Rainfall distribution and population dynamics of desert annuals

Martin Köchy, Florian Jeltsch, Katja Tielbörger — Potsdam University, Germany

Abstract

Precipitation patterns of Mediterranean and desert regions in Israel have become more similar since the 1930s. We used a spatially explicit model to simulate the effect of rainfall distribution and volume on three common desert annuals.

The model tracks soil moisture, germination, and plant growth in five–day steps for 100 years. The seedbank is updated annually. Germination depends on the number of available seeds, soil moisture near the surface, and a rain threshold. Plant growth including seed production is controlled by soil moisture and intraspecific competition. Daily rainfall is taken in sequence from random years of manipulated data sets.

We manipulated daily rainfall intensity to create data sets with skewed or normal distributions in combination with higher (≈100 mm), average (≈88 mm), and lower (≈ 70 mm) rainfall compared to a reference site.

In line with their demands for rainfall to initiate germination, population persistence of *Reboudia pinnata* (≥ 30 mm) and *Filago desertorum* (≥ 20 mm) decreased more strongly when rainfall was lower and more normally distributed than did *Schismus arabicus* (≥ 10 mm). In particular, *Reboudia*'s overall persistence under skewed rainfall distribution was 71 yr compared to 18 yr under normal distribution. *Filago* persistence was 90 yr (skewed) and 22 yr (normal). *Schismus* persistence was 95 yr (low volume, skewed), 61 yr (low volume, normal) and 100 yr in the remaining treatments.

Apparently, the replenishment of the seedbank depends on high seed production in years with very high rainfalls. Thus, the model predicts that the species' range will shrink if the rain distribution continues to become more normal.

This study is part of the GLOWA Jordan River project — a collaborative effort between Israel and Germany and Jordan and the Palestine Authority. GLOWA is financed by the German Federal Ministry of Education and Research (BMBF)

For more information see http://www.glowa.org

Introduction

The rainfall patterns of Mediterranean and desert regions in Israel have become more similar since the 1930s (Ben–Gai et al. 1998). In the Mediterranean region, years with high rainfall (compared to the local mean) occur more often, whereas in the desert region, years with high rainfall (again compared to the local mean) have become rarer. How will this change affect the population dynamics of desert annuals?

Methods

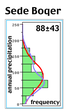
We used a spatially–explicit computer model to simulate rainfall, water infiltration, and plant growth. The model is based on published values and known or presumed functional relations.

We compared the effects of rainfall patterns on the persistence of populations of three annual plant species (*Reboudia pinnata*, *Filago desertorum*, *Schismus arabicus*) that differ in the amount of rain required to initiate germination.

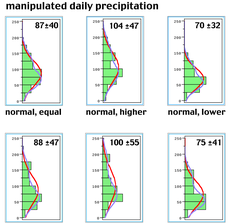
In addition, we tested whether persistence is higher in moister habitats like runnels. In runnels, germination of seeds has been observed after half the volume of rainfall required for germination on flat ground (Loria & Noy–Meir 1980).

We manipulated daily rain data of the Sede Boqer station (nothern Negev desert) to produce data sets with the same daily rainfall pattern but more normal or more extreme (skewed) distributions and lower, similar or higher annual sums.

Distribution and means (±SD) of annual precipitation



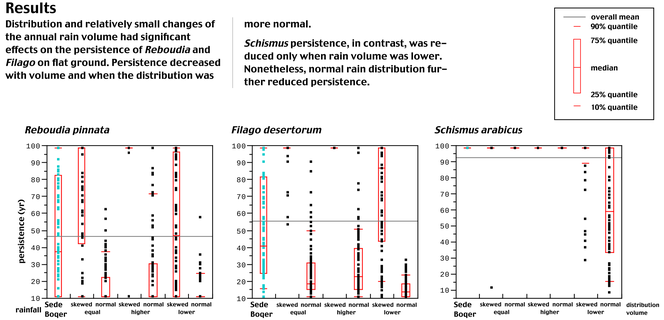
manipulated daily precipitation



Results

Distribution and relatively small changes of the annual rain volume had significant effects on the persistence of *Reboudia* and *Filago* on flat ground. Persistence decreased with volume and when the distribution was more normal.

***Schismus* persistence, in contrast, was reduced only when rain volume was lower. Nonetheless, normal rain distribution further reduced persistence.**



In runnels, the treatment effects were small. Only *Filago* and *Schismus* under lower volume, normal distribution conditions had reduced persistence.

