Environmental Management (2008) 41:676–684
DOI 10.1007/s00267-007-9064-4

RESEARCH

Grassland Plant Composition Alters Vehicular Disturbance Effects in Kansas, USA

Timothy L. Dickson · Brian J. Wilsey · Ryan R. Busby · Dick L. Gebhart

Published online: 18 January 2008

Abstract Many "natural" areas are exposed to military or recreational off-road vehicles. The interactive effects of different types of vehicular disturbance on vegetation have rarely been examined, and it has been proposed that some vegetation types are less susceptible to vehicular disturbance than others. At Fort Riley, Kansas, we experimentally tested how different plant community types changed after disturbance from an M1A1 Abrams tank driven at different speeds and turning angles during different seasons. The greatest vegetation change was observed because of driving in the spring in wet soils and the interaction of turning while driving fast (vegetation change was measured with Bray-Curtis dissimilarity). We found that less vegetation change occurred in communities with high amounts of native prairie vegetation than in communities with high amounts of introduced C_3 grasses, which is the first experimental evidence we are aware of that suggests plant communities dominated by introduced C_3 grasses changed more because of vehicular disturbance than communities dominated by native prairie grasses. We also found that vegetation changed linearly with vehicular disturbance intensity, suggesting that at least initially there was no catastrophic shift in vegetation beyond a certain disturbance intensity threshold. Overall, the intensity of vehicular disturbance appeared to play the greatest role in vegetation change, but the plant community type also played a strong role and this should be considered in land use planning. The reasons for greater vegetation change in introduced C_3 grass dominated areas deserve further study.

Keywords Vegetation change · Species composition · Catastrophic shift · Military lands

T. L. Dickson (✉) · B. J. Wilsey
Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames, IA 50011, USA
e-mail: dicksont@iastate.edu

R. R. Busby · D. L. Gebhart
U.S. Army Engineer Research and Development Center, Construction Engineering Research Lab, P.O. Box 9005, Champaign, IL 61826, US

Introduction

A great deal of both military and recreational off-road vehicular disturbance has occurred in parts of the United States (Kockelman 1983; Anderson and others 2005), as well as in other parts of the world (Vertegaal 1989; Hirst and others 2000). It is important to know how plant communities change in response to vehicle disturbance because vegetation can be a good indicator of soil and other environmental conditions (Philippi and others 1998) and because changes in vegetation can affect erosion, wildlife, and land use (Hobbs and others 1982; Tasser and others 2003; Wang and others 2007). It is also important to know which vegetation types are most susceptible to vehicular disturbance so that disturbances can be avoided in highly susceptible vegetation and so that the least susceptible vegetation can be used in restorations after disturbance. Vehicular disturbance is similar to other types of disturbance in that most disturbances can remove plant parts, cause soil compaction, and lead to increased erosion (Weaver and Dale 1978). However, large vehicles may cause high soil compaction and erosion rates, as well as expose large amounts of bare ground (Anderson and others 2006).

Many studies have examined the effects of vehicular disturbance on vegetation, although few of these studies have examined the interactive effects of multiple types of vehicular disturbance. Vegetative cover and biomass decreased more when vehicles were driven in wet conditions than in dry conditions (Althoff and Thien 2005), and vehicles decreased vegetative cover more when turning than when they were driving straight (Watts 1998; Haugen and others 2003; Li and others 2007), especially when vehicles were driven at high speeds (Foster and others 2006) or when soils were wet (Anderson and others 2006). There is also some evidence that the response of vegetation to disturbance differed across soil types (Yorks and others 1997; Leis and others 2005). In addition, vehicular disturbance has been shown to cause greater soil disturbance with decreased vehicle turning radius (Haugen and others 2003; Li and others 2007), heavier vehicles (Anderson and others 2006), and increased amounts of off-road traffic (Garten Jr. and others 2003; Debusk and others 2005).

Several studies have examined the effects of vehicular disturbance on measures of plant species composition and diversity. Short-statured vegetation increased in abundance relative to tall vegetation (Wilson 1988), and the abundance of introduced plants increased after vehicular disturbance (Wilson 1988; Shaw and Diersing 1990; Quist and others 2003). Also, vehicular disturbance often decreased the abundance of perennials and increased the abundance of annuals (Johnson 1982; Milchunas and others 2000; Hirst and others 2003; Quist and others 2003). Plant species richness was highest at intermediate vehicular disturbance levels in one study (Leis and others 2005), and tracked vehicles caused greater vegetation change in British chalk grassland than wheeled vehicles (Hirst and others 2003). It has also been shown that plant diversity levels can affect resistance and resilience to disturbance (Schläpfer and Schmid 1999). Lastly, a qualitative review by Yorks and others (1997) suggested that graminoids show the highest resistance and resilience to vehicle and trampling disturbance while broad-leaved forbs tend to suffer immediate losses from disturbance. The Yorks and others (1997) study also suggested that graminoids with tillers may show greater resistance and resilience to disturbance than strongly rhizomatous graminoids (sod-forming grasses).

