The stability of vegetation boundaries and the propagation of desertification in the American Southwest: A modelling approach

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ABSTRACT

A process-based approach to spatially distributed, overland-flow modelling is employed to assess the impact of water and nutrient redistribution at the landscape scale caused by short, high-intensity rainstorm events across grassland–shrubland vegetation boundaries of a semi-arid ecosystem in the south-western United States. The modelling scenarios showed that simulated fluxes from shrubland into grassland lead to a gain of water resources but to a loss of nutrient resources in the grassland areas close to the boundary. Simulated fluxes from grasslands into shrublands do not lead to a gain of water resources, but to an increase of nutrient resources for the shrubland areas close to the boundary. On the basis of the modelling results, a new hypothesis for the on-going desertification process in the south-western United States is proposed. It is hypothesised that a vegetation boundary is stable when two conditions prevail to balance the lower resistance of grassland within the existing environmental setting with the higher resistance of shrubland: that the depletion of soil nutrients by the action of overland flow in the grassland zone close to the boundary is in balance with the replenishment rates of grassland by other nutrient cycling, and that the grassland gains enough water resources from the upslope shrublands. In contrast, a vegetation boundary potentially becomes unstable when the grassland acquires a competitive disadvantage towards shrubland regarding water benefit and nutrient depletion due to the combined effects of overland-flow dynamics and some external forces such as extensive overgrazing or climate change. The modelling results suggest that landscape linkages through the redistribution of water and soil resources across vegetation-transition zones at the landscape scale and feedback dynamics of overland-flow processes play a significant role in the persistence of land degradation in the US Southwest.

1. Introduction

Desertification and land degradation in the south-western part of the United States have led to a significant vegeta-tion change from grassland to shrubland within the past 150 years (Buffington and Herbel, 1965). The degradation process continues even when external environmental stresses, such as heavy overgrazing, are removed (Whitford, 2002; Rango

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et al., 2002; Laycock, 1991); a fact which suggests that the ecosystem stability has been disturbed profoundly. The persistence and on-going propagation of desert shrubs has been related by Schlesinger et al. (1990) to the redistribution of water and nutrient resources at the plant–interspace scale. There is some suggestion in the results of Schlesinger et al. that redistribution at this scale leads to further redistributions at landscape scale (>5 km²), and this idea is reinforced by feedbacks observed in the transfer of water and sediment and the consequent reorganization of the land surface as observed by Abrahams et al. (1995), Parsons et al. (1996) and Wainwright et al. (2000). More recently, Peters and Havstad (2006) have outlined the need to use a multi-scale approach to understand the drivers of land degradation in these areas, taking into consideration variations at patch-mosaic and vegetation association scales as well as the plant interspace.

It is hypothesised in this paper that boundaries between different vegetation associations are likely to be foci for progressive change. In particular, the role of runoff across vegetation boundaries between shrubland and grassland in these degradation processes may be crucial in explaining the on-going degradation as significant amounts of overland flow are generated by high-intensity rainstorm events that frequently occur during the summer monsoon months in that region. Currently, only very limited quantitative information on this redistribution at the landscape scale is available as the spatial measurements of water and nutrient fluxes is problematic with increasing spatial extent. Parsons et al. (in press), for example, investigated the change of nutrient content of inter-rill runoff fluxes across shrubland and grassland boundaries in the Jornada Basin, Chihuahuan Desert. They argued that measurements from small runoff plots cannot be simply up-scaled to obtain estimates of landscape-scale nutrient fluxes. Thus, field plot measurements would only be able to give a very limited picture on the fluxes and are often not able to provide information on the spatial distributions of fluxes at the landscape scale, for example across vegetation boundaries, which might prove important for the explanation of land degradation processes.

To enable the investigation of spatial water and nutrient resource redistribution at the landscape scale, this research employed a previously tested, spatially distributed numerical modelling approach by Mueller et al. (in press) as an estimation approach for the assessment of ecosystem stability along vegetation boundaries between grasslands and shrublands. Once the water and nutrient fluxes are quantified through scenario calculations, the competitive advantage of shrubland towards grassland can be assessed and the stability and resilience of the ecosystem towards external factors such as overgrazing and climate change can be discussed.

1.1. Study area

The modelling studies concentrated on the computation of water and nutrient fluxes *between* vegetation associations across dominant vegetation boundaries between grassland and shrubland and *vice versa* in the Jornada Basin. The Jornada Basin (32°31′N, 106°47′W) is situated ca. 40 km NNE of Las Cruces, New Mexico, USA. The location experiences a semi-arid to arid climate with a mean annual precipitation

of 245 mm and a mean annual potential evapotranspiration of 2204 mm. The majority (65%) of the precipitation falls as intense, short-duration, convective summer storms (Wainwright, 2005). Dominant shrubland associations of the region are creosotebush (*Larrea tridentate*), honey mesquite (*Prosopis glandulosa*) and tarbush (*Flourensia cernua*). The soils in the Jornada Basin consist mostly of Aridisols such as Haplargids, and Entisols such as Toripsamments. Jornada soils are highly interactive with the vegetation through plant–soil feedback processes (Buffington and Herbel, 1965; Bulloch and Neher, 1980).

