

Chapter 13

Spatial Distribution of Plant Functional Types Along Stress Gradients – A Simulation Study Orientated Towards the Plant Succession on the Desiccating Aral Sea Floor

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13.1 Introduction

Since 1960 the Aral Sea has shrunk considerably, because the water of its two feeding rivers is intensively used for irrigation (Micklin and Aladin 2008). From 1960 to 2000 the irrigated area increased by approximately three million hectares and caused a negative water balance for the endorheic Aral Sea (Micklin 2007). During the desiccation a huge area of new land (approximately 54,000 km², Micklin and Aladin 2008) has been exposed, which is approximately 80% of the former sea surface (Micklin 2007). Plans to construct gigantic channel systems to transfer water from the major Siberian rivers into the Aral Sea have existed for decades but have not been applied (Badescu and Schuiling 2010). New satellite images (NASA) indicate a drastic retreat of the southern eastern basin in summer 2009; thus now almost 60,000 km² is desiccated seafloor (see Chap. 2). The new barren ground provides a complex mosaic of abiotic conditions, where soil salinity depends on the soil morphology, distance to the groundwater table and position along the gradient of the receding seawater. Sand and dust, salt dust in particular, which is blown off by strong winds (see Chaps. 5 and 7) and redistributed over the agricultural areas and villages is a serious economic (reduced crop yields) and health (respiratory illness, cancer, infant mortality) problem (O’Hara et al. 2000; Micklin 2007).

A fast and possibly dense colonization by plants could possibly help to attenuate those negative impacts of the desiccation. Therefore, a better understanding of the succession processes and the vegetation dynamics in this saline and arid environment is needed.

However, succession along environmental gradients is a complex and stochastic process, where multiple biotic and abiotic processes interact. Since the seawater has become more and more saline during the desiccation (Micklin and Aladin 2008), there is a tendency for the soil salinity to increase with distance from the former shoreline (Wucherer 1990). Continuous changes in the abiotic conditions can lead to abrupt changes in the species composition of plants and the spatial segregation of different species (Kenkel et al. 1991). Such zonation patterns have been found in

the newly established communities on the former seabed of the Aral Sea (Wucherer and Breckle 2001; see also Chaps. 9 and 10). Although zonation patterns along gradients are a well-known pattern in different ecological systems (Siccama 1974; Emery et al. 2001) it is not understood how the complex interplay of interspecific competition, seed dispersal and spatial heterogeneous abiotic conditions causes zonation. It is hypothesized that along stress gradients the lower end of a species occurrence (stressful end) is determined by its stress tolerance, whereas its upper end of occurrence (less stressful end) is determined by interspecific competition (Ungar 1998). To address these questions we have developed a spatially explicit, rule-based simulation model. In particular, we have investigated the effect of the magnitude and the scale of the spatial variability of the environmental conditions on the structure of the plant community.

13.2 Methods of Investigation – Model Description

13.2.1 General Structure

The following model description is based on previous more detailed model descriptions (Groeneveld 2003; Groeneveld et al. 2005). The main purpose of the model is to simulate the spatiotemporal vegetation dynamics along a stress gradient following the receding sea water. The spatial extension of the simulation arena ($40\text{ m} \times 6,000\text{ m}$) was chosen to facilitate comparison with the field site Bayan transect at the northeastern coast of the Large Aral Sea. The simulation arena is a grid, whereas the size of a single grid cell is related to the space requirements of an adult individual of the tallest species ($2\text{ m} \times 2\text{ m}$). Each grid cell is described by its position along the stress gradient and its state (empty, flooded or occupied by a dominant species). There are no shared grid cells, i.e., only one species can reach maturity in a given grid cell. Because individuals of different life forms differ in their space requirements, we assume that either a cohort of annual individuals or a single individual plant is occupying a grid cell. The grid is updated every time step (year) and typically one simulation runs for 640 time steps (years). Each time step biotic processes (germination, thinning, establishment, seed dispersal and mortality) and abiotic conditions (precipitation and stress) are modelled (see Fig. 13.1). To reduce the complexity of the model and the number of parameters, we model the dynamics of plant functional types (PFTs) instead of species. Each PFT is related to one of the dominant plant species of the study area (Bayan transect) and is defined by its longevity, its typical maximum seed dispersal distance and its stress tolerance (see Table 13.1), which is more or less the overall salinity tolerance. The names of the PFTs are a combination of the life form (p for “perennial” or a for “annual”) and its stress tolerance (from 0 for no stress tolerance – nonhalophytes to pseudohalophytes – to 5 for extreme stress tolerance – euhalophytes; see Chap. 12). We have considered four annual and three perennial PFTs which are related to dominant

