



Using resistance and resilience measurements for 'fitness' tests in ecosystem health

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*The resistance and resilience of perennial grasses and a small shrub to a natural disturbance (drought) were measured on stress gradients that were produced by domestic livestock in desert grassland ecosystems in the northern Chihuahuan Desert of New Mexico, USA. Both survivorship of grasses and a sub-shrub (*Gutierrezia sarothrae*) during a drought (a measure of resistance) and re-establishment of plant cover following a drought (a measure of resilience) were reduced in the intensely stressed ecosystems in comparison to the lightly stressed ecosystems. The compromise of the resistance and resilience characteristics of an ecosystem can be used as a 'fitness' test for the health of ecosystems. Fitness tests can provide early warning of ecosystem degeneration and allow intervention to reduce or eliminate anthropogenic stress on the ecosystems.*

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Introduction

The need to maintain the health and integrity of the world's ecosystems was one of the major conclusions of the Earth Summit (Rio Declaration on Environment and Development, 1992). However, in order to address that need, we must develop methods for assessing ecosystem health at the regional level. A healthy ecosystem may be characterised as free of 'ecosystem distress syndrome' (a set of signs such as reduced species diversity or alteration in values of critical physical environment parameters), self-sustaining and providing a full range of services such as water storage and harvestable productivity, and management options (Rapport, 1995). Critical to this definition is the capacity to rebound from disturbance (Stebbing, 1981; Kay, 1991; Costanza, 1995; Rapport and Regier, 1995). Approaches to assessing ecosystem health that focus on signs of ecosystem dysfunction generally provide an 'after the fact' confirmation of ecosystem breakdown but rarely provide

early warning of impending risk for degeneration. However, measurements of ecosystem resistance to disturbance and resilience following disturbance may provide an early warning of risk of degeneration of the ecosystem when it is exposed to stress and/or early warning of transition to an 'undesirable' state.

A perturbation that is part of evolutionary history (a disturbance) of the ecosystem generally results in a rapid and rejuvenated recovery (Vogel, 1980). A perturbation that is foreign to the system is a stress from which the system may recover only slowly or from which it may not recover and continue in a degraded state (Schlesinger *et al.*, 1990). Disturbance is a natural part of ecosystem dynamics. Natural disturbance can act as a stress when human actions such as fire suppression and levee construction alter the frequency and/or magnitude of the fire or flood. Natural disturbance may be severe, e.g. periodic floods resulting in stream scouring, and fire that destroys whole layers of vegetation but ecosystems have had long evolutionary exposure to such episodic disturbances and are adapted to recover. In

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contrast, stress may disrupt nutrient cycling, reduce productivity, cause the loss of biodiversity and other signs of ecosystem dysfunctions (Rapport *et al.*, 1985). The response of ecosystems to perturbations, therefore, depends upon the nature of the perturbation. Stress is seen as weakening system resilience. Stress may also weaken the capacity of a system to resist a natural perturbation such as periodic drought.

A measure of 'fitness' or counter-active capacity provides an integrated measure of the whole system response to stress. Such a measure can provide an early warning of risk of further degeneration and compromise of the resistance and resilience properties of the ecosystem. This kind of measure is analogous to measures of fitness of athletes in sports medicine. The attributes of resistance and resilience are commonly used to assess human fitness in athletics. For example, the pulse rate of a 'fit' runner may only increase by 30 beats min^{-1} during a 100 m run while that of a less 'fit' runner may increase by 60–80 beats min^{-1} . This measure of change in pulse rate is a measure of the resistance component. At the completion of a run, the pulse rate of a 'fit' runner may return to resting rate within 2–3 min while that of a less 'fit' runner may require 5–6 min to recover. The recovery rate is the resilience component.

While ecosystems do not engage in athletic contests, they are subject to episodic disturbance such as floods, fire and drought. Such natural disturbances can provide an unplanned 'fitness test' for ecosystems. For example measurements of resistance could include survivorship of selected species and extents to which primary productivity and nutrient cycling are maintained, extent to which biodiversity is maintained and mutualistic interactions persist. Measurements of resilience would focus on the rate of recovery of those variables measured to evaluate resistance.