An important aspect of increased vehicular disturbance is whether it affects vegetation in a linear or a nonlinear manner. Traditionally, ecologists have assumed a linear relationship between disturbance intensity and vegetation change. However, authors in more recent years have hypothesized that response to and recovery from disturbance might be nonlinear in many cases (Suding and others 2004; Temperton and others 2004; Groffman and others 2006). These authors predicted vegetation would only change dramatically above a certain threshold. In the case of vehicles, disturbance may cause changes in vegetation, for example from perennial to annual domination, only above the intensity levels that kill perennial roots and crowns. This would cause a nonlinear relationship between disturbance and vegetation change. It is important to test for the presence of disturbance intensity thresholds because vegetation recovery may take much longer once a threshold has been passed (Box 2 in Suding and others 2004).

We examined the interactive effects of military vehicular disturbance on vegetation at Fort Riley, Kansas, and determined which plant community types would show the least vegetation change after vehicular disturbance. The results of our experiment should be applicable to many types of vehicular disturbance, since Anderson and others (2006) found that tanks had more severe, but qualitatively similar, vegetation and soil disturbance effects compared to wheeled vehicles. In our study, we tested the following predictions: (1) pre-disturbance plant species composition and diversity would alter the effects of tank driving on vegetation change and biomass; (2) different tank driving conditions would individually and interactively alter disturbance intensity and cause different amounts of vegetation change; and (3) the amount of vegetation change would increase dramatically beyond some disturbance-intensity threshold (i.e., nonlinearly).

Materials and Methods

Study Site

We conducted the study at Fort Riley, in northeastern Kansas near the town of Riley (39° 30’ N, 96° 92’ W). Fort Riley consists of 40,000 + hectares (ha) of land, much of which is a mix of native prairie and introduced vegetation, and Fort Riley is located within a 1.6 million ha region in eastern Kansas containing the largest untilled tallgrass prairie landscape in the world (Knapp and Seastedt 1998). This study was conducted in the northwestern part of Fort Riley on former range and crop land acquired by Fort Riley in 1965. Little or no military training has occurred since 1965 in the area where we conducted our study. The soil at the experimental site consists of a Wymore-Irwin association of silt loams and silty clay loams composed of nearly level to sloping ground (Althoff and Thien 2005). The vegetation on the silt loam soil type was hayed during the summers of 2002–2004, and the entire area has been burned periodically since 1965 (no records have been kept of burning). Temperature and precipitation in the region is unimodal, with peak rainfall occurring in June (14 cm monthly average) and with an average yearly precipitation of 84 cm (Hayden 1998). Mean monthly temperatures range from −3° C in January to 27° C in July (Hayden 1998). Native and perennial species dominated the vegetation at our sites, comprising 91% and 90%, respectively of the total vegetative cover (estimated by us in plots outside tank tracks, see below), and functional group composition was C_4 grasses (46%), forbs (32%), legumes (11%), and C_3 grasses (11%). The most common species are listed in Table 1.

Experimental Design

We used a paired plot approach to examine plant communities in plots within tracks and approximately 50 cm outside (control) tracks created by an M1A1 main battle tank. The M1A1 weighs 57,150 kg, the tread width is 61 cm, and the average ground pressure applied by the tank is 0.98 kg cm^{-2}. A factorial set of treatments was applied to main plot (tank passes) using a randomized block split-plot design as described in Anderson and others (2006). Tanks drove at two different speeds (slow at approximately 11 km hr^{-1} or fast at approximately 21 km hr^{-1}) at two different times during the growing season (October 19, 2004 [11.5% soil moisture by weight] or April 12, 2005 [28.5% soil moisture]). This was done within two soil types: silty clay loam or silt loam soil, which served as blocks. Each of the eight treatment combinations was replicated twice for a total of 16 different tank passes (Fig. 1). Within each tank pass, we sampled two paired plots where the tank had driven straight and two paired plots (except in one instance) where the tank had driven at approximately 9 degrees, leading to 63 paired plots. All measurements within tank tracks were on the outside turning track. When a measurement was taken within a tank track, the same person made the measurements in the adjacent control plot, thereby removing sampler bias within paired plots. Also, the two vegetation samples were "calibrated" by having the two samplers (TLD and BJW) sample the same areas at the start of data collection to make sure their measurements were consistent.