Black grama grasslands occur typically on upland slopes and in the central plain of the basin with grass swards being degraded to various degrees. Creosotebush vegetation occurs within the lower and upper piedmont slopes of the basin. Tarbush vegetation is found within the lower piedmont slope and the alluvial plain. Mesquite shrubs exist predominantly in the eastern and central part of the Jornada Basin. Fig. 1 shows a vegetation map with the extent of the four vegetation types for the Jornada Experimental Range for the year 1998 (map data provided by the Jornada Experimental Range Agricultural Research Service, US Department of Agriculture, Las Cruces, New Mexico).

For the model scenarios of fluxes between vegetation associations, representative locations of currently existing vegetation boundaries from the vegetation map were selected for the model studies where overland flow occurred between relatively non-degraded, undisturbed black grama grassland and the three shrub types (and *vice versa*), and between creosotebush and mesquite and between creosotebush and tarbush within the Jornada Basin (Fig. 1). The other shrub combinations did not occur extensively in the Jornada Basin and were therefore not considered. The contributing area for each boundary scenario was chosen to extend over a distance of approximately 2 km upslope of the vegetation boundary, which was assumed to be large enough to avoid any edge effects. This perimeter was furthermore justified by the fact that high-intensity rainstorm events generally occur with a limited spatial coverage (Wainwright, 2005), and therefore the total area where significant amounts of overland flow is generated is assumed to be small. The exact locations of vegetation-boundary lines were identified by overlaying the vegetation-cover map from 1998 with high-resolution aerial photography provided by the Jornada Experimental Range Agricultural Research Service, US Department of Agriculture, Las Cruces, New Mexico.

1.2. Methods

1.2.1. Description of the modelling approach
Process-based, spatially distributed models were employed for the calculation of overland flow and dissolved nutrients in runoff generated by high-intensity rainstorm events. The hydrological model is based on a kinematic wave approximation to the St. Venant Equations for the routing of overland flow, Hortonian infiltration and Darcy-Weisbach flow equation as described by Scoging et al. (1992), Parsons et al. (1997) and Wainwright and Parsons (2002). The nutrient-transport is modelled by an advection–dispersion model as used by Havis et al. (1992) and Walton et al. (2000) and simulates the fluxes
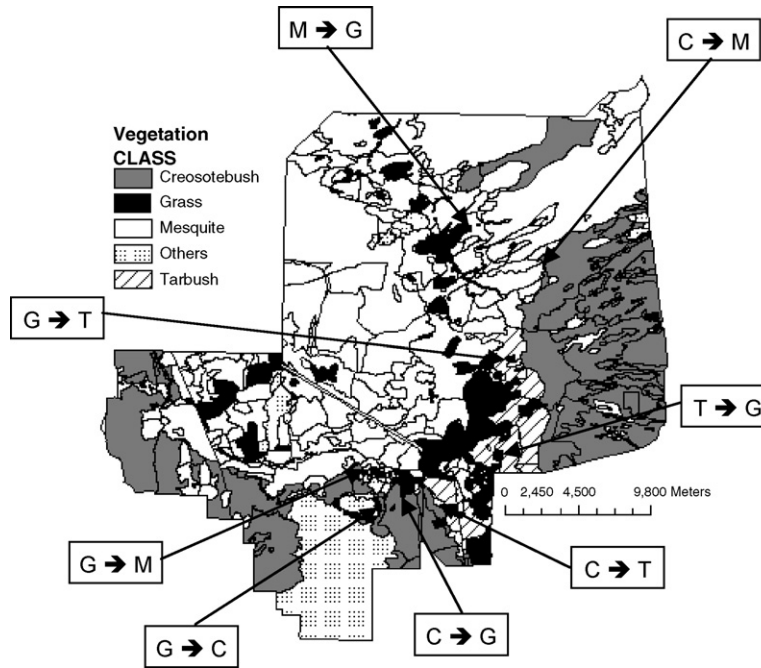
Fig. 1 – Location of vegetation-boundary scenarios within the Jornada Basin (map data provided by the Jornada Experimental Range Agricultural Research Service, US Department of Agriculture, Las Cruces, New Mexico).

of dissolved ammonium, nitrate and phosphorus in overland flow. These three nutrients were chosen for this investigation because they are the most crucial to primary production of the region as their reduced availability results in a limited plant-productivity (e.g. Whitford, 2002).

The model was run with a rectangular model cell size of $10\,\text{m} \times 10\,\text{m}$ and a time resolution of 1 s. The term flux is used in the following to denote the volume of water or the mass of nutrients per single rainstorm event. This modelling study uses a single scenario-based approach where we evaluated how single rainstorm events affects water and nutrient fluxes across shrubland–grassland boundaries. Although inter-storm dynamics and interactions of soil and vegetation along boundaries over longer time periods such as years and decades are obviously important, and briefly discussed, these long-term dynamics are beyond the scope of this modelling study.