Stress is hypothesised to compromise both the resistance and resilience components of the 'fitness' of ecosystems. Here we report a study designed to examine the resistance and resilience of stressed and relatively unstressed ecosystems to a natural disturbance (drought). We hypothesised that the relatively unstressed ecosystems would main-

tain more of their structure (resistance) during a drought and would return to the pre-disturbance structure quickly (resilience) following a drought when compared with stressed ecosystems.

Methods

Studies were conducted at the Chihuahuan Desert Rangeland Research Center which is located 40 km north of Las Cruces, New Mexico. The landscapes are northern Chihuahuan Desert grasslands. The climate is arid, subtropical. Average annual precipitation is 225 mm with 53% of the annual rainfall occurring between 1 July and 30 September. Average maximum temperature is 36°C with a number of days of maximum temperatures above 40°C in June through August. Winter minima are frequently below 0°C from December through February. Average winter maximum temperature is 13.3°C. The vegetation is a mix of C₄ grasses and C₃ shrubs. The growing season for grasses is defined by nightly minimum temperatures above 10°C (May through September).

In the desert grasslands of the southwestern US, domestic livestock create mosaics of stress gradients across the landscape. Cattle evolved in mesic, cool temperate grasslands and when placed in hot, dry environments remain in areas near water. As cattle tend to congregate near water sources, their impact is greatest close to a water point and that impact decreases exponentially at increasing distance from water (Fusco *et al.*, 1995). The ecosystems adjacent to water points are severely stressed while those more than 1 km from water are minimally stressed in the landscape selected for study. We utilised data from plots established on three grazing stress gradients for ecosystem health indicator studies (Whitford *et al.*, 1998) as baseline for this study and utilised those plots for studies of resistance and resilience to a natural disturbance (drought).

Measurements were made on the following dates: June 1994 (vegetation cover before the growing season droughts of 1994–1996), October 1994 (survivorship from summer drought) and repeat measurement of vegetation cover at the end of July 1997 when the grasses were at peak biomass (recovery from

the growing season droughts of 1994–1996). The June 1994 vegetation cover measurements were made as part of a study of indicators of rangeland health (Whitford *et al.*, 1998). The subsequent measurements were designed to address the questions of resistance and resilience of the ecosystems on the grazing stress gradients.

We measured survivorship and changes in cover of several species of perennial plants on plots located on 'stress' gradients extending from livestock watering points. We collected data on those species that were relatively abundant in the black-grama grassland that had low impact by cattle. The dominant grass is black-grama (*Bouteloua eriopoda*), a stoloniferous grass. Other abundant grasses include purple three awn, *Aristida purpurea*, and mesa dropseed, *Sporobolus flexuosus*. Other species of these grasses occur on some of the plots, i.e. *Sporobolus contractus*, *Sporobolus cryptandrus* and *Aristida ternipes*. Since these species cannot be readily separated in the field when the plants are senescent and inflorescences are absent, we recorded the data by genus for this study.

The study sites were in pastures that were established as a long-term seasonal grazing study in 1946. We used four, 1-h sites located at 50–150 m, 250–350 m, 500–600 m and 1000–1100 m from a livestock watering point in each of three pastures. The permanent plot corners were identified by 2-m iron rebar stakes sunk to 1 m depth. All of the study sites were on the same soil series (Bullock and Neher, 1980) and differed in vegetation cover, and size of patches of bare soil as a result of the activities of the cattle (Table 1). Each of the pastures has been stocked at comparable rates (5 ha/cow/month) since the initiation of the grazing study in 1946 (R. Beck, pers. comm.). Two of the transects were in pastures that were grazed only in winter and one was located in a pasture that was grazed throughout the year.

The infrequent, low volume precipitation events during most of the growing of 1994 were inadequate to stimulate growth of the grasses. September 1994 rainfall stimulated green-up of surviving tillers of the perennial grasses. We collected data on the percent of perennial bunch grasses that survived the growing season drought by recording the frequency of occurrence of grass clumps with no green tillers and frequency of clumps with

green tillers. Frequency data were collected by walking 100-m lines separated by 5 m on the permanent plots and recording the status of 100 plants of each genus. Due to the differences in abundance of plants on the plots near water and those distant from water, it was necessary to walk 10–12 lines on plots nearest water and only 2–3 lines on the plots most distant from water.