Vegetation Sampling

All vegetation data were collected July 20–28, 2005 in 50 cm × 50 cm plots. Without the use of cover classes, we visually estimated the percentage groundcover of all plant species, bare ground, and plant litter cover within each quadrat. The total percentage groundcover of all species, bare ground, and plant litter could sum to more than 100% because overlap of plants could occur in the vegetation canopy. We also measured the height of the three species with the highest percent groundcover in each plot to develop an index of biomass (see below).

To estimate disturbance intensity, we measured the difference in soil height between the inside of the tank track and immediately outside the tank track. Erosion over time is known to change soil height in some soil types (Halvorson and others 2001), but in our soil types we found that the depth of tank tracks remained largely the same even two years after disturbance (personal observations).

Data Analysis

All data analysis was completed in SAS for Windows 8.02. To examine whether the control plant species composition and diversity would alter the effects of tank driving on vegetation change and biomass, we performed multiple linear regression analyses using predictor variables from a principal component analysis (PCA). The PCA was performed to condense differences in control vegetation values into a small number of independent variables so that we would not include too many highly correlated predictor variables in the multiple linear regression. We performed both forward and backward multiple linear regression with a p-value to enter of 0.05 and a p-value to remove of 0.1. Both forward and backward multiple linear regression returned the same model in all cases.

Table 1 Abundance of species commonly found within plots (the total number of plots where a species could be found is 63; the average percent cover includes only those plots that contain a given species)

Species	Common name	Native or introduced	Functional Group[a]	Number of plots Control (track)	Average percent cover Control (track)
Ambrosia psilostachya	western ragweed	Native	PF	43 (40)	6.8% (7.7%)
Andropogon gerardii	big bluestem	Native	C_4-PG	27 (27)	17.9% (12.2%)
Bromus inermis	smooth brome	Introduced	C_3-PG	21 (21)	13.3% (4.3%)
Carex species	sedge	Native	C_3-PG	30 (27)	1.7% (1.6%)
Chamaecrista fasciculata	partridge pea	Native	AL	33 (29)	8.9% (9.2%)
Poa pratensis	Kentucky bluegrass	Introduced	C_3-PG	17 (12)	2.2% (1.4%)
Sorghastrum nutans	Indian grass	Native	C_4-PG	41 (35)	10.4% (8.4%)
Sporobolus compositus	rough dropseed	Native	C_4-PG	45 (39)	9.7% (7.3%)
Symphyotrichum ericoides	heath aster	Native	PF	51 (52)	9.3% (6.9%)

[a] A = annual, P = perennial, F = nonleguminous forb, L = leguminous forb, G = graminoid

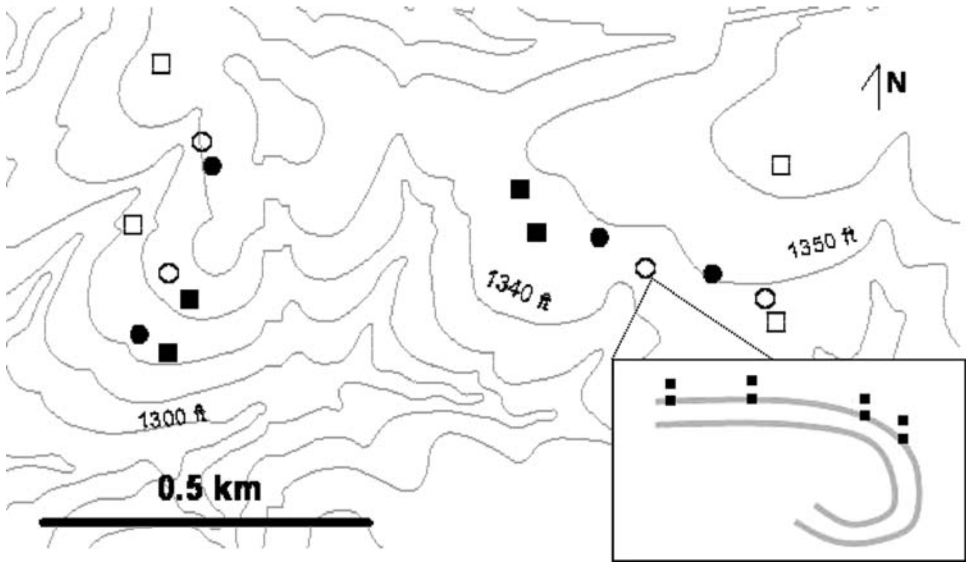

Fig. 1 Elevation map showing locations of tank spirals with an approximately 50 × 25-m inset showing approximate layout of plots within each tank spiral (the eight tank spirals to the west were in silty clay loam soil and the eight tank spirals to the east were in silt loam soil; circles were tank spirals driven in the fall and squares were driven in the spring; open circles and squares were tank spirals driven at slow speeds and closed were driven at fast speed)

