salt Lake range between 500-2000 seeds per square meter, depending on site rainfall, soil salinity, and land use practice. Different species had very different seed densities as a function of soil depth. Also, seed densities were much higher under shrub canopies and grass tussocks than in the open areas between shrubs.

Balda et al (1972) reported the following results from a Sonoran desert site near Tucson, Arizona:

(1) 90% of the seeds are in the top 2 cm of soil.

(2) Seed densities ranged from a high of 2300 seeds per square meter in July, 1970 to a low of 125 seeds per square meter in March, 1971. This represents a total loss of 95% of the seeds over this time period.

(3) The mean seed weight for all species of annuals (weighted by their relative abundance) was .001 gram.

(4) The major seed-eating rodents are one species of kangaroo rat and several species of pocket mouse. The report contains excellent data on the rodent's reproductive behavior and diets. However, since absolute densities of the rodents were not determined, rodent impact on the population dynamics of the annuals cannot be assessed.

Measurements of the densities of small mammals in deserts have been made by Chew and Butterworth (1965) on a Mojave site in California and by Chew and Chew (1970) on a Sonoran site in Arizona. Chew and Butterworth stated that the metabolic demand of an adult kangaroo rat (*Dipodomys merriami*) is about 12 Kcal per day (equivalent to 3 grams of seeds per day). Total rodent densities were between 0.5-3.7 per hectare during the study period. Chew and Chew (1970) found that small mammal densities averaged 17 per hectare on their Sonoran site, 70% of which was composed of the kangaroo rat, *D. merriami*. The small mammals consumed only 2% of the net above ground plant production (total of annuals and perennials), but they utilized over 85% of the seed production.

Other studies of desert rodents have been reported in Reynolds (1958), French *et al* (1966, 1967), Wood (1969), and Bradley and Mauer (1971).

There are several papers by Harper (with others) that deal with the germination, growth, and reproductive strategies of annual plants, particularly the so-called "weedy" species. Harper and

Gajic (1961) report on experimental studies of competiton effects between an annual weed grown in pots with various combinations of wheat and beet plants. They found that some characteristics (plant survival and seed weight) were fairly independent of the treatments, whereas some others (plant weight, number of seeds per plant, and total number of seeds produced per square meter) were quite dependent on the treatment.

Harper _et al_ (1965) and Harper and Benton (1966) introduce the concept of "safe sites" for seeds on a soil surface. They postulate that a given soil surface has a limited number of micro-sites where seeds are protected and have a moisture supply that is adequate enough to ensure germination and seedling establishment. They discuss the effects of the texture of the soil surface and the size and shape of the seed in determining the number of such safe sites.

Theoretical discussions of life cycle strategies for annual plants can be found in Harper (1967) and Harper and Ogden (1970). In the former paper, Harper stresses the importance of describing plant communities in terms of the numbers of _individuals_ of a plant species in an area, rather than in terms of plant biomass. He believes that using the life table approach of animal ecologists will help considerably in giving insight into the population dynamics of plant communities.

Harper and Ogden (1970) studied the growth characteristics of a common weed in terms of its energy allocation to different plant parts as a function of the age of the plant. In particular, they were interested in determining the "reproductive effort" of the plant, which they defined as the ratio: (total weight of seed per plant)/(total plant weight at maturity). They grew single plants in pots of various sizes to simulate the effects of crowding stress on the reproductive effort of the species. They found that at low stress (pot contained 1700 ml of soil) the reproductive effort was 19%. At medium stress (300 ml of soil), it was only reduced to 15%. At high stress (20 ml of soil), it was reduced to 6%.

A review article by Harper et al (1970) on the shapes and sizes of seeds indicates that the reproductive effort of most annuals (exclusive of grain crops) is in the range of 15-30%.

Palmblad (1966, 1968) made laboratory studies of factors which may regulate the size of populations weedy plant species, principally the effects of "safe site" germination controls and plant density effects (both intra- and inter-specific) on plant survival and plasticity (i.e., the effects of density on the size of mature individuals). He found that the size of the seedling population was mainly a function of the soil surface and was species specific. Vegetative dry matter production increased with sowing density, but finally reached a plateau. The number of seeds per plant decreased with increasing density. Seed weight for a given species varied only slightly with plant density. Palmblad concluded that the population size of these species was regulated by (1) self-controlled germination, (2) number of safe sites, (3) increased mortality with increasing plant density, and (4) decreased plant size and seed production per plant with increasing density.

A paper that has very direct relevance to the present study is that of Cohen (1966). He has used the economist's technique of investment decision making under risk to investigate optimum reproductive strategies for annual plants in a randomly varying environment. The factors that he uses to characterize the plant are (1) Y, the seed yield per germinating seed, (2) G, the germinating fraction of seed each year, and (3) D, the decaying fraction of seed each year. The parameters G and D are constants for a given species. Seed cohorts and age distributions are not considered. The environment is described in terms of a finite number of year types that have a probability of occurance of P_i and a corresponding seed yield of Y_i. Cohen then derives the value of the species long-term growth rate as a function of G and D for a given distribution of P_i and Y_i. His conclusions are the following:

(1) If there is a high probability of total failure, then the species must have a large Y when successful, good viability for ungerminated seeds, and a low yearly germinating fraction.

(2) Conversely, if there is a high probability for successful reproduction, then the optimum germinating fraction is high and the ability for seeds to survive a long time in the soil is relatively unimportant.

DESCRIPTIONS OF THE MODELS

After I decided to give up the weekly simulation approach and work on an annual time scale, I constructed a sequence of three distinctly different models. The first model was quite simple -- it did not deal with seed cohorts or a variable environment. After learning the behavior of this simple description of an annual's life cycle, I made the next model more complex by including seed cohorts. It was only after I had gained some experience with how different parameters affected the population's rate of growth and the age structure of the seed reserves in the soil that I constructed the final version (Model 3) with a randomly varying environment.

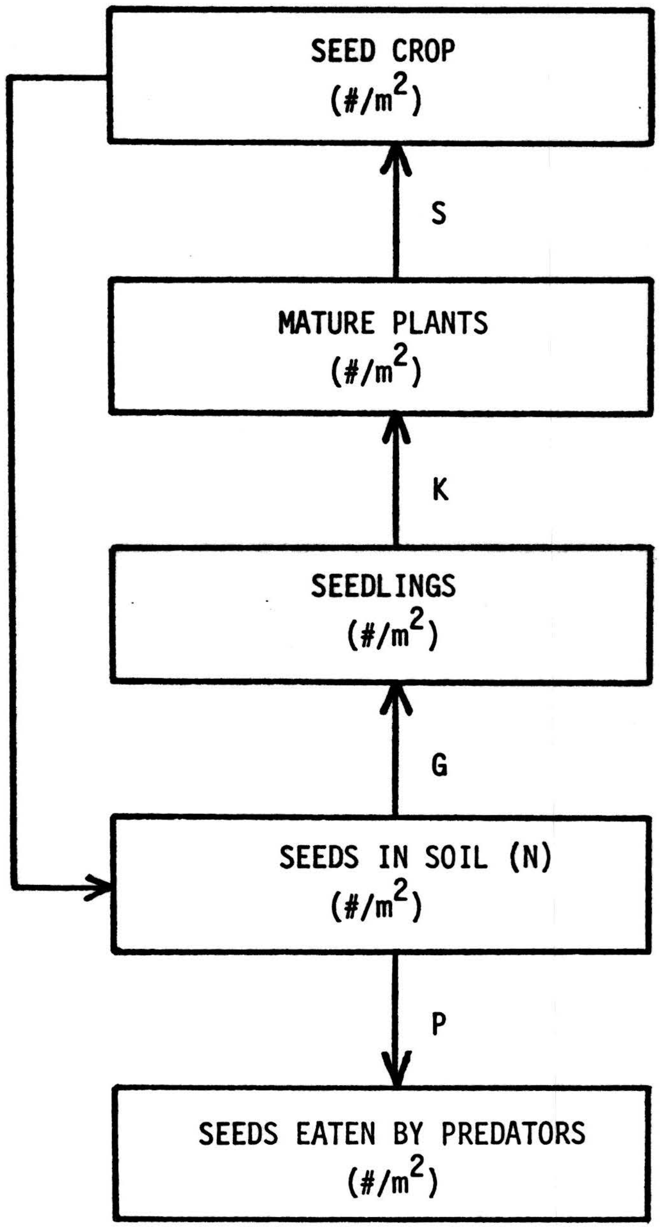
Model 1: Indistinguishable seed cohorts in a constant environment

Assume that the yearly life cycle of a species of annual which must re-seed itself from year to year can be diagrammed as shown in Figure 9 on the next page. What is the relationship between the four parameters G, K, S, and P such that the population will remain in equilibrium? Let N, the total density of seed reserves in the soil, be the measure of the species' well being. The equilibrium condition would then mean that when the plant goes through a yearly cycle there is no net change in N. Thus, if N_t is the seed density at time _t_, then the density the following year, _t_+1, is given by:

$$N_{t+1} = N_t(1-G)(1-P) + \text{Seed Crop} \qquad \text{(eq. 1)}$$

with the seed crop given by:

$$\text{Seed Crop} = N_t(GKS) \qquad \text{(eq. 2)}$$



G - fraction of the seeds that germinate per year $(0 < G < 1)$

K - fraction of the seedlings that survive to maturity $(0 < K < 1)$

S - number of seeds per mature plant $(S > 0)$

P - fraction of the seeds that are eaten per year (after germination losses) $(0 < P < 1)$

Figure 9. Diagram of Model 1.

For equilibrium, $N_{t+1} = N_t$. Combining equations 1 and 2 and equating N_{t+1} and N_t, we have:

$$N_t = N_t(1-G)(1-P) + N_t(GKS) \qquad \text{(eq. 3)}$$

Dividing through by N_t and rearranging terms we get the condition of equilibrium for this simple model:

$$GKS = P + G - PG \qquad \text{(eq. 4)}$$

The left side is the average number of seeds produced from each seed in the soil. The right side is the probability that a given seed will be "lost" from the seed reserves due to germination or predation. Equilibrium is attained when these two quantities are equal. In an expanding population, the relationship would be:

$$GKS > P + G - PG \qquad \text{(eq. 5)}$$

In a declining population, it would be:

$$GKS < P + G - PG \qquad \text{(eq. 6)}$$

In nature, the parameters G, K, S, and P are most certainly functions of environmental variables (e.g., rainfall) and vary in size from year to year. For the present model, let us assume that they are constant from year to year (i.e., a perfectly predictable environment) in order to study the effects of each parameter relative to the others.

There are four parameters in equation 4 and hence the behavior of the system at equilibrium cannot be examined graphically. However, K and S only appear as a single product, with that product being the number of seeds returned to the soil for each seed that germinates. Let us consider KS as a single parameter so that equation 4 may be arranged in the following forms:

$$KS = f(G,P) = \frac{P + G - PG}{G} \qquad \text{(eq. 7)}$$

$$G = f(P,KS) = \frac{P}{P + KS - 1} \qquad \text{(eq. 8)}$$

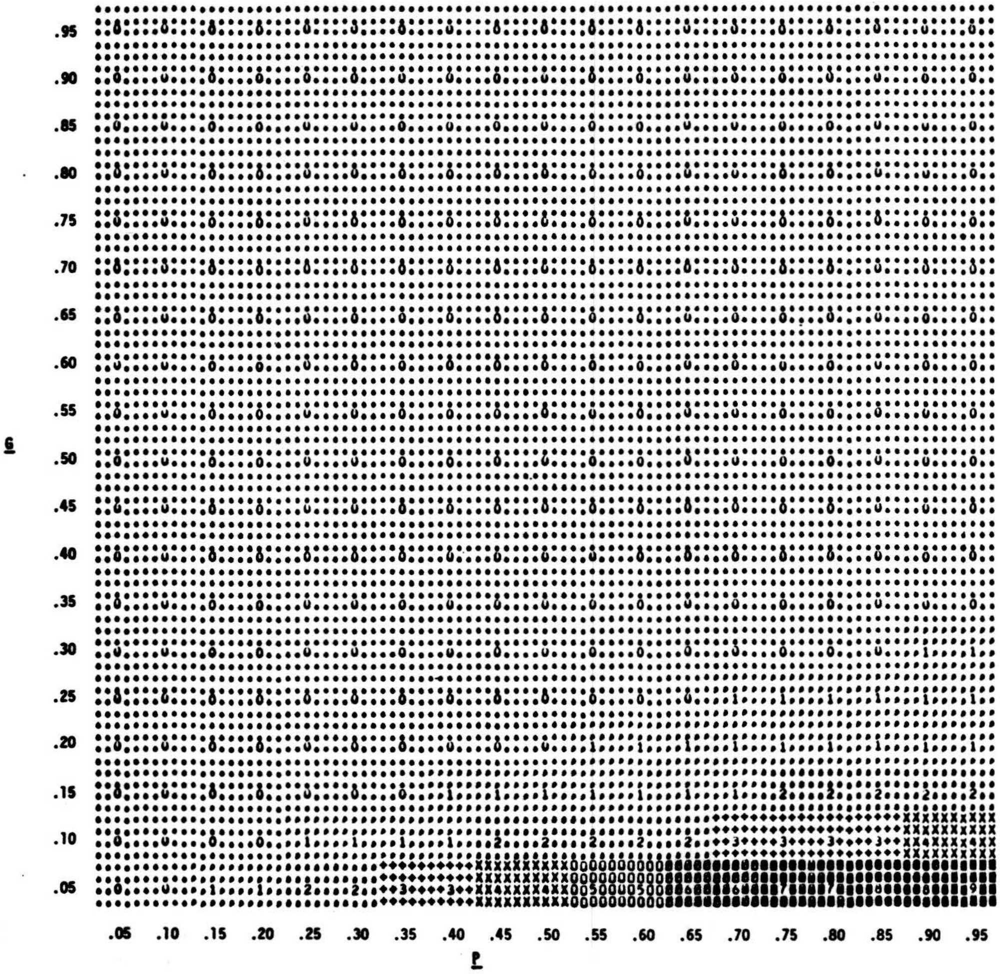
$$P = f(G,KS) = \frac{G(KS - 1)}{1 - G} \qquad \text{(eq. 9)}$$

The response surfaces described by these three equations, for various combinations of G, P, and KS, are shown in Figures 10-12, respectively.

Figure 10. In Figure 10 the KS surface is near 1.0 over most of the P-G plane. In fact it is only for low germinating fractions ($G < 0.3$) that KS rises above 3. Thus, in an environment where the plant can regularly germinate 30% or more of the seed reserves in the soil, KS can be near 1.0 for stability and the plant is insensitive to the seed predation rate.[5]

Of course, in harsher environments, it is known that even in good years less than 10% of the seed reserve may germinate. A population in such an environment would then be sensitive to the pressures of the seed eaters. Even so, at the lowest G value (5%) and the highest P value (95%) shown in Figure 10, KS need only be approximately 20 to insure year to year replacement. A KS of 20 is relatively conservative for most annuals (weeds in particular) and could be

[5]This insensitivity to seed predators has been "built in" to the model, since a value of G = 30% implies that the seed predators cannot eat more than 70% of the seeds in any one year. A P = 95% with G = 30% says that the seed predators eat 95% of the seeds remaining after germination, i.e., they in fact eat (.7)(.95) = .665 (66.5%) of the initial total seed.



Two-dimensional representation of the three-dimensional surface:

$$KS = \frac{P + G - PG}{G} \qquad \text{where } 0 < P < 1 \text{ and } 0 < G < 1$$

P is the horizontal (x) axis and takes on values .05, .10, .15, ...95

G is the vertical (y) axis and takes on values .05, .10, .15, ...95

The value of KS (height of surface above the P-G plane) is represented by the darkness of the overprinting symbolism, with its range divided into ten equal intervals from 1-21.

Symbols	Range of KS
. (0)	1 - 3
• (1)	3 - 5
• (2)	5 - 7
+ (3)	7 - 9
X (4)	9 - 11
O (5)	11 - 13
● (6)	13 - 15
● (7)	15 - 17
● (8)	17 - 19
■ (9)	19 - 21

Figure 10.

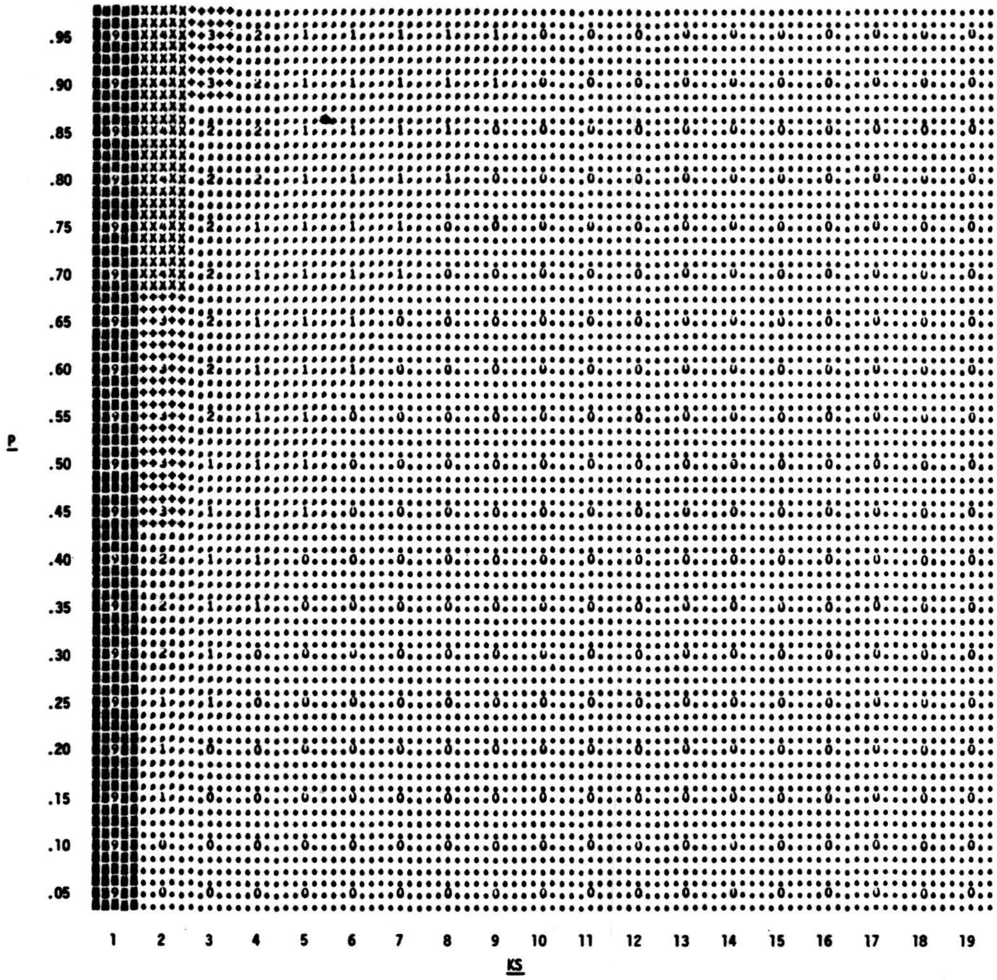
attained in a variety of ways:

K = 100% survival,	S = 20 seeds/plant	
K = 50% "	, S = 40	"
K = 10% "	, S = 200	"
K = 1% "	, S = 2000	"

Salisbury (1942) has recorded values of over 10,000 seeds per plant for some common English weeds. Desert annuals typically have K values near 50% (Beatley, 1967).

Figure 11. The equilibrium values of G as a function of P and KS are shown in Figure 11. Here we see that G can be quite small (less than 10%) over most of the range of P (0-1) and KS (1-19). It is only for small KS values (near 1.0) that G approaches 100%. Even with a KS of only 2.0 and a P of 95%, the plant need only germinate 40-50% each year for the population to persist. (Of course, the plant must be able to attain a given KS and G every year in this simple model. In nature it is the bad years that threaten the population's existence.)

Figure 12. In this figure, P is shown as a function of G (0-1) and KS (1-19). Those portions of the P surface that go above 1.0 have been blanked out, since they imply a seed eating rate (after germination losses) of more than 100% per year. It is amply clear that only restricted combinations of G and KS are such that the population can be controlled by the seed predators. In most of the figure (the blank upper-right portion) the plant population is an



Two-dimensional representation of the three-dimensional surface:

$$G = \frac{P}{P + KS - 1} \qquad \text{where } 0 < P < 1 \text{ and } 1 < KS < 20$$

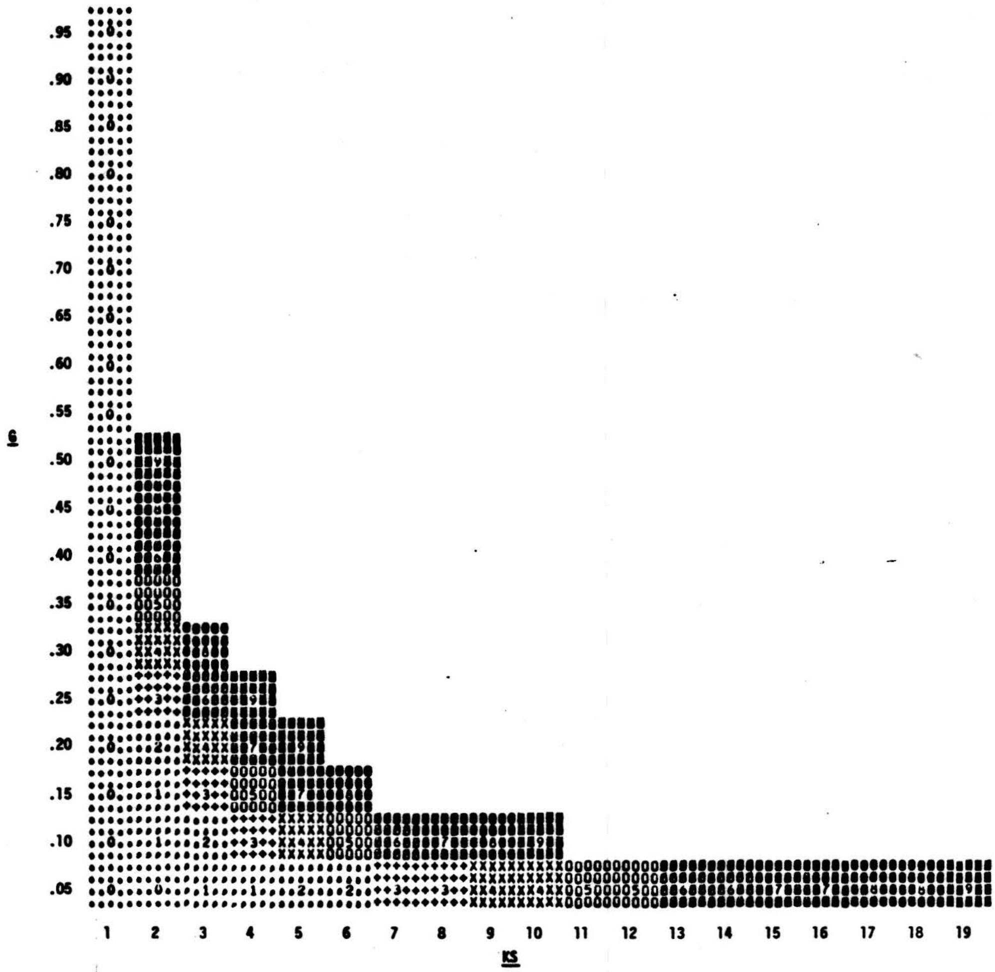
KS is the horizontal (x) axis and takes on values 1, 2, 3, . . . 19

P is the vertical (y) axis and takes on values .05, .10, .15, ...95

The value of G (height of surface above the KS-P plane) is represented by the darkness of the overprinting symbolism, with its 0-1 range divided into ten equal intervals.

Symbols	Range of G
. (0)	.0 - .1
• (1)	.1 - .2
• (2)	.2 - .3
+ (3)	.3 - .4
X (4)	.4 - .5
0 (5)	.5 - .6
▮ (6)	.6 - .7
▮ (7)	.7 - .8
▮ (8)	.8 - .9
▮ (9)	.9 -1.0

Figure 11.



Two-dimensional representation of the three-dimensional surface:

$$P = \frac{G(KS - 1)}{1 - G} \qquad \text{where } 0 < G < 1 \text{ and } 1 < K < 20$$

KS is the horizontal (x) axis and takes on values 1, 2, 3, . . . 19

G is the vertical (y) axis and takes on values .05, .10, .15, ...95

The value of P (height of surface above the KS-G plane) is represented by the darkness of the overprinting symbolism, with its 0-1 range divided into ten equal intervals. (Values of P greater than 1 are left blank)

Symbols	Range of P
. (0)	.0 - .1
, (1)	.1 - .2
; (2)	.2 - .3
+ (3)	.3 - .4
X (4)	.4 - .5
0 (5)	.5 - .6
● (6)	.6 - .7
● (7)	.7 - .8
● (8)	.8 - .9
■ (9)	.9 -1.0

Figure 12.

expanding one, assuming that P is the only controlling factor. Obviously, rainfall and density-dependent effects (to name only two other factors) are important in determining the population size of annuals in nature.

Model 2: Distinguishable seed cohorts in a constant environment

Careful readling of the literature on desert annuals had made it clear that I would have to consider seed cohorts if the model was to be at all realistic. Seed dormancy is a well established phenomenon in many species. Also, some seeds become "unavailable" to many predators through processes that bring about seed burial. These two factors imply that the population dynamics of these species would be quite sensitive to changes in the age structure of the seed reserves in the soil.

The simple model originally proposed in Figure 9 (p. 32) was therefore expanded to include seed cohorts. The following assumptions are made about the population dynamics of the species:

(1) The year begins immediately after seed set and ends as the annuals reach maturity and set seed again.

(2) Germination and growth occurs throughout the year, but seed set occurs synchronously at year's end.

(3) The age distribution of the seed cohorts in the soil and the plants that arise from them can be diagrammed as shown in Figure 13 on the next page, where

a) the subscripts denote the seed cohort age in years,

b) N_i = the seed density (seeds per square meter) of the ith cohort,

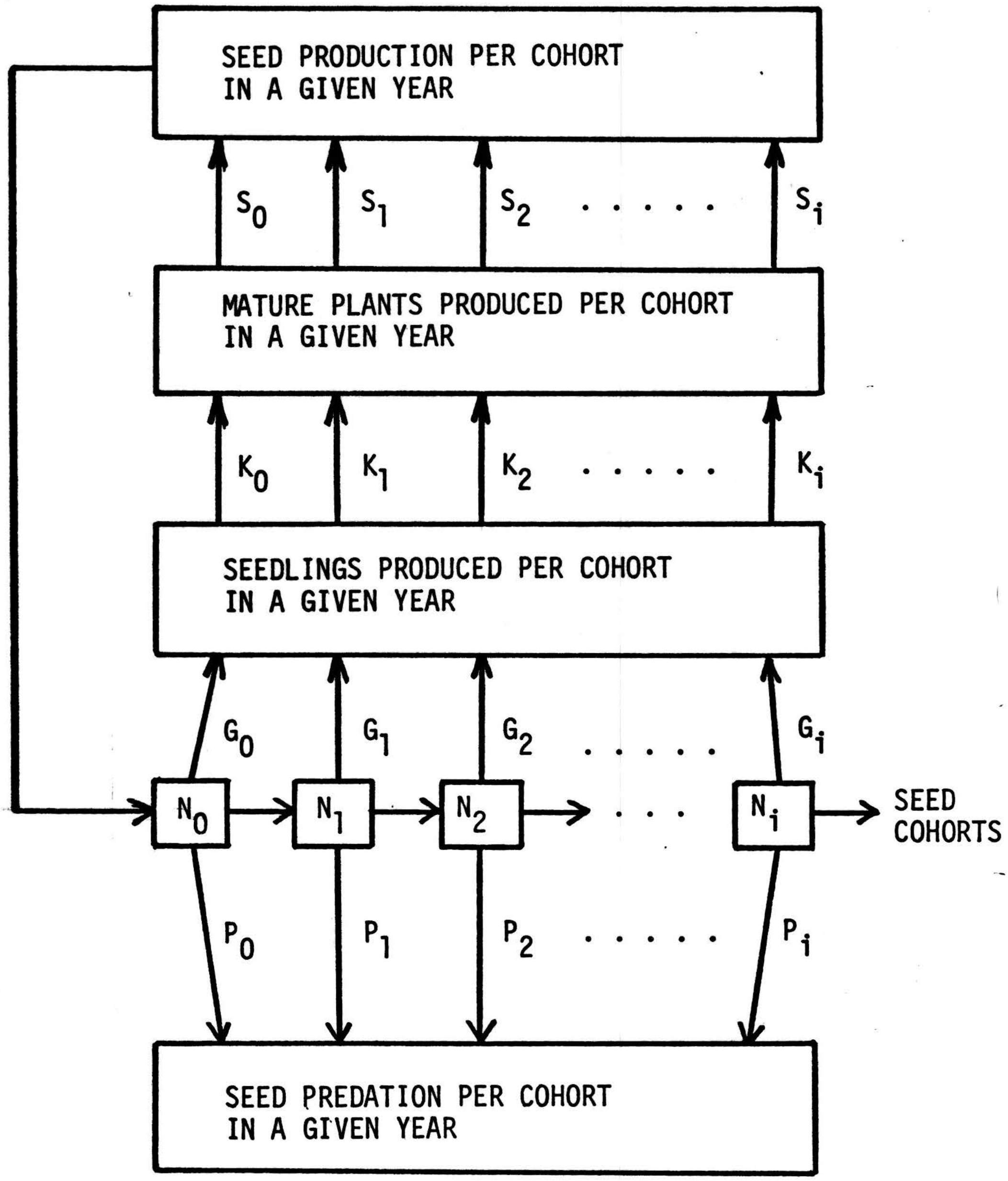


Figure 13. Diagram of Model 2.

c) G_i = the fraction of the ith cohort that germinates in a given year ($0 < G_i < 1$),

d) K_i = plant survival from germination to seed set for plants arising from a given seed cohort ($0 < K_i < 1$),

e) S_i = seed production (seeds per plant) at maturity for plants arising from a given seed cohort ($S_i > 0$), and

f) P_i = the fraction of the ith cohort (after germination losses) that are eaten (or otherwise lost to the system) per year ($0 < P_i < 1$).