Cover and composition were measured by line intercept on 10, 100-m lines with 10 m spacing between lines on each plot (Canfield, 1941) in June and July 1994. Cover and composition measurements were made on all of the same plots in July 1997. The July 1997 measurements were made using six, 30-m lines with 10 m line spacing. As drought conditions continued through 1995 (Table 2), we waited until 1997 to re-measure cover values to evaluate resilience.

Survivorship data were examined by linear and first-order polynomial regression analysis and by ANOVA followed by Student-Newman-Keuls method. The changes in cover of the selected plant species pre-drought and post-drought were examined by paired *t*-tests.

Results

The resistance of several species as measured by survivorship was affected by the intensity of exposure to the stress of livestock grazing (Figure 1). The survivorship of the three-awn grasses (*Aristida* spp.), dropseed grasses (*Sporobolus* spp.) and snakeweed (*Gutierrezia* spp.) were reduced in plots nearest the water source ($F = 4.9$, $P < 0.008$). Some of these species also exhibited higher survivorship in the plots subjected to intermediate levels of stress (Figure 1). The survivorship of both *Aristida* spp. and *Gutierrezia sarothrae* at varying distances from water points was best fit by first-order polynomial regressions ($r = 0.62$ and 0.65 , respectively). The survivorship of *Sporobolus* spp. was best fit by a linear regression ($r = 0.37$) (Figure 1). Black-grama grass (*Bouteloua eriopoda*), the dominant species in the areas least stressed by cattle grazing, was not present on any of the plots close to the water points. Most of the black-grama grass plants survived on the plots where black-grama occurred pre-drought (>95%) but there

Table 1. Characteristics of three stress gradients originating at water wells on the Chihuahuan Desert Rangeland Research Center desert grasslands in southern New Mexico

Site Code	Grass %	Shrub %	Bare (cm)	Soil
WW0	0.88	15.9	197.6	Berino Series, sandy loam, indurated calcareous layer at 40–100 cm
WW1	3.3	21.7	139.2	
WW2	8.9	13.7	133.1	
WW3	27.6	5.1	50.9	
CW0	0.47	5.7	396.2	Berino Series, sandy loam, indurated calcareous layer at 40–100 cm
CW1	2.4	8.6	126.0	
CW2	4.5	5.5	126.9	
CW3	20.8	4.3	68.5	
MW0	1.2	6.8	296.4	Berino Series, sandy loam, indurated calcareous layer at 40–100 cm
MW1	4.1	17.2	96.9	
MW2	5.7	10.9	90.2	
MW3	23.7	6.7	62.6	

Vegetation characteristics are reported as percent cover of perennial grass and shrubs. Average size of unvegetated patches is reported as average bare diameter in cm. Letter codes refer to well names, i.e. MW, Mayfield Well. Number codes refer to distance from water point of the 1-h study plots: 0 = 50–105 m, 1 = 250–350 m, 2 = 500–600 m, 3 = 1000–1100 m.

Table 2. Growing season (May through September) rainfall in mm for the year preceding the study and for the years spanning the study compared with the long-term average growing season

Year	May to September	Annual total	Percent
80 Year Average	152	225.5	
1993	190.5	125.0	279.9
1994	73.2	183.6	48.1
1995	119.4	169.5	78.6
1996	126.0	185.9	82.9
1997	155.9	255.0	105.2

Percent is the deviation from the long-term average. Long-term rainfall records from the Jornada Experimental Range Headquarters station 12 km east of the study sites. Growing season rainfall data are from a station 2.5 km east of the study transects.

was a significant reduction in the canopy cover of this species which did not recover following the drought in 1997 (Figure 2).