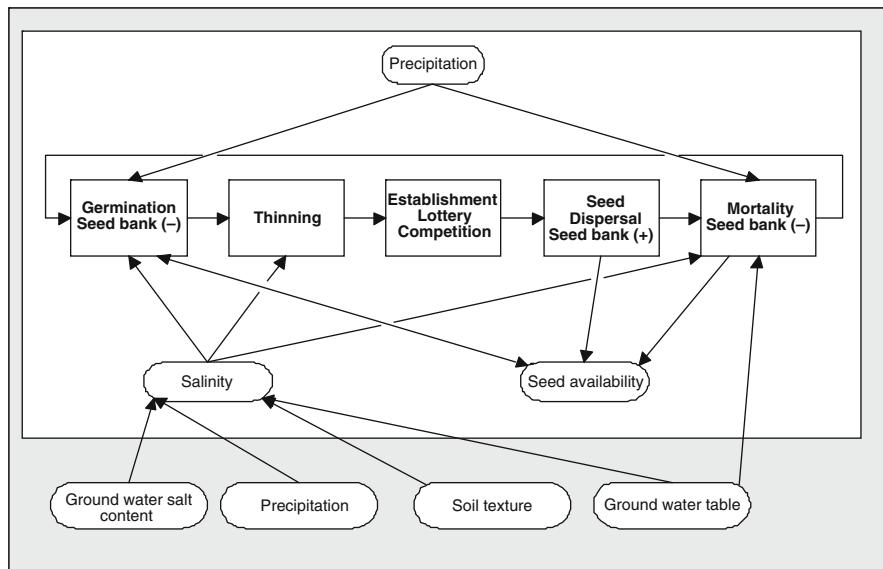


Fig. 13.1 Overview of the processes considered (*white background*). Germination, thinning, establishment, seed dispersal and mortality are simulated each year depending on precipitation, salinity and seed availability. Salinity depends on additional abiotic factors (e.g., groundwater salt content and grain size distribution in the soil – *grey background*) which are not considered explicitly in the model (Modified after Groeneweld 2003)

Table 13.1 The seven plant functional types. The functional types are named after their life form (*a* annual, *p* perennial) and their stress tolerance (5 is highest and 0 means no stress tolerance). Stress tolerance is here mainly salinity tolerance. The maximum seed dispersal distance represents the distance within which 99.9% of all seeds are dispersed

	p1	p3	p4	a2	a3	a4	a5	5
Stress tolerance σ	1	3	4	2	3	4	5	
Maximum seed dispersal distance (m)	500	500	500	1,000	1,000	1,000	1,000	
Longevity (years)	30	10	10	1	1	1	1	

species (Wucherer, unpublished data): *Petrosimonia triandra* a2, *Climacoptera aralensis* a3, *Suaeda acuminata* a4, *Salicornia europaea* a5, *Tamarix laxa* p1, *Halostachys caspica* p3, and *Halocnemum strobilaceum* p4. The stress tolerance level, which is a PFT-specific attribute, ranges from 0 to 5 (stress level where the plant species starts to suffer from stress), whereas the environmental stress conditions along the stress gradient range from 0 (no stress) to 11 (maximum stress).

13.2.2 Abiotic Conditions

We consider two abiotic factors which have an impact on the spatiotemporal vegetation dynamics. In arid areas, precipitation usually has a strong impact on

the vegetation (Lehouerou et al. 1988). Because of the lack of data, we introduce three abstract rainfall classes (good, average and bad), which occur randomly and are uncorrelated in time, with probabilities of 25%, 50% and 25%.