The PCA distilled control plot vegetation data into factor scores representing communalities in the different measures of vegetation (Table 2). All data in the PCA, except Simpson's diversity (1 / $\sum p_i^2$; Smith and Wilson 1996), represents percent cover (abundance) of different ground cover types. To improve normality we $\log_{10}$ transformed all the abundance variables in the PCA except total vegetative cover. We retained axes only if they had eigenvalues greater than 1.0 (Table 2; Kaiser 1960). We interpreted factor scores for each principal component (PC) as follows and used the factor scores as predictor variables in regression analysis (Stevens 1996): (PC1) a contrast between native species abundance and the abundance of introduced C_3 grasses (*Bromus inermis* was the most abundant introduced C_3 grass with small amounts of *Poa pratensis*); (PC2) vegetative cover; (PC3) a contrast between annual / biennial forb abundance and C_4 grass abundance; (PC4) a contrast between annuals / biennials and litter and nonleguminous forbs; and (PC5) a contrast between bare ground and litter. We also used the square root of track depth as a predictor variable in multiple linear regression, to account for disturbance intensity.

For estimates of vegetation change we used Bray-Curtis vegetation dissimilarity. We calculated Bray-Curtis vegetation dissimilarity (hereafter referred to as vegetation change) as follows (Bray and Curtis 1957):

Table 2 Loadings (correlations) of the vegetation variables on the five different principal component (PC) axes

	PC1	PC2	PC3	PC4	PC5
Annual and biennial cover	−0.498	−0.115	0.685	0.425	0.103
Perennial cover	0.316	0.826	−0.319	−0.105	0.085
Nonleguminous forb cover	0.026	0.481	0.469	−0.617	−0.263
Leguminous forb cover	−0.567	0.198	0.631	0.300	0.022
C_4 grass cover	−0.579	0.172	−0.577	0.319	0.232
C_3 grass cover	0.888	0.066	0.020	0.165	−0.002
Bromus inermis and *Poa pratensis* cover	0.899	0.071	0.262	0.134	0.103
Native cover	−0.661	0.609	−0.127	0.092	−0.043
Introduced cover	0.903	0.069	0.192	0.176	0.101
Bare ground cover	0.002	−0.697	−0.158	0.177	−0.623
Litter cover	−0.135	−0.578	0.096	−0.380	0.675
Total vegetative cover	0.115	0.942	0.058	0.231	0.021
Simpson's Diversity	−0.424	0.204	0.121	−0.412	−0.138
Eigenvalue	4.07	3.13	1.70	1.25	1.03
Variance explained	31.3%	24.1%	13.0%	9.6%	7.9%

$$\frac{\sum_{i=1}^{i=n} |Control_i - Track_i|}{\sum_{i=1}^{i=n} (Control_i + Track_i)}$$

where $Control_i$ is the percent cover of the ith species in the control plot (adjacent to the track) and $Track_i$ is the percent cover of the ith species within the paired track plot (with a total of n species). When the measure of vegetation change equals zero, there is no difference between the vegetation inside and outside the tank track, but when the measure of vegetation change equals one, then the vegetation is completely different inside the tank track versus outside. We found that 65% of the Bray-Curtis numerator value, on average, was determined by the change in abundance of the following seven species (from greatest contribution to least): *Sorghastrum nutans*, *Symphyotrichum ericoides*, *Andgropogon gerardii*, *Sporobolus compositus*, *Ambrosia psilostachya*, *Chamaecrista fasciculata*, and *Bromus inermis*. These species were generally the most abundant species in the experiment and, when present, were generally present in both paired plots, suggesting that changes in Bray-Curtis values were mostly caused by changes in the abundance of the most common species rather than changes in species identity (Table 1). We calculated the biomass index as follows:

$$Cover_{tot} * \left[\left(\sum_{i=1}^{i=3} Height_i * Cover_i \right) \div \left(\sum_{i=1}^{i=3} Cover_i \right) \right]$$

where $Cover_{tot}$ is the total percent cover of all species in the plot, $Height_i$ is the height of one of the three measured species, and $Cover_i$ is the percent cover of the ith species. We calculated the change in biomass between paired control and track plots by using the log response ratio [ln (control biomass index / track biomass index)] (Goldberg and others 1999; Hedges and others 1999).