The recovery of cover of the grass species and snakeweed was used as a measure of resilience. The cover of three awns, *Aristida* spp. was zero on all of the well gradient plots 50–150 m from the water points in 1997 (Figure 3). At two of the well gradients at 250–350 m, *Aristida* spp. cover was significantly lower in 1997 than the pre-drought cover of 1994 and at two of the well gradients,

Aristida spp. cover was significantly lower in 1997 on either the 500–600 m plot or the plot 1000–1100 m from the water point (Figure 3). Snakeweed, *Gutierrezia sarothrae*, exhibited complete recovery on most plots (Figure 4). At one of the well gradients at the 50–150 m distance, the cover of snakeweed was much higher post-drought than pre-drought, and on two of the plots at 1000–1100 m from water, *G. sarothrae* had lower post-drought cover than was recorded in the pre-drought sampling period. The dropseeds, *Sporobolus* spp. recovered to the pre-drought cover values on the plots farthest from the water points on two of the three well gradients (Figure 5). On one gradient (West Well), there were no *Sporobolus* spp. plants on the plot nearest the water point and on that well gradient *Sporobolus* spp. cover did not recover to pre-drought values (Figure 5).

Discussion

The data from these studies are consistent with the hypothesis that both the resistance and resilience components of fitness are compromised by exposure to the environmental stresses generated by the activities of domestic livestock. Ecosystem-level responses

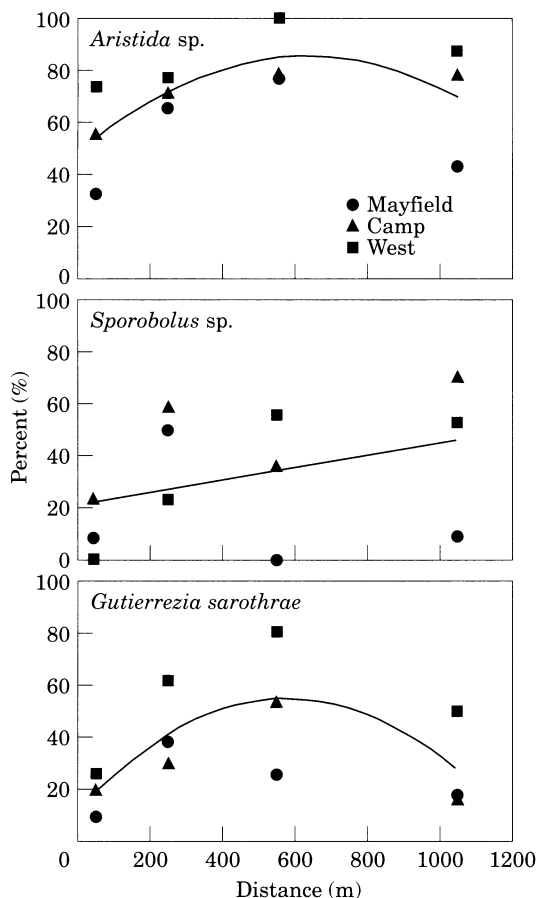


Figure 1. Best-fit linear or first-order polynomial regression lines for the survivorship (percent alive) of selected plant species on stress gradients produced by domestic livestock activity centered on watering points.

to natural or experimentally induced perturbations can be the ecological equivalent of a 'fitness test' or natural 'treadmill test' and provide an integrative measure of the health of the ecosystem. Our studies addressed only the perennial plant component of the desert grassland ecosystem but that component responded as hypothesised. The heavily stressed ecosystems exhibited less resistance to drought (a natural disturbance) as measured by survivorship of perennial plants than the less stressed ecosystems. With the exception of *G. sarothrae*, recovery following drought resulted in a similar pattern with the stressed ecosystems showing reduced resilience (lower recovery of plant cover) than the less stressed ecosystems.

The behavior of *G. sarothrae* in response to drought and its pattern of recovery following drought was suggested in the results from early studies of this species. *Gutierrezia sarothrae* was shown to be susceptible to drought damage and to 'invade' areas around livestock watering installations and other areas of livestock concentration (Talbot, 1926). This species has also been reported to reestablish rapidly following die-off after drought. Since *G. sarothrae* is toxic to livestock (Matthews, 1936) it has an advantage in re-establishing in areas where livestock congregate. In these areas there is little competition for water and nutrients with other perennial species. The data from this study show that *G. sarothrae* suffered higher mortality in the areas where livestock congregate