Furthermore, we consider stress as an abiotic component. Stress is presented in the model as an abstract stress index s , which combines the effects of salinity and inundation (0 for no stress, 11 for maximum stress).

Both stress factors increase along the transect at our study site. Inundation will be more frequent at the end of the gradient, where the elevation is at its minimum. Salt stress will also increase along the transect of receding seawater, because the salinity of the retreating seawater increases with time and the salinity of the groundwater increases with the distance from the former seashore. Furthermore, the average grain size of the soil particles decreases along the transect (Wucherer 1990). Therefore, the coarse-grained sand of the former beach will desalinize more quickly than the fine loamy soil of the new areas, because capillarity depends on grain size. In this chapter we discuss two types of spatial heterogeneous stress conditions: (1) a linear gradient ranging from no stress (0) to maximum stress (11) – see Fig. 13.2 for details; (2) no spatial correlation in the stress conditions, i.e., stress randomly fluctuates in a uniform manner around a mean of 5.5 (see Fig. 13.2).

13.2.3 Biotic Processes

The biological processes implemented are germination, seed bank dynamics, thinning, establishment, seed dispersal and mortality. For a complete model description, see Groeneveld (2003). A precipitation-dependent fraction of seeds germinate

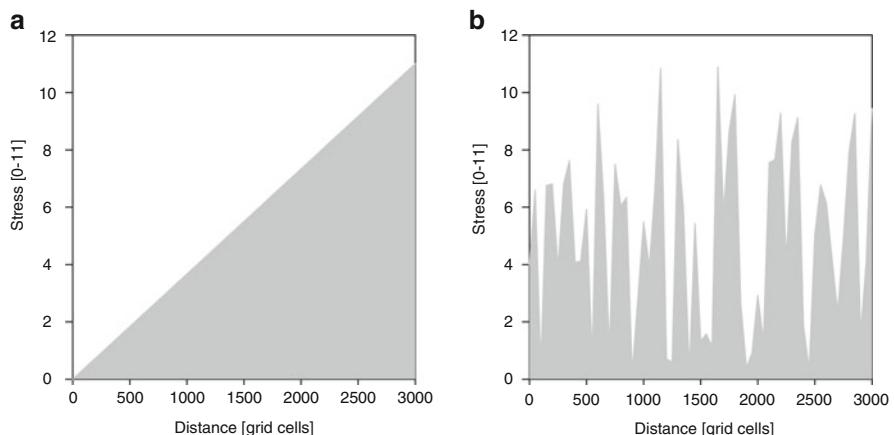


Fig. 13.2 Shapes of the stress gradients. (a) Linear stress gradient (0 for no stress, 11 for maximum stress). (b) No spatial correlation of stress along the transect

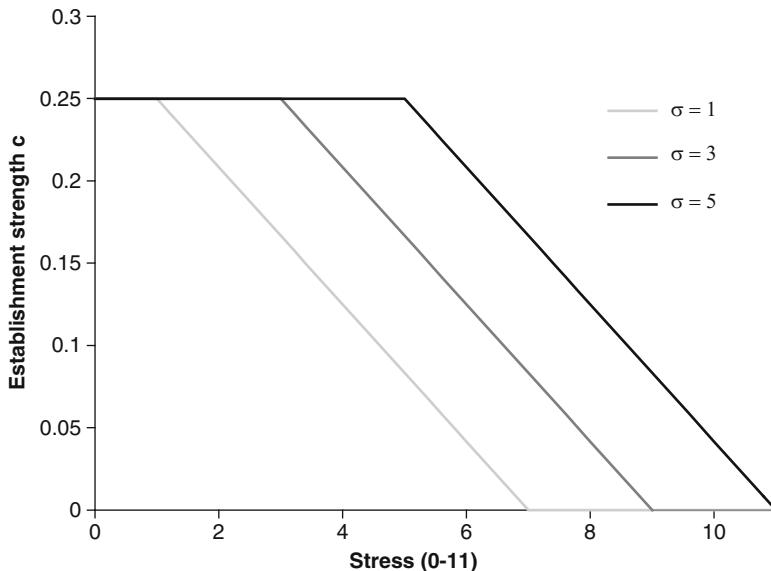


Fig. 13.3 Plant functional type (PFT)-specific reduction of the establishment strength c_i due to stress. Starting from the same seedling density, all PFTs have the same establishment strength under nonsaline conditions. As soon as stress exceeds the PFT-specific tolerance level σ , the establishment strength c_i declines linearly to zero (Modified after Groeneveld 2003)