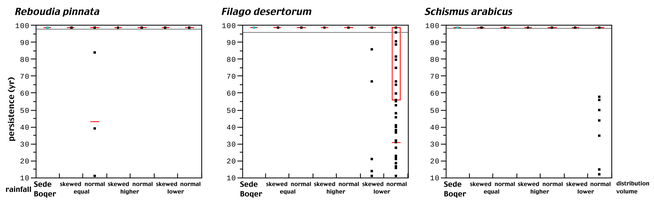


Photo credits: Claus Holzapfel, Katja Tielbörger

Discussion

The resilience to changes in rain pattern is in line with the species' demand for rain to initiate germination. *Reboudia*, germinating after ≥30 mm rainfall and *Filago*, germinating after ≥20 mm rainfall responded more strongly to treatments than *Schismus* (≥10 mm).

Populations persisted longer when the distribution of rainfall was more skewed, because the species produced many seeds during the rare years with extremely high rainfall. In such years, the seed bank was replenished and allowed the species to persist during drought years.

The results emphasize that even a small change (compared to the SD) of the average annual rainfall can have pronounced effects on the persistence of populations in the desert. Based on our results we predict that the species' range will shrink if the change of the rainfall pattern continues.

Research needs

Despite the importance of the seed bank for species persistence, seed bank dynamics are not well known. The model assumes that 40% of seeds in the seed bank are lost between years. This is much less than the 60 – 98 % found in experiments for other annual species in the Negev (Tielbörger 1997). It was necessary to assume a high value, though, to achieve at least temporary persistence in the model; all other important model parameters are backed by published studies. The rain requirements for germination (Loria & Noy–Meir 1980) are probably valid only for a fine sandy–silty loam and, in our experience, are lower for sandy soils. This highlights the need to study seed bank processes in the desert more closely.

References

Aronson, J.A., Kigel, J., Shmida, A. and Klein, J. 1992. Adaptive phenology of desert and mediterranean populations of annual plants grown with and without water stress. – Oecologia 89: 17–26.

Ben–Gai, T., Bitan, A., Manes, A., Alpert, P. and Rubin, S. 1998. Spatial and temporal changes in rainfall frequency distribution patterns in Israel. – Theoretical and Applied Climatology 61: 177–190.

Benecke, P. [1992]. Stoffhaushalt von Wald–Ökosystemen: Wasserhaushalt. Lecture notes. – Institut für Bodenkunde und Waldernährung der Universität Göttingen, Göttingen.

Cabin, R.J., Marshall, D.L. and Mitchell, R.J. 2000. The demographic role of soil seed banks. II. Investigations of the fate of experimental seeds of the desert mustard *Lesquerella fendleri*. – Journal of Ecology 88: 293–302.

Dyer, A.R., Turkington, R., Goldberg, D.E. and C.Sayre, C.Sayre. 2001. Effects of growing conditions and source habitat on plant traits and functional group definition. – Functional Ecology 15: 85–95.

Freas, K.E. and Kemp, P.R. 1983. Some relationships between environmental reliability and seed dormancy in desert annual plants. – *Journal of Ecology* 71: 211217.

Kigel, J. 1995. Seed germination in arid and semiarid regions. In: Kigel, J. (ed.), Seed development and germination. Books in soils, plants, and the environment. – Marcel Dekker, New York, New York, U.S.A., pp. 645–699.

Loria, M. and Noy–Meir, I. 1980. Dynamic of some annual populations in a desert loess plain. – Israel Journal of Botany 28: 211–225.

Meidan, E. 1990. The effects of soil water potential on seed germination of four winter annuals in the Negev desert. – Journal of Arid Environments 19: 77–83.

Pake, C.E. and Venable, D.L. 1996. Seed banks in desert annuals: implications for persistence and coexistence in variable environments. – Ecology 77: 1427–1435.

Tielbörger, K. 1997. Effect of shrubs on population dynamics of annual plants in a sandy desert ecosystem. Dissertation. Ludwig–Maximilian–Universität München, Munich.

Program Flow

set seedbank to mean seed production / loss rate
for each year
  select a year from the rain database
  calculate seed loss
  for each five-day-period ("week")
    get sum of rainfall and maximum rainfall event of the current week of the selected year
    calculate rain infiltration
    do plant life cycle
      calculate germination
      calculate plant growth
      calculate seed production
disperse seeds

Rain infiltration

"Infiltration" here is a net process and includes evaporation, drainage, and plant water use.

for each grid cell (periodic 10 × 10 grid)
  reduce available soil water content by 20%
  add amount of rain to soil water content
soil potential (Ψ) = $-e^{-1.38+0.029 \cdot \text{soil water content}}$ (Meidan 1990)