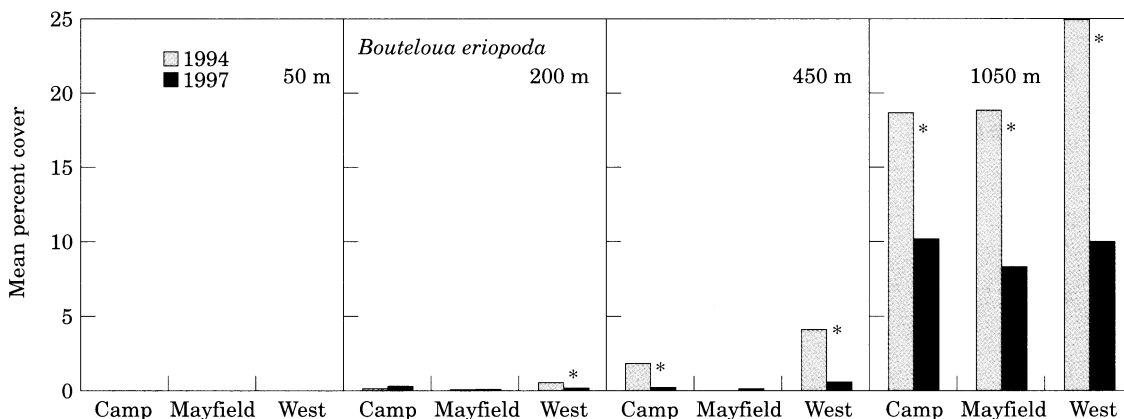


Figure 2. Percent cover of black-grama grass, *Bouteloua eriopoda*, at varying distances from domestic livestock watering points, pre-drought (1994) and 1 year post-drought (1997). Bar pairs marked with an asterisk (*) are significantly different at $P < 0.05$.

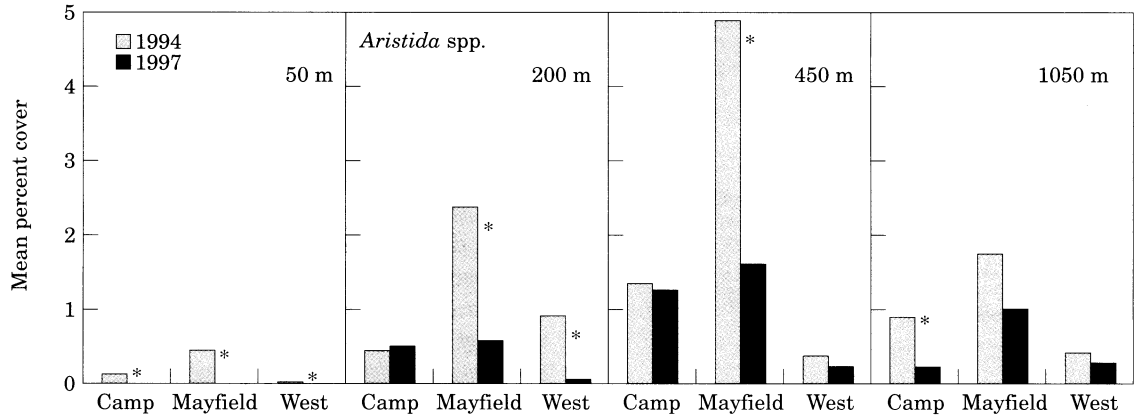


Figure 3. Percent cover of three-awn grasses, *Aristida* spp., at varying distances from domestic livestock watering points, pre-drought (1994) and 1 year post-drought (1997). Bar pairs marked with an asterisk (*) are significantly different at $P < 0.05$.