For any particular year the seed crop is given by:

$$\text{Seed Crop} = \sum_{i=0}^{\infty} N_i G_i K_i S_i \qquad \text{(eq. 10)}$$

(Note: It has been explicitly shown here that the G_i, K_i, S_i, and P_i are functions of seed age. They may also be functions of plant density, rainfall, etc. This is dealt with in Model 3.)

Equation 10 is not particularly informative, especially with regard to whether the population is stable, increasing, or decreasing. In the case of a stable population (thus implying a stable environment), the N_i are all constant from year to year and are given by:

N_0 = the yearly seed crop

$$N_1 = N_0(1-G_0)(1-P_0)$$

$$N_2 = N_1(1-G_1)(1-P_1) = N_0(1-G_0)(1-G_1)(1-P_0)(1-P_1)$$

or in general for $i > 0$,

$$N_i = N_0 \prod_{j=0}^{i-1} (1-G_j)(1-P_j) \qquad \text{(eq. 11)}$$

But since N_0 = the seed crop, equations 10 and 11 may be combined (writing out the first term of the sum explicitly) to give:

$$N_0 = N_0 G_0 K_0 S_0 + \sum_{i=1}^{\infty} G_i K_i S_i \prod_{j=0}^{i-1} (1-G_j)(1-P_j) \qquad \text{(eq. 12)}$$

Dividing through by N_0 and exchanging sides gives the condition of stability for a population with distinguishable seed cohorts:[6]

$$G_0 K_0 S_0 + \sum_{i=1}^{\infty} G_i K_i S_i \prod_{j=0}^{i-1} (1-G_j)(1-P_j) \qquad \text{(eq. 13)}$$

For a given set of functions G, K, S, and P, the left side of equation 13 would show whether the population is stable (the left side equals 1), increasing (the left side greater than 1), or decreasing (the left side less than 1).

At this point it became obvious that I would have to write a computer program to deal with equation 13. My goals were (1) to investigate how different functions for G, K, S, and P affected the stable age distribution and (2) to determine if these functions described populations that were stable, expanding, or declining.[7] Example output from two runs of this program (called STRATEGY2) are described on the next few pages.

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[6]Distinguishable by differences in the degree of dormancy and the rate at which they are eaten by seed predators. It is assumed that seed age is a sufficient measure of these differences.

[7]A stable age distribution means that the proportion of the total population in each age class is constant through time. A stable population means that the size of the total population is constant through time. One can have a stable age distribution in either an increasing or a decreasing population. In the present example, all that is required is that G, K, S, and P are not functions of time.

Figures 14-17 show the functions used for G, K, S, and P for the first example. In fact, these functions are actually constants and effectively reduce this model to the "indistinguishable cohort" model described above. The set of values has been chosed so as to satisfy equation 4 on page 33 (the condition of equilibrium for Model 1). G is 1.0%, K is 50%, S is 42 seeds per plant, and P is 20%. The seed age distribution is shown in histogram form in Figure 18 and in tabular form in Table 1. Also in Table 1 is the expected density of seedlings, mature plants, and seed produced from each seed cohort over one growing season. Equation 4 is validated in this example, since the total seeds produced (10,000 seeds per square meter) equals the seed density in the zeroth cohort (10,000 seeds per square meter). The zeroth cohort represents the previous year's seed crop.

Figures 19-22 show a case where G and P <u>are</u> functions of seed age, but K and S are still constant.[8] Table 2 and Figure 23 show a very different age structure than the previous example. It turns out that the percent of the total seed population in the youngest age group is approximately the same numerically as the total seed "mortality" in the first year, i.e., the combined losses of a given year's seed crop through germination and predation. Table 2 shows that this population is definitely expanding (by a factor of 4.5 per year), with the largest proportion of the seed production coming from the

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[8]There is no compelling reason to assume that the growth characteristics, K and S, are dependent upon the age of the seed from which the plant germinates. One might possibly want to give lower K and S values to seeds in the youngest age group because they may still be lying in exposed positions that are not favorable for good seedling establishment and subsequent growth.

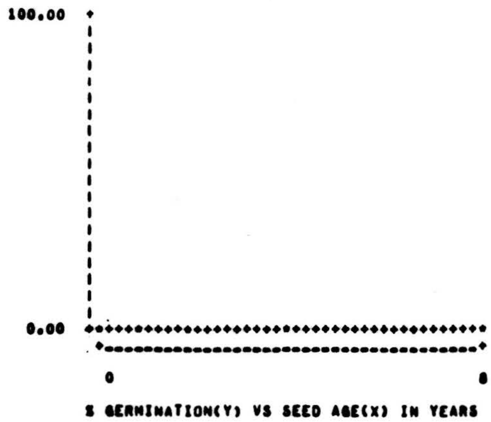

Figure 14.

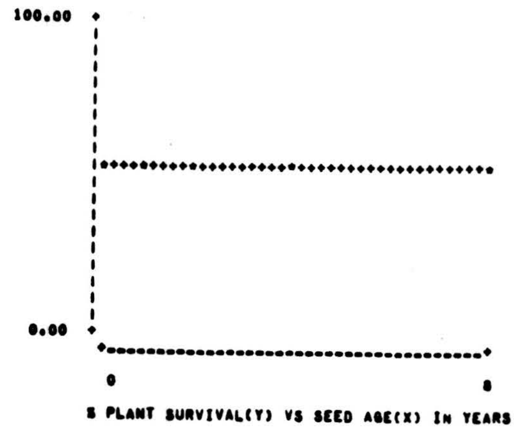

Figure 15.

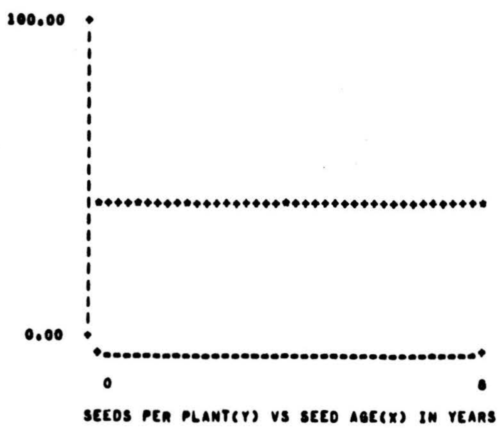

Figure 16.

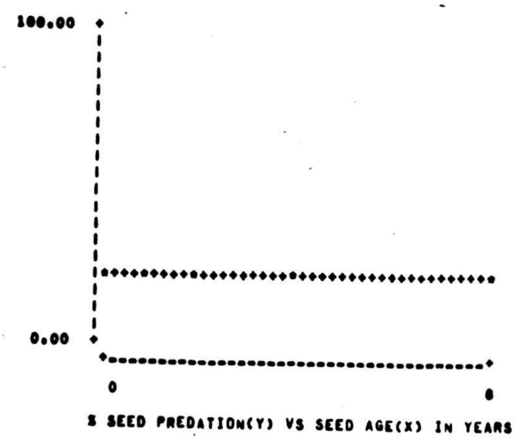

Figure 17.

STRATEGY2, first example.

Table 1. Output from STRATEGY2, first example.

SEED AGE (YEARS)	SEED DENSITY	% EATEN PER YEAR	% GERMINABLE PER YEAR	% PLANT SURVIVAL	SEEDS PER PLANT	REPRODUCTIVE POTENTIAL	SEEDLINGS	MATURE PLANTS	SEEDS PRODUCED
0	10000	20.0	1.0	50.0	42.0	0.21	100.0	50.0	2100.0
1	7920	20.0	1.0	50.0	42.0	0.21	79.2	39.6	1663.2
2	6272	20.0	1.0	50.0	42.0	0.21	62.7	31.4	1317.3
3	4967	20.0	1.0	50.0	42.0	0.21	49.7	24.8	1043.3
4	3934	20.0	1.0	50.0	42.0	0.21	39.3	19.7	826.3
5	3116	20.0	1.0	50.0	42.0	0.21	31.2	15.6	654.4
6	2468	20.0	1.0	50.0	42.0	0.21	24.7	12.3	518.3
7	1954	20.0	1.0	50.0	42.0	0.21	19.5	9.8	410.5
8	1548	20.0	1.0	50.0	42.0	0.21	15.5	7.7	325.1
9	1226	20.0	1.0	50.0	42.0	0.21	12.3	6.1	257.5
10	971	20.0	1.0	50.0	42.0	0.21	9.7	4.9	203.9
11	769	20.0	1.0	50.0	42.0	0.21	7.7	3.8	161.5
12	609	20.0	1.0	50.0	42.0	0.21	6.1	3.0	127.9
13	482	20.0	1.0	50.0	42.0	0.21	4.8	2.4	101.3
14	382	20.0	1.0	50.0	42.0	0.21	3.8	1.9	80.2
15	302	20.0	1.0	50.0	42.0	0.21	3.0	1.5	63.5
16	239	20.0	1.0	50.0	42.0	0.21	2.4	1.2	50.3
17	189	20.0	1.0	50.0	42.0	0.21	1.9	0.9	39.9
18	150	20.0	1.0	50.0	42.0	0.21	1.5	0.8	31.6
19	118	20.0	1.0	50.0	42.0	0.21	1.2	0.6	25.0
	47623						476.2	238.1	10000.9

**** SEED PRODUCTION RATIO IS 1.000 ****

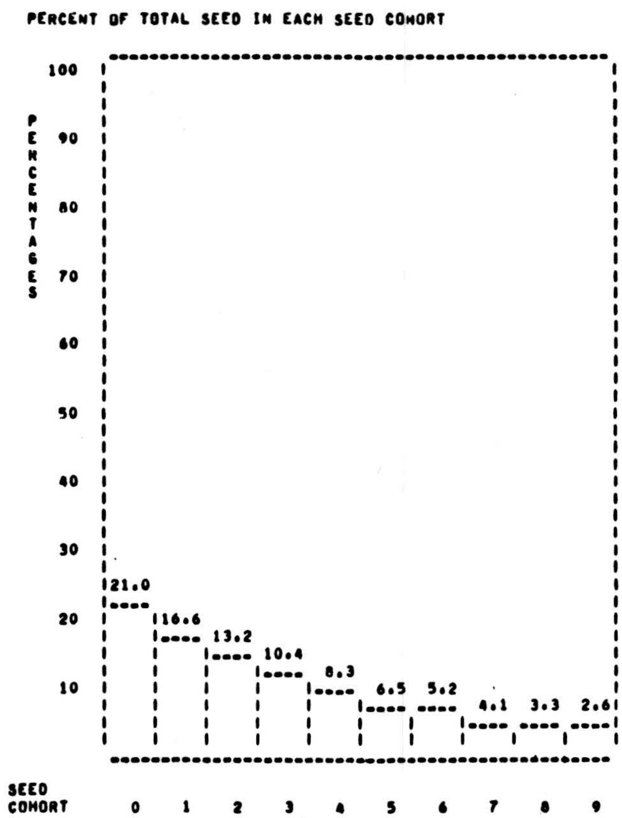

Figure 18. Distribution of seed age from STRATEGY2, first example.

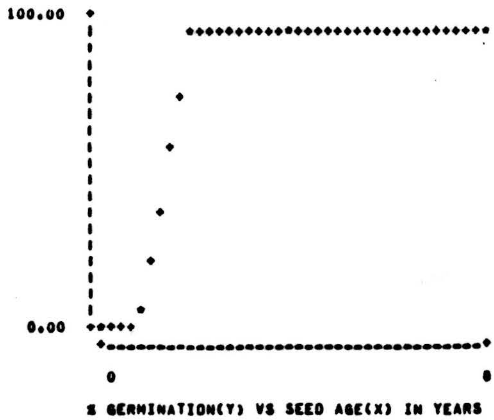

Figure 19.

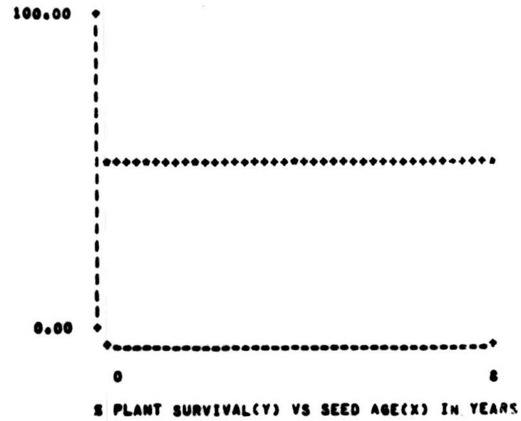

Figure 20.

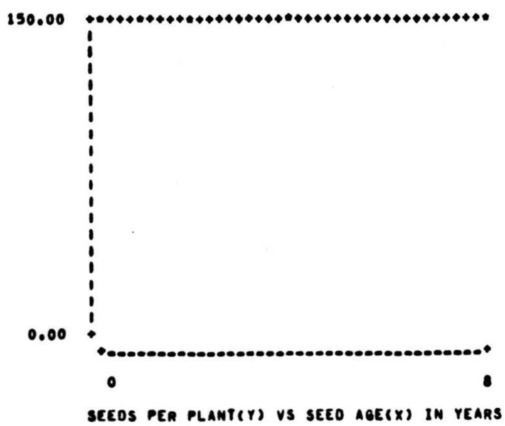

Figure 21.

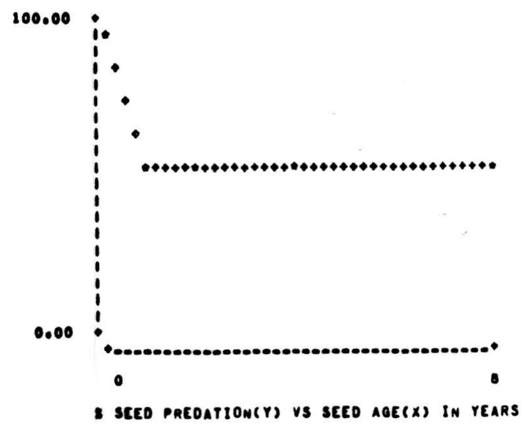

Figure 22.

STRATEGY2, second example.

Table 2. Output from STRATEGY2, second example.

SEED AGE (YEARS)	SEED DENSITY	% EATEN PER YEAR	% GERMINABLE PER YEAR	% PLANT SURVIVAL	SEEDS PER PLANT	REPRODUCTIVE POTENTIAL	SEEDLINGS	MATURE PLANTS	SEEDS PRODUCED
0	10000	90.0	1.0	50.0	150.0	0.75	100.0	50.0	7500.0
1	990	50.0	5.0	50.0	150.0	3.75	49.5	24.8	3712.5
2	470	50.0	90.0	50.0	150.0	67.50	423.2	211.6	31741.9
3	23	50.0	90.0	50.0	150.0	67.50	21.2	10.6	1587.1
4	1	50.0	90.0	50.0	150.0	67.50	1.1	0.5	78.8
	11484						594.9	297.5	44620.8

**** SEED PRODUCTION RATIO IS 4.462 ****

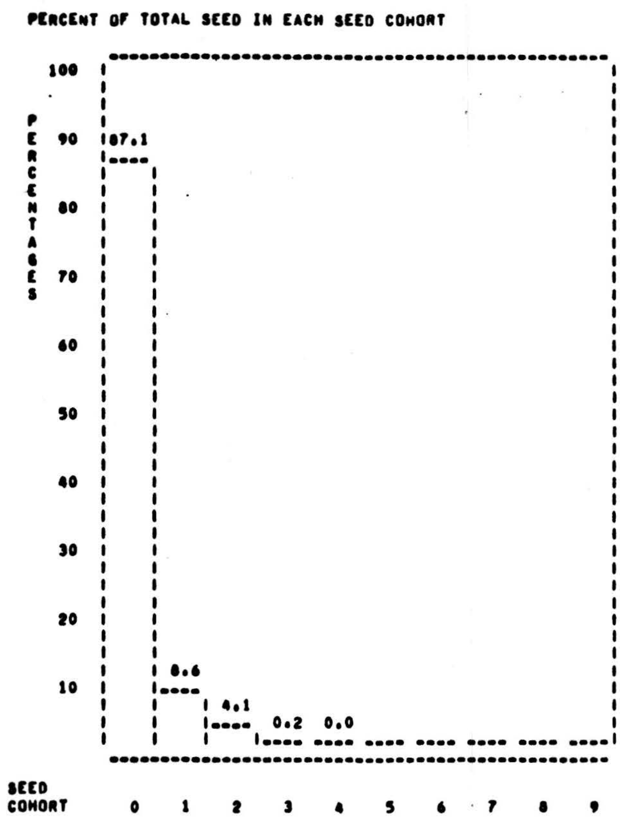

Figure 23. Distribution of seed age from STRATEGY2, second example.

germination of 2-year-old seeds. It is clear that different curves of G and P can cause drastic differences in the age structure of the seed reserves in the soil and, hence, on the population dynamics of the species.

One of my stated objectives for STRATEGY2 was to determine whether a given combination of functions for G, K, S, and P described an expanding or declining population. After a few runs of this model I discovered that the rate of increase (or decrease) of the population was sensitive to the age structure of its seed reserves.[9] In a rapidly expanding or declining population, the age structure as computed with equation 11 (p. 41) could be very much in error. In an expanding population, the equation underestimates the younger cohorts in relation to the older cohorts. The reverse is true for a declining population. STRATEGY2 would then overestimate the rate of growth in an expanding population and underestimate it in a declining population. Concerned about this difficulty, I consulted the animal ecology literature dealing with dynamic life tables on a finite time interval. It turns out that Leslie (1945, 1948) developed a matrix method for this type of problem that is quite elegant. However, this technique cannot be solved analytically for populations with more than four cohorts -- numerical methods are required for solving an nth order algebraic equation, where n is the number of cohorts. In this case with seed cohorts, I would certainly want to keep track of more than four cohorts.

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[9]The analogous situation in animal populations (humans, in particular) is quite well known.

But Leslie also proved that, if the demographic parameters are not changing with time, any population will eventually reach a stable age distribution and then maintain it, even though it may be an expanding or declining population. Thus the answer for my problem was to take several iterations (i.e., run the population through several generations with a given set of G, K, S, and P functions) to determine the stable age distribution. With this distribution STRATEGY2 could then accurately calculate the rate at which the population was increasing or decreasing. I added an iteration loop in STRATEGY2 and found that the age distribution did indeed reach a stable form within 5-10 generations, depending on the number of cohorts involved. I also found that the difference between the initial age distribution (equation 11) and the one obtained after several iterations was not as great as I had anticipated. However, the true growth rate <u>was</u> very much smaller (in an expanding population) then the initial calculation indicated. Conversely, the growth rate in a declining population was not as low as the initial calculation indicated.

In retrospect, it seems that my concern about the accuracy of the construction of the stable age distribution was a needless worry. When I began work on Model 3 with a randomly varying environment, the concept of a stable age distribution proved to be a bit ridiculous. Since seed production varied tremendously from year to year, the age structure was dominated by the recent rainfall history during the run. However, I could use the approximate form of the age distribution as the initial condition for a given run in Model 3.

Model 3: Distinguishable seed cohorts in a randomly varying environment

Figure 24 displays the structure of Model 3. The symbols labeled S, K, and GR represent "valves" controlling the amount of flow from one plant stage to the next. The arrows entering the right sides of these valves indicate what variables determine the degree to which the valves are open or closed.

Since I intended to test the model with data on desert annuals, rainfall is the only environmental variable that is considered in the present version.[10] In deserts the germinating rainfall can be as little as 10% or as much as 90% of the total rainfall over the growing season. Both the total rainfall and the germinating rainfall are treated as random variables in Model 3. The distributions used for these two random variables are determined from historical records for the site in question.

Only the parameters P and G are still assumed to be functions of seed age. The value of K (% survival from seedling to mature plant) is now assumed to be a function of (1) the total rainfall over the growing season and (2) the density of seedlings following a 2-3 week germination period at the beginning of the growing season. The value of S (number of seeds per mature plant) is assumed to be a function of (1) the total rainfall over the growing season and (2) the density of mature plants at the end of the

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[10]A possible later addition would be a growing season of varying length.

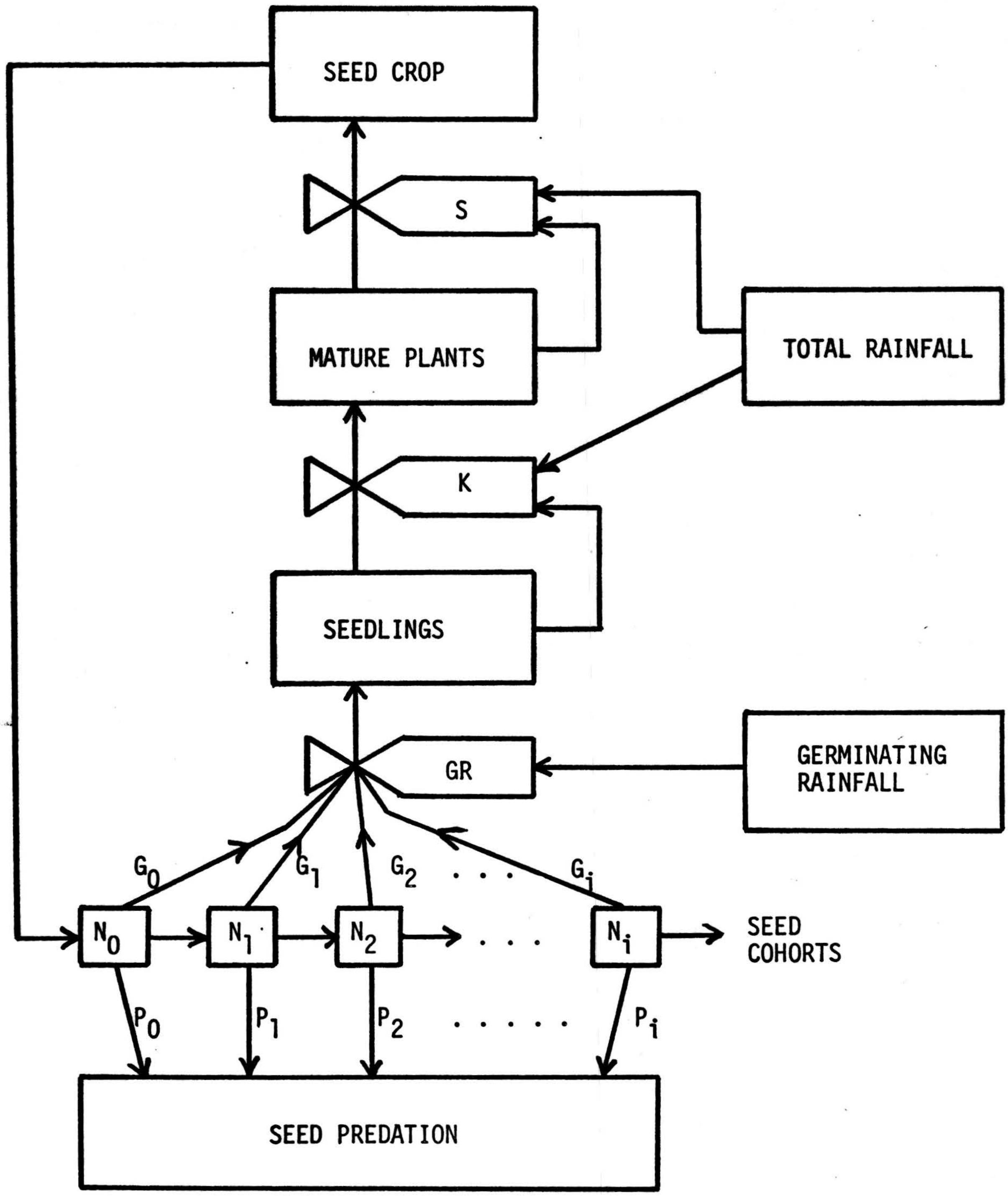

Figure 24. Diagram of Model 3

growing season.[11]

The number of seeds that germinate in a given year is now determined by (1) the pattern of seed dormancy (expressed by G as a function of seed age) and (2) the amount of the total rainfall that comes in the time of the year suitable for germination. The effect of the germinating rainfall on seed germination has been shown in Figure 24 as the valve labeled GR.

The best way to describe Model 3 is to outline the sequence of steps that the computer program, STRATEGY3, carries out in one complete run. The first step is the reading in of all the data required by the program and the calculation of the initial conditions. During any one year (actually, one growing season) of the simulation, the sequence of steps that occur can be labeled as (1) stochastic generation of total rainfall over the growing season and the fraction that comes as germinating rainfall, (2) the determination of the total density of seeds that are potentially germinable, (3) the determination of how many of these potentially germinable seeds respond to the germinating rainfall in that year and produce seedlings, (4) the calculation of the density of seedlings that survive to maturity as determined by the total rainfall over the growing season and the density of seedlings, (5) the calculation of the seed crop as determined by the total rainfall over the growing

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[11]The growing season and the period of germination are defined externally to the model. The rainfall data (read into the program at run time) are analyzed according to the typical growing season for the annual plant whose population dynamics is being simulated. See Appendix 2.

season and the density of mature plants, (6) the reduction of each seed cohort by losses due to germination and predation, and (7) the advancing of all seed cohorts in age by one year and placing the seed crop into the zeroth cohort at year's end. Each subsequent year is then just a repeat of steps 1-7.

The example set of functions next described are called the base run. They incorporate the "best guesses" that I could make for them, using all of the available data for winter annuals. Since most of this data is from Beatley's work at the Nevada Test Site, the rainfall data used is that from the US Weather Bureau at Las Vegas.[12]

Beatley's data are for winter annuals as a group. The implicit assumption that has been made with all three models is that they each describe a single species. However, it is well known that the bulk of the production of annuals on a given desert site is usually supplied by just one or two dominant species. The output of STRATEGY3 will be compared with this group data as if the model were describing the mean plant responses for these dominant species.

Initial conditions. Apart from supplying STRATEGY3 with the number of years to run, the rainfall distributions, and the functions describing the plant's responses, the only initial condition required at the beginning of a simulation run is the densities of seeds in each age class. As mentioned in the discussion of Model 2, the initial age structure is calculated in STRATEGY3 with the use of equation 11 on page 41, using the values read in at run time for the functions

[12]Las Vegas is at a lower elevation than most of the Nevada Test Site and, hence, its mean rainfall is somewhat lower as well.

G, P, and N_0, the initial seed crop. For the base run, N_0 is set equal to 2000 seeds per square meter -- a value that is consistent with the range of seed production for the Nevada Test Site (see below, page 62). The initial age distribution for the total seed density used in the base run is shown in Figure 25.

Stochastic rainfall generator. STRATEGY3 assumes that the distribution of total rainfall over the growing season has been classified into six rainfall classes. The corresponding mean rainfall amounts for these classes and their probabilities of occurance are read in as data. A random number is then used to decide what the total rainfall is for a given growing season. Table 3 shows the base run data for Las Vegas. The cummulative probabilities for each rainfall class k are given by:

$$\text{cummulative probability } (k) = \sum_{i=1}^{k} (\text{rainfall probability for class } i)$$

The random numbers are drawn from a uniform distribution on the interval (0,1).[13] Assume that a particular random number turns out to be 0.632. Looking at the last column in Table 3, we see that this is larger than the cummulative probability for class 1, but less than that for class 2. This implies that the predicted rainfall amount falls somewhere within the range of class 2. STRATEGY3 then sets the total rainfall amount equal to 75 mm, the mid-point of class 2. If the random number had been 0.013, the total rainfall would be 25 mm. If it had been 0.984, the total rainfall would be 175 mm.

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[13] If desired, a given sequence of random numbers can be repeated from run to run. This allows one to assess the effects of changes in plant parameters on the output of the model while keeping the sequence of rainfall years the same.