The principal model parameters required are the saturated hydraulic conductivity (K_{sat}) and the friction factor (ff) for the hydrological model, and the mass-transfer coefficient (K) and the nutrient concentration C_s in the soil-solution zone for the nutrient-transport model. These parameters were varied as a function of vegetation type and vegetation cover. The parameterisation approach and data of Mueller (2004) and Mueller et al. (in press) were used, based on extensive field studies to derive adequate input parameters for the model. Table 1 summarises the parameter values, which in all cases except for the C_s parameter are distributed differently for both bare and vegetated surface covers. According to the scaling scheme as derived by Mueller (2004), a model cell is assumed to behave as a vegetated cell with field parameters derived from vegetated surface covers if a critical vegetation-cover threshold of 43% for mesquite, 35% for creosotebush and 48% for tarbush is exceeded, and like a bare cell oth-

erwise. The parameter scaling concept via vegetation-cover thresholds was tested by comparison to observed hydrographs from four instrumented shrubland catchments with an area of ca. $0.15\,\text{km}^2$ within the Jornada Basin and proved appropriate for the incorporation of statistically significant differences of parameters as a function of vegetation cover. No testing data were available for grassland catchments due to the problem of identifying well-defined grassland catchments within the Jornada Basin. Therefore, the assessment of fluxes from or into grassland areas concentrates on uniformly vegetated grassland areas. The potential limitations of this simplification on the understanding of grassland–shrubland transitions are discussed below. The required vegetation cover was derived from high-resolution aerial photography (Mueller, 2004).

1.2.2. Method for the spatial interpretation of modelling results across vegetation boundaries

For the vegetation-boundary scenario, the total water and nutrient fluxes were assessed for a distance of approximately 150 m upslope and downslope of the vegetation boundary. This distance proved large enough to evaluate the intrinsic changes of fluxes associated with the change of vegetation associations and small enough to prevent the influence of the local topography and the associated merging of larger rills from becoming prevalent. The total fluxes along straight contour-parallel strips above and below the vegetation boundary were evaluated with an average strip length of around 150 m and a strip interval of 20–30 m.

Fig. 2 exemplifies the methodology employed for the spatial derivation of the fluxes at the vegetation boundary between tarbush (upslope) and black grama grassland (downslope). Fig. 2a displays an aerial photograph of the tarbush and grass-

Table 1 – Input parameters for the hydrological and nutrient-transport model (Mueller, 2004; Mueller et al., in press)

		Black grama grass	Mesquite	Creosote	Tarbush
K_{sat}: saturated hydraulic conductivity, ff: friction factor					
K_{sat} (mm/h)	Bare	–	30	11	15
	Vegetated	106	153	33	40
ff (–)	Bare	–	1	1	1
	Vegetated	114	20	20	20
		Black grama grass	Mesquite	Creosote	Tarbush
C_s: nutrient concentration in the soil solution zone					
C_s, ammonium (mg/l)		92 ± 61	31 ± 28	60 ± 35	51 ± 17
C_s, nitrate (mg/l)		44 ± 37	10 ± 12	12 ± 12	10 ± 8
C_s, phosphorus (mg/l)		148 ± 57	36 ± 28	120 ± 30	15 ± 6
		Vegetated (mm/s)			Bare (mm/s)
K: mass-transfer coefficient					
$K_{Ammonium}$		4×10^{-4}			3×10^{-5}
$K_{Nitrate}$		5×10^{-4}			7×10^{-5}
$K_{Phosphorus}$		2×10^{-4}			4×10^{-5}

land sites and their vegetation boundary. The square marks the boundary area where the fluxes were assessed. Fig. 2b shows an enlargement of this area containing a 10-m resolution map with the simulated total water fluxes, the vegetation boundary and 15 strips covering the area above and below the boundary.

The fluxes are calculated as the sum of modelled total water and nutrient discharge along each individual red strip, starting 140 m upslope of the vegetation boundary, in 20-m intervals, as far as 140 m downslope of the boundary. For this purpose, the spatial model output on water and nutrient fluxes were imported into the ENVI geographical information system, and the required information were extracted by defining regions of interest along each of the 15 strips. The sum of the fluxes rather than the average or maximal flux values along each strip was selected for the analysis, because both the mean and the maximal values produce a distortion of the relative change if two rills merge just above or below a strip, for example. The sum of the fluxes for each strip was then scaled

by dividing by the length of the strips to obtain an effective, average flux value in m^3 flux per metre vegetation boundary (i.e. given as a unit flux across the boundary). For the assessment of the percentage change of fluxes across the boundary, the scaled flux values are then divided by the flux value of the most upslope strip. The presentation of the percentage relative flux changes across the boundary is advantageous in the sense that it allows the fluxes of different boundary scenarios to be compared directly. In contrast, a quantitative comparison of the total fluxes per metre is only possible to a limited extent due to the different sizes of contributing areas and topographic variations between the locations of the boundary scenarios.

For the study of water and nutrient fluxes between vegetation associations, the subsequent results are presented for a rainstorm scenario with a storm duration of 5 min and a rainfall intensity of 109.7 mm/h. This event has a return interval of 10 years, as derived from the intensity–duration–frequency statistics by Wainwright (2005). This rainstorm event was