Seed loss

Seeds are lost due to mortality including predation. Seed loss in deserts is high (Kigel 1995, Cabin et al. 2000, Pake & Venable 1996). In the Negev it ranges from 50 to 98% depending on species, habitat, and year (Tielbörger 1997). Seed loss in this simulation is underestimated.

for each grid cell (periodic 10 × 10 grid)
  reduce seedbank by 40%

Germination

Seeds germinate when rainfall is above a certain threshold (Meidan 1990, Loria & Noy–Meir 1980, Freas & Kemp 1983) and when their dormancy is low (Meidan 1990, Aronson et al. 1992). The germination rate increases with the soil water potential near the soil surface (Meidan 1990) and the germinability (inverse of dormancy). The probability that one seed germinates is proportional to the number of seeds in the seed bank. The rainfall threshold refers to a fine sandy–silty loam.

for each grid cell (periodic 10 × 10 grid)
  plants germinate
    when no plant has germinated yet in the same place
    and when the amount of rain on one day > R_{min}
    germination rate (G) = $G_\Psi \cdot G_i$
      $G_\Psi = G_{max}$ when $\Psi \geq -0.0361$ MPa (field capacity), else
      $G_\Psi = -0.1 + 0.015/-\Psi$ **(Fig. 1)**
      $G_i = \left(\left[\sin\left(\frac{\text{week}}{72} \cdot 2\pi + \frac{5}{2}\pi\right) + 1\right] \cdot 0.5\right)^{0.-k}$, $k = 3$ **(Fig. 2)**
    seed germinates if $P' \leq G_i$; P': random number [0;1), n: seeds in seed bank
  initial plant mass equals seed mass

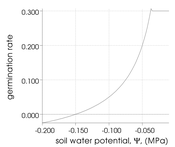


Fig. 1

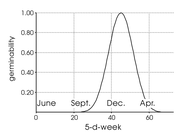


Fig. 2

Plant growth

Plant growth is basically logistic (m_{max} = final mass in wet years). In addition, growth rate increases with the soil water potential and decreases with the average mass of neighbours. After the plant has reached maturity (defined by 70 % of final mass in dry years), 60 % of new biomass is used for seed production (Loria & Noy–Meir 1980).

for each grid cell (periodic 10 × 10 grid)
  produced biomass = old biomass · (relative growth rate – 1)
    relative growth rate (RGR) =
      $\left(RGR_{max} - \frac{RGR_{max}}{m_{max}} \cdot m\right)$ · water availability ·
      dominance ratio
    water availability = $(1+0.0001 \cdot e^{-30 \cdot \Psi})^{-1}$ **(Fig. 3, after Benecke 1992)**
    dominance ratio (D) = target mass / average neighbour mass (6 nbs in hexagonal design) when target mass < average neighbour mass, else D = 1± random number [0;0.01)
  mass for seed production = 60 % of produced biomass when $m > m_{mature}$
  fruit and inflorescence mass do not contribute to plant growth

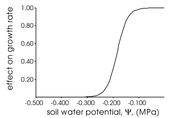


Fig. 3

Seed production

Seed production is proportional to the mass of the reproductive tissue, including inflorescences and fruit tissue. In wet years the plants produce more seeds per unit biomass (SM ratio) than in dry years.

for each grid cell
  number of seeds = reproductive mass · SM

$$SM = (SM_{max} - SM_{min}) \cdot \frac{m - m_{mature}}{m_{max} - m_{mature}} + SM_{min}$$

  seed numbers are accumulated

Seed dispersal

Seeds are dispersed in packages of 1/3 of the produced number into the same cell or adjacent neighbour cells.

for each grid cell
  do three times
    choose one neighbour cell (square design, eight neighbours plus target cell)
    add one third of produced seeds to existing seed bank

Important parameters

		Reboudia pinnata	*Filago desertorum*	*Schismus arabicus*
net weight of seed (mg)	1,2	0.22	0.037	0.07
biomass (mg)/plant, dry year	1	15.87	7.01	5.20
biomass (mg)/plant, wet year	1	710.80	21.95	18.83
reproductive effort	1	0.6	0.6	0.6
minimum rain (mm) for germination	1	30	20	10
shoot RGR max (mg · mg^{-1} · d^{-1})	1	0.166	0.166	0.166
shoot GR, 5 days	1	2.29	2.29	2.29
max germination rate	1	0.5	0.3	0.3
seeds/reprod. tissu (mg)e, dry year	1	40	104	41
seeds/reprod. tissu (mg)e, wet year	1	1777	326	148

[1] Loria & Noy-Meir 1980
[2] Dyer et al. 2001
[3] Meidan 1990