THIS IS THE INITIAL AGE DISTRIBUTION

TOTAL SEED DENSITY IS 2827 PER SQUARE METER

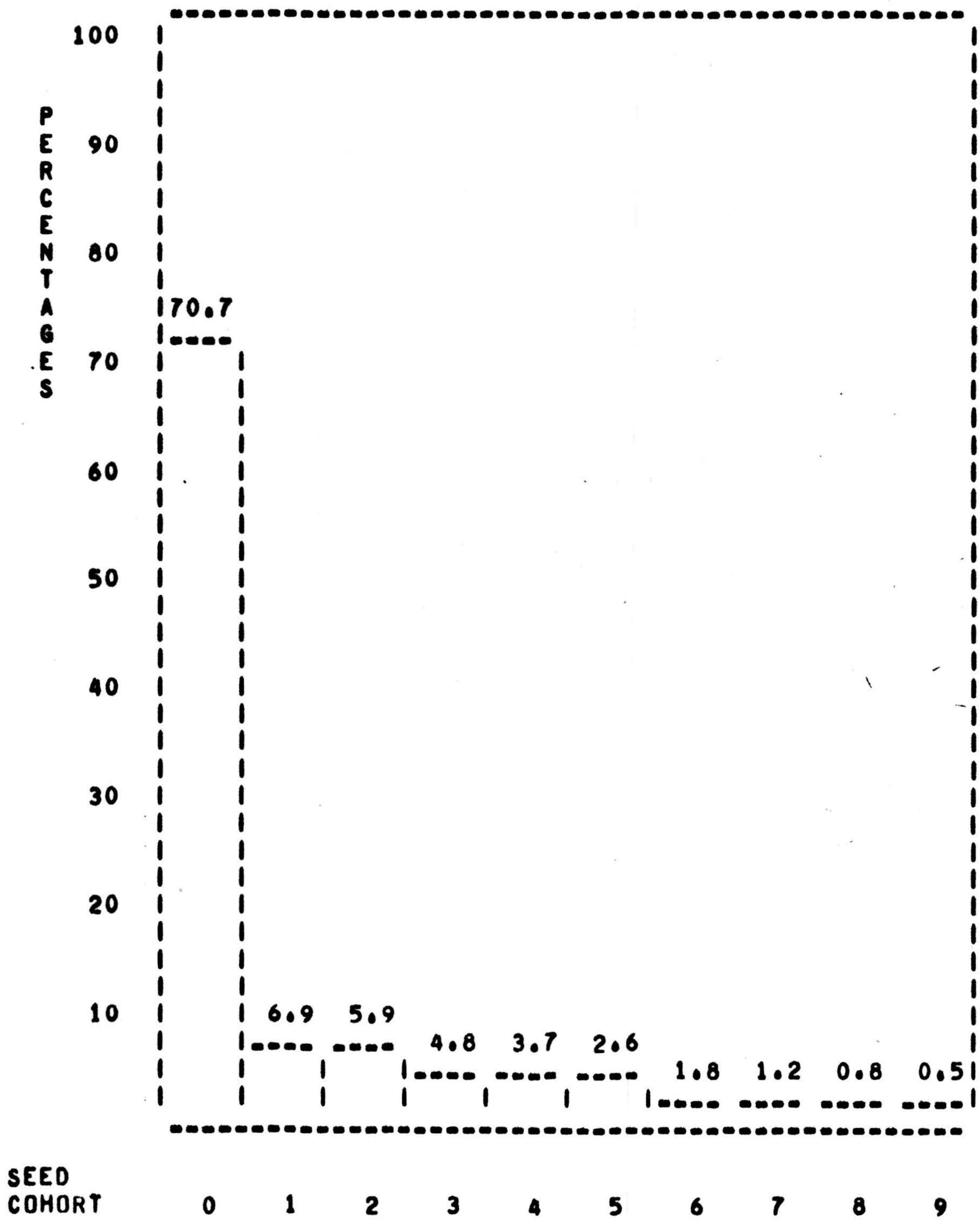


Figure 25.

Table 3. Distribution of the total rainfall over the growing season for Las Vegas

Class	Total Rainfall Interval (mm)	Interval Mid-point (mm)	Probability of Occurance	Cummulative Probability
1	0 - 50	25	.475	.475
2	50 - 100	75	.350	.825
3	100 - 150	125	.150	.975
4	150 - 200	175	.025	1.000
5	200 - 250	225	.000	1.000
6	250 - 300	275	.000	1.000

Table 4. Distribution of the ratio (germinating rainfall/ total rainfall) for years with total rainfall in rainfall class 2, for Las Vegas

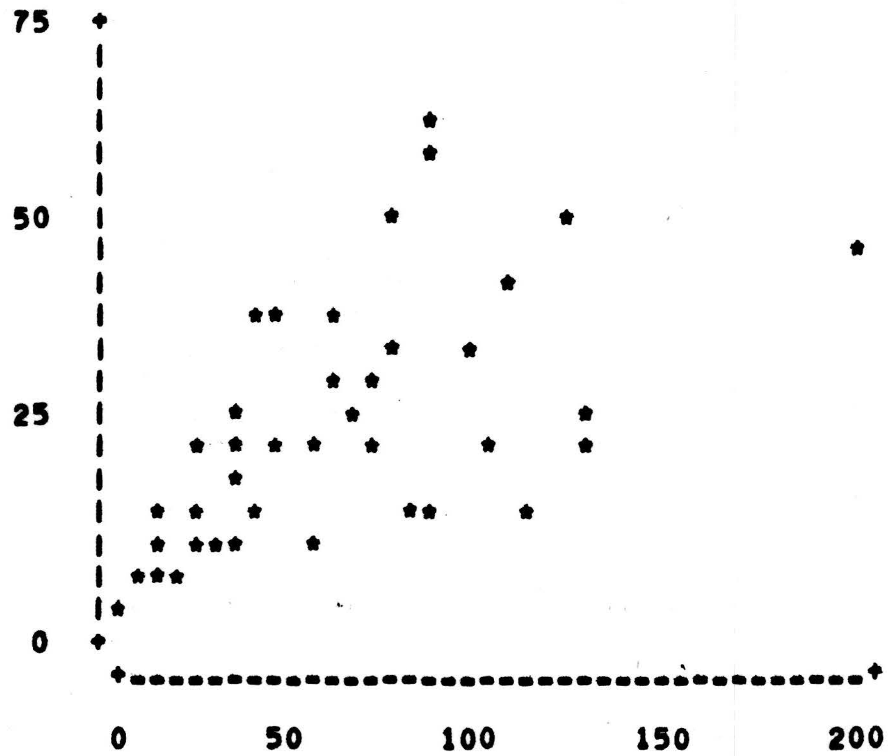
Ratio Interval	Interval Mid-point	Historical Probability	"Smoothed" Probability	Cummulative Probability
.0 - .1	.05	.000	.000	.000
.1 - .2	.15	.143	.167	.167
.2 - .3	.25	.071	.167	.334
.3 - .4	.35	.214	.167	.501
.4 - .5	.45	.285	.167	.668
.5 - .6	.55	.000	.167	.835
.6 - .7	.65	.285	.167	1.000
.7 - .8	.75	.000	.000	1.000
.8 - .9	.85	.000	.000	1.000
.9 -1.0	.95	.000	.000	1.000

Once the total rainfall has been determined, the amount that comes as germinating rainfall must be calculated. I had originally hoped to use a regression equation relating germinating rainfall to total rainfall. Figure 26 shows the set of historical data points for Las Vegas. It is clear that a regression equation would not be suitable (these data have $r^2 = 0.35$). However, the correlation is too high to allow the germinating rainfall to be completely independent of the total rainfall.

I then looked at the distribution of the ratio of (germinating rainfall)/(total rainfall) within each of the six classes of total rainfall. Table 4 shows the distribution of this ratio for Las Vegas for years when the total rainfall fell within class 2 (50-100 mm). Since the number of original data points is small, I decided to "smooth" the historical probabilities by allocating equal probabilities to the set of ratio intervals bounded by the historical data. Similar sets of ratio probabilities were calculated for the other five classes of total rainfall years and are shown in Appendix 2.

Carrying through on our example where the total rainfall was determined to be 75 mm (class 2), a second random number is then chosen to compare with the appropriate set of cummulative probabilities listed in Table 4. Assuming this second random number is 0.532, then the corresponding ratio would be .45, the mid-point of the ratio interval 0.4-0.5. Since the total rainfall is 75 mm, the germinating rainfall is the product: (.45)(75 mm) = 34 mm.

<u>Seedlings.</u> STRATEGY3 keeps track of the seed densities of 20 cohorts -- last year's seed crop (age = 0 at the beginning of the year),



GERMINATING RAINFALL IN MM (Y-AXIS) VS
TOTAL RAINFALL (MM) OVER GROWING SEASON (X-AXIS)
LAS VEGAS DATA YEARS: 1931-1971

Figure 26.

plus seeds from 1-19 years of age. As in Model 2, the dormancy pattern for the seeds is contained in the function G. The base run form of G is shown in Figure 27. I have assumed that the seeds are quite dormant the first year (age class 0), with the percent germinable slowly rising to 30% for seeds that are eight years old or older.

The total density of potentially germinable seeds is found by calculating the density of germinable seeds in each age class and then summing these values. In a given year, not all of the potentially germinable seeds may germinate. The amount of germinating rainfall will in fact determine what fraction germinates. In STRATEGY3 the factor called <u>germination response</u> (the valve labeled GR in Figure 24) is a function that ranges between 0-1, depending on the magnitude of the germinating rainfall. Figure 28 displays the base run form for GR. It is in agreement with the field observations that usually one inch of rain (25 mm) is required to get maximum germination response and that rains of less than 0.5 inch are totally ineffective.

The density of seedlings is given by the product of the total density of germinable seeds and the value of GR corresponding to the germinating rainfall in the current year.

<u>Mature plants.</u> The probability of survival (K) from seedling to maturity is now a function of two variables: total rainfall and seedling density. The base run form of K is shown as families of curves in Figures 29 and 30. The values have been chosen such that the curve labeled 100 (seedlings per square meter) is in approximate

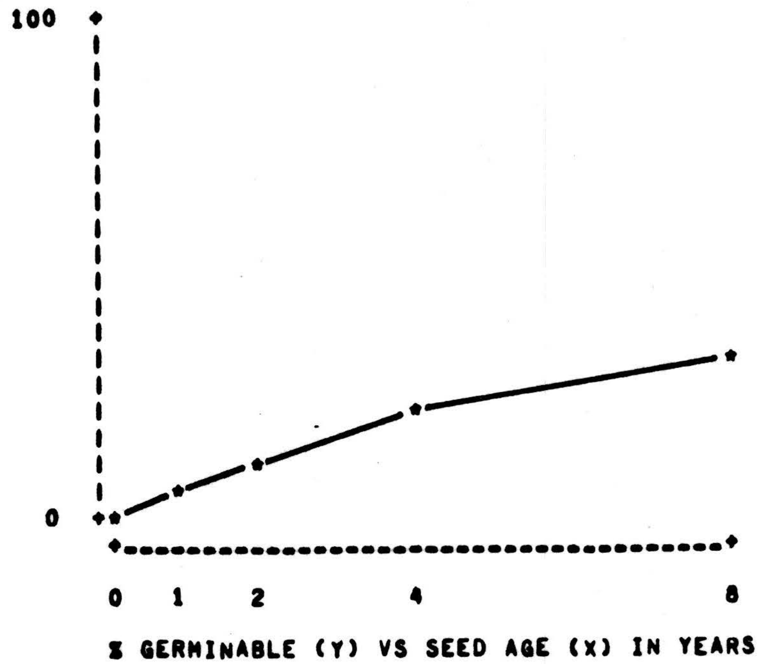


Figure 27.

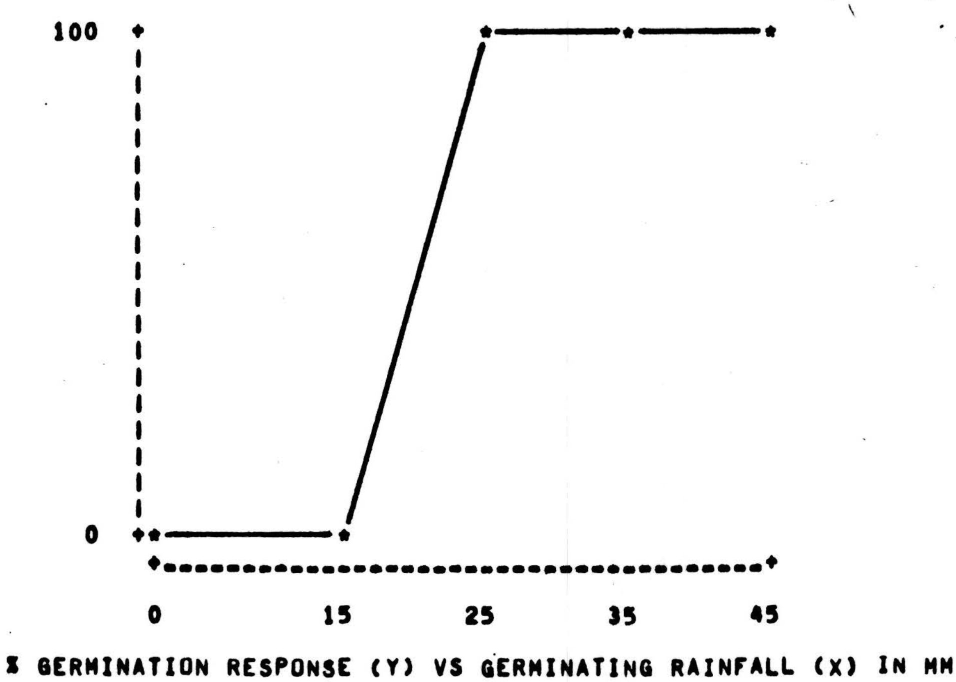
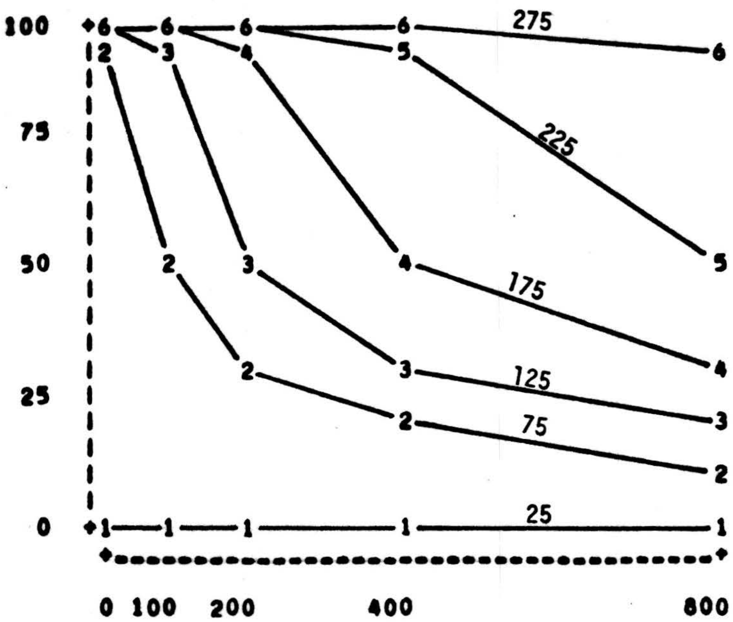
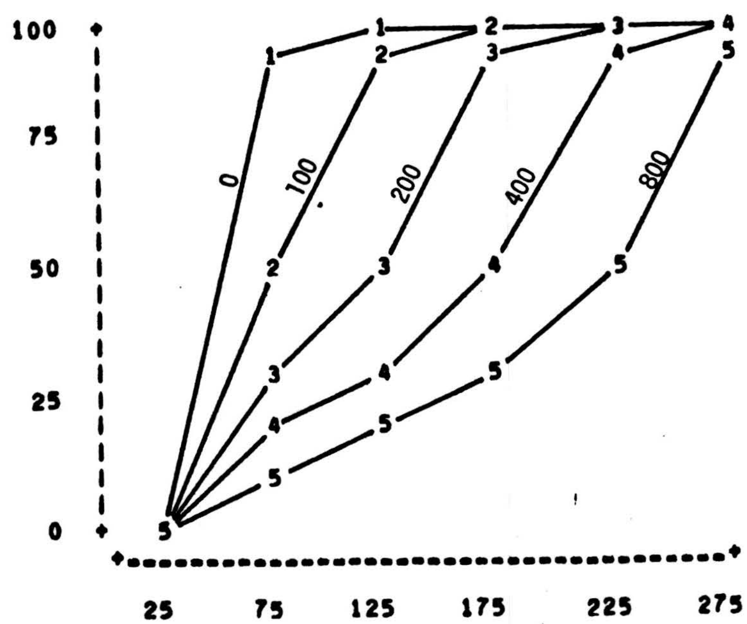


Figure 28.



% PLANT SURVIVAL (Y-AXIS) VS
SEEDLING DENSITY IN #/SQ METER (X-AXIS)
FOR DIFFERENT TOTAL RAINFALL AMOUNTS IN MM

Figure 29.



% PLANT SURVIVAL (Y-AXIS) VS
RAINFALL (MM) OVER GROWING SEASON (X-AXIS)
FOR DIFFERENT SEEDLING DENSITIES IN #/SQ METER

Figure 30.

agreement with the data of Beatley (1967) shown in Figure 1, page 17. The shapes of the curves for the other densities are just guesses at the moment.

STRATEGY3 reduces the seedling population by the appropriate value of K as determined by the current year's values for total rainfall and seedling density.[14]

Seed crop. The number of seeds per plant (S) at maturity is now a function of the total rainfall and of the density of mature plants. The base run form of S is shown in Figures 31 and 32. These curves are almost complete speculation at this point. From Tevis (1958c) one can calculate a range of values for S of 350-2000 seeds per plant for the species of annuals on his watered plots near Indio, California. These values are certainly too high for plants growing without supplemental water. A rough measure of S for annuals on the Nevada Test Site may be made with information from four sources: Baker (1972), Harper et al (1970), and Beatley (1967, 1969b). Baker has found that the mean seed weight for semi-arid annuals in California is about 0.001 gram. Harper et al report that most "weedy" species have 15-30% of their total biomass as seed at maturity. From Beatley's two papers we find that a density of 70 plants per square meter has a total biomass of 100 kgm per hectare. This would give a total seed biomass of 1.5-3.0 grams per square

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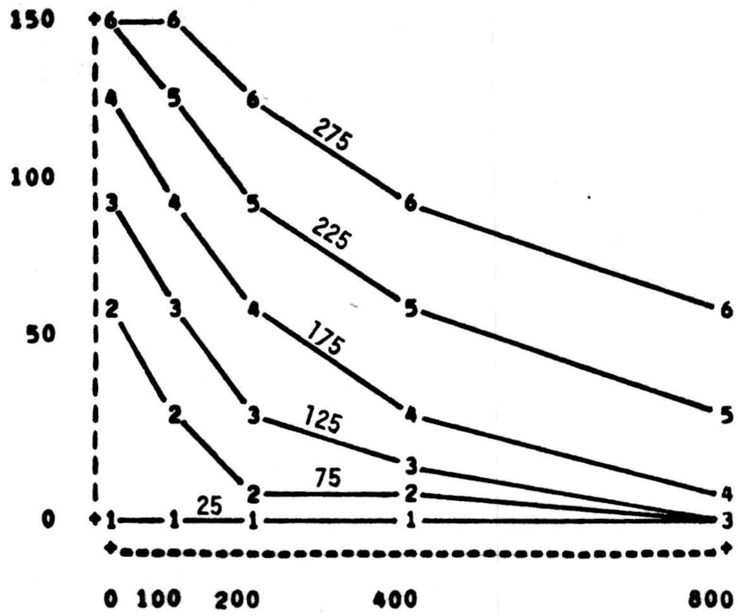
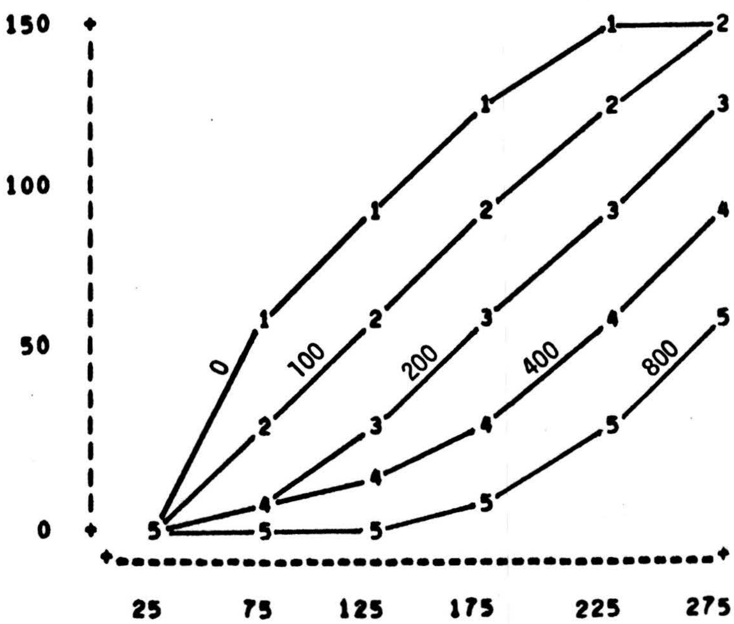
[14]STRATEGY3 calculates K by linear interpolation along one of the rainfall curves in Figure 29. If the total rainfall was not restricted to a finite number of values, interpolation on a surface would have been required. This consideration is one of the reasons I decided to limit the total rainfall to a few discrete possibilities.



SEEDS PER PLANT (Y-AXIS) VS
MATURE PLANT DENSITY IN #/SQ METER (X-AXIS)
FOR DIFFERENT TOTAL RAINFALL AMOUNTS IN MM

Figure 31.



SEEDS PER PLANT (Y-AXIS) VS
RAINFALL (MM) OVER GROWING SEASON (X-AXIS)
FOR DIFFERENT MATURE PLANT DENSITIES (#/SQ METER)

Figure 32.

meter. The number of seeds per plant is then in the range of 20-40.

I have assumed that the species that is represented by the curves in Figures 31 and 32 has a genetic maximum of 150 seeds per plant.[15] This is a quite conservative figure. The maximum is only reached at low plant densities and high rainfall. The seed crop is given by the product of the density of mature plants and the appropriate value of S as determined by the current year's total rainfall and the mature plant density.

Seed losses. Seeds are lost from a given cohort each year either by germination or predation. After the year's germination calculations have been completed, the seed density in each seed cohort is reduced by the density of seedlings that arose from each of them. As in Model 2, the rate at which seed predators consume a given seed age is given by the function P. The base run values for P are shown in Figure 33. The shape of this curve has been inferred from information from several sources. Chew and Chew (1970) found that small mammals were eating about 85% of the seed crop on a Sonoran desert site. The base run curve specifies that 90% of the seed crop (after germination losses) will be eaten or otherwise lost to the system in one year's time. Balda et al (1972) found that the total loss of seed (predation plus germination) was approximately 95% per year. This would be consistent with the above predation curve and with total germination rates of the order of

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[15]Previous experience with STRATEGY2 had shown that, with reasonable choices for the other functions in the model (e.g., seed predation rate), a positive growth rate could be achieved with S values in the range of 40-100.

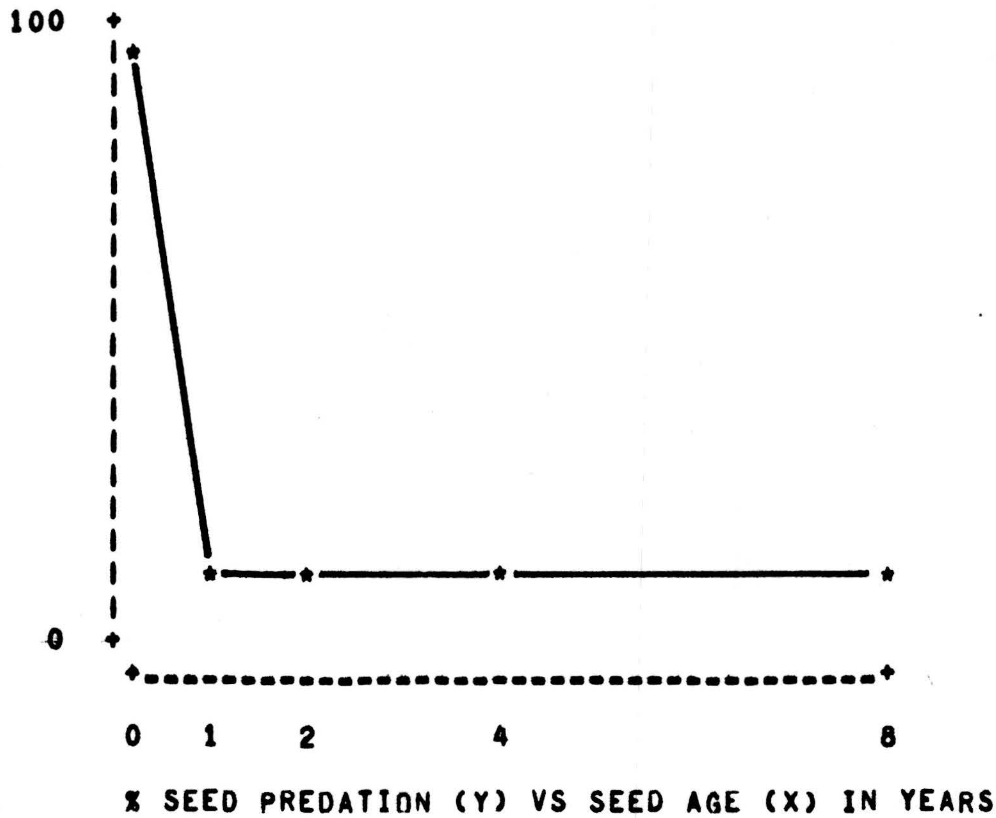

Figure 33.

10-20% per year.

The low seed-eating rate for older seeds is justified on the basis of two pieces of evidence: (1) the existence of large seed reserves in the soil at depths of several centimeters and (2) the existence of certain rare species of desert annuals that only appear at intervals of several years. Neither of these two conditions could persist in the face of continued heavy losses from the older seed cohorts.

Advance the seed cohorts. At the end of each year of simulation, the remaining seeds in each cohort are advanced into the next older age class. The seed crop is placed in the youngest cohort (age = 0). Any seeds still present that are 19 years old are totally "lost" at this point. It is assumed that such cases will be rare and that the seed densities involved are quite negligible. If the model is to be applied to situations where 20 year old seeds are a common occurance, one need only increase the number of cohorts in the computer program.

Base run output. The output of the base run is shown in the next set of figures and tables. Figure 34 displays the name of the site and the distribution of the total rainfall over the growing season for that site. Figures 35-38 show "snapshots" of the seed age distribution at years 2, 4, 8, and 20 (the initial distribution is shown in Figure 25 on page 55). They amply demonstrate how the recent rainfall history affects the relative abundance of different age seeds. Year 20 is in the middle of a string of very low rainfall years.

THIS IS THE DISTRIBUTION OF TOTAL RAINFALL FOR LAS VEGAS

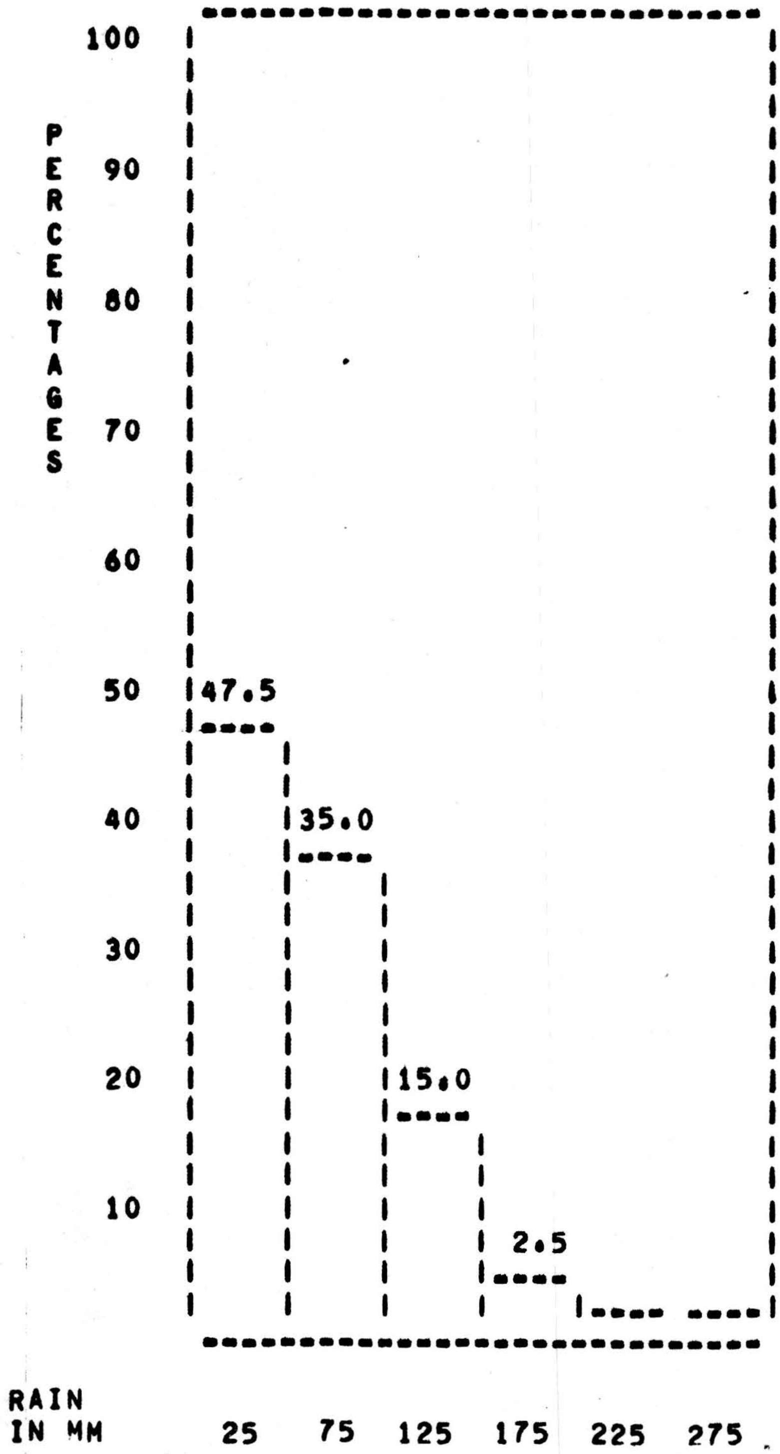

Figure 34.