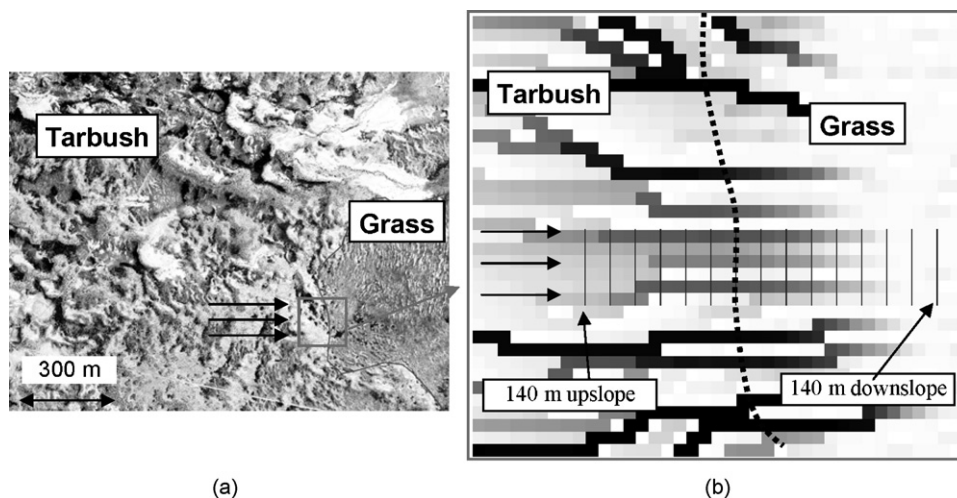(a)   (b)

Fig. 2 – (a) and (b) Methodology for the flux calculations at the vegetation boundary exemplarily between tarbush (upslope) and grassland (downslope).

selected for illustration because it represents a moderately frequent, high-intensity event that proved to generate substantial water and nutrient fluxes within the various vegetation associations.

1.3. Results and interpretation

Fig. 3 displays the plots for the percentage change of water fluxes across the eight vegetation boundaries: the plots in the left column display the scenarios for fluxes from the shrublands (creosote, mesquite, tarbush) into grasslands, the right one the scenarios for the fluxes from grasslands into shrublands. The lowest row depicts the creosote–tarbush and the creosote–mesquite scenarios.

For the transitions from the three shrub associations into the grasslands, the water fluxes remain constant or decrease slightly upslope of the vegetation boundary and decrease substantially below the boundary to between 11% and 49% over a distance of ca. 300 m (left column in Fig. 3). The flux reduction is more pronounced for the mesquite and tarbush than for the creosotebush scenarios. The decrease of water fluxes across the vegetation boundaries implies that significant amounts of the water resources that are generated within the upslope shrubland areas are infiltrated and therefore retained by the grasslands. The modelling results imply that the grasslands downslope of shrublands are gaining water resources and thus are able to store and utilise the water within their root systems.

The water fluxes from the grassland into the three shrublands remain constant or increase slightly upslope of the boundary. Below the boundary, the fluxes increase substantially by 150–621% over a distance of ca. 300 m (right column in Fig. 3). In contrast to the opposite configuration, the water that was generated in the upslope grassland is not retained by the shrublands. On the contrary, even more runoff is produced within the shrublands and transferred to further downslope areas.

The water fluxes between the creosotebush and the tarbush and mesquite associations remain approximately constant (lowest row in Fig. 3).

Fig. 4 displays the plots for the percentage change of total ammonium, nitrate and phosphorus mass fluxes across the various vegetation boundaries. The change of nutrient fluxes across the grass and shrubland boundaries shows qualitatively the opposite behaviour of the water fluxes: nutrient fluxes increase from the three shrub associations into the grasslands, and decrease when moving from the grass into the shrub associations.

For the fluxes from the shrublands into the grasslands, the nutrient fluxes remain more or less constant upslope of the vegetation boundary, increase substantially and then level off downslope of the boundary (left column in Fig. 4). Nutrient fluxes increase by 200–1000% for ammonium, by 380–1200% for nitrate and by 110–2000% for phosphorus masses over a distance of ca. 300 m. In contrast to the water fluxes from shrubland into grassland, the grasslands just downslope of the boundaries do not retain the nutrients. Quite the opposite, due to the large water fluxes that were generated upslope of the boundary in the shrubland areas, a significant amount of nutrients are washed out of the nutrient-high grassland areas

close to the vegetation boundary, according to the modelling results (right column in Fig. 4). This finding has important implications with regard to the ecological balance between shrublands and grasslands at the vegetation boundary.

The increased amounts of nutrients that are washed out of the grassland could potentially lead to a depletion of nutrient resources for grassland areas close to the vegetation boundary and therefore to a competitive disadvantage of grassland towards the more resistant shrublands. The modelling study only evaluates processes that occur during one single rainstorm event, and does not consider processes associated with long-term nutrient cycling. While grassland loses nutrients by the runoff processes described, at the same time it gains nutrients by atmospheric dry and wet fall and by decomposition of organic litter. Schlesinger et al. (2000) studied the nutrient losses in runoff from grassland and shrubland associations on field plots in the Jornada Basin. They reported that nitrogen losses in runoff are lower than the inputs by atmospheric deposition, i.e. the grassland experiences net gain rather than a net loss of nitrogen. Thus, if the grassland close to the boundary is able to replenish its nutrient resources in the soil at the same rate as it loses nutrients by the action of overland-flow events, then the grassland ecosystem at the transition zone does not acquire a competitive disadvantage in regard to nutrient budgeting. However, in the opposite case, i.e. if the grassland exhibits greater losses of nutrients through the action of overland flow than it gains by nutrient cycling, then over time the soil in the grassland close to the boundary becomes depleted of vital nutrients. The subsequent decrease of soil nutrients in the grassland might potentially lead to the degradation or even deletion of grassland within the boundary zone. As shrubs are more resistant towards nutrient limitations for primary production than grassland (Whitford, 2002), they acquire a competitive advantage over grassland at the boundary zone, i.e. in this case, the transition zone becomes unstable in regard to nutrient budgeting. The implications of these scenarios on degradation processes in the form of shrub invasion into grassland are discussed in detail below.