To examine whether the amount of vegetation change would increase dramatically beyond some disturbance-intensity threshold (i.e., nonlinearly), we examined whether the relationship between vegetation change and the untransformed depth of tank tracks was nonlinear. We used polynomial regression models that included a quadratic term and a cubic term, as well as a linear term, to test for both linear and nonlinear relationships.

To test whether tank driving would alter disturbance intensity and cause different amounts of vegetation change, we completed a randomized block split-plot ANOVA with PROC GLM in SAS (Littell and others 2002). Response variables were square root transformed track depth, vegetation change, change in the biomass index, and difference (track plots minus control plots) in Simpson's diversity. Soil type was treated as a blocking effect. Season, tank speed, and their interaction were included as main plot effects. Tank trajectory was included as a subplot effect. Thus, main plot effects used [replicate (Season × Tank speed)] as the error term, whereas subplot effects used the residual error term.

All standard errors in the figures were calculated as the square root of (MSE / n) where MSE is the mean square error term of the associated analysis and n is the number of replicates for each treatment (Sokal and Rohlf 1995). We back-transformed standard errors when statistical tests were performed on the transformed data, but nontransformed data were presented in the figures.

Results

Effects of Community Composition and Severity of Disturbance on Vegetation

Vegetation change increased as the depth of tracks increased (Fig. 2a). Vegetation change was also higher when a high proportion of introduced C_3 grasses (PC1) were initially present (Fig. 2b). No other variables were significantly

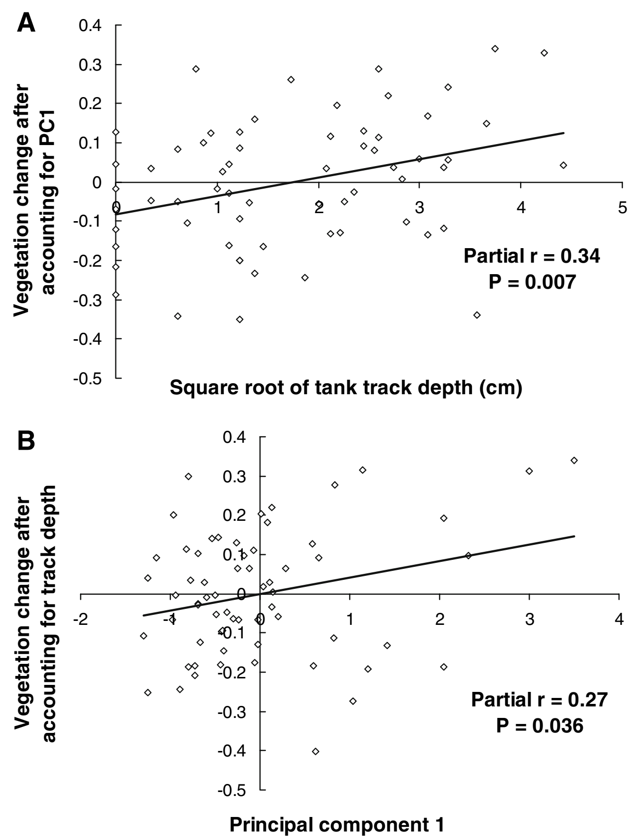

Fig. 2 The relationship between vegetation change (Bray-Curtis dissimilarity) and the square root of tank track depth (**a**) and the first principal component that represents the abundance of introduced C_3 grasses (**b**)

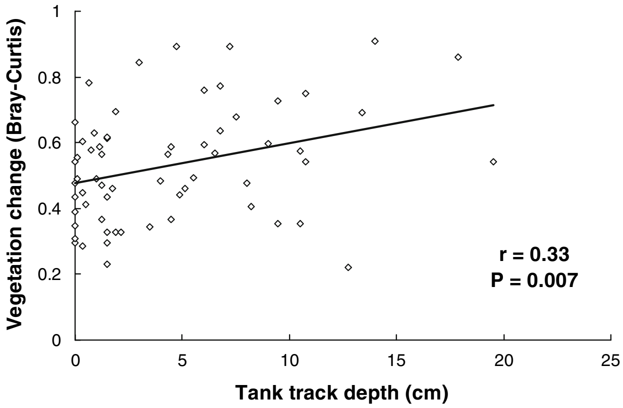

Fig. 3 The relationship between vegetation change (Bray-Curtis dissimilarity) and tank track depth (cm)

related to vegetation change (p-values > 0.1). The overall model had an r^2 of 0.18 with $f_{2,\ 60} = 6.7$; $p = 0.002$.