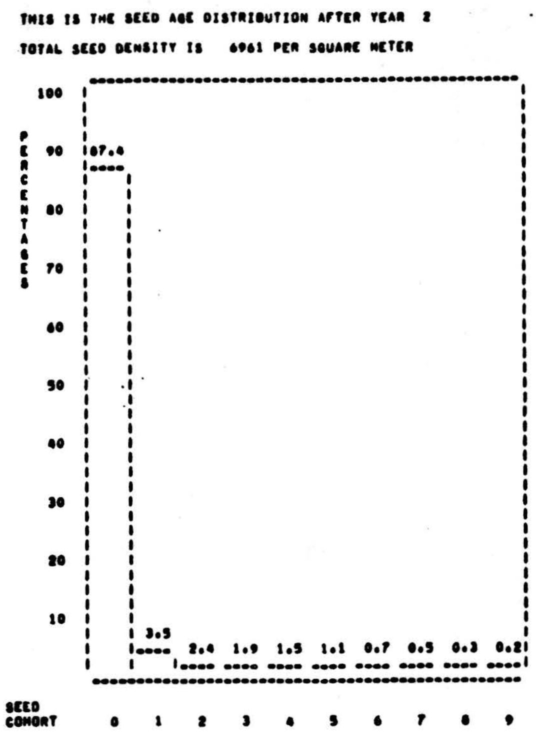

Figure 35.

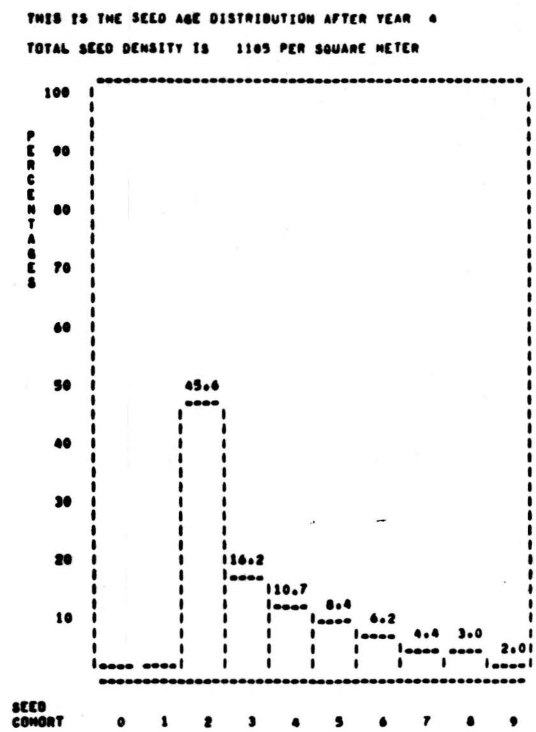

Figure 36.

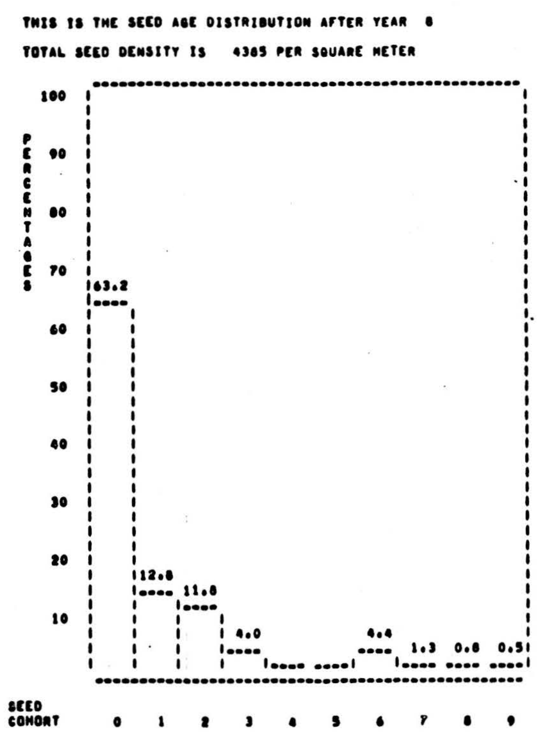

Figure 37.

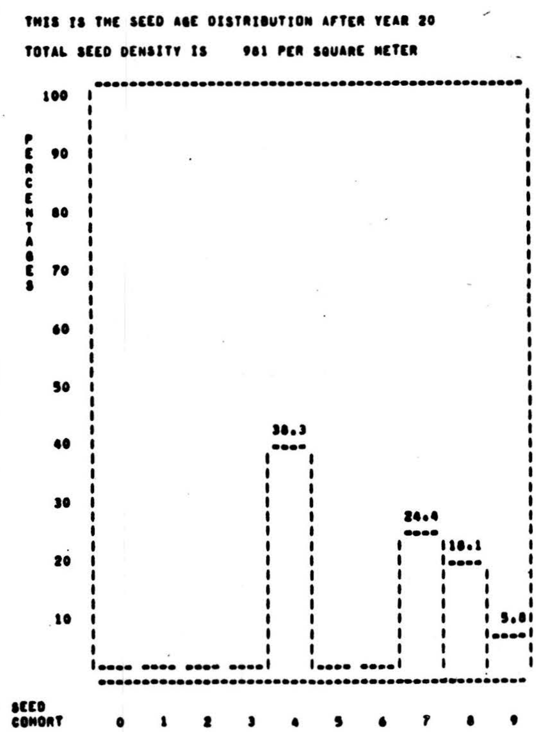

Figure 38.

Table 5 shows the tabulated output for this base run. The column labeled 'GERM FACTOR' is the value of GR. The plant and seed variables are all in units of numbers per square meter. The first five seed cohorts are shown, as well as the seed crop and the total seed density (sum of all cohorts).

Table 6 displays some simple statistical analyses that were done on some of the major variables at the end of the run. This table is a valuable aid in comparing the relative performances of two or more runs that use the same sequence of rainfall years, but have one or more plant functions that are different. The means and standard deviations of the total rainfall and the germinating rainfall indicate how severe and/or variable the physical environment is. The remaining means and standard deviations show how well the plant has adapted to these conditions. In general, higher means and lower standard deviations are the mark of the better adapted plants.

Comparison of base run output with field data. Examination of Table 6 shows that the mean values for the plant and seed variables agree pretty well with the field data. Average plant survival is about 30%. The mean seed crop is in the range calculated on page 62. The mean total seed is a believable figure, considering that field observations have ranged between 500 and 20,000 seeds per square meter.[16]

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[16]Although most of these data on seed reserves undoubtedly reflect the total of both summer and winter annuals, most of the sites in question have the bulk of their yearly production as winter annuals.

Table 5. Output of the 80-year base run, STRATEGY3.

*** INITIAL SEED DENSITY IS 2827 PER SQUARE METER ***

YEAR	TOTAL RAIN	GERM RAIN	GERM FACTOR	% SEEDS GERMINABLE	SEEDLINGS	MATURE PLANTS	SEED CROP	SEED1	SEED2	SEED3	SEED4	SEED5	TOTAL SEED
1	75	33	1.0	5.86	165	61	2504	196	167	135	103	74	3331
2	125	31	1.0	5.28	175	104	6084	245	167	135	103	74	6961
3	25	21	0.6	3.59	156	0	0	600	213	141	110	81	1317
4	75	11	0.0	12.14	0	0	0	0	540	192	127	99	1185
5	75	26	1.0	16.32	193	60	2483	0	0	438	147	91	3376
6	125	43	1.0	6.68	225	106	6098	243	0	0	335	106	6987
7	125	18	0.4	4.03	105	92	5748	605	214	0	0	278	7099
8	75	41	1.0	4.22	299	74	2772	563	517	174	0	0	4385
9	75	33	1.0	5.88	257	69	2725	271	481	419	133	0	4266
10	75	33	1.0	6.40	273	71	2734	267	232	390	320	95	4191
11	75	33	1.0	6.70	280	72	2770	267	228	188	298	230	4145
12	125	31	1.0	6.67	276	117	6325	271	229	184	143	214	7635
13	125	31	1.0	4.43	338	122	6485	619	232	185	141	103	8093
14	25	23	0.9	4.33	306	0	0	637	533	190	145	105	1910
15	25	23	0.9	13.07	218	0	0	0	548	438	149	107	1522
16	125	18	0.4	16.63	94	85	5499	0	0	475	372	124	6784
17	25	21	0.6	5.48	232	0	0	543	0	0	387	293	1551
18	25	21	0.6	16.92	164	0	0	0	473	0	0	305	1248
19	75	11	0.0	19.53	0	0	0	0	0	426	0	0	1123
20	25	16	0.1	22.63	31	0	0	0	0	0	376	0	981
21	75	11	0.0	25.56	0	0	0	0	0	0	0	338	882
22	75	48	1.0	27.12	239	67	2617	0	0	0	0	0	3194
23	125	31	1.0	6.69	213	103	6027	256	0	0	0	0	6658
24	125	18	0.4	3.63	90	82	5357	598	226	0	0	0	6482
25	75	33	1.0	3.85	249	68	2680	525	511	183	0	0	4088
26	25	23	0.9	5.26	188	0	0	263	451	420	143	0	1401
27	125	18	0.4	13.34	70	65	4564	0	232	391	356	119	5760
28	25	21	0.6	5.21	187	0	0	450	0	196	319	280	1408
29	75	41	1.0	15.82	222	64	2572	0	385	0	150	229	3638
30	75	48	1.0	6.89	250	68	2684	252	0	312	0	108	3715
31	75	18	0.4	6.29	87	48	2167	266	222	0	265	0	3299
32	25	16	0.1	7.20	29	0	0	216	238	197	0	232	1210
33	25	18	0.4	17.54	79	0	0	0	190	206	168	0	1013
34	25	23	0.9	20.58	182	0	0	0	0	156	161	124	748
35	75	18	0.4	23.00	64	41	1946	0	0	0	133	134	2561
36	125	31	1.0	7.61	194	101	5982	190	0	0	0	95	6584
37	125	18	0.4	3.63	89	81	5301	593	168	0	0	0	6396
38	175	61	1.0	3.85	246	198	11936	519	507	136	0	0	13315
39	75	18	0.4	3.00	149	59	2518	1184	458	439	115	0	4889
40	25	16	0.1	6.06	37	0	0	251	1059	407	388	101	2357

Table 5. continued

YEAR	TOTAL RAIN	GERM RAIN	GERM FACTOR	% SEEDS GERMINABLE	SEEDLINGS	MATURE PLANTS	SEED CROP	SEED1	SEED2	SEED3	SEED4	SEED5	TOTAL SEED
41	75	26	1.0	13.78	324	77	2778	0	214	858	311	279	4608
42	25	13	0.0	8.18	0	0	0	277	0	193	772	280	1922
43	25	16	0.1	19.03	45	0	0	0	248	0	170	677	1695
44	125	31	1.0	21.97	370	122	6470	0	0	201	0	122	7651
45	75	33	1.0	5.44	416	81	2854	634	0	0	153	0	4291
46	25	8	0.0	7.04	0	0	0	285	570	0	0	138	1578
47	75	18	0.4	17.47	103	50	2243	0	252	494	0	0	3568
48	25	16	0.1	8.74	38	0	0	223	0	224	436	0	1385
49	125	43	1.0	20.21	279	117	6350	0	191	0	171	314	7343
50	25	13	0.0	4.71	0	0	0	635	0	172	0	154	1526
51	75	41	1.0	16.22	247	68	2667	0	542	0	131	0	3816
52	25	16	0.1	6.98	33	0	0	266	0	482	0	115	1276
53	75	11	0.0	18.26	0	0	0	0	239	0	434	0	1148
54	125	43	1.0	21.60	248	112	6279	0	0	193	0	312	7089
55	25	8	0.0	4.44	0	0	0	627	0	0	174	0	1355
56	25	11	0.0	16.09	0	0	0	0	565	0	0	157	1211
57	25	18	0.4	19.18	87	0	0	0	0	489	0	0	1004
58	25	21	0.6	22.05	138	0	0	0	0	0	399	0	763
59	75	33	1.0	24.45	186	60	2500	0	0	0	0	287	3016
60	75	26	1.0	6.08	183	61	2505	245	0	0	0	0	3095
61	25	18	0.4	5.03	58	0	0	248	216	0	0	0	740
62	25	11	0.0	15.22	0	0	0	0	223	194	0	0	666
63	75	41	1.0	18.91	126	56	2427	0	0	181	148	0	2914
64	25	8	0.0	5.23	0	0	0	242	0	0	163	134	673
65	125	18	0.4	17.07	43	41	3177	0	214	0	0	135	3741
66	25	8	0.0	4.66	0	0	0	317	0	192	0	0	825
67	75	18	0.4	15.83	49	34	1690	0	280	0	163	0	2386
68	25	16	0.1	7.02	20	0	0	168	0	249	0	143	779
69	125	43	1.0	18.41	143	104	6043	0	144	0	190	0	6608
70	125	31	1.0	3.59	237	109	6260	592	0	116	0	137	7256
71	25	21	0.6	3.40	153	0	0	618	516	0	95	0	1443
72	25	8	0.0	11.12	0	0	0	0	556	464	0	85	1299
73	25	13	0.0	15.39	0	0	0	0	0	500	418	0	1169
74	75	18	0.4	19.67	86	47	2154	0	0	0	425	348	3121
75	25	18	0.4	8.43	98	0	0	213	0	0	0	354	1010
76	125	43	1.0	20.66	208	102	6048	0	182	0	0	0	6769
77	25	8	0.0	4.19	0	0	0	604	0	164	0	0	1253
78	75	26	1.0	15.53	194	60	2479	0	517	0	125	0	3432
79	75	33	1.0	6.40	219	63	2548	242	0	418	0	90	3494
80	75	33	1.0	5.85	204	60	2494	249	207	0	320	0	3455

Table 6. Statistical summary of the base run.

RAINFALL LOCATION: LAS VEGAS

NUMBER OF YEARS OF SIMULATION: 80

	MEAN	STD DEVIATION
TOTAL RAIN (MM)	67	40
GERMINATING RAIN (MM)	24	11
% SEEDS GERMINABLE	11	6
SEEDLINGS (#/SQ METER)	140	108
MATURE PLANTS (#/SQ METER)	44	45
SEED CROP (#/SQ METER)	2232	2554
TOTAL SEED (#/SQ METER)	3376	2519

Consulting Table 5, we see that the density of mature plants for a given total rainfall year are in qualitative agreement with Beatley's data in Figure 4 on page 19. Years with a total rainfall of 75 mm have mature plant densities that range between 0-80, with a mean of 53. Years with a total rainfall of 125 mm have mature plant densities between 40-125, with a mean of 98. The single year with a total rainfall of 175 mm has a mature plant density of 198.

The effect of the germination response function on the density of seedlings produced in a given year can be readily detected in two types of years: (1) 25 mm years when most of the total comes as germinating rainfall and (2) 75 mm years when a small fraction of the total comes as germinating rainfall. In the first type of year (see years 14, 15, and 20) the plant is "fooled" into germinating a large density of seedlings, none of which will mature in this dry of a year. In the second type of year (see years 4 and 19) the plant "misses an opportunity" by not germinating any seeds in what turns out to be an average rainfall year. This is probably the best that the plant can do because of the unreliability of the germinating rainfall as a trigger in deserts. The relationship between germinating rainfall and total rainfall for Las Vegas is such that the type 1 condition will occur about 22% of the time and the type 2 condition will occur about 6% of the time. Investigations of forms for the germination response function that describe more "opportunistic" or more "cautious" plants will be discussesd in the next section.

RESULTS

The set of base run functions describes the population dynamics of winter annuals as a group quite well. The next question that arises is: What degree of latitude is there in variations in these functions that still describe species which can persist in a given desert environment? The broader theoretical question is: In a given environment (rainfall and seed predators), is there an optimal set of plant response functions?

The results of a number of 80-year simulations with various combinations of plant response functions and environments are presented in this section. Runs that looked as if the plant were going extinct were re-run for a longer period to determine the year of extinction. These runs constitute a sensitivity analysis of the system that Model 3 represents.

Variations in seed dormancy

Table 7 displays how different forms for the seed dormancy function (G) affect the 80-year mean values for the plant variables when all of the other functions in the model have been kept at their base run form. The values given in the table for the shape of the seed dormancy curve are the fraction germinable at seed ages 0, 1, 2, 4, and 8, respectively.[17] When the fraction germinable is

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[17]There are three variables in the model that deal with germination: the function G (% germinable), germinating rainfall, and GR (germination response). Through a variety of reasons, I decided at this point to refer to G as the dormancy curve, even though the values for the curve are the fraction germinable, rather than the fraction dormant.

Table 7. Effects of variations in the dormancy curve on 80-year runs of STRATEGY3.

Dormancy Curve	Percent Germinable	Seedling Density	Mature Plant Density	Seed Crop Density	Total Seed Density
.02,.05,.10,.20,.30(BASE)	11	140	44	2233	3378
.05,.10,.20,.30,.40	16	211	50	2372	3370
.02,.05,.10,.20,.40	12	148	45	2254	3360
.01,.01,.01,.20,.40	10	119	40	2138	3267
.00/.10	6	65	31	1777	2897
.00/.20	11	116	40	2121	3138
.00/.30	16	147	44	2223	3083
.00/.40	21	164	45	2243	2972
.01/.10	6	81	35	1959	3179
.02/.10	6	98	38	2073	3353
.04/.10	7	126	41	2148	3459
.10/.10	10	208	46	2233	3539
.20/.10	14	336	56	2226	3444
.40/.10	22	536	75	2018	2972
.01/.01		extinction in 71 years*			
.02/.02		extinction in 195 years*			
.05/.05	5	97	35	1892	3255
.20/.50	35	451	66	2416	3004
.50/.90	69	766	103	2183	2452

*These were run with STRATEGY3 keeping track of 50 cohorts the same for all ages greater than 0, this is shown in the table in abbreviated form with a '/'. Figure 39 shows a few selected curves with the corresponding value of the total seed density given in parenthesis. It seems that with base run values for the other functions almost any form for G will describe a viable plant -- it is only for very low germinating fractions (1-2%) that extinction occurs.[18]

Another feature of the model that is discernable in Table 7 is the surprising constancy of the mean values for mature plant density, seed crop, and total seed density. It appears that the density dependence incorporated into the curves for percent survival and seeds per plant is quite strong and that these curves effectively dictate a "constant yield" situation. This is particularly evident in the short and moderate dormancy curves (the last two entries). Seedling densities are high (766 and 451, respectively), but mean plant survival and mean seeds per plant are such that the resulting mean seed crop and mean total seed are lower than for runs where the dormancy curve is more restrictive.

The dormancy curve .10/.10 is labeled "optimum" because it has the largest value for the mean total seed density. However, I did ~~not~~ choose it as the base run form on biological (and aesthetic!) grounds. It would seem that whatever the mechanism is for attaining seed dormancy, it probably wears off gradually (e.g., leaching of

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[18]This is because the base run form for the seed predation curve is .90/.10, i.e., when the germination rate is only 1-2% then the older seeds are being eaten at 5-10 times the rate at which they are germinating.

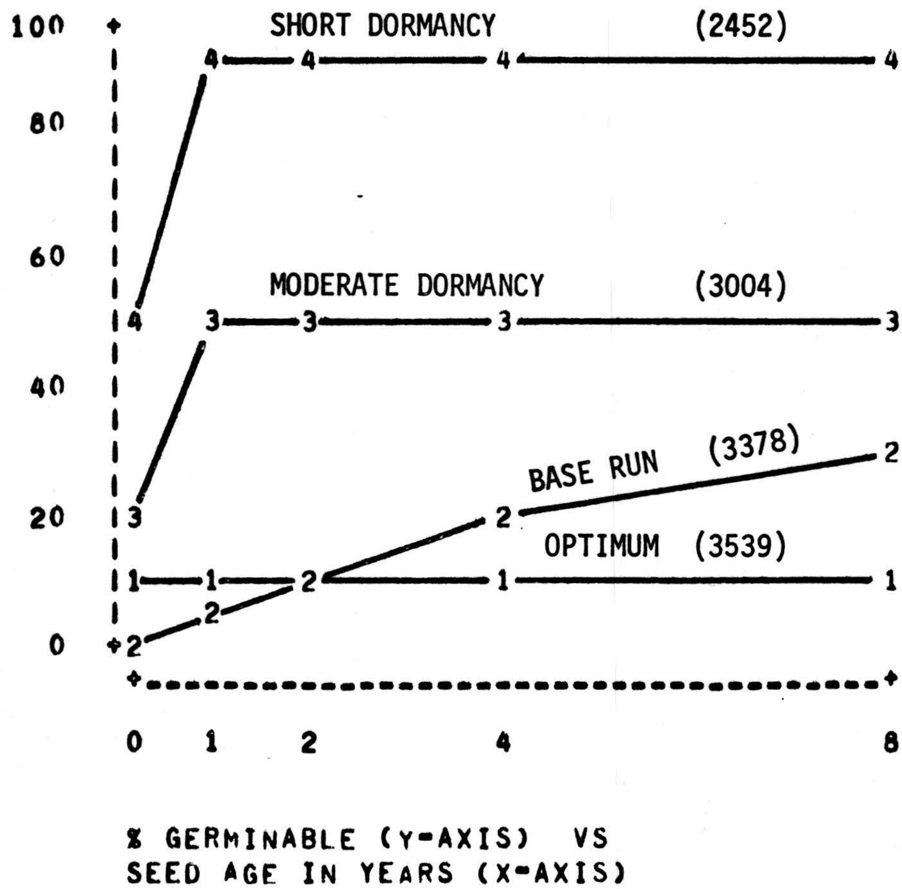
100
80
60
40
20
0
SHORT DORMANCY (2452)
MODERATE DORMANCY (3004)
BASE RUN (3378)
OPTIMUM (3539)
0 1 2 4 8
% GERMINABLE (Y-AXIS) VS
SEED AGE IN YEARS (X-AXIS)

Figure 39.

an inhibitor from the seed coat). The base run curve would reflect this kind of aging process, but with the stipulation that the seeds never become very germinable.[19]

Variations in germination response

Table 8 shows how the action of the valve labeled 'GR' in Figure 24 affects the behavior of the model. The five numbers that describe the germination response curve are the fraction of germinable seeds that in fact do germinate in response to germinating rainfall of 0, 15, 25, 35, and 45 mm, respectively.

Figure 40 displays three of these curves, along with the corresponding mean values of the total seed density given in parenthesis. The curve labeled "opportunistic" allows full germination to occur every year, regardless of the size of the germinating rainfall. In type 1 years (see page 73) all seedlings will die and no seeds are produced. In type 2 years seed production will occur that the base run and "cautious" curves will miss. Since the opportunistic curve yields a higher total seed density, these runs indicate that there is a net gain for a plant with the base run curves for dormancy, percent survival, and seeds per plant to take this risk in low rainfall years. Other combinations for these curves would not produce this result (see below, Table 15).

The curve labeled "cautious" describes a plant that only

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[19]Keeping the value for percent germinable the same for seeds eight years old or older is a programming restriction that could easily be changed. I expect that doing so would not change the qualitative behavior of the model.

Table 8. Effects of variations in the germination response curve on 80-year runs of STRATEGY3.

Germination Response	Percent Germinable	Seedling Density	Mature Plant Density	Seed Crop Density	Total Seed Density
1,1,1,1,1	9	199	48	2412	3418
0,1,1,1,1	9	195	48	2426	3444
0,0,1,1,1 (BASE)	11	140	44	2233	3378
0,0,0,1,1	14	65	29	1552	2530
0,0,0,0,1	19	9	7	459	866

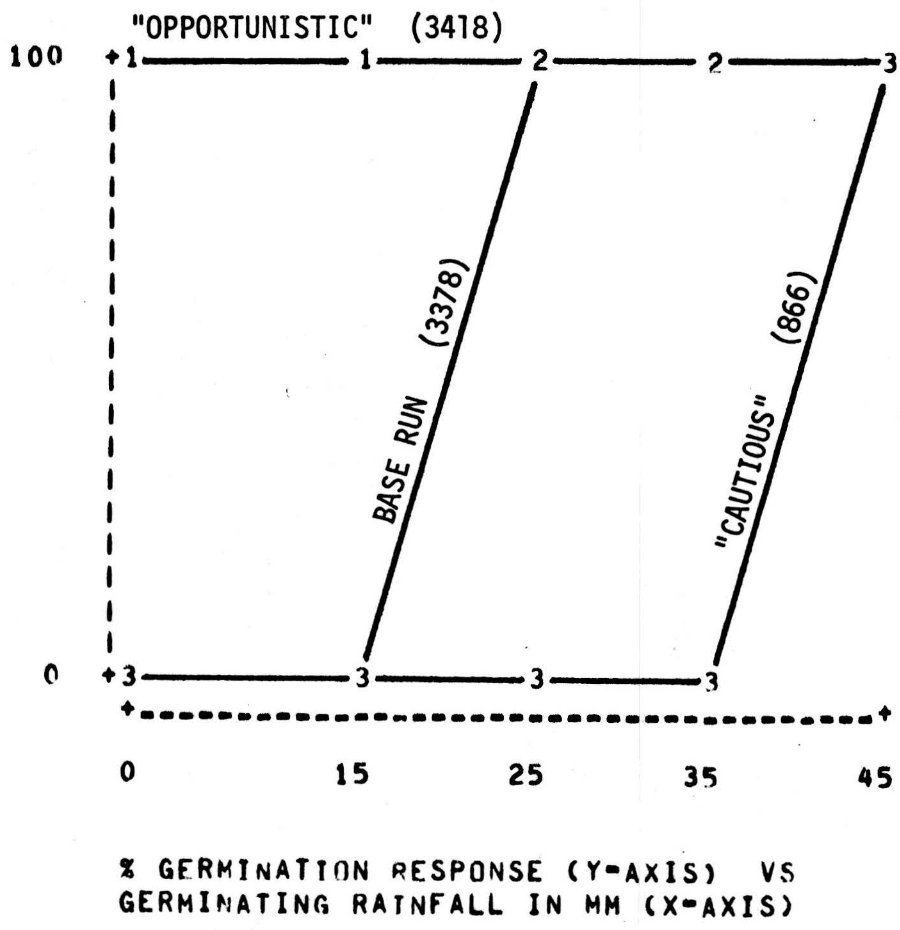


Figure 40.

germinates in exceptionally rainy years. The output from the first 40 years of this run is shown in Table 9. This is probably representative of the species of rare plant that only appear at long intervals on the desert. Although the absolute value of the total seed density is undoubtedly too high for a rare species, changes in the other plant functions could remedy this.

<u>Variations in seed predation</u>

Table 10 displays how different forms for the seed predation curve (P) affect the 80-year mean values when all of the other functions in the model have been kept at their base run form. The values given in the table for the shape of the predation curve are the fraction eaten (or otherwise lost to the system) from the seed crop and from all older seeds, respectively. Thus the first curve (.90/.01) indicates that 90% of the seed crop and 1% of all older seeds are removed from the system each year.

Figure 41 shows three of these curves with the mean total seed in parenthesis. Curve .80/.50 (denoted with '2') tests the relative sensitivity of the seed crop loss rate and the loss rate of older seeds. Comparison with the base run (.90/.10) shows that (1) the fraction of the seed crop that survives to one year of age has been doubled (from 10% survival to 20% survival), but (2) the loss rate from the older seeds has been doubled as well (from 10% loss to 20% loss). The mean total seed is significantly higher with the .80/.20 curve. This would indicate that, given a seed predation curve that is qualitatively like the base run curve, the plant would

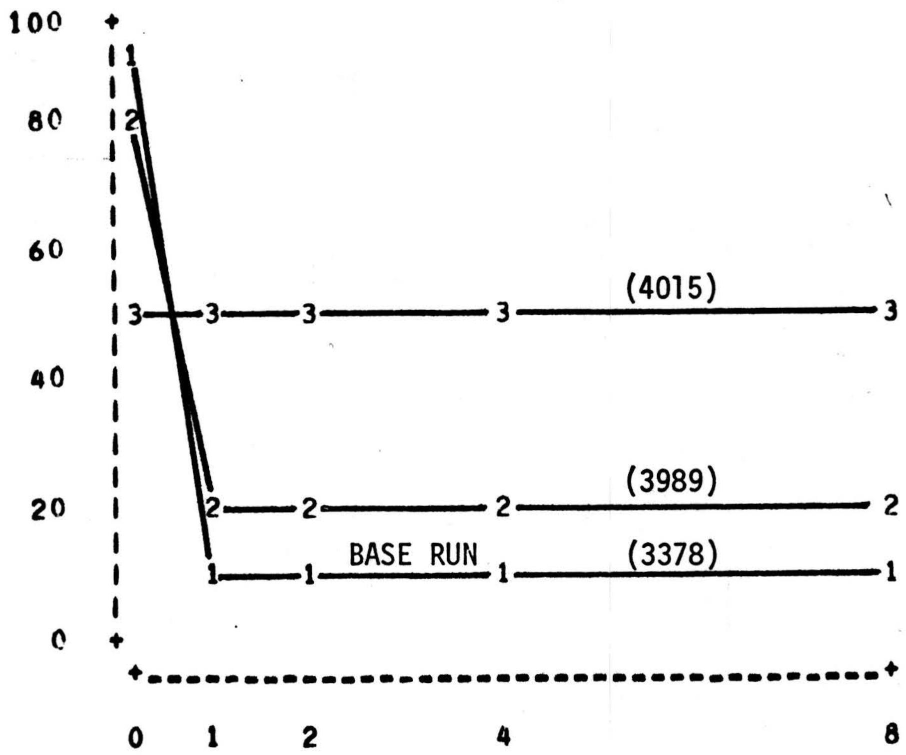
Table 9. Output of the first 40 years of the "cautious" run, STRATEGY3.