In Fig. 4, showing the nutrient fluxes from the grasslands into the shrublands, the decrease of fluxes is not as pronounced as was the above-described increase in the opposite cases: varying by 35–75% for ammonium, by 35–59% for nitrate and by 30–91% for phosphorus over a distance of ca. 300 m. The reduction of nutrient fluxes denotes that the shrublands in the vicinity of the vegetation boundary retain the nutrients that were washed out of the grasslands upslope. In other words, the shrublands gain nutrients due to the infiltration of nutrient-enriched overland flow generated in the grasslands. However, the shrublands do not gain a large amount of nutrients in absolute terms, as both the water and nutrient fluxes generated from the grasslands are relatively small.

For the creosotebush to tarbush transition, the fluxes of ammonium and nitrate increase by 152%, whereas the flux of phosphorus decreases by 26% over a distance of ca. 300 m (lowest row in Fig. 4). As with the shrubland–grassland scenarios, the modelling results suggest that ammonium and nitrate resources are not retained within the tarbush association, but that a significant amount of them are washed out of the soil close to the boundary. No information is currently available on the replenishment rates of nutrients in tarbush vegetation
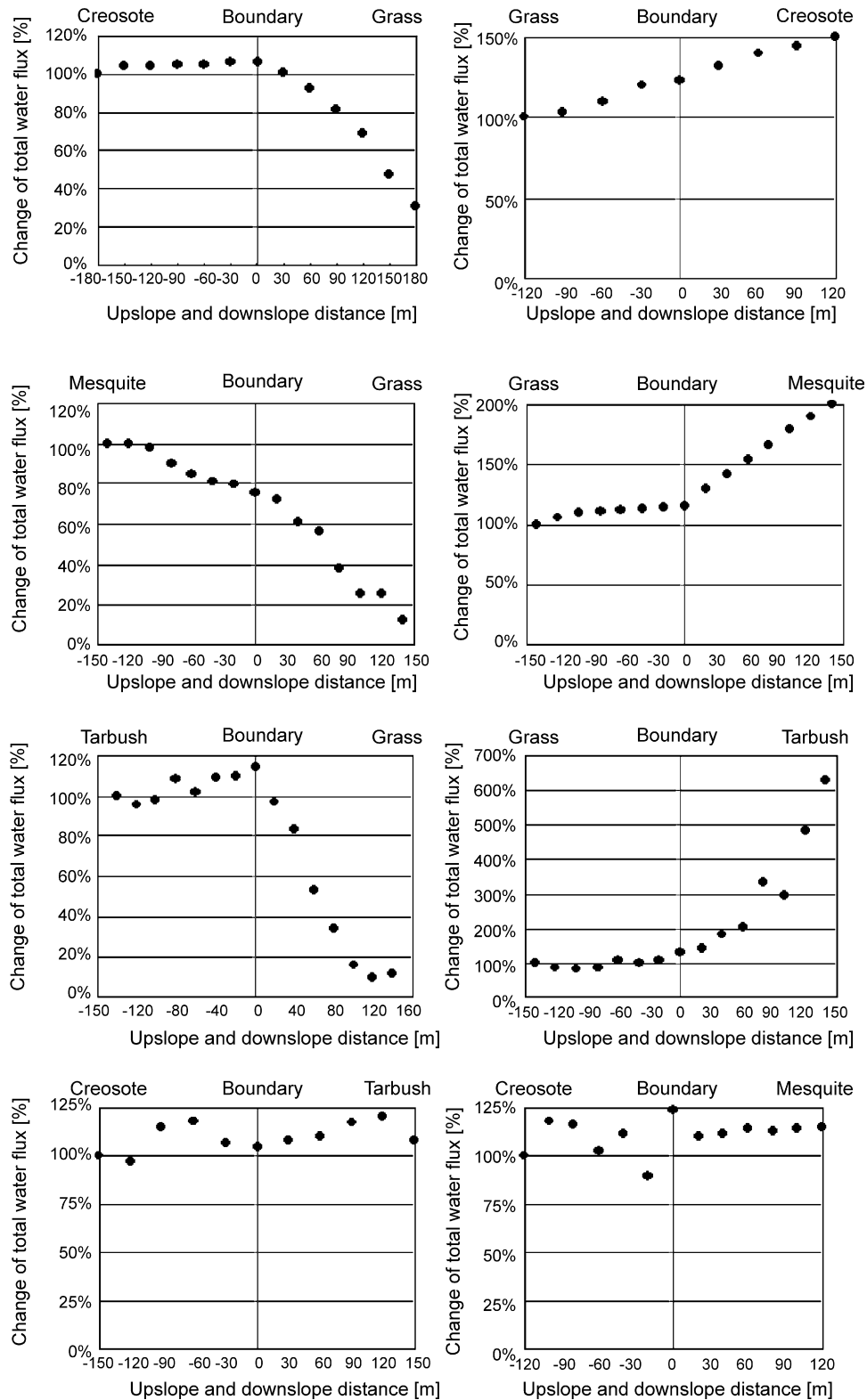
Fig. 3 – Simulated water fluxes across vegetation boundaries.

and it is therefore not possible to evaluate the net gain or loss rate of nutrients both as a function of runoff losses and gains through atmospheric dry and wet fall and litter decomposition. For the creosotebush to mesquite transition, the fluxes of all three nutrients remain essentially constant (lowest row in Fig. 4).