The relationship between untransformed tank track depth and vegetation change was linear (Fig. 3). Neither the quadratic term nor the cubic term had p-values low enough to be included in the polynomial regression ($p = 0.53$ and 0.60, respectively).

The change in the biomass index increased as the depth of tank tracks increased (data not shown). The overall model had an r^2 of 0.19 *with* $f_{1,\ 61} = 14$; $p < 0.001$ (change in biomass index = 0.38 + 0.28 × square root of tank track depth). No other variables were significantly related to the change in the biomass index (p-values > 0.1).

Effects of Season and Tank Driving Style on Disturbance Intensity

Track depth (disturbance intensity) was much greater when tanks were driven in the spring than when tanks were driven in the fall (Table 3; Fig. 4). Track depth was also greater when tanks were turning than when they were driving straight.

Effects of Soil Condition and Tank Driving Style on Vegetation

Vegetation change was greatest when tanks were driven in the spring (Table 3; Fig. 5). There was also a nearly significant ($p = 0.055$) interaction between tank trajectory and tank speed whereby turning caused a larger increase in vegetation change when tanks were driving fast than when they were driving more slowly. The change in the biomass index was greatest when tanks were driven in the spring and when tanks were turning (Table 3; Fig. 6). No factors or interactions between factors had significant effects on the difference in Simpson's species diversity (Table 3; data not shown).

Discussion

Vegetation change in our study was the result of both disturbance intensity and the pre-disturbance plant community. Our results suggest that the types of vehicular disturbance that have been shown to cause the most severe soil and biomass disturbances in the past also cause the greatest change in species composition. Specifically, conditions present in the spring appeared to play the greatest role in increasing disturbance intensity and vegetation change, and sites dominated by introduced C_3 grasses were more susceptible to vegetation change than sites dominated by native species.

It is well known that different plant species respond differently to disturbance (Palazzo and others 2005), but it

Table 3 Analysis of variance results using four different response variables

		Track depth (disturbance intensity)		Vegetation change (Bray-Curtis)		Change in biomass index		Difference in simpson's diversity	
Predictor variable	d.f.	M.S.	*p*-value	M.S.	*p*-value	M.S.	*p*-value	M.S.	*p*-value
Soil type (St)	1	0.12	0.61	0.003	0.71	1.5	0.24	8.6	0.24
Season (Se)	1	63	<0.001	0.19	0.028	6.7	0.046	0.099	0.89
Tank speed (Ts)	1	0.010	0.88	0.052	0.15	0.32	0.57	2.5	0.50
Se × Ts	1	0.022	0.83	0.004	0.66	0.069	0.79	3.3	0.45
Error = rep(Se × Ts)	4	0.40		0.017		0.81		4.6	
Tank trajectory (Tt)	1	2.33	0.016	0.056	0.15	1.9	0.036	1.6	0.45
Tt × Se	1	0.009	0.88	0.056	0.15	0.84	0.15	0.36	0.72
Tt × Ts	1	0.36	0.34	0.10	0.055	0.16	0.53	2.2	0.38
Tt × Se × Ts	1	0.29	0.38	0.001	0.86	0.20	0.48	2.1	0.38
Error = M.S.E.	50	0.38		0.026		0.40		2.7	

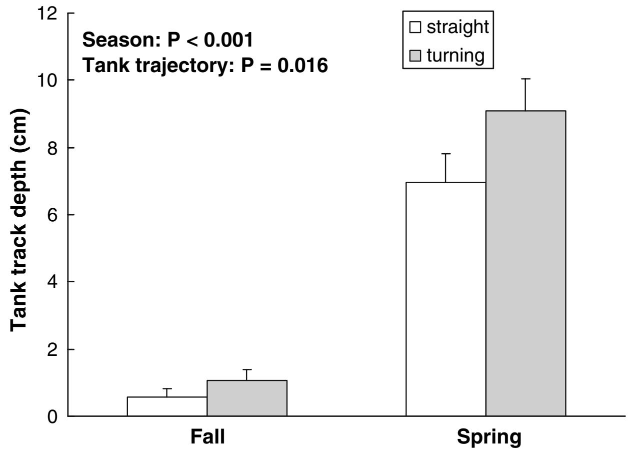

Fig. 4 The effects of different types of tank driving on the depth of tank tracks (all error bars represent + 1 SE)