*** INITIAL SEED DENSITY IS 2827 PER SQUARE METER ***

YEAR	TOTAL RAIN	GERM RAIN	GERM FACTOR	% SEEDS GERMINABLE	SEEDLINGS	MATURE PLANTS	SEED CROP	SEED1	SEED2	SEED3	SEED4	SEED5	TOTAL SEED
1	75	33	0.0	5.86	0	0	0	200	176	150	122	93	944
2	125	31	0.0	16.06	0	0	0	0	180	158	135	109	849
3	25	21	0.0	19.72	0	0	0	0	0	162	142	122	764
4	75	11	0.0	22.86	0	0	0	0	0	0	145	128	687
5	75	26	0.0	25.35	0	0	0	0	0	0	0	131	618
6	125	43	0.9	27.07	146	104	6066	0	0	0	0	0	6490
7	125	18	0.0	3.73	0	0	0	606	0	0	0	0	987
8	75	41	0.6	14.43	89	48	2179	0	528	0	0	0	2986
9	75	33	0.0	6.03	0	0	0	217	0	476	0	0	943
10	75	33	0.0	16.66	0	0	0	0	196	0	428	0	847
11	75	33	0.0	20.31	0	0	0	0	0	176	0	385	759
12	125	31	0.0	22.71	0	0	0	0	0	0	158	0	679
13	125	31	0.0	25.11	0	0	0	0	0	0	0	142	606
14	25	23	0.0	26.95	0	0	0	0	0	0	0	0	538
15	25	23	0.0	28.81	0	0	0	0	0	0	0	0	475
16	125	18	0.0	29.39	0	0	0	0	0	0	0	0	416
17	25	21	0.0	30.00	0	0	0	0	0	0	0	0	361
18	25	21	0.0	30.00	0	0	0	0	0	0	0	0	309
19	75	11	0.0	30.00	0	0	0	0	0	0	0	0	261
20	25	16	0.0	30.00	0	0	0	0	0	0	0	0	217
21	75	11	0.0	30.00	0	0	0	0	0	0	0	0	195
22	75	48	1.0	30.00	58	39	1876	0	0	0	0	0	1999
23	125	31	0.0	3.73	0	0	0	187	0	0	0	0	298
24	125	18	0.0	14.30	0	0	0	0	168	0	0	0	268
25	75	33	0.0	17.44	0	0	0	0	0	151	0	0	241
26	25	23	0.0	20.58	0	0	0	0	0	0	136	0	162
27	125	18	0.0	21.57	0	0	0	0	0	0	0	123	145
28	25	21	0.0	23.68	0	0	0	0	0	0	0	0	110
29	75	41	0.6	25.00	17	14	790	0	0	0	0	0	875
30	75	48	1.0	4.45	38	28	1478	77	0	0	0	0	1610
31	75	18	0.0	3.10	0	0	0	147	69	0	0	0	267
32	25	16	0.0	10.93	0	0	0	0	133	62	0	0	240
33	25	18	0.0	15.01	0	0	0	0	0	119	56	0	216
34	25	23	0.0	19.08	0	0	0	0	0	0	107	50	194
35	75	18	0.0	22.50	0	0	0	0	0	0	0	97	175
36	125	31	0.0	24.54	0	0	0	0	0	0	0	0	157
37	125	18	0.0	26.58	0	0	0	0	0	0	0	0	141
38	175	61	1.0	28.62	40	40	4345	0	0	0	0	0	4436
39	75	18	0.0	2.58	0	0	0	434	0	0	0	0	516
40	25	16	0.0	8.97	0	0	0	0	391	0	0	0	464

Table 10. Effects of variations in the seed predation curve on 80-year runs of STRATEGY3.

Predation Curve	Percent Germinable	Seedling Density	Mature Plant Density	Seed Crop Density	Total Seed Density
.90/.01	13	235	52	2420	4233
.90/.05	12	186	49	2358	3834
.90/.10 (BASE)	11	140	44	2233	3378
.90/.20	9	84	35	1965	2686
.90/.30	8	48	23	1414	1816
.90/.40		extinction in 159 years			
.90/.50		extinction in 58 years			
.80/.20	10	169	46	2303	3989
.80/.50	6	37	17	1054	1458
.50/.50	7	127	39	2077	4015
.60/.60	6	60	24	1410	2310
.70/.70		extinction in 73 years			



% SEED PREDATION (Y-AXIS) VS
SEED AGE IN YEARS (X-AXIS)

Figure 41.

do better by concentrating on strategies that achieve a larger survival rate for the seed crop than by attempting to lower the long-term loss rate of older seeds.

The seed predation curve .50/.50 shows that a constant loss of 50%, regardless of seed age, is comparable to curves similar to the base run. However, consulting Table 10 we see that if the loss rate is much higher than .60/.60, the plant goes extinct.

Runs with seed predation curves that are less severe than those shown in Table 10 were not attempted, since they would certainly yield mean values even higher than those listed.

<u>Variations in plant survival, seeds per plant, and rainfall</u>

Table 11 shows the effects of changes in the rainfall distribution, percent plant survival, and seeds per plant on the 80-year mean values. These variations are made one at a time, while all other functions in the model are held at their base run values. The variation labeled '+10% Survival' is arrived at by raising the family of curves shown in Figure 29 (page 61) upward by 10% (with 100% as the upper bound). A similar procedure is carried out on the curves in Figure 31 (page 63) to produce the variation labeled '+10% Seeds/Plant'. The '+10% Rainfall' variation is obtained by "enhancing" the historical distribution for Las Vegas. The resulting distribution is shown in Figure 42. The probability for a 25 mm year has been cut in half and added to the probability for a 75 mm year (compare with Figure 34 on page 67). This modification raises the 80-year mean value for total rainfall from 67 mm to 75 mm and the germinating rainfall from 24 mm to 26 mm.

Table 11. Effects of variations in plant survival, seeds per plant, and rainfall on 80-year runs of STRATEGY3.

Variation	Percent Germinable	Seedling Density	Mature Plant Density	Seed Crop Density	Total Seed Density
BASE RUN	11	140	44	2233	3378
+10% Survival	11	146	49	2348	3548
+10% Seeds/Plant	11	156	46	2517	3802
+10% Rainfall	9	168	53	2575	3838
Tucson Rainfall	8	534	154	7700	11204

THIS IS THE DISTRIBUTION OF TOTAL RAINFALL
FOR LAS VEGAS (ENHANCED)

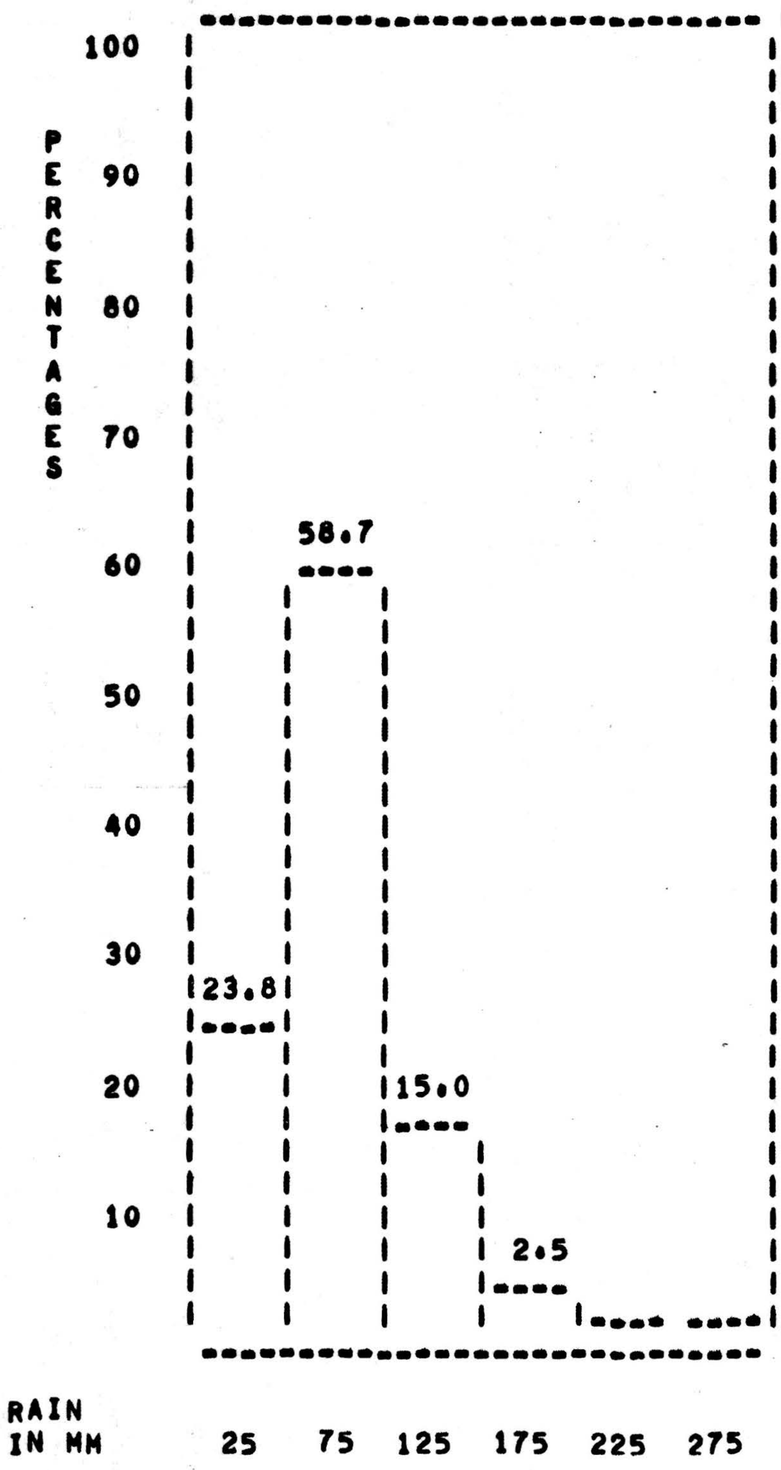


Figure 42.

The Tucson rainfall distribution is shown in Figure 43. The 80-year mean value for total rainfall is 122 mm and for germinating rainfaill it is 34 mm. The output of the first 40 years of this run is shown in Table 12.

Looking back at Table 11 again, we see that increasing the survival rate is not nearly as beneficial as increasing the seeds produced per plant. The previously mentioned density dependence in these two functions is the probable cause for this difference. Increasing the value for seeds per plant is a clear gain for the plant, whereas some of the gain in increasing the survival rate is lost because an increased density of mature plants (in any given rainfall year) will result in lower seed production per plant due to density dependent effects.

These two runs would indicate that for a plant with curves similar to the base run, it would do best to adopt a growth pattern that would trade an increase in the number of seeds per mature plant for a decrease in the survival rate from the seedling stage to maturity. One can imagine this being accomplished in two ways: (1) put less biomass into root material in order to increase the proportion of mature plant that is in seed form or (2) decrease the mean seed weight so that a given fraction of total plant biomass as seed represents a larger number of seeds per plant. It is clear that either of these two strategies will result in lowered plant survival -- the former through reduced ability of the plant to extract water from the soil (either alone or in competition with

THIS IS THE DISTRIBUTION OF TOTAL RAINFALL
FOR TUCSON

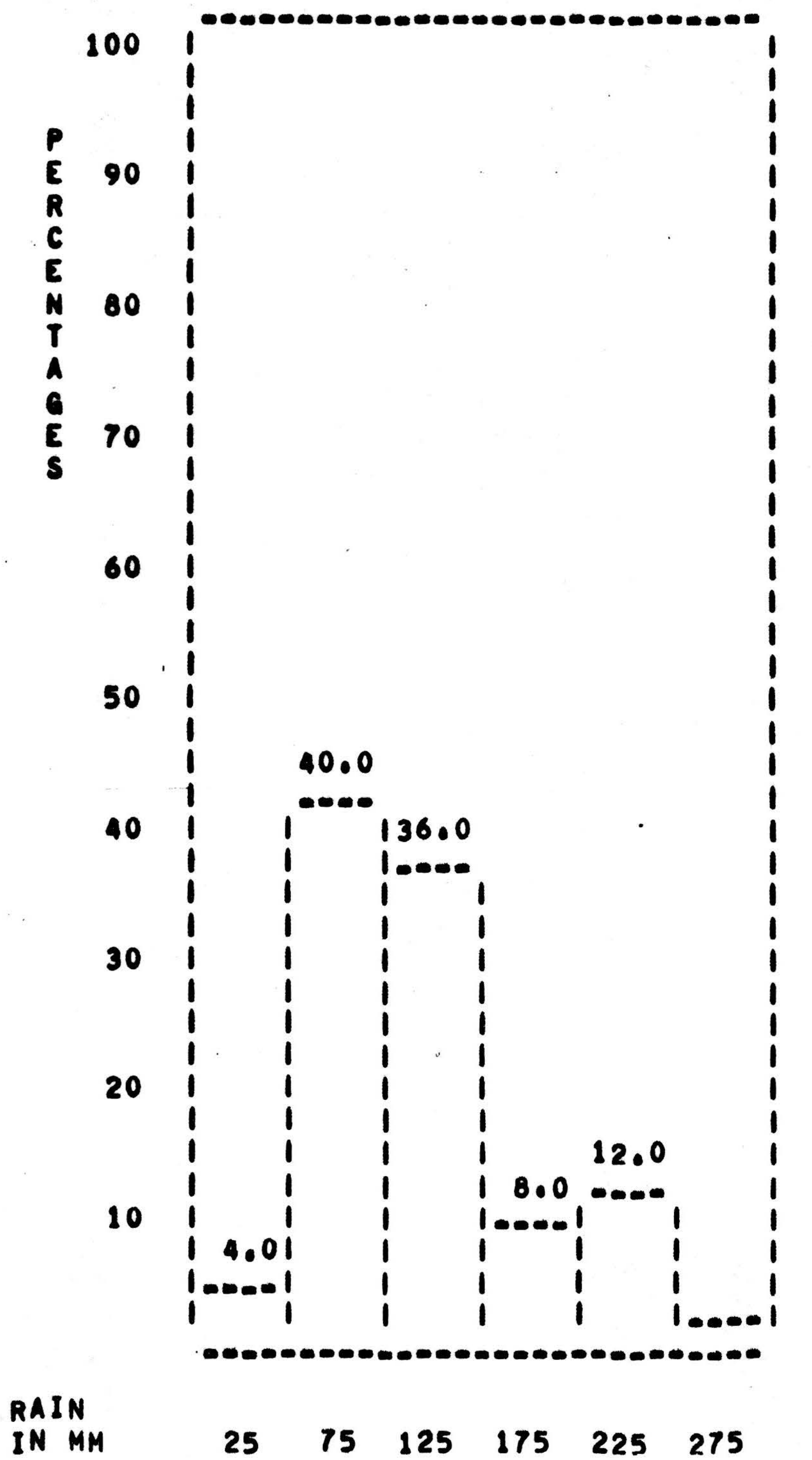


Figure 43.

Table 12. Output of the first 40 years of the Tucson rainfall run, STRATEGY3.

*** INITIAL SEED DENSITY IS 2827 PER SQUARE METER ***

YEAR	TOTAL RAIN	GERM RAIN	GERM FACTOR	% SEEDS GERMINABLE	SEEDLINGS	MATURE PLANTS	SEED CROP	SEED1	SEED2	SEED3	SEED4	SEED5	TOTAL SEED
1	125	31	1.0	5.86	165	105	6123	196	167	135	103	74	6950
2	175	61	1.0	3.57	248	199	11968	600	167	135	103	74	13199
3	75	33	1.0	2.92	385	79	2876	1172	513	135	103	74	5025
4	125	6	0.0	5.31	0	0	0	287	1055	461	122	93	2222
5	125	18	0.4	13.08	108	94	5743	0	253	914	392	101	7645
6	175	78	1.0	5.82	445	212	12329	562	0	205	699	282	14305
7	225	33	1.0	4.00	572	416	24152	1208	481	0	157	503	26846
8	175	78	1.0	3.09	828	248	12923	2366	1033	389	0	113	17404
9	125	31	1.0	4.12	716	158	6646	1266	2023	836	298	0	11533
10	125	43	1.0	6.18	712	158	6639	651	1082	1639	640	214	11167
11	125	43	1.0	7.02	784	159	6717	650	556	877	1254	460	10856
12	225	56	1.0	7.40	803	401	23688	658	556	451	671	902	27470
13	175	43	1.0	4.05	1111	333	13002	2321	562	450	345	483	18153
14	75	41	1.0	5.16	937	93	2905	1274	1984	455	344	248	8205
15	75	41	1.0	9.55	783	81	2854	284	1089	1607	348	248	7256
16	175	26	1.0	10.74	779	241	12817	279	243	882	1229	251	16408
17	75	33	1.0	5.66	929	92	2973	1256	239	197	675	885	6855
18	75	41	1.0	10.02	687	88	2907	291	1073	193	150	486	6127
19	125	18	0.4	10.15	233	108	6206	288	257	930	164	125	9202
20	75	26	1.0	7.62	701	87	2885	608	246	208	711	118	5670
21	125	18	0.4	10.04	213	103	6024	286	537	213	177	592	8644
22	125	56	1.0	7.25	626	152	6709	590	244	435	163	127	9201
23	225	56	1.0	6.21	571	416	24149	657	504	198	332	117	26655
24	225	33	1.0	3.32	886	443	24814	2366	562	408	151	239	29073
25	125	43	1.0	3.34	969	193	6013	2431	2023	455	312	109	11851
26	75	41	1.0	6.26	741	84	2889	589	2079	1639	348	225	8173
27	225	33	1.0	9.49	775	406	23997	283	503	1684	1253	250	28388
28	75	33	1.0	4.30	1219	121	3049	2351	242	408	1288	902	8686
29	125	56	1.0	9.75	846	169	6602	298	2010	196	312	927	11267
30	125	56	1.0	7.90	889	177	6407	647	255	1628	150	224	10569
31	125	18	0.4	7.99	316	121	6434	635	571	221	1383	124	10573
32	25	8	0.0	8.45	0	0	0	643	572	514	199	1245	4366
33	75	33	1.0	19.11	834	83	2836	0	550	463	393	143	6013
34	75	41	1.0	12.22	734	85	2905	277	0	445	354	283	5432
35	125	18	0.4	11.11	226	107	6110	288	245	0	378	295	8488
36	175	43	1.0	7.55	640	243	12891	598	246	198	0	272	15162
37	175	26	1.0	4.46	675	244	12969	1263	511	199	152	0	15899
38	225	78	1.0	4.16	662	422	24496	1270	1080	414	152	109	28042
39	125	18	0.4	3.32	349	122	6492	2431	1122	935	352	127	11965
40	75	26	1.0	6.27	749	84	2869	636	2078	909	715	253	7872

other individuals) and the latter because the newly germinated seedlings would have a smaller food reserve to draw upon.

Selected combinations

Considering the above sets of variations, it is apparent that the most interesting interactions among the five functions P, G, GR, K, and S are the three that regulate the loss rates from the seed reserves, namely seed predation, dormancy, and germination response. Several combinations of these three functions are displayed in the next three tables.

Table 13 shows the statistical summary for a run with very low (1%) loss rates of older seeds due to both predation and germination. The curves used are .90/.01 and .01/.01, respectively. The low germination rate makes this run mimic a rare species and the low predation rate allows for a relatively large seed reserve to accumulate. The standard deviation of the total seed density is only one third the size of the mean value. This shows that the plant is well buffered, since the total seed reserve is even less variable than the rainfall. In all of the other runs of the model the standard deviation of the total seed density is almost the same size as (or larger than) the mean. For runs with a short dormancy curve the standard deviation is significantly larger than the mean.

Table 14 displays the effect of variations of the germination response curve when the seed dormancy is .50/.90, i.e., a short dormancy period. It is clear that when dormancy is short that there must be some control on the response of the germinable seeds to the

Table 13. Statistical summary for the run with 1% loss rate, STRATEGY3.

RAINFALL LOCATION: LAS VEGAS

NUMBER OF YEARS OF SIMULATION: 80

	MEAN	STD DEVIATION
TOTAL RAIN (MM)	67	40
GERMINATING RAIN (MM)	24	11
% SEEDS GERMINABLE	1	0
SEEDLINGS (#/SQ METER)	10	8
MATURE PLANTS (#/SQ METER)	7	7
SEED CROP (#/SQ METER)	499	587
TOTAL SEED (#/SQ METER)	1908	661

Table 14. Effects of variations in the germination response curve on 80-year runs of STRATEGY3 when dormancy curve is .50/.90

Germination Response	Percent Germinable	Seedling Density	Mature Plant Density	Seed Crop Density	Total Seed Density
1,1,1,1,1	extinction in 58 years				
0,1,1,1,1	near extinction in years 18, 34, and 58				
0,0,1,1,1	69	766	103	2183	2452
0,0,0,1,1	75	349	59	1695	2136
0,0,0,0,1	83	48	14	735	1119

Table 15. Effects of variations in dormancy and germination response curves on 80-year runs of STRATEGY3 when seed predation curve is .90/.50

Variation	Percent Germinable	Seedling Density	Mature Plant Density	Seed Crop Density	Total Seed Density
BASE RUN	extinction in 58 years				
Dormancy .50/.90	68	679	94	2023	2212
GR 1,1,1,1,1	extinction in 85 years				

germinating rainfall. In fact, the base run form for GR is the optimum amount of control for long-term viability of the plant in this situation.

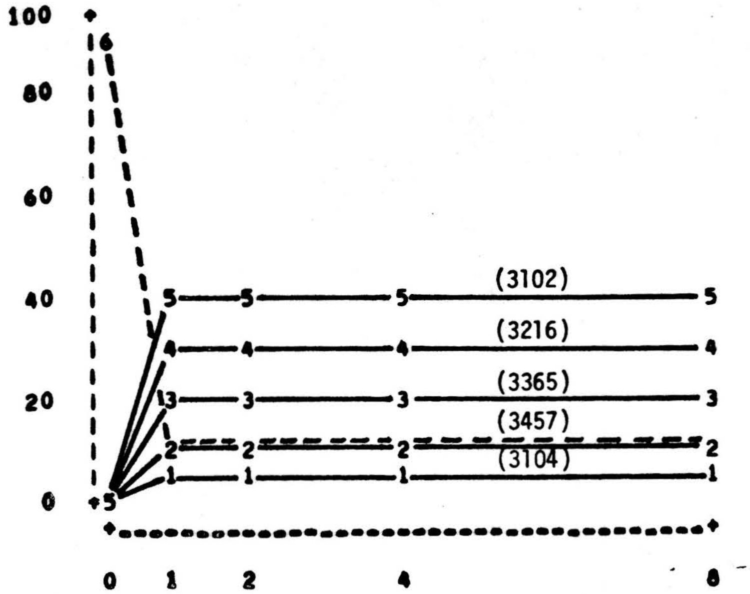
Table 15 shows how the plant can adapt to increasing predation pressures. These runs have a seed predation curve of .90/.50 and they show that the base run forms for dormancy and germination response cannot cope with this large of a seed loss. Changing GR to the "opportunistic" form is only of marginal help -- it just delays extinction for a few years. However, a shortened dormancy <u>does</u> result in long-term viability for the plant.

Optimum seed dormancy and factors affecting it

Cohen (1966) indicated that the optimum germination rate (all age classes treated the same) is strongly influenced by the severity of the rainfall environment. The above sensitivity analysis of Model 3 (distinguishable age classes) shows that the form of the dormancy curve is strongly dependent upon the form of the seed predation curve. Several runs were made to test the relative importance of rainfall and predation rate on the optimum form for the dormancy curve.

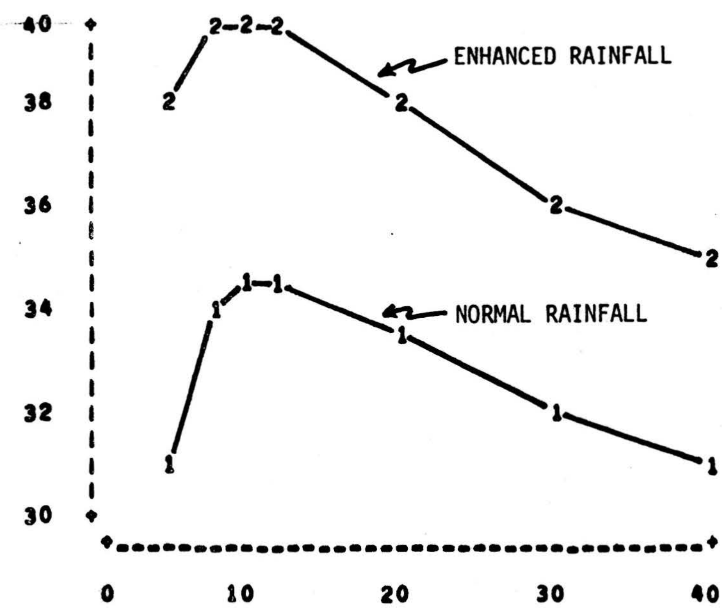
Figure 44 shows the assumed seed predation curve that the plant faces (dashed curve) and the kinds of dormancy curves that the plant is allowed to take in response. The predation curve is .90/.10 and the dormancy curves are all of the form .02/X, where X is the fraction germinable for seeds one year old or older.[20] The numbers

[20]When the fraction germinable for the previous year's seed crop was not held at a constant value, no relationship could be discerned between the predation curve and various dormancy curves. I somewhat arbitrarily decided upon a constant value of 2%.



% GERMINABLE (Y-AXIS) VS
SEED AGE IN YEARS (X-AXIS)
WHEN % PREDATION IS 90/10. 80-YEAR RUNS.

Figure 44.



MEAN TOTAL SEED DENSITY (X100/SQ METER) VS
% GERMINABLE FOR SEEDS 1 YEAR OLD OR OLDER,
WHEN % PREDATION IS 90/10. 80-YEAR RUNS.

Figure 45.

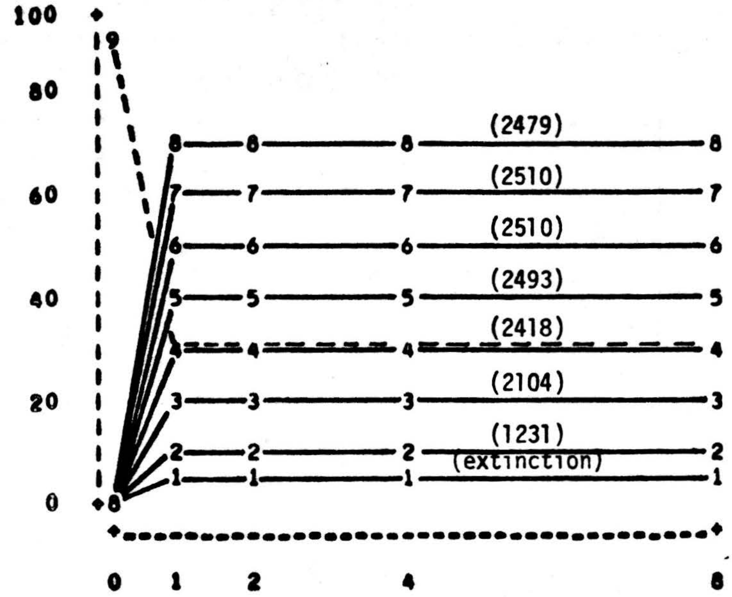
in parenthesis in Figure 44 are the corresponding mean values for the total seed density after an 80-year simulation when the historical rainfall distribution for Las Vegas was used, along with base run curves for the other functions in the model.

These same mean values are plotted as a function of X in Figure 45 and are labeled as the NORMAL RAINFALL curve. An optimum value for X is clearly evident and is numerically the same as the seed predation rate for these older seeds.

The second curve in Figure 45 shows a similar series of runs where the rainfall distribution was the ENHANCED rainfall of Figure 42 (page 85). This demonstrates that in this model the optimum value of X is not particularly affected by the "harshness" of the rainfall environment.

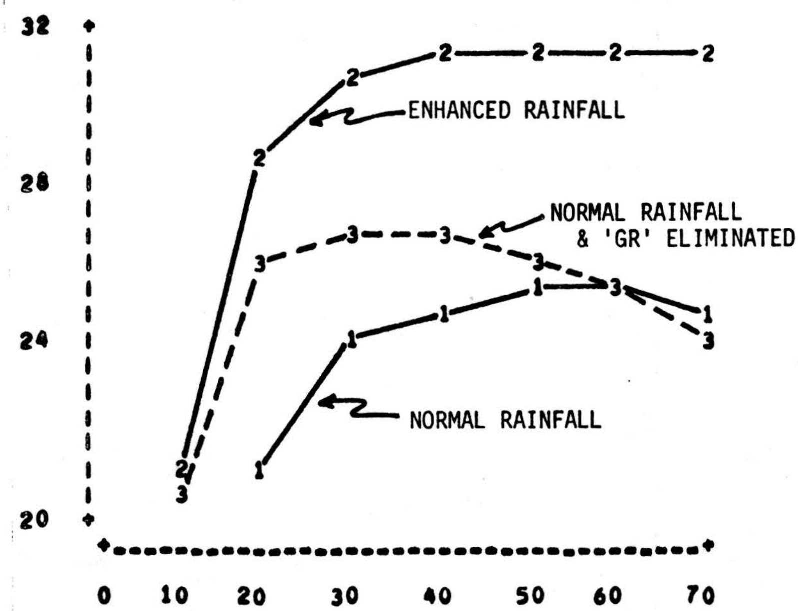
To further test this observation that the long-term germinable fraction should be the same size as the fraction lost to seed predators, several additional runs were made with a predation curve of .90/.30. The results are shown in Figure 46 and 47. There is now no well-defined peak in the two solid-line curves. Believing that the peak was now obscured by the effect of the germination response function (GR), I re-ran the normal rainfall set again with GR taking the "opportunistic" form. This set is plotted as the dashed curve in Figure 47 and a peak at 30% is clearly evident.

The above result can be made more understandable by referring back to the original diagram for Model 3 on page 51. The question that has been posed in this optimization section is: What are the



% GERMINABLE (Y-AXIS) VS
SEED AGE IN YEARS (X-AXIS)
WHEN % PREDATION IS 90/30. 80-YEAR RUNS.