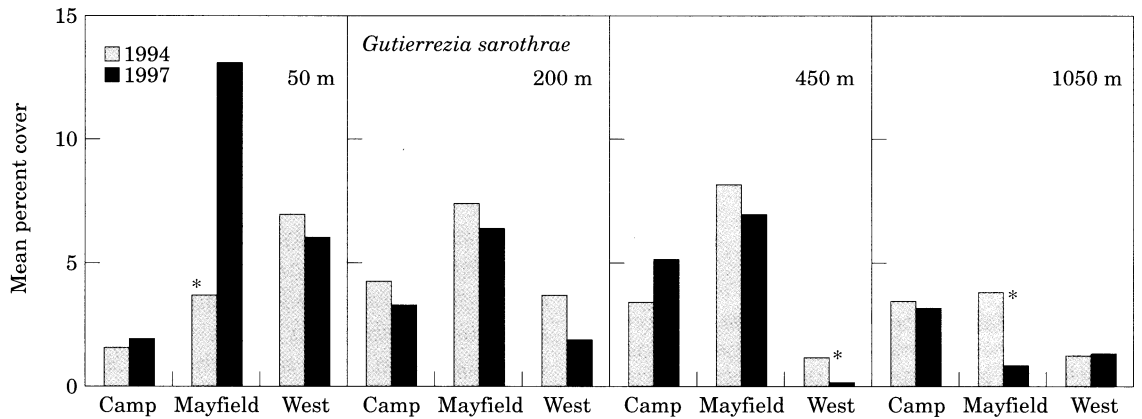


Figure 4. Percent cover of snakeweed shrubs, *Gutierrezia sarothrae*, at varying distances from domestic livestock watering points, pre-drought (1994) and 1 year post-drought (1997). Bar pairs marked with an asterisk (*) are significantly different at $P < 0.05$.

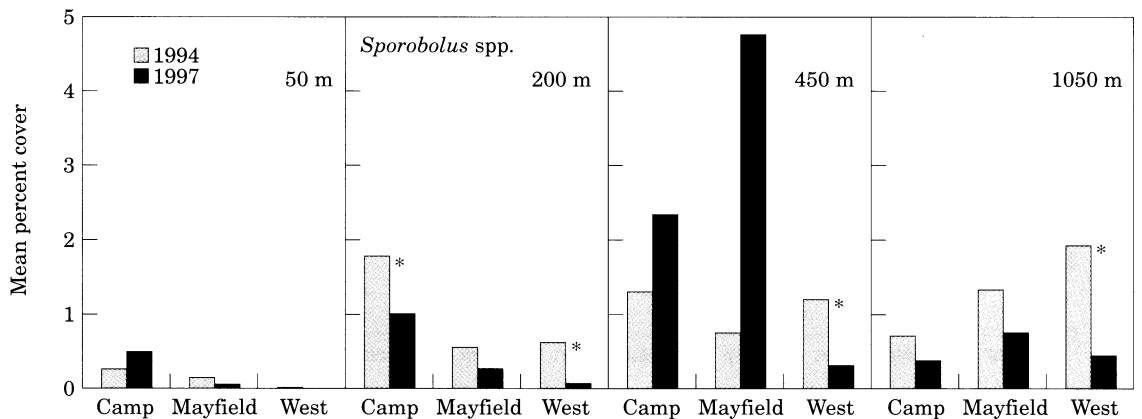


Figure 5. Percent cover of dropseed grasses, *Sporobolus* spp., at varying distances from domestic livestock watering points, predrought (1994) and 1 year post-drought (1997). Bar pairs marked with an asterisk (*) are significantly different at $P < 0.05$.

but re-established in these areas rapidly at the end of the drought. The low re-establishment rate of *G. sarothrae* in the black-grama grasslands more than 1000 m from water was probably the result of the competitive disadvantage of seedlings with the surviving black-grama grass. Low re-establishment of this shrub may also result from the differential effects of grazing and competition on seed production (Freeman and Emlen, 1995).

The changes in cover of the perennial grasses reflect differences in reproduction and mortality. *Sporobolus* spp. and *Aristida* spp. are bunch grasses that reproduce by seed. *Bouteloua eriopoda* reproduces by primarily by stolons but also from seeds. Drought death of *Sporobolus* spp. and *Aristida* spp. originated with tillers at the center of the clump and moved outward toward the periphery. In October 1994, the live tillers of the surviving bunch grasses were on the edges of the clumps. Drought death in *B. eriopoda* originated at the fringe of the clumps and moved toward the center. In this grass the live tillers were in the center of a clump. The root systems of surviving bunches of *Aristida* and *Sporobolus* were using the same volume of soil post-drought as before and during the drought. The reduction in size of *B. eriopoda* canopies opened areas for the root systems of other grasses and drought should have reduced the competitive effect of this grass on the other species.