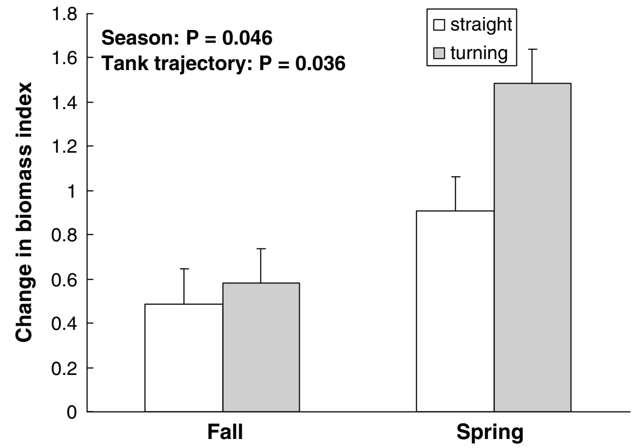

Fig. 6 The effects of different types of tank driving on the change in the biomass index between control and track plots (all error bars represent + 1 SE)

was still somewhat surprising to find that sites dominated by introduced C_3 grasses showed the greatest vegetation change after vehicular disturbance. This result is consistent with the suggestion that tillering graminoids show greater resistance and resilience to disturbance than graminoids with rhizomes (sod-forming grasses; Yorks and others 1997), because introduced C_3 grasses such as *Bromus inermis* and *Poa pratensis* tend to be strongly rhizomatous (Great Plains Flora Association 1986). Native prairie plants also tend to have deeper root systems than introduced species, which may help prairie plants to survive soil disturbance (Wilsey and Polley 2006). For example, *Andropogon gerardii* and *Schizachyrium scoparium* both have fairly deep root systems, with the following percentage of fine root biomass at different depths in Minnesota: 57% and 64%, respectively, at 0–24 cm; 27% and 25% at 24–56 cm; and 16% and 11% at 56–96 cm (Craine and others 2002). *Poa pratensis* has 99% of its fine roots in the top 24 cm of soil, with the remaining 1% located at 24–56 cm (Craine and others 2002). We cannot directly compare the root growth of *Bromus inermis* to these other species because no study grows all of the species under similar conditions. However, in two different soil types in Wisconsin, *B. inermis* had 91–93% of its root biomass at 0–20 cm and 9–7% at 20–41 cm (Lamba and others 1949).

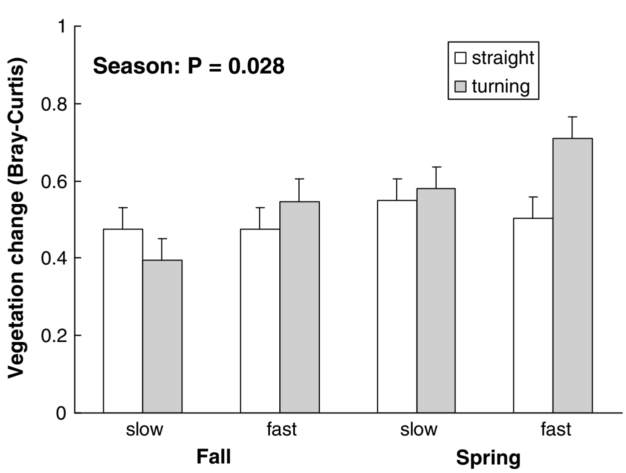

Fig. 5 The effects of different types of tank driving on Bray-Curtis vegetation change (all error bars represent + 1 SE)

This study represents the only experiment we are aware of that examines the interactions among multiple types of vehicular disturbance on plant species composition. Overall, the interactions among multiple types of vehicular disturbance did not have significant effects, even though there was a nearly significant interaction between tank speed and turning on vegetation change. We are somewhat surprised to find that driving at different times of the year under different soil moisture conditions never significantly changed the effects of turning or driving fast, especially since previous studies have found evidence suggesting that vegetation damage in wet conditions is especially severe when vehicles are turning (Anderson and others 2006). However, the turns we examined were not as sharp as in some other studies, and vegetation damage was so severe when tanks were driving straight in wet spring conditions that damage could not become much more severe by turning.

We suspect soil moisture conditions affected the results more than the different amounts of time between the fall and spring disturbances and sampling. Vegetation had approximately the same amount of time to recover after both fall and spring disturbances because both disturbances occurred during the same cold, dormant period. The fall disturbance occurred shortly before the end of the growing season and the spring disturbance occurred at the beginning of the next growing season, shortly before temperatures below −3° C either killed or retarded the growth of plants

(NCDC and NOAA 2005). The importance of soil moisture conditions is also suggested by previous studies that show vehicles decrease biomass and vegetation percent cover the most in wet conditions (Payne and others 1983; Althoff and Thien 2005; Anderson and others 2006). We therefore suggest that wet soil conditions played the greatest role in increasing disturbance intensity and vegetation change in our study.