Figure 46.



MEAN TOTAL SEED DENSITY (X100/SQ METER) VS
% GERMINABLE FOR SEEDS 1 YEAR OLD OR OLDER,
WHEN % PREDATION IS 90/30. 80-YEAR RUNS.

Figure 47.

relative magnitudes of the two loss rates from the older seeds (N_1, N_2, N_3 . . .) in the soil so that the plant does best? The conclusion reached is that there should be approximately equal loss rates, i.e., $G_1 = P_1$, $G_2 = P_2$, etc. However, if the predation rate is high, then the optimum becomes much broader and the relationships between the two loss rates becomes $G_1 \geq P_1$, $G_2 \geq P_2$, etc. Thus, if the plant must "err", it is safest to err on the high side of the long-term predation rate.

The output from all of the optimization runs is shown in tabular form in Appendix 3.

CONCLUSIONS

The working hypothesis that has guided me in this research was originally stated in the introduction and bears repeating now: Seed dormancy and germination controls are the most important adaptive strategies of desert annuals. Have the results validated this assertion? The answer is a qualified yes. The 80-year simulation runs indicate that extinction will occur in a rainfall environment as severe as that at Las Vegas unless (1) the seeds have a minimum dormancy period of one year and a threshold of 15-25 mm for germinating rainfall or (2) the seeds have a moderate-to-long dormancy period, in which case the threshold for germinating rainfall can be somewhat less. The qualification is that the pattern of seed dormancy is also strongly influenced by the rates at which seed predators eat different aged seeds.

General observations

There are several general observations about the life cycle of desert annuals that the sensitivity analysis of Model 3 has made apparent:

(1) Short dormancy species can withstand a higher seed predation rate than can species whose seeds have a longer dormancy period.

(2) The age distribution of the seeds in the soil and the total fraction that is germinable in any given year is strongly dependent upon the recent rainfall history of the site.

(3) Evidently the soil serves as a sanctuary for the seeds of desert annuals. Assuming that older seeds are eaten at a reduced

rate as compared to the losses from the seed crop, mechanisms that increase the proportion of seeds surviving the first year is more important than a further reduction in the loss rate of the older seeds.

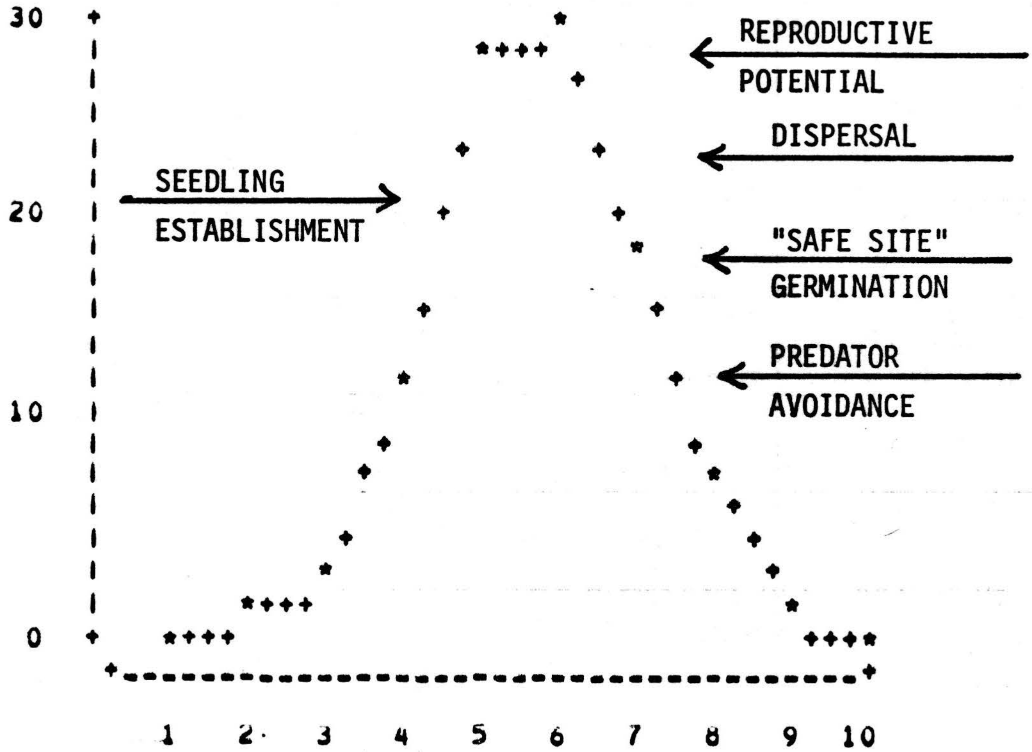
(4) The maximum loss rates for seeds of desert annuals is probably 90% for the current seed crop and 50% for all older seeds.

(5) The optimum balance between the non-productive loss of older seeds (predation) and the productive loss of older seeds (germination) is when they are approximately the same size. This condition is relatively insensitive to the degree of severity of the rainfall environment, provided the conditions mentioned in the opening paragraph of the conclusions section are met.

(6) Mechanisms that can increase the number of seeds per plant are of greater benefit than mechanisms that increase the probability of survival from seedling to maturity.

(7) Rare species must have a high threshold for germinating rainfall (possibly along with other special environmental conditions) and a low loss rate for the older seeds.

(8) In the light of all of the above observations, it seems that factors that control the rate of seed burial are of critical importance to desert annuals. Seed size and morphology should be such that seeds can easily fall between soil particles and work their way down into the soil profile. Referring again to the seed weight data of Baker (1972), Figure 48 indicates the selection pressures that are probably acting on seed weight to create this rather striking pattern. Reduced probability of seedling establishment



% FREQUENCY OF SEED WEIGHT CLASS (Y-AXIS)
VS SEED WEIGHT CLASS (X-AXIS, LOG SCALE)
(DATA SOURCE: BAKER 1972)

FIGURE 48.

(Finished figure not done yet)

due to limited food reserves in small seeds is the major pressure from the left. Increased reproductive potential, seed dispersal, and "safe site" germination are often-cited pressures from the right. The results of this study indicate that there may be another pressure from the right -- that of predator avoidance. The seed size corresponding to a seed weight of .001 gram may be such that on most arid soils they are buried at a faster rate than are the larger seeds.

Suggested experiments

There are a host of experiments that the present research suggests. The most significant ones are:

(1) Measure the effects of total rainfall over the growing season (natural or simulated rainfall) and density dependent effects on plant survival rates and seeds produced per plant. The literature on desert annuals is woefully lacking with regard to seed production by individual plants.

(2) Identify the seed burying mechanism(s) and the factors affecting it.

(3) Use exclosure experiments to determine the effects of seed predators on the level of seed reserves in the soil. By monitoring the buildup of older seeds at deeper levels, one can make some inferences about the seed predation rate as a function of seed age.

(4) Initiate a long-term study to measure the dormancy curves for selected species of desert annuals. Start the experiment after one or two good rainfall years to insure a reasonable initial

age distribution for the seed reserves. The experiment would probably require both conventional exclosures for seed predators and "seed exclosures" of some kind. One could then (a) allow germination, growth, flowering, and fruiting to occur each year, but harvest the seeds before they are released and (b) measure the rate of attrition of the seed reserves in the soil. Coupled with the measured germination rates, one could construct a dormancy curve for each species.

(5) See if the pattern of distribution of individual species in the desert correlates with soil surface characteristics that would affect the seed burying rates.

(6) See if the distribution of seed with depth in the soil profile correlates with the recent rainfall history of the site and/or with seed size and shape.

ACKERMAN, T L AND S A BAMBERG (1972) PHENOLOGY STUDIES IN THE MOJAVE DESERT AT ROCK VALLEY, NTS, NEVADA, 1972 AIBS SYMPOSIUM: PHENOLOGY AND SEASONALITY

ALIZAI, H U (1970) EFFECTS OF SOIL TEXTURE ON EVAPORATIVE LOSS AND AVAILABLE WATER IN SEMI-ARID CLIMATES, SOIL SCI 110: 328-332

ARKLEY, RODNEY J (1963) RELATIONSHIPS BETWEEN PLANT GROWTH AND TRANSPIRATION, HILGARDIA 34: 559-584

BAKER, HERBERT G (1972) SEED WEIGHT IN RELATION TO ENVIRONMENTAL CONDITIONS IN CALIFORNIA, ECOL 53: 997-1010

BALDA, R, G C BATEMAN AND T A VAUGHAN (1972) DIETS, FOOD PREFERENCES, AND REPRODUCTIVE CYCLES OF SOME DESERT RODENTS, US/IBP DESERT BIOME RM 72-29

BARTON, LELA (1967) BIBLIOGRAPHY OF SEEDS, COLUMBIA U PRESS

BEATLEY, JANICE C (1966) ECOLOGICAL STATUS OF INTRODUCED BROME GRASSES (BROMUS SPP.) IN DESERT VEGETATION OF SOUTHERN NEVADA, ECOLOGY 47:548-554

BEATLEY, JANICE C (1967) SURVIVAL OF WINTER ANNUALS IN THE NORTHERN MOJAVE DESERT, ECOLOGY 48:745-750

BEATLEY, JANICE C (1969) (A) DEPENDENCE OF DESERT RODENTS ON WINTER ANNUALS AND PRECIPITATION, ECOLOGY 50:722-724

BEATLEY, JANICE C (1969) (B) BIOMASS OF DESERT WINTER ANNUAL PLANT POPULATIONS IN SOUTHERN NEVADA, OIKOS 20:261-273

BEATLEY, JANICE C (1970) PERENNATION IN ASTRAGALUS LENTIGINOSUS AND TRIDENS PULCHELLUS IN RELATION TO RAINFALL, MADRONO 20:326-332

BEATLEY, JANICE C (1972) (A) PREDICTIVE MODEL FOR MOJAVE DESERT PHENOLOGICAL EVENTS AND THEIR ENVIRONMENTAL TRIGGERS, UCLA, LABORATORY NUCLEAR MED & RAD BIOL, NOVEMBER, 1972

BEATLEY, JANICE C (1972) (B) EFFECTS OF RAINFALL AND TEMPERATURE ON DISTRIBUTION AND BEHAVIOR OF LARREA TRIDENTATA IN THE MOJAVE DESERT OF NEVADA, UCLA, LABORATORY OF NUC MED AND RAD BIOL, AUG 1972

BLAINEY, H F AND W D CRIDDLE (1950) DETERMINING WATER REQUIREMENTS IN IRRIGATED AREAS FROM CLIMATOLOGICAL AND IRRIGATION DATA, US SOIL CONS SERV TP-96

BLANEY, H F (1952) DETERMINING EVAPOTRANSPIRATION OF PHREATOPHYTES FROM CLIMATOLOGICAL DATA, AMER GEOPHYS UNION TRANS 33: 61-66

BRADLEY, W GLENN AND ROGER A MAUER (1971) REPRODUCTION AND FOOD HABITS OF MERRIAM'S KANGAROO RAT, DIPODOMYS MERRIAMI, J MAMM 52: 497-507

BRIGGS, L J AND H L SHANTZ (1916) DAILY TRANSPIRATION DURING THE NORMAL GROWTH PERIOD AND ITS CORRELATION WITH THE WEATHER, J AGR RES 7: 155-212

BRYSON, R A (1957) THE ANNUAL MARCH OF PRECIPITATION IN ARIZONA, NORTHERN MEXICO, AND NORTHWESTERN NEW MEXICO, U ARIZONA, INST ATMOSPHERIC PHYSICS, TECH REPORT 6

BUOL, S W (1964) CALCULATED ACTUAL AND POTENTIAL EVAPOTRANSPIRATION IN ARIZONA, U ARIZONA, AGR EXP STA TECH BULL 162

CABLE, DWIGHT R (1969) COMPETITION IN THE SEMI-DESERT GRASS-SHRUB TYPE AS INFLUENCED BY ROOT SYSTEMS, GROWTH HABITS, AND SOIL MOISTURE EXTRACTION, ECOLOGY 50:27-38

CHEW, ROBERT M AND BERNARD B BUTTERWORTH (1964) ECOLOGY OF RODENTS IN INDIAN COVE (MOJAVE DESERT), JOSHUA TREE NATIONAL MONUMENT, CALIFORNIA, J MAMM 45:203-225

CHEW, ROBERT M AND ALICE EASTLAKE CHEW (1965) THE PRIMARY PRODUCTIVITY OF A DESERT-SHRUB (LARREA TRIDENTATA) COMMUNITY, ECOL MONOGR 35: 355-375

CHEW, ROBERT M AND ALICE EASTLAKE CHEW (1970) ENERGY RELATIONSHIPS OF THE MAMMALS OF A DESERT SHRUB (LARREA TRIDENTATA) COMMUNITY, ECOL MONOGR 40: 1-21

CHRISTIANSEN, J E (1968) PAN EVAPORATION AND EVAPOTRANSPIRATION FROM CLIMATIC DATA, J IRRIG DRAIN DIV, AMER SOC CIVIL ENG PROC 243-265

COHEN, D (1966) OPTIMIZING REPRODUCTION IN A RANDOMLY VARYING ENVIRONMENT, J THEOR BIOL 12: 119-129

COHEN, D (1970) EXPECTED EFFICIENCY OF WATER UTILIZATION IN PLANTS UNDER DIFFERENT COMPETITION AND SELECTION REGIMES, ISRAEL J BOT 19: 50-54

CUNNINGHAM, G L AND B R STRAIN (1969) AN ECOLOGICAL SINIFICANCE OF SEASONAL LEAF VARIABILITY IN A DESERT SHRUB, ECOLOGY 50: 400-408

DASBERG, S AND K MENDEL (1971) THE EFFECT OF SOIL WATER AND AERATION ON SEED GERMINATION, J EXP BOT 22: 992-998

DASBERG, S (1971) SOIL WATER MOVEMENT TO GERMINATING SEEDS, J EXP BOT 22: 999-1008

DENMEAD, O T AND R H SHAW (1962) AVAILABILITY OF SOIL WATER TO

PLANTS AS AFFECTED BY SOIL MOISTURE CONTENT AND METEOROLOGICAL CONDITIONS, AGRON J 45: 385-390

DYE, A J (1969) GERMINATION POTENTIALS AND ACCUMULATION OF NATIVE PLANT SEEDS FROM SOUTHERN NEW MEXICO, NEW MEXICO STATE U, MS THESIS

FOGEL, M M (1968) THE EFFECT OF THE SPATIAL AND TEMPORAL VARIATIONS OF RAINFALL ON RUNOFF FROM SMALL SEMIARID WATERSHEDS, U ARIZONA, PHD DISSERTATION

FRENCH, NORMAN R, BERNARDO G MAZA AND ARNOLD P ASCHWANDEN (1966) PERIODICITY OF DESERT RODENT ACTIVITY, SCIENCE 154:1194-1195

FRENCH, NORMAN R, BERNARDO G MAZA AND ARNOLD P ASCHWANDEN (1967) LIFE SPANS OF DIPODOMYS AND PEROGNATHUS IN THE MOJAVE DESERT, J MAMM 48:537-548

GARDNER, W R (1958) SOME STEADY-STATE SOLUTIONS OF THE UNSATURATED MOISTURE FLOW EQUATION WITH APPLICATION TO EVAPORATION FROM A WATER TABLE, SOIL SCI 85: 228-234

GARDNER, W R (1960) DYNAMIC ASPECTS OF WATER AVAILABILITY TO PLANTS, SOIL SCI 89: 63-73

GARDNER, W R (1964) RELATION OF ROOT DISTRIBUTION TO WATER UPTAKE AND AVAILABILITY, AGRON J 56: 41-45

GASHWILER, JAY S (1970) FURTHER STUDY ON CONIFER SEED SURVIVAL IN A WESTERN OREGON CLEARCUT, ECOLOGY 51: 849-854

GIFFORD, R O, G L ASHCROFT AND M D MAGNUSON (1967) PROBABILITY OF SELECTED PRECIPITATION AMOUNTS IN THE WESTERN REGION OF THE UNITED STATES, U NEVADA AGR EXP STA

GOODALL, D W, S CHILDS AND H WEIBE (1972) METHODOLOGICAL AND VALIDATION STUDY OF SEED RESERVES IN DESERT SOILS, US/IBP DESERT BIOME RM 72-8

GREEN, CHRISTINE R (1962) ARIZONA CLIMATE: PROBABILITIES OF TEMPERATURE OCCURRENCE IN ARIZONA AND NEW MEXICO, U ARIZONA, INSTITUTE OF ATMOSPHERIC PHYSICS

GREEN, C R (1964) (A) SEASONAL PRECIPITATION AND TEMPERATURE DATA FOR SELECTED ARIZONA STATIONS, U ARIZONA, INST ATMOSPHERIC PHYSICS, TECH REPORT 12

GREEN, C R (1964) (B) DISTRIBUTION OF RAINFALL IN ARIZONA, U ARIZONA, INST ATMOSPHERIC PHYSICS, TECH REPORT 13

GRIGAL, D G AND J E HUBBARD (1971) SOGGY: A SOIL TENSION EVAPOTRANSPIRATION MODEL, IN: SUMMER COMPUTER SIMULATION CONFERENCE, 1971, SESSION V

HANKS, R J AND S A BOWERS (1962) NUMERICAL SOLUTION OF THE MOISTURE FLOW EQUATION FOR INFILTRATION INTO LAYERED SOILS, SOIL SCI SOC AMER PROC 26: 530-534

HANKS, R J, A KLUTE AND E BRESLER (1969) A NUMERIC METHOD FOR ESTIMATING INFILTRATION, REDISTRIBUTION, DRAINAGE, AND EVAPORATION OF WATER FROM SOIL, WATER RESOUR RES 5: 1064-1069

HARPER, JOHN L (ED) (1960) THE BIOLOGY OF WEEDS, BLACKWELL

HARPER, JOHN L AND DANICA GAJIC (1961) EXPERIMENTAL STUDIES ON THE MORTALITY AND PLASTICITY OF A WEED, WEED RES 1: 91-104

HARPER, JOHN L (1964) THE INDIVIDUAL IN THE POPULATION, J ECOLOGY 52 (SUPPL): 149-158

HARPER, JOHN L, J T WILLIAMS AND G R SAGAR (1965) THE BEHAVIOR OF SEEDS IN SOIL. I. THE HETEROGENEITY OF SOIL SURFACES AND ITS ROLE IN DETERMINING THE ESTABLISHMENT OF PLANTS FROM SEED, J ECOL 53: 273-286

HARPER, J L AND R A BENTON (1966) THE BEHAVIOR OF SEEDS IN SOIL. II. THE GERMINATION OF SEEDS ON THE SURFACE OF A WATER SUPPLYING SUBSTRATE, J ECOLOGY 54: 151-166

HARPER, JOHN L (1967) A DARWINIAN APPROACH TO PLANT ECOLOGY, J ECOLOGY 55: 247-270

HARPER, J L (1968) THE REGULATION OF NUMBERS AND MASS IN PLANT POPULATIONS, IN: LEWONTIN (ED), POPULATION BIOLOGY AND EVOLUTION.

HARPER, JOHN L (1969) THE ROLE OF PREDATION IN VEGETATIONAL DIVERSITY, IN: DIVERSITY AND STABILITY IN ECOLOGICAL SYSTEMS

HARPER, JOHN L AND JOHN OGDEN (1970) THE REPRODUCTIVE STRATEGY OF HIGHER PLANTS. I. THE CONCEPT OF STRATEGY WITH SPECIAL REFERENCE TO SENECIO VULGARIS L, J ECOLOGY 58: 681-698

HARPER, J L, P H LOVELL AND K G MOORE (1970) THE SHAPES AND SIZES OF SEEDS, ANN REV ECOL SYSTEM 1: 327-356

HETTINGER, LOREN ROBERT (1969) ENERGY DYNAMICS AND NET PRODUCTIVITY OF ANNUAL PLANTS IN SOUTHERN NEW MEXICO, NEW MEXICO STATE U, MS THESIS

HOFF, C C (ED) AND M L (ED) RIEDESEL (1969) PHYSIOLOGICAL SYSTEMS IN SEMIARID ENVIRONMENTS, U NEW MEXICO PRESS

HOUGHTON, JOHN G (1969) CHARACTERISTICS OF RAINFALL IN THE GREAT BASIN, U NEVADA AT RENO, DESERT RESEARCH INSTITUTE

HULBERT, L C (1955) ECOLOGICAL STUDIES OF BROMUS TECTORUM AND OTHER ANNUAL BROMEGRASSES, ECOL MONOGR 25: 181-213

HUMPHREY, R R (1933) A DETAILED STUDY OF DESERT RAINFALL, ECOLOGY 14: 31-34

JAEGER, EDMUND C (1957) THE NORTH AMERICAN DESERTS, STANFORD U PRESS

JAMESON, D A (1969) RAINFALL PATTERNS ON VEGETATION ZONES IN NORTHERN ARIZONA, PLATEAU 41: 105-111

JANZEN, DANIEL H (1971) SEED PREDATION BY ANIMALS, ANN REV ECOL & SYSTEM 2:465-492

JUHREN, MARCELLA, F W WENT AND EDWIN PHILLIPS (1956) ECOLOGY OF DESERT PLANTS, IV. COMBINED FIELD AND LABORATORY WORK ON GERMINATION OF ANNUALS IN THE JOSHUA TREE NATIONAL MONUMENT, CALIFORNIA, ECOLOGY 37:318-330

KLEMMEDSON, JAMES O AND JUSTIN G SMITH (1964) CHEATGRASS (BROMUS TECTORUM L), BOT REV 30: 226-262

KLIKOFF, LIONEL G (1966) COMPETITIVE RESPONSE TO MOISTURE STRESS OF A WINTER ANNUAL OF THE SONORAN DESERT, AM MID NAT 75:383-391

KOLLER, D (1955) THE REGULATION OF GERMINATION IN SEEDS, BULL RES COUNC ISRAEL 50:85-108

KRAMER, PAUL J (1969) PLANT AND SOIL WATER RELATIONSHIPS: A MODERN SYSNTHESIS, MCGRAW-HILL

LEE, R (1967) THE HYDROLOGIC IMPORTANCE OF TRANSPIRATION CONTROL BY STOMATA, WATER RES RES 3: 737-752

LESLIE, P H (1945) THE USE OF MATRICES IN CERTAIN POPULATION MATHEMATICS, BIOMETRIKA 33: 183-212

LESLIE, P H (1948) SOME FURTHER NOTES ON THE USE OF MATRICES IN POPULATION MATHEMATICS, BIOMETRIKA 35: 213-245

LEWONTIN, R C (1965) SELECTION FOR COLONIZING ABILITY, IN: BAKER & STEBBINS (EDS), GENETICS OF COLONIZING SPECIES

MARSHALL, D R AND S K JAIN (1970) SEED PREDATION AND DORMANCY IN THE POPULATION DYNAMICS OF AVENA FATUA AND A. BARBATA, ECOLOGY 51: 886-891

MAYER, A M AND A POLJAKOFF-MAYBER (1963) THE GERMINATION OF SEEDS, MACMILLAN

MCDONALD, JAMES E (1956) VARIABILITY OF PRECIPITATION IN AN ARID REGION: A SURVEY OF CHARACTERISTICS FOR ARIZONA, U ARIZONA, INSTITUTE OF ATMOSPHERIC PHYSICS

MOLZ, F J AND I REMSON (1970) EXTRACTION TERM MODELS OF SOIL

MOISTURE USE BY TRANSPIRING PLANTS, WAT RES RES 6: 1346-1356

MULLER, C H (1953) THE ASSOCIATION OF DESERT ANNUALS WITH SHRUBS, AMER J BOT 40:53-60

MULLER, C H (1956) TOXICITY OF ENCELIA, FRANSERIA, AND THAMNOSMA TO DESERT ANNUALS, AMER J BOT 43:354

MULLER, W H AND C H MULLER (1956) ASSOCIATION PATTERNS INVOLVING DESERT PLANTS THAT CONTAIN TOXIC PRODUCTS, AMER J BOT 43:354-361

NIMAH, MUSA N (1972) MODEL FOR ESTIMATING SOIL WATER FLOW, WATER CONTENT, EVAPOTRANSPIRATION AND ROOT EXTRACTION, UTAH STATE U, PH D THESIS

NORERO, A (1969) A FORMULA TO EXPRESS EVAPOTRANSPIRATION AS A FUNCTION OF SOIL MOISTURE AND EVAPORATIVE DEMANDS OF THE ATMOSPHERE, UTAH STATE U, PH D DISSERTATION

NOY-MEIR, I (1973) DESERT ECOSYSTEMS, ANN REV ECOL & SYSTEM (IN PRESS)

OGATA, G, L A RICHARDS AND W R GARDNER (1960) TRANSPIRATION OF ALFALFA DETERMINED FROM SOIL WATER CONTENT CHANGES, SOIL SCI 89: 179-182

OSBORN, H B AND L LANE (1969) PRECIPITATION-RUNOFF RELATIONS FOR VERY SMALL SEMIARID RANGELAND WATERSHEDS, WATER RES RES 5: 419-425

PALMBLAD, IVAN GORDEN (1966) EXPERIMENTAL STUDIES ON INTERFERENCE IN WEEDY PLANT SPECIES, U WASHINGTON, PHD THESIS

PALMBLAD, IVAN G (1968) COMPETITION IN EXPERIMENTAL POPULATIONS OF WEEDS WITH EMPHASIS ON THE REGULATION OF POPULATION SIZE, ECOLOGY 49: 26-34

PELTON, W L, K M KING AND C B TANNER (1960) AN EVALUATION OF THE THORNTHWAITE AND MEAN TEMPERATURE METHODS IN DETERMINING POTENTIAL EVAPOTRANSPIRATION, AGRON J 52: 387-395

PELTON, W L AND H C KORVEN (1969) EVAPOTRANSPIRATION ESTIMATES IN A SEMIARID CLIMATE, CAN AGR ENG 11: 50-53

PENMAN, H L (1948) NATURAL EVAPORATION FROM OPEN WATER, BARE SOIL, AND GRASS, PROC ROYAL SOC LONDON, SERIES A, 193: 120-145

PENMAN, H L (1956) EVAPORATION: AN INTRODUCTORY SURVEY, NETH J AGR SCI 4: 9-29

REYNOLDS, H G (1950) RELATION OF MERRIAM KANGAROO RATS TO RANGE VEGETATION IN SOUTHERN ARIZONA, ECOLOGY 31:456-463

REYNOLDS, H G (1958) THE ECOLOGY OF THE MERRIAM KANGAROO RAT (DIPODOMYS MERRIAMI MEARNS) ON THE GRAZING LANDS OF SOUTHERN ARIZONA, ECOL MONOGR 28:111-127

REYNOLDS, HUDSON G (1960) LIFE HISTORY NOTES ON MERRIAM'S KANGAROO RAT IN SOUTHERN ARIZONA, J MAMM 41: 48-58

RICKARD, W H AND J R MURDOCK (1963) SOIL MOISTURE AND TEMPERATURE SURVEY OF A DESERT VEGETATION MOSAIC, ECOLOGY 44: 821-824

RICKARD, W H AND JANICE C BEATLEY (1965) CANOPY COVERAGE OF THE DESERT SHRUB VEGETATION MOSAIC OF THE NEVADA TEST SITE, ECOLOGY 46:524-529

RICKARD, W H (1967) SEASONAL SOIL MOISTURE PATTERNS IN ADJACENT GREASEWOOD AND SAGEBRUSH STANDS, ECOLOGY 48: 1034-1038

SALISBURY, E J (1942) THE REPRODUCTIVE CAPACITY OF PLANTS, G BELL & SONS, LONDON

SELIGMAN, N G, N H TADMOR, I NOY-MEIR AND A DOVRAT (1971) AN EXERCISE IN SIMULATION OF A SEMI-ARID MEDITERRANEAN GRASSLAND, (UNPUBLISHED)

SHANTZ, H L AND L N PIEMEISEL (1927) THE WATER REQUIREMENT OF PLANTS AT AKRON, COLORADO, J AGR RES 34: 1093-1190

SHIFFLER, W J (1968) PHENOLOGY OF DESERT EPHEMERALS IN SOUTHERN NEW MEXICO, NEW MEXICO STATE U, MS THESIS

SHREVE, E B (1924) FACTORS GOVERNING SEASONAL CHANGES IN TRANSPIRATION OF ENCELIA FARINOSA, BOT GAZ 77: 432-439

SHREVE, F (1942) THE DESERT VEGETATION OF NORTH AMERICA, BOT REV 8: 195-264

SHREVE, F (1951) VEGETATION OF THE SONORAN DESERT, CARNEGIE INST WASH PUBL 591

SHREVE, F AND I L WIGGINS (1964) VEGETATION AND FLORA OF THE SONORAN DESERT, STANFORD U PRESS

SLATYER, R O (1956) EVAPOTRANSPIRATION IN RELATION TO SOIL MOISTURE, NETH J AGR SCI 4: 73-76

SLATYER, R O (1967) PLANT WATER RELATIONSHIPS, ACADEMIC PRESS

STRAIN, B R (1969) SEASONAL ADAPTATIONS IN PHOTOSYNTHESIS AND RESPIRATION IN FOUR DESERT SHRUBS GROWING IN SITU, ECOLOGY 50: 511-513

STRUIK, GWENDOLYN J AND J R BRAY (1970) ROOT-SHOOT RATIO OF NATIVE FOREST HERBS AND ZEA MAYS AT DIFFERENT SOIL-MOISTURE LEVELS, ECOL 51: 892-893

TADMOR, N H AND L SHANAN (1969) RUNOFF INDUCEMENT IN AN ARID REGION BY REMOVAL OF VEGETATION, SOIL SCI SOC AMER PROC 33: 790-794