in empty grid cells at the start of each time step (see Fig. 13.1). Intraspecific density regulation caps the local seedling densities and stress reduces the local seedling densities even further if the stress index s exceeds the PFT-specific stress tolerance level. Above the stress tolerance level, seedling densities decrease linearly until all seedlings die (Fig. 13.3). This reflects the assumption that stress-adapted species perform best in low-stress environments.

Finally, in all mixed grid cells, i.e., where more than one PFT is present, the winning PFT has to be chosen. This central establishment process is modelled by a lottery competition (*sensu* Chesson and Warner 1981), where one winner is chosen from several juvenile individuals competing for dominance in a grid cell. The local PFT-specific establishment probabilities ρ_i are given by Eq. 13.1.

$$\rho_i = \frac{c_i}{\sum_{j=1}^S c_j} \quad (13.1)$$

where ρ_i is the establishment probability of PFT i , c_i is the establishment strength of PFT i and S is the total number of PFTs.

The establishment strength of PFT i , c_i , characterizes its weight in the lottery competition and can be identified as the density of competing juveniles. Seeds, seedlings and juveniles are not modelled individually in the simulation and

therefore the competition strength c_i describes not a discrete number of individuals, but a density. The absolute values of these densities and the establishment strength c_i are less important because the establishment probability is determined by the weight of the establishment strength of PFT i relative to the establishment strength of all PFTs.

After the establishment phase, all mature perennial individuals and annual cohorts disperse seeds. There are two seed dispersal scenarios:

1. Global seed bank scenario: Each fertile individual or cohort contributes seeds to the nonspatial global seed bank. The establishment probability of a PFT is proportional to its relative abundance in this global seed bank; therefore, establishment probabilities are the same for all sites.
2. Local dispersal scenario: In this scenario all individuals or cohorts disperse their seeds following a spatial dispersal kernel. Perennial PFTs and annual PFTs have dispersal kernels described by an exponential decay distribution that is parameterized such that 99.9% of all seeds are distributed within a radius of 500 m for seeds from perennial PFTs and 1,000 m for annual PFTs. Seed banks are finally determined by the superposition of all normalized dispersal kernels.

All annual cohorts and all perennial individuals which have reached their maximum age die at the end of each time step. Juvenile perennial individuals survive with an age-, stress- and precipitation-dependent probability. Adult perennial individuals always survive until they reach their longevity (see Table 13.1). Finally, only a fraction of the seeds that have not germinated survive to the next year. An overview of all processes considered is shown in Fig. 13.1 together with their dependencies on abiotic factors.

13.3 Simulation Experiments and Results

In the first scenario, environmental stress is described by a linear gradient (see Fig. 13.2a). Seed dispersal is simulated nonspatially, i.e., each fertile plant or cohort increases the density of its PFT in the global seed bank (see Sect. 13.2 for details).

In the second scenario, a linear stress gradient is also used (see Fig. 13.2a), but seed dispersal is local (see Fig. 13.2 for details).

In the third scenario, we also used localized dispersal. However, the stress conditions are not spatially correlated. Stress is allocated at random (uniform 0–11) along the transect. Environmental conditions do not change in the direction which is rectangular to the main direction of the transect (following the receding seawater). All simulations were run for 640 time steps. Abundances of PFTs were counted along 24 subplots for the first year of average rainfall conditions after 600 years of simulation time.