Combining the behaviour of both water and nutrient fluxes across the boundaries, the following rule statements can be

Fig. 4 – Simulated nutrient fluxes across vegetation boundaries (*, ammonium; ▲, nitrate; ×, phosphorus).

derived from the modelling results: modelled fluxes from shrubland into grassland lead to a gain of water resources but to a loss of nutrient resources in the grassland areas close to the boundary. In contrast, the fluxes in the opposite case, i.e. from grasslands into shrublands, do not lead to a gain of water resources, but to an increase of nutrient resources for the shrubland areas close to th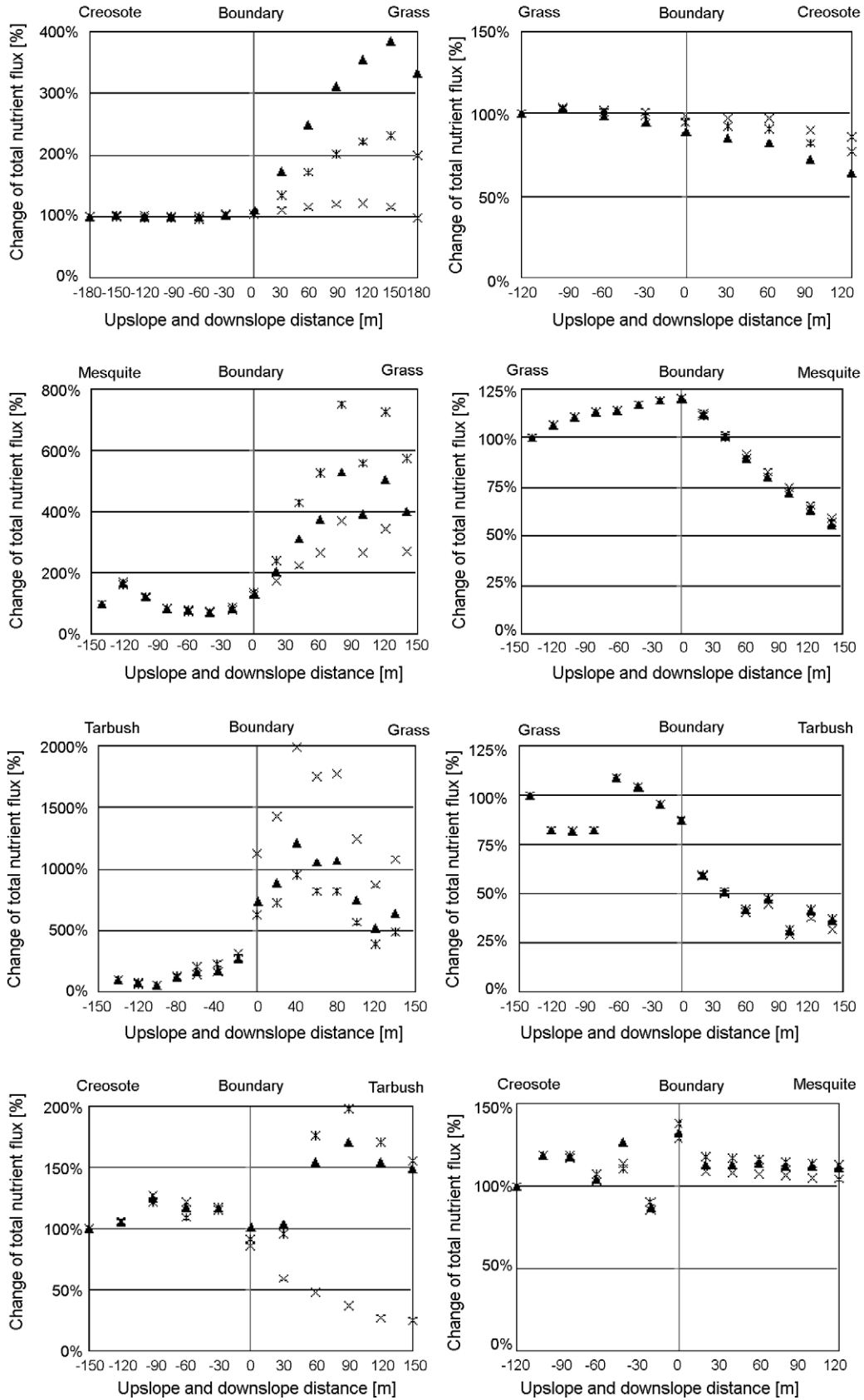e boundary. In the case of shrubland–shrubland boundaries, there seems to be little influence of the boundary on water and nutrient fluxes (Figs. 3 and 4), so that in these cases there seems to be little sensitivity to the role of the boundary. Within the stated limitations and assumptions of the modelling approach, the insights on the qualitative behaviour of flux dynamics across vegetation boundaries that were gained from this modelling study can now be used to discuss and interpret the role of overland flow on the stability of vegetation boundaries between grasslands and shrublands in the Jornada Basin.