TANNER, C B AND W L PELTON (1960) POTENTIAL EVAPOTRANSPIRATION ESTIMATES BY THE APPROXIMATE ENERGY BALANCE METHOD OF PENMAN, GEOPHYS RES 65: 3391-3413

TAYLOR, G B AND R C ROSSITER (1967) GERMINATION RESPONSE TO LEACHING IN DORMANT SEED OF TRIFOLIUM SUBTERRANUM L., NATURE 216: 389-390

TEVIS, LLOYD JR (1958) (A) GERMINATION AND GROWTH OF EPHEMERALS INDUCED BY SPRINKLING A SANDY DESERT, ECOLOGY 39:681-688

TEVIS, LLOYD JR (1958) (B) A POPULATION OF DESERT EPHEMERALS GERMINATED BY LESS THEN ONE INCH OF RAIN, ECOLOGY 39:688-695

TEVIS, LLOYD JR (1958) (C) INTERRELATIONS BETWEEN THE HARVESTER ANT VEROMESSOR PERGANDEI (MAYR) AND SOME DESERT EPHEMERALS, ECOLOGY 39:695-704

THRONTHWAITE, C W (1948) AN APPROACH TOWARD A RATIONAL CLASSIFICATION OF CLIMATE, GEOGRAPH REV 38: 55-94

THRONTHWAITE, C W AND J R MATHER (1955) THE WATER BUDGET AND ITS USE IN IRRIGATION, USDA YEARBOOK, PP 346-357

VAN BAVEL, C H M (1966) (A) POTENTIAL EVAPORATION: THE CONCEPT AND ITS EXPERIMENTAL VERIFICATION, WATER RES RES 2: 455-467

VAN BAVEL, C H M (1966) (B) COMBINATION (PENMAN TYPE) METHODS, AMER SOC AGR ENG, DEC, 48-51

VEIHMEYER, F J AND A H HENDRICKSON (1955) DOES TRANSPIRATION DECREASE AS THE SOIL MOISTURE DECREASES?, AM GEOPHYS UNION TRANS 36: 425-428

WENT, F W (1948) ECOLOGY OF DESERT PLANTS, I. OBSERVATIONS ON GERMINATION IN THE JOSHUA TREE NATIONAL MONUMENT, CALIFORNIA, ECOLOGY 29:242-253

WENT, F W (1949) ECOLOGY OF DESERT PLANTS, II. THE EFFECT OF RAIN AND TEMPERATURE ON GERMINATION AND GROWTH, ECOLOGY 30:1-13

WENT, F W AND M WESTERGAARD (1949) ECOLOGY OF DESERT PLANTS, III. DEVELOPMENT OF PLANTS IN THE DEATH VALLEY NATIONAL MONUMENT, CALIFORNIA, ECOLOGY 30:26-38

WILLIAMS, GEORGE J (1971) PRODUCER FUNCTION ON THE INTENSIVE

AND COMPREHENSIVE SITES IN: FRENCH, N R (ED), PRELIMINARY ANALYSIS OF, STRUCTURE AND FUNCTION IN GRASSLANDSRANGE SCI DEPT SCI SER NO 10, COLORADO STATE U

WINKWORTH, R E (1971) LONGEVITY OF BUFFEL GRASS SEED SOWN IN AN ARID AUSTRALIAN RANGE, J RANGE MAN 24: 141-145

WOOD, JOHN E (1969) RODENT POPULATIONS AND THEIR IMPACT ON DESERT RANGELANDS, NEW MEXICO STATE U, AGR EXP STA BULL 555

APPENDICES

Appendix 1.

```
"SET XREF"
STRATEGY3: PROC OPTIONS(MAIN);
/*************************************************************************/
/*                                                                       */
/*      CURTIS WILCOTT                                                   */
/*      UTAH STATE UNIVERSITY                                            */
/*      MAY 10, 1973                                                     */
/*                                                                       */
/*      STRATEGY MODEL FOR DESERT ANNUALS                                */
/*      VERSION 3                                                        */
/*                                                                       */
/*************************************************************************/
DCL #_CURVES FIXED BIN;                                  /* DIMENSIONLESS*/
DCL #_PAIRS FIXED BIN;                                   /* DIMENSIONLESS*/
DCL #_X_AXIS_POINTS FIXED BIN;                           /* DIMENSIONLESS*/
DCL #_Y_AXIS_POINTS FIXED BIN;                           /* DIMENSIONLESS*/
DCL #_YEARS FIXED BIN;                                   /* DIMENSIONLESS*/
DCL DENSITY_AXIS(5) FLOAT(6);                            /* DIMENSIONLESS*/
DCL DUM CHAR(1);                                         /* DIMENSIONLESS*/
DCL FACTOR FLOAT(6);                                     /* DIMENSIONLESS*/
DCL FRACTION_GERMINABLE(0:19) FLOAT(6);                  /* DIMENSIONLESS*/
DCL FRACTION_EATEN(0:19) FLOAT(6);                       /* DIMENSIONLESS*/
DCL FUNCTIONS BIT(1);                                    /* DIMENSIONLESS*/
DCL GERMINATING_RAIN FLOAT(6);                           /* MILLIMETERS  */
DCL GERMINATING_RAIN_AXIS(5) FLOAT(6);                   /* MILLIMETERS  */
DCL GERMINATION_AXIS(5) FLOAT(6);                        /* DIMENSIONLESS*/
DCL GERMINATION_RESPONSE FLOAT(6);                       /* DIMENSIONLESS*/
DCL GERMINATION_RESPONSE_AXIS(5) FLOAT(6);               /* DIMENSIONLESS*/
DCL GRAPHS PRINT;                                        /* PRINT FILE   */
DCL INITIAL_SEED_CROP FLOAT(6);                          /* #/SQ METER   */
DCL INTERPOLATE BIT(1);                                  /* DIMENSIONLESS*/
DCL LAMDA(6) FLOAT(6);                                   /* DIMENSIONLESS*/
DCL LOCATION CHAR(20);                                   /* DIMENSIONLESS*/
DCL MATURE_PLANTS FLOAT(6);                              /* #/SQ METER   */
DCL MEAN(7) FLOAT(6);                                    /* DIMENSIONLESS*/
DCL NUM FIXED BIN INIT(10);                              /* DIMENSIONLESS*/
DCL PERCENT_ARRAY(10) FLOAT(6);                          /* DIMENSIONLESS*/
DCL PERCENT_AXIS(5) FLOAT(6);                            /* DIMENSIONLESS*/
DCL PERCENT_AXIS2(6) FLOAT(6);                           /* DIMENSIONLESS*/
DCL PERCENT_GERMINABLE FLOAT(6);                         /* DIMENSIONLESS*/
DCL PLANT_SURVIVAL FLOAT(6);                             /* DIMENSIONLESS*/
DCL PLANT_SURVIVAL_ARRAY(6,5) FLOAT(6);                  /* DIMENSIONLESS*/
DCL PLANT_SURVIVAL_VECTOR(5) FLOAT(6);                   /* DIMENSIONLESS*/
DCL PLOT FIXED BIN;                                      /* DIMENSIONLESS*/
DCL PREDATION_AXIS(5) FLOAT(6);                          /* FRACTION/YEAR*/
DCL PROBABILITY(6) FLOAT(6);                             /* DIMENSIONLESS*/
DCL RAIN_CLASS FIXED BIN;                                /* DIMENSIONLESS*/
DCL RAIN_HISTOGRAMS BIT(1);                              /* DIMENSIONLESS*/
DCL RAIN_RANDOM_NUMBER FLOAT(6);                         /* DIMENSIONLESS*/
DCL RATIO_CLASS FLOAT(6);                                /* DIMENSIONLESS*/
DCL RATIO_PROBABILITIES(6,10) FLOAT(6);                  /* DIMENSIONLESS*/
DCL SEED_AGE FIXED BIN;                                  /* YEARS        */
DCL SEED_AGE_AXIS(5) FLOAT(6);                           /* YEARS        */
DCL SEED_CROP FLOAT(6);                                  /* #/SQ METER   */
DCL SEED_DENSITY(0:19) FLOAT(6);                         /* #/SQ METER   */
DCL SEED_POTENTIAL(6) FLOAT(6);                          /* #/SQ METER   */
DCL SEED_SURVIVAL(0:19) FLOAT(6);                        /* FRACTION/YEAR*/
DCL SEEDLINGS FLOAT(6);                                  /* #/SQ METER   */
DCL SEEDS_PER_PLANT FIXED BIN;                           /* #/PLANT      */
DCL SEEDS_PER_PLANT_ARRAY(6,5) FLOAT(6);                 /* #/PLANT      */
DCL SEEDS_PER_PLANT_VECTOR(5) FLOAT(6);                  /* #/PLANT      */
```

```
DCL SIZE CHAR(11);                                           /* DIMENSIONLESS*/
DCL STATS BIT(1);                                            /* DIMENSIONLESS*/
DCL SUMS(7) FLOAT;                                           /* DIMENSIONLESS*/
DCL SUM_SQUARES(7) FLOAT;                                    /* DIMENSIONLESS*/
DCL TABLE2 PRINT;                                            /* PRINT FILE   */
DCL TABLE3 PRINT;                                            /* PRINT FILE   */
DCL TITLE(3) CHAR(80);                                       /* DIMENSIONLESS*/
DCL TOO_BIG BIT(1) INIT('0'B);                               /* DIMENSIONLESS*/
DCL TOTAL_GERMINABLE FLOAT(6);                               /* #/SQ METER   */
DCL TOTAL_LAMDA FLOAT(6);                                    /* DIMENSIONLESS*/
DCL TOTAL_RAIN FLOAT(6);                                     /* MILLIMETERS  */
DCL TOTAL_RAIN_AXIS(6) FLOAT(6);                             /* MILLIMETERS  */
DCL TOTAL_RAIN_PROBABILITIES(6) FLOAT(6);                    /* DIMENSIONLESS*/
DCL TOTAL_SEED FLOAT(6);                                     /* #/SQ METER   */
DCL VARIANCE(7) FLOAT(6);                                    /* DIMENSIONLESS*/
DCL WEIGHTED_LAMDA(6) FLOAT(6);                              /* DIMENSIONLESS*/
DCL X FLOAT(6);                                              /* DIMENSIONLESS*/
DCL X_AXIS(10) FLOAT(6);                                     /* DIMENSIONLESS*/
DCL Y_AXIS(10) FLOAT(6);                                     /* DIMENSIONLESS*/
DCL YEAR FIXED BIN;                                          /* DIMENSIONLESS*/
/*****************************************************************************/
/*                                                                           */
/*      READ IN THE DATA                                                     */
/*                                                                           */
/*****************************************************************************/
GET EDIT(#_YEARS) (COL(21),F(3));
PUT SKIP(4) EDIT('# YEARS TO RUN IS',#_YEARS)
      (COL(10),A,F(3));
GET EDIT(LOCATION) (COL(1),A(20));
PUT SKIP(2) EDIT('LOCATION:',LOCATION) (COL(10),A,X(3),A);
GET SKIP EDIT(X) (COL(21),E(20,5));
PUT SKIP(2) EDIT('RANDOM NUMBER PRIMER IS',X) (COL(10),A,E(15,5));
GET SKIP EDIT(TOTAL_RAIN_AXIS) (COL(21), (6) F(5));
PUT SKIP(2) EDIT('TOTAL RAIN AXIS:',TOTAL_RAIN_AXIS)
      (COL(10),A,COL(38), (6) F(7));
GET EDIT(TOTAL_RAIN_PROBABILITIES) (COL(21), (6) F(5,3));
PUT SKIP(2) EDIT('TOTAL RAIN PROBABILITIES:',
      TOTAL_RAIN_PROBABILITIES) (COL(10),A,COL(38), (6) F(7,3));
GET EDIT((RATIO_PROBABILITIES(I,*) DO I = 1 TO 6))
      (COL(21), (10) F(5,3));
PUT SKIP(2) EDIT('RATIO PROBABILITIES:',
      (RATIO_PROBABILITIES(I,*) DO I = 1 TO 6))
      (COL(10),A,SKIP,  (6) (COL(10), (10) F(7,3)));
GET EDIT(GERMINATING_RAIN_AXIS) (COL(21), (5) F(5));
PUT SKIP(2) EDIT('GERMINATING RAIN AXIS:',GERMINATING_RAIN_AXIS)
      (COL(10),A,COL(34), (5) F(7));
GET EDIT(GERMINATION_RESPONSE_AXIS) (COL(21), (5) F(5,2));
PUT SKIP(2) EDIT('GERMINATION RESPONSE:',GERMINATION_RESPONSE_AXIS)
      (COL(10),A,COL(34), (5) F(7,2));
GET EDIT(INITIAL_SEED_CROP) (COL(21),F(5));
PUT SKIP(2) EDIT('INITIAL SEED CROP:',INITIAL_SEED_CROP)
      (COL(10),A,F(8));
GET EDIT(SEED_AGE_AXIS) (COL(21), (5) F(5));
PUT SKIP(2) EDIT('SEED AGE AXIS:',SEED_AGE_AXIS)
      (COL(10),A,COL(33), (5) F(6));
GET EDIT(GERMINATION_AXIS) (COL(21), (5) F(5,3));
PUT SKIP(2) EDIT('FRACTION GERMINABLE:',GERMINATION_AXIS)
      (COL(10),A,COL(33), (5) F(6,2));
GET EDIT(PREDATION_AXIS) (COL(21), (5) F(5,2));
PUT SKIP(2) EDIT('PREDATION:',PREDATION_AXIS)
      (COL(10),A,COL(33), (5) F(6,2));
```

```
GET EDIT(DENSITY_AXIS) (COL(21), (5) F(5));
PUT SKIP(2) EDIT('DENSITY AXIS:',DENSITY_AXIS)
       (COL(10),A,COL(35), (5) F(6));
GET EDIT((PLANT_SURVIVAL_ARRAY(I,*) DO I = 1 TO 6))
       (COL(21), (5) F(5,2));
PUT SKIP(2) EDIT('PLANT SURVIVAL ARRAY:',
       (PLANT_SURVIVAL_ARRAY(I,*) DO I = 1 TO 6))
       (COL(10),A, (6) (COL(35), (5) F(6,2)));
GET EDIT((SEEDS_PER_PLANT_ARRAY(I,*) DO I = 1 TO 6))
       (COL(21), (5) F(5));
PUT SKIP(2) EDIT('SEEDS PER PLANT ARRAY:',
       (SEEDS_PER_PLANT_ARRAY(I,*) DO I = 1 TO 6))
       (COL(10),A, (6) (COL(35), (5) F(6)));
GET EDIT(FACTOR) (COL(21),F(5,2));
PUT SKIP(2) EDIT('FACTOR:',FACTOR) (COL(10),A,X(3),F(5,2));
GET EDIT(DUM) (COL(21),A(1));
PUT SKIP(2) EDIT('RAIN HISTOGRAMS:',DUM) (COL(10),A,X(3),A);
RAIN_HISTOGRAMS=DUM;
GET EDIT(DUM) (COL(21),A(1));
PUT SKIP(2) EDIT('STATS:',DUM) (COL(10),A,X(3),A(1));
STATS=DUM;
GET EDIT(DUM) (COL(21),A(1));
PUT SKIP(2) EDIT('FUNCTIONS:',DUM) (COL(10),A,X(3),A);
FUNCTIONS=DUM;
PUT PAGE;
/*********************************************************************/
/*                                                                   */
/*       PRINT THE FUNCTIONS USED IN THIS RUN                        */
/*                                                                   */
/*********************************************************************/
IF FUNCTIONS THEN DO;
PERCENT_AXIS=100*GERMINATION_AXIS;
CALL PUT_CURVE('            % GERMINABLE (Y) VS SEED AGE (X)'||
       ' IN YEARS',SEED_AGE_AXIS,PERCENT_AXIS);
PUT FILE(GRAPHS) SKIP(4);
PERCENT_AXIS=100*PREDATION_AXIS;
CALL PUT_CURVE('            % SEED PREDATION (Y) VS SEED AGE (X)'||
       ' IN YEARS',SEED_AGE_AXIS,PERCENT_AXIS);
PUT FILE(GRAPHS) PAGE;
PERCENT_AXIS=100*GERMINATION_RESPONSE_AXIS;
CALL PUT_CURVE('% GERMINATION RESPONSE (Y) VS GERMINATING'||
       ' RAINFALL (X) IN MM',GERMINATING_RAIN_AXIS,
       PERCENT_AXIS);
PLANT_SURVIVAL_ARRAY=100*PLANT_SURVIVAL_ARRAY;
DO PLOT = 1 TO 4;
    GET EDIT(TITLE) (COL(1),A(80));
    PUT SKIP(1) EDIT(TITLE) (COL(10),A(80));
    GET EDIT(DUM) (COL(21),A(1));
    PUT SKIP(1) EDIT('INTERPOLATE',DUM) (COL(10),A,X(3),A);
    INTERPOLATE=DUM;
    GET EDIT(#_X_AXIS_POINTS,#_Y_AXIS_POINTS) (COL(21), (2) F(5));
    PUT SKIP(1) EDIT('# OF X-AXIS POINTS, # OF Y-AXIS POINTS',
           #_X_AXIS_POINTS,#_Y_AXIS_POINTS)
           (COL(10),A, (2) F(10));
    GET EDIT((X_AXIS(I) DO I = 1 TO #_X_AXIS_POINTS))
              (COL(21), (10) F(5));
    PUT SKIP EDIT('X-AXIS:', (X_AXIS(I) DO I = 1 TO #_X_AXIS_POINTS))
           (COL(10),A,X(3), (10) F(6));
    GET EDIT((Y_AXIS(I) DO I = 1 TO #_Y_AXIS_POINTS))
              (COL(21), (10) F(5));
    PUT SKIP EDIT('Y-AXIS:', (Y_AXIS(I) DO I = 1 TO #_Y_AXIS_POINTS))
```

```
            (COL(10),A,X(3), (10) F(6));
    GET EDIT(SIZE) (COL(1),A(11));
    PUT SKIP(1) EDIT('SIZE:',SIZE) (COL(10),A,X(3),A);
    GET SKIP EDIT(#_CURVES) (COL(21),F(5));
    PUT SKIP(1) EDIT('# CURVES:',#_CURVES) (COL(10),A,X(1),F(5));
    GET SKIP EDIT(#_PAIRS) (COL(21),F(5));
    PUT SKIP EDIT('# OF POINTS:',#_PAIRS) (COL(10),A,F(5));
    PUT SKIP(2);
    CALL PLOTTER;
    END;
PLANT_SURVIVAL_ARRAY=.01*PLANT_SURVIVAL_ARRAY;
PUT PAGE;
END;
/*********************************************************************
/*                                                                   *
/*      PRINT THE HISTOGRAM OF THE TOTAL RAINFALL DISTRIBUTION       *
/*                                                                   *
/*********************************************************************
PROBABILITY(1)=TOTAL_RAIN_PROBABILITIES(1);
DO RAIN_CLASS = 2 TO 6;
    PROBABILITY(RAIN_CLASS)=TOTAL_RAIN_PROBABILITIES(RAIN_CLASS)
                -TOTAL_RAIN_PROBABILITIES(RAIN_CLASS-1);
    END;
IF RAIN_HISTOGRAMS THEN DO;
PUT SKIP(4) EDIT('THIS IS THE DISTRIBUTION OF TOTAL RAINFALL')
        (COL(10),A);
PUT SKIP(2) EDIT('FOR ',LOCATION) (COL(10),A,A);
PUT SKIP(2);
NUM=6;
PERCENT_AXIS2=100*PROBABILITY;
CALL HISTOGRAM(NUM,PERCENT_AXIS2);
PUT SKIP(2) EDIT('RAIN','IN MM',TOTAL_RAIN_AXIS)
        (COL(10),A,SKIP,COL(10),A,COL(18), (6) F(5));
PUT PAGE;
END;
/*********************************************************************
/*                                                                   *
/*      CALCULATE THE SEED COHORT PARAMETERS                         *
/*                                                                   *
/*********************************************************************
SEED_DENSITY(0)=INITIAL_SEED_CROP;
DO SEED_AGE = 0 TO 19;
    FRACTION_GERMINABLE(SEED_AGE)=
                CURVE(SEED_AGE,SEED_AGE_AXIS,GERMINATION_AXIS);
    FRACTION_EATEN(SEED_AGE)=
                CURVE(SEED_AGE,SEED_AGE_AXIS,PREDATION_AXIS);
    SEED_SURVIVAL(SEED_AGE)=(1-FRACTION_GERMINABLE(SEED_AGE))
            *(1-FRACTION_EATEN(SEED_AGE));
    IF SEED_AGE > 0 THEN SEED_DENSITY(SEED_AGE)=
            SEED_DENSITY(SEED_AGE-1)*SEED_SURVIVAL(SEED_AGE-1);
    END;
/*********************************************************************
/*                                                                   *
/*      PRINT THE INITIAL SEED COHORT HISTOGRAM                      *
/*                                                                   *
/*********************************************************************
TOTAL_SEED=SUM(SEED_DENSITY);
DO J = 1 TO 10;
    PERCENT_ARRAY(J)=100*SEED_DENSITY(J-1)/TOTAL_SEED;
    END;
PUT SKIP(2) EDIT('THIS IS THE INITIAL AGE DISTRIBUTION') (COL(12),A);
```

```
PUT SKIP(2) EDIT('TOTAL SEED DENSITY IS',
                              TOTAL_SEED,' PER SQUARE METER')
        (COL(12),A,F(7),A);
PUT SKIP;
NUM=10;
CALL HISTOGRAM(NUM,PERCENT_ARRAY);
PUT SKIP(2) EDIT('SEED','COHORT','0','1','2','3','4','5','6',
        '7','8','9') (COL(10),A,SKIP,COL(10),A,
        COL(22), (10) (A,X(4)));
/*****************************************************************
/*                                                               *
/*      PRINT TABLE HEADINGS                                     *
/*                                                               *
/*****************************************************************
PUT FILE(TABLE3) SKIP(3) EDIT('*** INITIAL SEED DENSITY IS',
        TOTAL_SEED,' PER SQUARE METER ***') (COL(10),A,F(7),A);
PUT FILE(TABLE3) SKIP(4) EDIT('YEAR','TOTAL','GERM','GERM  ',
        '% SEEDS   ',
        'SEEDLINGS','MATURE',' SEED','SEED1','SEED2','SEED3','SEED4',
        'SEED5','TOTAL',
        'RAIN','RAIN','FACTOR','GERMINABLE','PLANTS',' CROP','SEED')
        (COL(8), (14) (X(2),A),SKIP,
        COL(16),A,X(3),A,X(2),A,X(2),A,COL(60),A,X(2),A,COL(110),A);
PUT FILE(TABLE3) SKIP;
/*****************************************************************
/*                                                               *
/*      BEGIN THE YEAR LOOP                                      *
/*                                                               *
/*****************************************************************
DO YEAR = 1 TO #_YEARS;
/*****************************************************************
/*                                                               *
/*      DETERMINE THIS YEAR'S RAINFALL                           *
/*                                                               *
/*****************************************************************
    RAIN_RANDOM_NUMBER=RANDOM(X);
    DO RAIN_CLASS = 1 TO 6 WHILE (RAIN_RANDOM_NUMBER
            >= TOTAL_RAIN_PROBABILITIES(RAIN_CLASS));
        END;
    TOTAL_RAIN=TOTAL_RAIN_AXIS(RAIN_CLASS);
/*****************************************************************
/*                                                               *
/*      DETERMINE THE GERMINATING RAINFALL                       *
/*                                                               *
/*****************************************************************
    RAIN_RANDOM_NUMBER=RANDOM(X);
    DO RATIO_CLASS = 1 TO 10 WHILE (RAIN_RANDOM_NUMBER
            >= RATIO_PROBABILITIES(RAIN_CLASS,RATIO_CLASS));
        END;
    GERMINATING_RAIN=TOTAL_RAIN*(0.1*RATIO_CLASS - .05);
    GERMINATION_RESPONSE=CURVE(GERMINATING_RAIN,
            GERMINATING_RAIN_AXIS,GERMINATION_RESPONSE_AXIS);
/*****************************************************************
/*                                                               *
/*      CALCULATE # OF SEEDLINGS AND REDUCE THE SEED RESERVES    *
/*      ACCORDLINGLY                                             *
/*                                                               *
/*****************************************************************
    TOTAL_GERMINABLE=SUM(FRACTION_GERMINABLE*SEED_DENSITY);
    PERCENT_GERMINABLE=100*TOTAL_GERMINABLE/SUM(SEED_DENSITY);
    SEEDLINGS=TOTAL_GERMINABLE*GERMINATION_RESPONSE;
```

```
    SEED_DENSITY=SEED_DENSITY
                *(1-FRACTION_GERMINABLE*GERMINATION_RESPONSE);
/******************************************************************/
/*                                                                */
/*      CALCULATE # OF MATURE PLANTS AND THIS YEAR'S SEED CROP    */
/*                                                                */
/******************************************************************/
    PLANT_SURVIVAL_VECTOR=PLANT_SURVIVAL_ARRAY(RAIN_CLASS,*);
    PLANT_SURVIVAL=CURVE(SEEDLINGS,DENSITY_AXIS,
            PLANT_SURVIVAL_VECTOR);
    MATURE_PLANTS=SEEDLINGS*PLANT_SURVIVAL;
    SEEDS_PER_PLANT_VECTOR=SEEDS_PER_PLANT_ARRAY(RAIN_CLASS,*);
    SEEDS_PER_PLANT=CURVE(MATURE_PLANTS,DENSITY_AXIS,
            SEEDS_PER_PLANT_VECTOR);
    SEED_CROP=MATURE_PLANTS*SEEDS_PER_PLANT;
/******************************************************************/
/*                                                                */
/*      REDUCE SEED RESERVES DUE TO THIS YEAR'S PREDATION         */
/*                                                                */
/******************************************************************/
    SEED_DENSITY=SEED_DENSITY*(1-FRACTION_EATEN);
/******************************************************************/
/*                                                                */
/*      ADVANCE SEEDS IN AGE, ADD IN THIS YEAR'S SEED CROP, AND   */
/*      UPDATE TOTAL SEED                                         */
/*                                                                */
/******************************************************************/
    DO SEED_AGE = 19 TO 1 BY -1;
        SEED_DENSITY(SEED_AGE)=SEED_DENSITY(SEED_AGE-1);
        END;
    SEED_DENSITY(0)=SEED_CROP;
    TOTAL_SEED=SUM(SEED_DENSITY);
/******************************************************************/
/*                                                                */
/*      PRINT THE YEARLY OUTPUT TABLE                             */
/*                                                                */
/******************************************************************/
    PUT FILE(TABLE3) SKIP EDIT(YEAR,TOTAL_RAIN,GERMINATING_RAIN,
            GERMINATION_RESPONSE,PERCENT_GERMINABLE,SEEDLINGS,
            MATURE_PLANTS,
            (SEED_DENSITY(I) DO I = 0 TO 5),TOTAL_SEED)
            (COL(10),F(3),COL(16),F(4),COL(23),F(4),COL(30),F(4,1),
            COL(38),F(6,2),COL(50),F(6),COL(60),F(5),
            COL(66), (7) (X(1),F(6)));
    IF (MOD(YEAR,40) = 0) & (YEAR ¬= #_YEARS) THEN DO;
    PUT FILE(TABLE3) PAGE;
    PUT FILE(TABLE3) SKIP(4) EDIT('YEAR','TOTAL','GERM','GERM  ',
         '% SEEDS   ',
         'SEEDLINGS','MATURE',' SEED','SEED1','SEED2','SEED3','SEED4',
         'SEED5','TOTAL',
         'RAIN','RAIN','FACTOR','GERMINABLE','PLANTS',' CROP','SEED')
         (COL(8), (14) (X(2),A),SKIP,
         COL(16),A,X(3),A,X(2),A,X(2),A,COL(60),A,X(2),A,COL(110),A);
    PUT FILE(TABLE3) SKIP;
    END;
/******************************************************************/
/*                                                                */
/*      STATISTICAL ANALYSIS                                      */
/*                                                                */
/******************************************************************/
  IF STATS THEN DO;
```

```
    SUMS(1)=SUMS(1)+TOTAL_RAIN;
    SUMS(2)=SUMS(2)+GERMINATING_RAIN;
    SUMS(3)=SUMS(3)+PERCENT_GERMINABLE;
    SUMS(4)=SUMS(4)+SEEDLINGS;
    SUMS(5)=SUMS(5)+MATURE_PLANTS;
    SUMS(6)=SUMS(6)+SEED_CROP;
    SUMS(7)=SUMS(7)+TOTAL_SEED;
    SUM_SQUARES(1)=SUM_SQUARES(1)+TOTAL_RAIN**2;
    SUM_SQUARES(2)=SUM_SQUARES(2)+GERMINATING_RAIN**2;
    SUM_SQUARES(3)=SUM_SQUARES(3)+PERCENT_GERMINABLE**2;
    SUM_SQUARES(4)=SUM_SQUARES(4)+SEEDLINGS**2;
    SUM_SQUARES(5)=SUM_SQUARES(5)+MATURE_PLANTS**2;
    SUM_SQUARES(6)=SUM_SQUARES(6)+SEED_CROP**2;
    SUM_SQUARES(7)=SUM_SQUARES(7)+TOTAL_SEED**2;
    END;
/*********************************************************************/
/*                                                                   */
/*      SEE IF THE POPULATION HAS GONE EXTINCT OR IS ABSURDLY LARGE  */
/*                                                                   */
/*********************************************************************/
    IF (TOTAL_SEED < 1) | (TOTAL_SEED > 100000) THEN DO;
        PUT FILE(TABLE3) SKIP(4) EDIT('*** TOTAL SEED DENSITY ',
            'HAS GONE OUT-OF-BOUNDS ***') (COL(20),A,A);
        GO TO QUIT;
        END;
/*********************************************************************/
/*                                                                   */
/*      END OF THE YEAR LOOP                                         */
/*                                                                   */
/*********************************************************************/
    END;    /* END OF YEAR LOOP */
/*********************************************************************/
/*                                                                   */
/*      PRINT THE SEED COHORT HISTOGRAM                              */
/*                                                                   */
/*********************************************************************/
QUIT:
IF TOTAL_SEED = 0 THEN DO;
    PUT SKIP(4) EDIT('*** TOTAL SEED DENSITY IS ZERO ***') (COL(20),A);
    GO TO STAT;
    END;
DO J = 1 TO 10;
    PERCENT_ARRAY(J)=100*SEED_DENSITY(J-1)/TOTAL_SEED;
    IF PERCENT_ARRAY(J) > 95 THEN TOO_BIG = '1'B;
    END;
YEAR=MIN(YEAR,#_YEARS);
PUT PAGE;
PUT SKIP(2) EDIT('THIS IS THE SEED AGE DISTRIBUTION AFTER YEAR',
       YEAR) (COL(12),A,F(3));
PUT SKIP(2) EDIT('TOTAL SEED DENSITY IS',
                           TOTAL_SEED,' PER SQUARE METER')
       (COL(12),A,F(7),A);
PUT SKIP;
IF ¬ TOO_BIG THEN DO;
    CALL HISTOGRAM(NUM,PERCENT_ARRAY);
    PUT SKIP(2) EDIT('SEED','COHORT','0','1','2','3','4','5','6',
        '7','8','9') (COL(10),A,SKIP,COL(10),A,
       COL(22), (10) (A,X(4)));
    END;
ELSE PUT SKIP(4) EDIT('MORE THAN 95% OF THE SEEDS ARE ',
       'IN ONE AGE COHORT') (COL(15),A);
```

```
/*********************************************************************
/*                                                                   *
/*      CALCULATE AND PRINT THE MEANS AND STANDARD DEVIATIONS        *
/*                                                                   *
/*********************************************************************
STAT;
IF STATS & YEAR > 1 THEN DO;
    DO M = 1 TO 7;
         MEAN(M)=SUMS(M)/YEAR;
         VARIANCE(M)=SQRT((SUM_SQUARES(M)-YEAR*MEAN(M)**2)/(YEAR-1));
         END;
    PUT FILE(TABLE2) SKIP(10) EDIT('RAINFALL LOCATION:',LOCATION,
         'NUMBER OF YEARS OF SIMULATION:',YEAR)
         (COL(14),A,X(3),A,SKIP(2),COL(14),A,X(2),F(3));
    PUT FILE(TABLE2) SKIP(3) EDIT('MEAN','STD DEVIATION')
         (COL(47),A,COL(55),A);
    PUT FILE(TABLE2) SKIP(2) EDIT
        ('TOTAL RAIN (MM)',MEAN(1),VARIANCE(1),
         'GERMINATING RAIN (MM)',MEAN(2),VARIANCE(2),
         '% SEEDS GERMINABLE',MEAN(3),VARIANCE(3),
         'SEEDLINGS (#/SQ METER)',MEAN(4),VARIANCE(4),
         'MATURE PLANTS (#/SQ METER)',MEAN(5),VARIANCE(5),
         'SEED CROP (#/SQ METER)',MEAN(6),VARIANCE(6),
         'TOTAL SEED (#/SQ METER)',MEAN(7),VARIANCE(7))
         (COL(14),A,COL(45),F(6),COL(57),F(6));
    END;
/*********************************************************************
/*                                                                   *
/*      PUT_CURVE PROCEDURE                                          *
/*                                                                   *
/*********************************************************************
PUT_CURVE: PROC(H,XVAL,YVAL);
           DCL XVAL(*),YVAL(*),H CHAR(*),GRAPH(20,40)CHAR(1);
           DCL(ISTORE,JSTORE)(20);
/*THIS MAY BE TOO SMALL IN SOME CASES*/
           NDIM=DIM(XVAL,1);
               IF NDIM>20 THEN
                  DO;
                  PUT SKIP LIST(H, ' TOO SMALL');
                  RETURN;
                  END;
           XMIN=XVAL(1);
           XMAX=XVAL(NDIM);
           YMAX=100;
           YMIN=0;
           DO II = 1 TO NDIM;
              YMAX=MAX(YMAX,YVAL(II));
              END;
           XDIV=(XMAX-XMIN)*0.025;
           YDIV=(YMAX-YMIN)*0.05;
           GRAPH(*,*)=' ';
               DO K=1 TO NDIM;
               J=CEIL((XVAL(K)-XMIN)/XDIV-0.5);
                  IF J>40 THEN
                  J=40;
                  IF J<1 THEN
                  J=1;
               I=CEIL((YMAX-YVAL(K))/YDIV-0.5);
                  IF I>20 THEN
                  I=20;
                  IF I<1 THEN
```

```
                  I=1;
                ISTORE(K)=I;
                JSTORE(K)=J;
                GRAPH(I,J)='*';
                END;
                DO M=1 TO 20;
                   IF M=1 THEN
       PUT FILE(GRAPHS) SKIP EDIT(YMAX,'+',GRAPH(1,*))
                              (COL(27),F(5),COL(34),A,COL(35),40 A);
                   ELSE
                      IF M=20 THEN
         PUT FILE(GRAPHS) SKIP EDIT(YMIN,'+',GRAPH(20,*))
                              (COL(27),F(5),COL(34),A,COL(35),40 A);
                      ELSE
         PUT FILE(GRAPHS) SKIP EDIT('I',GRAPH(M,*))
                                (COL(34),A,COL(35),40 A);
                END;
PUT FILE(GRAPHS) SKIP EDIT('+----------------------------------------+')
                       (COL(35),A);
          PUT FILE(GRAPHS) SKIP(2);
          DO K=1 TO NDIM;
PUT FILE(GRAPHS) SKIP(0) EDIT(XVAL(K))(COL(32+JSTORE(K)),F(3));
             END;
PUT FILE(GRAPHS) SKIP(2)EDIT(H)(COL(26),A);
          END PUT_CURVE;
/************************************************************************
/*                                                                      *
/*       INTERPOLATION PROCEDURE                                        *
/*                                                                      *
/************************************************************************
CURVE : PROC(X,XVAL,YVAL);
DCL I FIXED BIN INTERNAL, X FLOAT DEC;
DCL XVAL(*), YVAL(*);
  NDIM=DIM(XVAL,1);
IF X <= XVAL(1) THEN RETURN (YVAL(1));
IF X >= XVAL(NDIM) THEN RETURN (YVAL(NDIM));
DO I = 1 TO NDIM;
  IF XVAL(I) > X THEN DO;
      AM = (YVAL(I)-YVAL(I-1))/(XVAL(I)-XVAL(I-1));
      C = YVAL(I)-AM*XVAL(I);
      RETURN (AM*X+C);
  END;
END;
END CURVE;
/************************************************************************
/*                                                                      *
/*       HISTOGRAM PROCEDURE                                            *
/*                                                                      *
/*       ARRAY SHOULD HAVE VALUES BETWEEN 0-100                         *
/*       NUM = # OF HISTOGRAM INTERVALS (# OF DIMENSIONS OF THE         *
/*             ARRAY IN THE CALL STATEMENT)                             *
/*       WDTH = # OF PRINT SPACES GIVEN TO EACH HISTOGRAM INTERVAL      *
/*       LEN = TOTAL HEIGHT OF THE HISTOGRAM (# OF PRINT LINES)         *
/*             LEN MUST BE A MULTIPLE OF 10                             *
/*                                                                      *
/************************************************************************
HISTOGRAM: PROC(NUM,ARRAY);
       DCL NUM BIN FIXED INIT(11),
           LEN BIN FIXED INIT(40),
           WDTH BIN FIXED INIT(5),
           ARRAY(*) FLOAT(6) ;
```

```
            DCL PLOTER(LEN) CHAR(WDTH*NUM+1),
                BLNK CHAR(5*NUM+1) INIT(' '),
                STR CHAR(LEN) INIT('   PERCENTAGES ');
            NW=WDTH-1 ;
              DO I=1 TO LEN ;
              PLOTER(I)=BLNK ;
              END ;
            BLNK=REPEAT('_',120) ;
              DO I=1 TO NUM-1 ;
              IV=ARRAY(I)*LEN/100;
              IIV=ARRAY(I+1)*LEN/100;
                IF IIV < IV THEN
                IIV=IV ;
                DO K=1 TO IIV ;
                SUBSTR(PLOTER(K),WDTH*I+1,1)='|' ;
                END ;
              SUBSTR(PLOTER(IV+1),WDTH*(I-1)+2,NW)='__________' ;
                IF ARRAY(I) > 0 THEN
                PUT STRING(SUBSTR(PLOTER(IV+2),WDTH*(I-1)+2,NW)) EDIT(
                ARRAY(I)) (F(NW,1)) ;
              END ;
            IV=ARRAY(NUM)/2 ;
            SUBSTR(PLOTER(IV+1),WDTH*(NUM-1)+2,NW)='__________' ;
              IF ARRAY(NUM) > 0 THEN
              PUT STRING(SUBSTR(PLOTER(IV+2),WDTH*(I-1)+2,NW)) EDIT(
              ARRAY(NUM)) (F(NW,1)) ;
            PUT SKIP ;
            PUT EDIT(BLNK)(COL(20),A(WDTH*NUM-1)) ;
              DO I=LEN TO 1 BY -1 ;
              SUBSTR(PLOTER(I),1,1)='|' ;
              SUBSTR(PLOTER(I),WDTH*NUM+1,1)='|' ;
              PUT EDIT(SUBSTR(STR,LEN-I+1,1))(COL(12),A) ;
                IF MOD(I,LEN/10) = 0 THEN
                PUT EDIT(I*100/LEN)(COL(14),F(3)) ;
              PUT EDIT(PLOTER(I))(COL(19),A) ;
              END ;
            PUT EDIT(BLNK)(SKIP(0),COL(20),A(WDTH*NUM-1)) ;
          RETURN ;
      END HISTOGRAM;
  /****************************************************************
  /*                                                              *
  /*      PLOTTER PROCEDURE                                       *
  /*                                                              *
  /****************************************************************
  PLOTTER: PROC;
  DCL ARRAY(6,5) FLOAT(6);
  DCL GRAPH(40,80) CHAR(1);
  DCL ISTORE(100);
  DCL JSTORE(100);
  DCL PAIR FIXED BIN;
  DCL X(6) FLOAT(6);
  DCL Y(6) FLOAT(6);
      DCL XMAX,YMAX FLOAT(6);
      DCL NP,NL FIXED BIN;
      DCL XMIN,YMIN FLOAT(6) INIT(0);
      DCL NUM(9) CHAR(1) INIT('1','2','3','4','5','6','7','8','9');
  GRAPH(*,*)=' ';
  IF SIZE = 'SMALL GRAPH' THEN EDGE = 40;
  ELSE IF SIZE = 'LARGE GRAPH' THEN EDGE = 80;
  ELSE DO;
      PUT SKIP(6) EDIT('*** CARD STATING THE GRAPH SIZE',
```

```
            ' IS MISSING OR MISS-SPELLED ***') (COL(20),A,A);
        STOP;
        END;
    IF PLOT < 3 THEN ARRAY = PLANT_SURVIVAL_ARRAY;
    ELSE ARRAY = SEEDS_PER_PLANT_ARRAY;
    DO NL = 1 TO #_CURVES;
    DO PAIR = 1 TO #_X_AXIS_POINTS;
        X(PAIR)=X_AXIS(PAIR);
        END;
    DO PAIR = 1 TO #_PAIRS;
        IF #_PAIRS = 5 THEN Y(PAIR) = ARRAY(NL,PAIR);
        ELSE Y(PAIR) = ARRAY(PAIR,NL);
        END;
    XMAX=X_AXIS(#_X_AXIS_POINTS);
    YMAX=Y_AXIS(#_Y_AXIS_POINTS);
    NP=#_PAIRS;
                XDIV=(XMAX-XMIN)/EDGE;
                YDIV=(YMAX-YMIN)*2/EDGE;
                  DO K = 1 TO NP;
                   J=CEIL((X(K)-XMIN)/XDIV-0.5);
                      IF J > EDGE THEN J = EDGE;
                      IF J<1 THEN
                      J=1;
                   I=CEIL((YMAX-Y(K))/YDIV-0.5);
                      IF I > EDGE/2 THEN I = EDGE/2;
                      IF I<1 THEN
                      I=1;
                   GRAPH(I,J)=NUM(NL);
                   IF INTERPOLATE THEN DO;
                       ISTORE(K)=I;
                       JSTORE(K)=J;
                       END;
                   END;
                   IF INTERPOLATE THEN DO;
                   DO N=2 TO NP;
                      DO J=JSTORE(N-1)+1 TO JSTORE(N)-1;
                      GRAD=(ISTORE(N)-ISTORE(N-1))/(JSTORE(N)-JSTORE(N-1));
                      C=ISTORE(N)-(GRAD*JSTORE(N));
                      I=CEIL(GRAD*J+C);
                      GRAPH(I,J)='+';
                      END;
                   END;
                   END;  /* END OF INTERPOLATION LOOP */
    END;   /* END OF NL LOOP */
        DO K = 1 TO #_X_AXIS_POINTS;
            J=CEIL((X_AXIS(K)-XMIN)/XDIV-0.5);
            IF J > EDGE THEN J = EDGE;
            ELSE IF J < 1 THEN J = 1;
            JSTORE(K)=J;
            END;
        DO K = 1 TO #_Y_AXIS_POINTS;
            I=CEIL((YMAX-Y_AXIS(K))/YDIV-0.5);
            IF I > EDGE/2 THEN I = EDGE/2;
            ELSE IF I < 1 THEN I = 1;
            ISTORE(K)=I;
            END;
    PUT FILE(GRAPHS) PAGE;
                PUT FILE(GRAPHS) SKIP(7);
                   DO M=1 TO EDGE/2;
                      IF M=1 THEN
        PUT FILE(GRAPHS) SKIP EDIT(YMAX,'+',(GRAPH(M,L) DO L = 1 TO EDGE))
```

```
                   (COL(27),F(5),COL(34),A,COL(35),80 A);
            ELSE
               IF M = EDGE/2 THEN
        PUT FILE(GRAPHS) SKIP EDIT(YMIN,'+',(GRAPH(M,L) DO L=1 TO EDGE))
                   (CUL(27),F(5),COL(34),A,COL(35),80 A);
               ELSE DO;
        PUT FILE(GRAPHS) SKIP EDIT('I',(GRAPH(M,L) DO L = 1 TO EDGE))
                          (COL(34),A,COL(35),80 A);
               DO K = 2 TO #_Y_AXIS_POINTS-1;
                   IF M = ISTORE(K) THEN PUT FILE(GRAPHS) SKIP(0)
                         EDIT (Y_AXIS(K)) (COL(27),F(5));
                   END;
               END;
         END;
      IF EDGE = 40 THEN
PUT FILE(GRAPHS) SKIP EDIT('+----------------------------------------+')
                   (COL(35),A);
      ELSE
PUT FILE(GRAPHS) SKIP EDIT('+----------------------------------------',
                    '----------------------------------------+')
                   (COL(35),A,A);
      PUT FILE(GRAPHS) SKIP(2);
      DO K = 1 TO #_X_AXIS_POINTS;
PUT FILE(GRAPHS) SKIP(0) EDIT(X_AXIS(K))(COL(32+JSTORE(K)),F(3));
        END;
PUT FILE(GRAPHS) SKIP(3) EDIT(TITLE) (COL(35),A(80));
END PLOTTER;
END STRATEGY3;
```