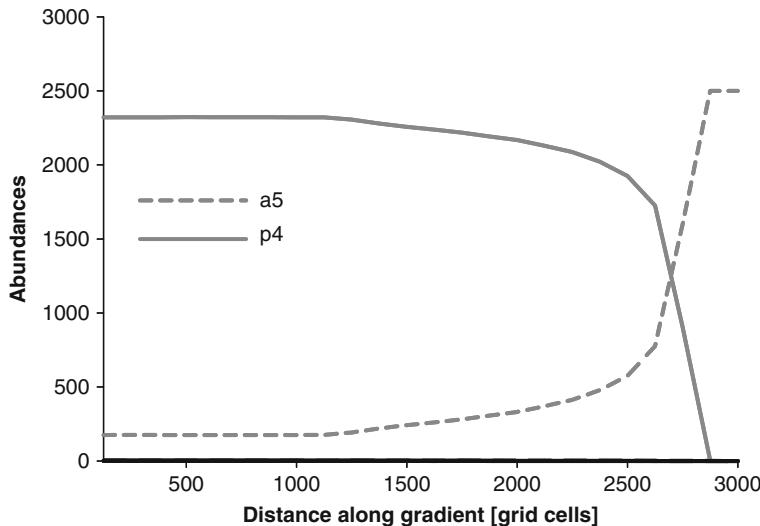


Fig. 13.4 Spatial distribution of different PFTs (a annual or p perennial and different stress tolerances: 5 is highest and 0 means no stress tolerance) after 600 years for a representative single run. For these simulations the spatially explicit dispersal process was replaced by a nonspatial global seed bank. Only two types persist for 600 years in the system and the perennial species could not outcompete the annual type at any locality (Modified after Groeneveld 2003)

13.3.1 Results for the First Scenario: Global Nonspatial Seed Bank

The spatial distribution of two dominating PFTs is shown in Fig. 13.4 for simulations after 600 years where seed dispersal was implemented as a nonspatial global seed bank. Only the best adapted PFTs of each life form, a5 and p4, persist under these conditions. Environmental stress conditions increase linearly with the distance along the gradient. The annual type a5 is present along the whole transect and cannot be outcompeted by the perennial type p4. At the stressful end of the transect, p4 cannot survive and the annual type a5 dominates.

13.3.2 Results for the Second Scenario: Local Dispersal

If seed dispersal is a spatially explicit process (Fig. 13.5a) the number of PFTs which can coexist for 600 years is doubled (four PFTs) compared with the nonspatial situation (two PFTs). Three PFTs segregate along the stress gradient (p1, p4, a5), whereas the intermediate stress-tolerant perennial type p3 can persist in the overlap zone, where p1 and p4 dominate. Compared with the nonspatial global seed

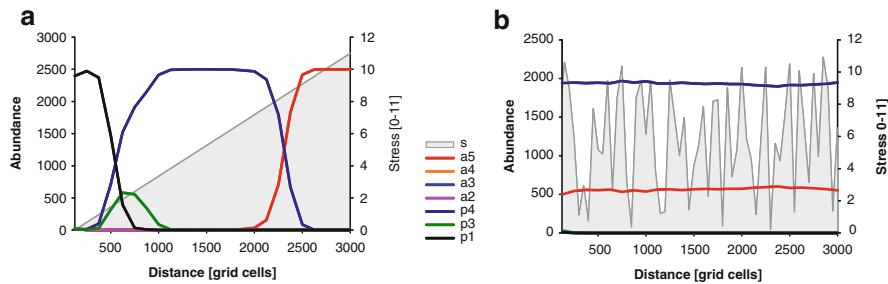


Fig. 13.5 Spatial distribution of different PFTs (*a* annual or *p* perennial and different stress tolerances: 5 is highest and 0 means no stress tolerance) after 600 years for a representative single run. (a) Spatially explicit seed dispersal and a linear stress gradient allow four PFTs to coexist. (b) No spatial correlation of stress conditions and spatially explicit seed dispersal allow only two PFTs to coexist

bank scenario (first scenario), the extremely stress tolerant annual type a5 is now restricted to the most stressful end of the gradient.

13.3.3 Results for the Third Scenario: High Spatial Variability of Stress Conditions

If the spatial stress conditions change on a smaller spatial scale (Fig. 13.2b), only two PFTs can persist (p4 and a5), whereas the perennial PFT dominates the community (Fig. 13.5b). These results are similar to those for the first scenario (nonspatial global seed dispersal and linear stress gradient), where the most-stress-tolerant perennial PFTs dominate most of the transect.