1.4.   Discussion and conclusion

Table 2 summarises the flux changes qualitatively in terms of the increase or the reduction of water and nutrient fluxes across the eight vegetation-boundary scenarios. The modelling results suggest that the generation of overland flow by high-intensity rainstorm events plays a fundamental role in the redistribution of water and soil resources across vegetation boundaries and consequently across the landscape.

The stability of vegetation boundaries could now be discussed with reference to the current concepts of rangeland stability and resilience that has been applied to on-going desertification processes. Laycock (1991), for example, introduced the concept of stability and thresholds of environmental change to rangeland research. Laycock stated that if stability is resistance to change imposed by external forces, then a system is stable, if it returns to the original steady-state after being disturbed or deflected. In contrast, an unstable state does not return to the original level after disturbance but rather crosses a threshold and continues to be deflected toward some new state. Closely linked to the concept of ecosystem stability is the term resilience, which refers to the ability of an ecosystem to remain in its current state (resist change) and return to this state (recover) if disturbed (e.g. Ludwig et al., 2001).

In this context, the vegetation boundary between shrubland and grassland may be defined as stable if it remains at the same position independently of any external stresses, and unstable, if some properties of the system are altered in such

a way that the vegetation boundary shifts downslope, i.e. if shrubs invade and replace the grassland downslope of the former boundary line. The latter case essentially describes the vegetation scenario of the Jornada Basin, where productive grassland was replaced by shrubland within the past 150 years (Buffington and Herbel, 1965). For a stable vegetation boundary between grassland and shrubland, the above-described nutrient depletion by overland flow in the grassland zone close the boundary is in balance with the replenishment rates by nutrient cycling of grass. At the same time, the grassland at the boundary zone gains water resources from upslope shrublands. Both effects balance the lower resistance of the grassland to the existing environmental conditions with the higher resistance of shrublands. In this equilibrium case, no species exhibits a smaller or greater competitive advantage and the ecosystem can be thought of as being stable. This pattern is essentially the stable-state scenario of grassland and shrubland species that is thought to have been predominant in the Jornada Basin before the first signs of vegetation change were reported at the end of the 19th century (Buffington and Herbel, 1965). The boundary scenario becomes unstable when the grassland acquires a competitive disadvantage towards the shrubland. With regard to the role of overland flow, the disadvantage for grassland may be characterised either by its decreased ability to replenish its nutrient sources causing an increased net loss of nutrient resources or by its decreased ability to gain and store water resources generated within the upslope shrublands. Both factors may lead to the degradation of grassland and to a subsequent invasion of the more resistant shrubs at the boundary zone, i.e. the vegetation boundary becomes unstable. The two factors may occur if the grassland properties with regard to nutrient budgeting and water storage are altered by some environmental stresses.

Possible external factors and triggers that are thought to have led to the invasion of shrubs into formerly non-degraded grassland are overgrazing and other related effects of cattle, climatic variations, effects of natural fire suppression and actions of rodents and jackrabbits, as comprehensively discussed in Whitford (2002), Hastings and Turner, 1965; Conley et al., 1992; Drewa and Havstad, 2001; Valone and Thornhill, 2001). The first two factors, overgrazing and climatic variations, can be related to the derived stability concept of vegetation boundaries as a function of the overland-flow mechanism and the resulting redistribution of water and soil resources. The following paragraphs review hypothetical scenarios where these factors might have changed the properties of grassland so that it acquires a competitive disadvantage

Table 2 – Comparison of relative changes of water and nutrient fluxes between different vegetation associations at vegetation boundaries

	Water	Ammonium	Nitrate	Phosphorus
Creosote → grass	Decrease	Increase	Increase	Increase
Mesquite → grass	Decrease	Increase	Increase	Increase
Tarbush → grass	Decrease	Increase	Increase	Increase
Grass → creosote	Increase	Decrease	Decrease	Decrease
Grass → mesquite	Increase	Decrease	Decrease	Decrease
Grass → tarbush	Increase	Decrease	Decrease	Decrease
Creosote → tarbush	No change	Increase	Increase	Decrease
Creosote → mesquite	No change	No change	No change	No change

towards shrublands in regard to the above-described modelled flux dynamics across vegetation boundaries.

Overgrazing and the resulting spatially extensive reduction of vegetation cover fundamentally alter the hydrological properties and the related transport processes of the grassland. Severe overgrazing results in the development of bare, possibly interconnected patches within the grasslands. A reduction of the grass cover is accompanied by a decrease in surface roughness. Trampling by livestock leads to the compaction of the soil resulting in decreased infiltration capacities (Hastings and Turner, 1965). Both the decrease of roughness and of the infiltration capacities result in a substantial increase of overland-flow velocities and in runoff production (Whitford, 2002; Rietkerk et al., 1997). The qualitative changes of water and nutrient fluxes across vegetation boundaries as derived for non-degraded grassland in the modelling studies above can now be projected to the possible flux behaviour at vegetation boundaries between shrublands and degraded grasslands. The more the vegetation cover of the grassland is degraded, the more water that was generated in the scenarios with upslope shrublands is transported through interconnected bare patches within the grassland further downslope. This dynamics results in a reduced retention of water resources for degraded grassland in comparison to non-degraded grassland close to the vegetation boundary, in other words, a lower capacity of the grassland to gain and utilise the inflowing water fluxes in their root system. Due to the increased water flows within the grassland close to the boundary, the disturbed grassland would lose even more nutrient resources than the non-degraded grassland.