HERE IS A COMPLETE LISTING OF THE DATA DECK USED FOR THE BASE RUN:

```
# YEARS               80
LAS VEGAS
RANDOM PRIMER         9.45637E11
TOTAL RAIN AXIS         25   75  125  175  225  275
TOTAL RAIN PROB       .475 .825 .9751.00 1.00 1.00
GERM. RATIO  25       .000 .000 .000 .143 .286 .429 .572 .715 .8581.000
GERM. RATIO  75       .000 .167 .334 .501 .668 .8351.00 1.00 1.00 1.00
GERM. RATIO 125       .000 .333 .6661.00 1.00 1.00 1.00 1.00 1.00 1.00
GERM. RATIO 175       .000 .333 .6661.00 1.00 1.00 1.00 1.00 1.00 1.00
GERM. RATIO 225      1.00 1.00 1.00 1.00 1.00 1.00 1.00 1.00 1.00 1.00
GERM. RATIO 275      1.00 1.00 1.00 1.00 1.00 1.00 1.00 1.00 1.00 1.00
GERM RAIN AXIS           0   15   25   35   45
GERM RESPONSE         0.0  0.0  1.0  1.0  1.0
INITIAL SEED CROP     2000
SEED AGE AXIS            0    1    2    4    8
DORMANCY              .020 .050 .100 .200 .300
PREDATION             0.90 0.10 0.10 0.10 0.10
DENSITY AXIS             0  100  200  400  800
PLANT SURVIVAL  25    0.00 0.00 0.00 0.00 0.00
PLANT SURVIVAL  75    0.90 0.50 0.30 0.20 0.10
PLANT SURVIVAL 125    1.00 0.90 0.50 0.30 0.20
PLANT SURVIVAL 175    1.00 1.00 0.90 0.50 0.30
PLANT SURVIVAL 225    1.00 1.00 1.00 0.90 0.50
PLANT SURVIVAL 275    1.00 1.00 1.00 1.00 0.90
SEEDS/PLANT  25          0    0    0    0    0
SEEDS/PLANT  75         60   30   10    5    2
SEEDS/PLANT 125         90   60   30   10    5
SEEDS/PLANT 175        120   90   60   30   10
SEEDS/PLANT 225        150  120   90   60   30
SEEDS/PLANT 275        150  150  120   90   60
FACTOR                1.00
RAIN HISTOGRAMS      1
STATS                1
FUNCTIONS            1
% PLANT SURVIVAL (Y-AXIS)  VS
SEEDLING DENSITY IN #/SQ METER (X-AXIS)
FOR DIFFERENT TOTAL RAINFALL AMOUNTS IN MM
INTERPOLATE          0
# X,Y AXIS POINTS         5    5
X AXIS                   0  100  200  400  800
Y-AXIS                   0   25   50   75  100
SMALL GRAPH
# CURVES                 6
# PAIRS                  5
% PLANT SURVIVAL (Y-AXIS)  VS
RAINFALL (MM) OVER GROWING SEASON (X-AXIS)
FOR DIFFERENT SEEDLING DENSITIES IN #/SQ METER
INTERPOLATE          0
# X,Y AXIS POINTS         6    5
X-AXIS                  25   75  125  175  225  275
Y-AXIS                   0   25   50   75  100
SMALL GRAPH
```

```
# CURVES                 5
# X-Y PAIRS              6
SEEDS PER PLANT (Y-AXIS)  VS
MATURE PLANT DENSITY IN #/SQ METER (X-AXIS)
FOR DIFFERENT TOTAL RAINFALL AMOUNTS IN MM
INTERPOLATE            0
# X,Y AXIS POINTS        5    4
X-AXIS                   0  100  200  400  800
Y-AXIS                   0   50  100  150
SMALL GRAPH
# CURVES                 6
# X-Y PAIRS              5
SEEDS PER PLANT (Y-AXIS)  VS
RAINFALL (MM) OVER GROWING SEASON (X-AXIS)
FOR DIFFERENT MATURE PLANT DENSITIES (#/SQ METER)
INTERPOLATE            0
# X,Y AXIS POINTS        6    4
X-AXIS                  25   75  125  175  225  275
Y-AXIS                   0   50  100  150
SMALL GRAPH
# CURVES                 5
# X-Y PAIRS              6
```

Appendix 2.

Rainfall data

As was mentioned in footnote 11 on page 52, the growing season and the period of germination is defined by the annual plant whose life cycle is being modeled. For winter annuals, the growing season is typically from mid-autumn to mid-spring.

Forty-one years of daily rainfall data (1931-1971) from the US Weather Bureau at Las Vegas were analyzed to determine (1) the time and amount of the germinating rainfall (which marked the beginning of the growing season) and (2) the total rainfall from the time of germination until the end of April. For years when there was insufficient rainfall in autumn to initiate germination, a second possible germination period was looked for between February 1st and March 15th (Beatley, 1967). This original data is shown in Table 16. Tables 17-19 contain the processed data that are then used as input to STRATEGY3.

Twenty-five years of rainfall data (1946-1971) from the US Weather Bureau at Tucson were similarly analyzed. These data are shown in Tables 20-23.

Table 16. Original yearly rainfall data for Las Vegas.

YEAR	GERMINATING RAINFALL (mm)	TOTAL RAINFALL (mm)	RAINFALL RATIO: (GERMINATING/TOTAL)
1931-32	21.8	123.4	.18
1932-33	34.3	93.7	.37
1933-34	8.1	15.7	.52
1934-35	14.0	78.7	.18
1935-36	14.5	17.0	.85
1936-37	22.9	100.3	.23
1937-38	36.8	44.7	.82
1938-39	16.0	86.6	.18
1939-40	47.2	118.1	.40
1940-41	44.7	196.9	.23
1941-42	24.1	53.3	.45
1942-43	25.7	64.0	.40
1943-44	23.6	68.1	.35
1944-45	38.9	40.1	.97
1945-46	16.5	23.1	.71
1946-47	24.9	32.8	.76
1947-48	28.7	67.8	.42
1948-49	58.4	84.1	.70
1949-50	3.3	5.6	.59
1950-51	4.1	6.1	.67
1951-52	24.9	122.9	.20
1952-53	22.1	37.3	.59
1953-54	23.1	44.2	.52
1954-55	13.0	57.4	.23
1955-56	5.8	7.9	.74
1956-57	6.6	20.6	.32
1957-58	28.2	59.4	.47
1958-59	38.9	61.5	.63
1959-60	39.9	103.6	.38
1960-61	47.8	73.7	.65
1961-62	9.7	31.0	.31
1962-63	11.4	34.8	.33
1963-64	11.7	23.1	.50
1964-65	15.7	109.2	.14
1965-66	56.4	84.8	.66
1966-67	20.6	34.8	.59
1967-68	32.0	73.4	.44
1968-69	14.5	38.9	.37
1969-70	20.8	27.4	.76
1970-71	9.7	14.2	.68
	mean: 24.0	mean: 59.5	

Table 17. Historical distribution of the total rainfall over the growing season for Las Vegas.

TOTAL RAINFALL INTERVALS (mm)	INTERVAL MID-POINT (mm)	# OF YEARS	FREQUENCY
0 - 50	25	19	.475
50 - 100	75	14	.350
100 - 150	125	6	.150
150 - 200	175	1	.025
200 - 250	225	0	.000
250 - 300	275	0	.000

Table 18. Historical distribution of the germinating rainfall ratio for Las Vegas

	TOTAL RAINFALL INTERVALS (mm)				
RATIO	0-50	50-100	100-150	150-200	200-250
.0-.1					
.1-.2		2	2		
.2-.3		1	2	1	
.3-.4	4	3	2		
.4-.5	1	4			
.5-.6	5				
.6-.7	2	4			
.7-.8	4				
.8-.9	2				
.9-1.0	1				

Table 19. Smoothed distribution of the germinating rainfall ratio for Las Vegas

	TOTAL RAINFALL INTERVALS (mm)				
RATIO	0-50	50-100	100-150	150-200	200-250
.0-.1	.000	.000	.000	.000	
.1-.2	.000	.167	.333	.333	
.2-.3	.000	.167	.333	.333	
.3-.4	.143	.167	.333	.333	
.4-.5	.143	.167	.000	.000	
.5-.6	.143	.167	.000	.000	
.6-.7	.143	.167	.000	.000	
.7-.8	.143	.000	.000	.000	
.8-.9	.143	.000	.000	.000	
.9-1.0	.143	.000	.000	.000	

Table 20. Original yearly rainfall data for Tucson.

YEAR	GERMINATING RAINFALL (mm)	TOTAL RAINFALL (mm)	RAINFALL RATIO: (GERMINATING/TOTAL)
1946-47	43.2	117.1	.37
1947-48	19.1	105.4	.18
1948-49	26.7	113.3	.24
1949-50	13.5	101.1	.13
1950-51	17.5	83.8	.21
1951-52	48.5	209.8	.23
1952-53	37.1	109.5	.34
1953-54	7.6	72.1	.11
1954-55	44.5	100.1	.44
1955-56	8.4	57.4	.15
1956-57	6.4	111.5	.06
1957-58	35.8	190.8	.19
1958-59	28.7	65.8	.44
1959-60	21.3	118.1	.18
1960-61	16.8	78.2	.21
1961-62	22.9	117.6	.19
1962-63	66.5	160.5	.41
1963-64	29.0	93.5	.31
1964-65	20.8	96.3	.22
1965-66	88.6	239.3	.37
1966-67	11.7	37.3	.31
1967-68	36.8	227.3	.16
1968-69	47.2	110.7	.43
1969-70	24.1	96.5	.25
1970-71	43.9	82.6	.53
	mean: 30.7	mean: 115.8	

Table 21. Historical distribution of the total rainfall over the growing season for Tucson.

TOTAL RAINFALL INTERVALS (mm)	INTERVAL MID-POINT (mm)	# OF YEARS	FREQUENCY
0 - 50	25	1	.040
50 - 100	75	10	.400
100 - 150	125	9	.360
150 - 200	175	2	.080
200 - 250	225	3	.120
250 - 300	275	0	.000

Table 22. Historical distribution of the germinating rainfall ratio for Tucson.

	TOTAL RAINFALL INTERVALS (mm)				
RATIO	0-50	50-100	100-150	150-200	200-250
.0-.1			1		
.1-.2		2	4	1	1
.2-.3		4	1		1
.3-.4	1	1	2		1
.4-.5		1	2	1	
.5-.6		1			
.6-.7					
.7-.8					
.8-.9					
.9-1.0					

Table 23. Smoothed distribution of the germinating rainfall ratio for Tucson.

	TOTAL RAINFALL INTERVALS (mm)				
RATIO	0-50	50-100	100-150	150-200	200-250
.0-.1	.000	.000	.100	.000	.000
.1-.2	.000	.200	.300	.250	.333
.2-.3	.333	.200	.200	.250	.333
.3-.4	.333	.200	.200	.250	.333
.4-.5	.333	.200	.200	.250	.000
.5-.6	.000	.200	.000	.000	.000
.6-.7	.000	.000	.000	.000	.000
.7-.8	.000	.000	.000	.000	.000
.8-.9	.000	.000	.000	.000	.000
.9-1.0	.000	.000	.000	.000	.000

Appendix 3.

Table 24. Effects of variations in the dormancy curve on 80-year runs of STRATEGY3 with the predation curve at .90/.10 and normal Las Vegas rainfall.

Dormancy Curve	Percent Germinable	Seedling Density	Mature Plant Density	Seed Crop Density	Total Seed Density
.02/.05	3	61	29	1724	3104
.02/.08	5	88	37	2010	3410
.02/.10	6	102	39	2102	3457
.02/.12	7	114	41	2148	3441
.02/.20	12	151	45	2274	3365
.02/.30	17	180	47	2326	3216
.02/.40	22	199	48	2353	3102

Table 25. Effects of variations in the dormancy curve on 80-year runs of STRATEGY3 with the predation curve at .90/.10 and enhanced Las Vegas rainfall.

Dormancy Curve	Percent Germinable	Seedling Density	Mature Plant Density	Seed Crop Density	Total Seed Density
.02/.05	3	79	40	2169	3820
.02/.08	5	109	46	2370	3950
.02/.10	6	126	48	2450	3964
.02/.12	7	140	50	2492	3928
.02/.20	10	182	54	2604	3782
.02/.30	15	216	57	2670	3624
.02/.40	18	238	59	2707	3508

Table 26. Effects of variations in the dormancy curve on 80-year runs of STRATEGY3 with the predation curve at .90/.30 and normal Las Vegas rainfall.

Dormancy Curve	Percent Germinable	Seedling Density	Mature Plant Density	Seed Crop Density	Total Seed Density
.02/.05	extinction in 68 years				
.02/.10	extinction in 202 years				
.02/.20	11	70	29	1672	2104
.02/.30	16	102	36	1961	2418
.02/.40	21	125	39	2055	2493
.02/.50	26	142	41	2100	2510
.02/.60	30	157	42	2125	2510
.02/.70	35	169	42	2122	2479

Table 27. Effects of variations in the dormancy curve on 80-year runs of STRATEGY3 with the predation curve at .90/.30 and enhanced Las Vegas rainfall.

Dormancy Curve	Percent Germinable	Seedling Density	Mature Plant Density	Seed Crop Density	Total Seed Density
.02/.05	3	20	12	759	1012
.02/.10	5	51	28	1639	2111
.02/.20	9	101	43	2269	2841
.02/.30	13	137	49	2458	3015
.02/.40	17	165	52	2543	3065
.02/.50	21	188	54	2602	3091
.02/.60	25	207	56	2638	3094
.02/.70	29	223	57	2653	3078

Table 28. Effects of variations in the dormancy curve on 80-year runs of STRATEGY3 with the predation curve at .90/.30, normal Las Vegas rainfall, and 'GR' eliminated.

Dormancy Curve	Percent Germinable	Seedling Density	Mature Plant Density	Seed Crop Density	Total Seed Density
.02/.10	5	77	28	1621	2062
.02/.20	10	136	39	2118	2589
.02/.30	14	173	44	2245	2676
.02/.40	19	198	45	2281	2665
.02/.50	23	215	46	2270	2611
.02/.60	27	224	45	2217	2518
.02/.70	31	226	43	2132	2396

VITA

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