13.4 Discussion

A multi-PFT simulation model was developed to study the spatiotemporal vegetation dynamics along stress gradients. Parameterization and PFT definition were orientated towards the situation at the Aral Sea (see Chaps. 9, 10 and 12 for further details). One of the aims of the model was to study the effect of spatial processes as seed dispersal and the spatial distribution of abiotic conditions on the spatial structure and richness of the simulated plant community. Zonation as one potential spatial outcome is a common pattern along environmental gradients that has been reported for many systems (Siccama 1974; Kenkel et al. 1991), especially in marshland communities (Bertness and Hacker 1994; Emery et al. 2001; Greiner et al. 2001; see Chaps. 9 and 10 for the specific situation at the Aral Sea).

Our results show that abrupt changes in the vegetation structure (zonation) can evolve along continuous environmental gradients if the competitive abilities of PFTs differ. The zonation is facilitated by a trade-off between longevity and stress tolerance. Under low-stress conditions, the long-lived PFT p1 could outcompete all other PFTs, simply because individuals of this PFT occupy a grid cell much longer than that of the competing species and therefore had locally a higher per capita growth rate. This positive feedback results in the monodominance of this particular PFT. DeAngelis and Post (1991) also showed with a coupled partial differential equation (PDE) system that positive feedbacks can lead to the spatial segregation of species along subtle gradients. Although PDE models benefit from a compact description and sophisticated mathematical theory, PDE models of this type cannot consider stochastic processes and are hardly applicable to multispecies systems (but see Kohyama 1992). In general, equation-based models such as PDE models cannot incorporate neighbourhood interactions. In recent years substantial progress has been made to approximate neighbourhood interactions by analytical methods such as pair approximation, moment equations and coalescence methods (Dieckmann and Law 2000; Rosindell et al. 2008). Nevertheless, for some of these methods spatially explicit simulations are essential to test whether these approximations are valid and often it is not possible to include stochastic processes in these models. Equation-based models usually assume that the system will end in some sort of equilibrium, but most often ecological systems will not be in or will never reach an equilibrium. Thus, a grid-based approach seems to be more appropriate for most of the complex multispecies problems in ecology.

Spatial processes such as local competition and seed dispersal are key drivers for plant community structure and dynamics (Tilman and Kareiva 1997). We have shown here that along environmental gradients local seed dispersal resulted in zonation and therefore spatial aggregation of species, which enhanced the overall species richness. The same is true for spatially homogeneous environments, where local dispersal causes a clumped and aggregated spatial distribution of plants (Bolker and Pacala 1999). Aggregation increases intraspecific competition and reduces interspecific competition, which is a fundamental requirement for stable coexistence (Wissel 1989). Furthermore, dispersal limitation has been found to be important to explain fundamental community measures as rank abundance distributions in neutral models of biodiversity (Hubbell 1997). The spatial nature of seed dispersal is not only important on the local scale. Rare long-distance seed dispersal events are crucial for invasions, metapopulation and metacommunity dynamics (Cain et al. 2003). This highlights the importance of the consideration of spatial processes in ecological theory (Jeltsch and Moloney 2002) and casts further doubt on the applicability of so-called mean field approaches (Tilman and Kareiva 1997; Dieckmann and Law 2000).

Our study also highlights the importance of the spatial resolution of the spatial variability in abiotic conditions for species coexistence (Palmer 1992). In general, spatial variability promotes persistence and coexistence in a wide range of ecological systems (Braak and Prentice 1988). However, the spatial scale of this variability

matters. If suitable habitats are becoming too small, if spatial variability is too high, the most-stress-tolerant PFTs will dominate.

The complex nature of ecological systems requires flexible modelling tools such as grid-based, stochastic and rule-based simulation models (Wissel 2000). Advances in ecological theory, computer science and statistics enable us to analyse, calibrate and perform complex simulation models efficiently to improve our understanding of the fundamental mechanisms that structure ecological systems (Grimm et al. 2005; Elith et al. 2008).

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