At the same time, the replenishment rate of nutrients by litter decomposition is decreased due to the lower areal extent of vegetation cover. This scenario suggests that the grassland in the direct vicinity of vegetation boundaries becomes increasingly degraded by depletion of nutrients and deficiency of water resources, and therefore acquires a competitive disadvantage towards shrubs. As shrubs are more resistant to their physical environment, they increasingly invade the degraded grasslands which would consequently lead to a shifting of the vegetation boundary progressively downslope. In the context of stability, the vegetation boundary becomes unstable and continues to shift downslope until a new stable state is reached where the shrubland replaces the grassland entirely.

Another external factor that could have caused an imbalance at the boundary between shrubland and grassland associations is climatic variation, either in the form of excessive droughts or in the form of an increase in high-intensity rainstorm events. Several severe droughts were reported to haven taken place within the last 100 years during the summer season, winter season or both together in the years 1908–1913, 1934–35, 1951–1956, 1963–1965, 1971 and 1976 (Wainwright, 2005). The droughts might have led to a spatially extensive degradation of the grassland due to the decreased decomposition rates of organic litter to replenish nutrient resources in the soil and due to limited water availability (Whitford et al., 1995). In the event of a large rainstorm after the drought, the grassland might be too degraded to replenish nutrient resources that were washed away with the overland flow quickly enough. Due to the resulting net losses of soil nutrients, the grass-

land acquires a competitive disadvantage towards shrubland in the boundary zones, which displaces the ecosystem stability. The gradual shifting of the vegetation boundary over the last 150 years could then be related to the frequent reoccurrence of droughts approximately every one to two decades that prevented the grassland to recover from the combined degradation effects of drought and of depletion of soil by the action of overland flow.

At this point, it is not possible to quantify the degree of resilience of the grassland to the effects of overgrazing or climatic variations. However, the qualitative insights into the redistribution of water and nutrient resources across vegetation boundaries at the landscape scale, as derived from the modelling studies, enable an enhanced understanding of degradation mechanism in regard to overland-flow processes. The previous discussion stresses the potential importance of landscape linkages, i.e. the water and soil resource flux dynamics and their redistribution at the landscape scale, on the vegetation-change processes. A similar finding was made by van de Koppel and Rietkerk (2004) who stressed the importance of large-scale mechanisms on feedback mechanism at the smaller scale in regard to irreversible and continuing vegetation shifts within semi-arid grasslands. Previous studies and conceptual models of desertification processes have concentrated on the plant–interplant scale. However, field measurements and process understanding derived from field plots did not enable a linear extrapolation of this information to explain patterns and dynamics at the landscape scale (Peters and Havstad, 2006). This is illustrated by the fact that remediation measures failed and shrub invasion continued even when the environmental stress was removed from the grassland, as was shown, e.g. by Rango et al. (2002), Whitford (2002) and Hennessy et al. (1983).

The following positive feedback mechanisms at three spatial scales can now be identified in regard to overland-flow dynamics for a semi-arid environment such as the Jornada Basin. First, at the plant–interplant scale, the invasion by shrubs results in a concentration of water and soil resources beneath individual shrubs, resulting in a positive feedback to shrub persistence and fewer resources available to grass species, i.e. the development of the 'island of fertility' concept after Schlesinger et al. (1990).

Second, at the landscape scale, due external environmental stress, vegetation boundaries between shrublands and grasslands become unstable which results in the shifting of the boundary downslope while the shrubs invade and eventually replace the grassland within the former boundary zone. The following positive feedback mechanism is created at the landscape scale: the shift of the boundary results in an increase of the areal extent of shrublands, which consequently leads to the production of larger runoff amounts within the shrublands just above the new vegetation boundary. The larger the runoff production, the larger is the depletion of nutrients in the grassland close to the boundary, and the larger the degradation of grassland and subsequent invasion of shrubs which again increases the areal extent of shrublands.

Third, at the regional scale, biogeophysical feedback mechanisms may occur between the atmosphere and the vegetation that can result in an increased albedo due to the reduction of vegetation cover, followed by a decreased

net radiation and surface cooling, the subsidence of upper atmosphere air masses, reduced convection and cloud formation and consequently a reduction of rainfall (Charney, 1975). Reduced rainfall rates would then lead to a continuing degradation of grassland due to its lower resistance against drought conditions.

In conclusion, for a complete system understanding of desertification processes, feedback mechanisms at the local, at the landscape, and at the regional scale as well as the interaction between vegetation and soil dynamics have to be assessed. This modelling study uses a scenario-based approach to determine landscape stability along vegetation boundaries in regard to water and nutrient fluxes for single rainstorm events and does not consider inter-storm dynamics and long-term interactions of soil and vegetation characteristics over larger temporal scales such as years or decades. However, the modelling results suggest that those dynamics are potentially crucial to explain the on-going propagation of desertification. The notion of stable and unstable vegetation boundaries as a function of water and nutrient gain or loss provides now a working hypothesis for future fieldwork and modelling efforts along vegetation boundaries that should implicitly consider vegetation and soil nutrient dynamics and inter-storm processes and combine them with the horizontal movement of water and nutrient resources across the landscape.

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