The variation in both the resistance and resilience measures among well gradients emphasises the necessity of having sufficient replication for 'fitness' testing. Much of the variation in survivorship and recovery following drought is attributable to competition between *B. eriopoda* and other species for soil resources (water and nutrients) on those plots dominated by *B. eriopoda*. At the intermediate distances, overgrazing of *B. eriopoda* by livestock had virtually eliminated this species. Re-establishment of *Sporobolus* spp. on the highest impact plots could not be evaluated because its initial low cover and abundance. The variability in re-establishment of this species on the other plots could result from differences in soil seed bank and competition with other grasses on the high vegetation cover plots. The lower impact by trampling and grazing at intermediate distances allowed for higher abundance and

cover of other species. The lower impact by trampling also eliminated the development of a compaction layer at 10 cm (Herrick, USDA Jornada Experimental Range, unpubl. data). The absence of a compaction layer and reduced hoof action contributes to the higher rates of germination and establishment of *Aristida* spp. and *Sporobolus* spp. on most of these plots. This variation did not reduce the value of survivorship and recovery of canopy cover as tests of resistance and resilience of stressed and relatively unstressed ecosystems.

The compromised resistance and resilience of stressed ecosystems was in response to a single stressor (livestock grazing). However, ecosystems are generally beset by multiple stresses some of which are easily identified and others that are only suspected (Rappport *et al.*, 1985; Hilden and Rappport, 1993; Rappport and Regier, 1995). The effects of such stresses may be synergistic. Frequently, by the time the symptoms of ecosystem pathology are evident, the system is in advanced stages of breakdown. The capacity of an ecosystem to absorb multiple stresses is unknown. The mechanisms linking sources of stress to impacts on ecosystems given the temporal and spatial lags and synergistic and/or antagonistic effects are poorly defined. This appears to be so in most cases of anthropogenic stress on large-scale ecosystems (Regier and Hartman, 1973; Rappport, 1989; Whitford, 1995).

It is in the assessment of the impact of stressors on ecosystems that monitoring resistance to natural disturbance and recovery from natural disturbance becomes a valuable tool. Ecosystems that display reduced capacity to resist periodic disturbance and/or to recover quickly from such disturbance are at high risk of further degradation. One of the earliest signs that ecosystems are overstressed is reduced capacity to resist disturbance and to recover from normal disturbances e.g. drought, fire, spring scouring of streams, floods etc. Cumulative impacts of stress tend to lower ecosystem fitness by damaging the mechanisms that normally assist in recovery, e.g. maintenance of species pools, seed banks, soil fertility, maintenance of soil properties and maintenance of habitat structure. Stress may also change the physical environment in ways that affect competitive ability or survivorship. In this study,

soil compaction produced by trampling on the high impact plots probably reduced water storage and rooting soil volume thereby compromising the ability of perennial plants to survive the drought.

Although livestock grazing using the current water well and paddock system imposes a stress on subtropical arid grasslands, other grazing systems may not generate 'stress'. The stress on the Chihuahuan Desert grasslands results from the behavioral characteristics of the animals chosen by the pastoralists. It is likely that similar densities of desert adapted herbivores would not generate stress gradients in these landscapes because they would not congregate at water points. However, we have not invested in the domestication of desert adapted grazing animals, hence, this alternative is not viable. The most difficult problem of pastoralists is providing water in a temporal and spatial pattern that allows for grazing pressure to be spread relatively evenly across the landscape. Alternative grazing systems are perceived as too labor or capital intensive to be implemented. Pastoralists need to be made aware of the impact of their grazing systems on the 'fitness' of the ecosystems that provide the basic resources for their industry.

This study examined the responses of one kind of ecosystem to one kind of stress. There are many kinds of stress that affect ecosystems and which probably affect the resistance and resilience of those systems. Fitness tests can be designed for different kinds of ecosystems. The general applicability of this type of 'fitness' test to other ecosystems depends upon the ability to identify natural disturbances that can be used to examine the resistance and resilience of the stressed and unstressed ecosystems.

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