Even though there was a positive relationship between disturbance intensity and vegetation change, we did not find any indication of a disturbance-intensity threshold whereby short-term vegetation change increased dramatically beyond some level of disturbance. This suggests that vegetation changes will initially respond in a linear manner to disturbance intensity in this tallgrass prairie habitat. However, the longer term recovery may be nonlinear if sites below some disturbance-intensity threshold recover over time and sites above some disturbance-intensity threshold do not recover (Scheffer and others 2001; Suding and Gross 2006). Vegetation in our study had approximately two months of growing season to recover after disturbance and it did not appear that either biomass or species composition had completely recovered by this time.

In conclusion, because of the linear relationship between disturbance intensity and vegetation change, there does not appear to be any level of vehicular disturbance intensity below which no vegetation change will occur. However, vegetation change can be kept to a minimum primarily by limiting vehicular disturbance in wet conditions and by minimizing turning. It also appears that introduced C_3 grasses had not recovered well shortly after vehicular disturbance. A mechanistic study of the traits underlying the different responses to disturbance between native tillering grasses and introduced sod-grasses is needed, and further studies are needed to determine whether these grasses show the same response to disturbance in other locations. It would also be interesting to examine the effects of different types of tank driving on vegetation change at different spatial scales (Dale and others 2005), in more hilly terrain, and after repeated passes (although Braunack and Williams [1993] find that one tank pass while turning is equivalent to at least eight passes while driving straight). However, for single passes in gently sloping grassland regions, it appears advisable to minimize vehicular disturbance during wet periods, and to maximize the abundance of native tillering grasses and limit the abundance of sod-forming, introduced C_3 grasses.

Acknowledgments We thank Chris Otto and Phil Woodford for help with logistics at Fort Riley, Thuy Bui for field work, and Terence Yorks and two anonymous reviewers for comments. Funding was provided by a grant from the Upper Middle Mississippi Valley (UMMV) Cooperative Ecosystems Studies Unit (CESU) Agreement W9132T-06-2-0007.

References

Althoff PS, Thien SJ (2005) Impact of M1A1 main battle tank disturbance on soil quality, invertebrates, and vegetation characteristics. Journal of Terramechanics 42:159–176

Anderson AB, Howard H, Ayers P, Butler C, Wu C, Woodford P, Otto C (2006) Soil property influence on military vehicle impacts. American Society of Agricultural and Biological Engineers, Portland, Oregon, USA: paper number 061183

Anderson AB, Palazzo AJ, Ayers PD, Fehmi JS, Shoop S, Sullivan P (2005) Assessing the impacts of military vehicle traffic on natural areas. Introduction to the special issue and review of the relevant military vehicle impact literature. Journal of Terramechanics 42:143–158

Braunack MV, Williams BG (1993) The effects of initial soil water content and vegetative cover on surface soil disturbance by tracked vehicles. Journal of Terramechanics 30:299–311

Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27:325–349

Craine JM, Wedin DA, Chapin FS, Reich PB (2002) Relationship between the structure of root systems and resource use for 11 North American grassland plants. Plant Ecology 165:85–100

Dale V, Druckenbrod DL, Baskaran L, Aldridge M, Berry M, Garten C, Olsen L, Efroymson R, Washington-Allen R (2005) Vehicle impacts on the environment at different spatial scales: observations in west central Georgia, USA. Journal of Terramechanics 42:383–402

Debusk WF, Skulnick BL, Prenger JP, Reddy KR (2005) Response of soil organic carbon dynamics to disturbance from military training. Journal of Soil and Water Conservation 60:163–171

Foster JR, Ayers PD, Lombardi-Przybylowicz AM, Simmons K (2006) Initial effects of light armored vehicle use on grassland vegetation at Fort Lewis, Washington. Journal of Environmental Management 81:315–322

Garten CT Jr, Ashwood TL, Dale VH (2003) Effect of military training on indicators of soil quality at Fort Benning, Georgia. Ecological Indicators 3:171–179

Goldberg DE, Rajaniemi T, Gurevitch J, Stewart-Oaten A (1999) Empirical approaches to quantifying interaction intensity: Competition and facilitation along productivity gradients. Ecology 80:1118–1131

Great Plains Flora Association (1986) Flora of the Great Plains. University Press of Kansas, Lawrence, Kansas

Groffman PM, Baron JS, Blett T, Gold AJ, Goodman I, Gunderson LH, Levinson BM, Palmer MA, Paerl HW, Peterson GD, Poff NL, Rejeski DW, Reynolds JF, Turner MG, Weathers KC, Wiens J (2006) Ecological thresholds: The key to successful environmental management or an important concept with no practical application? Ecosystems 9:1–13

Halvorson JJ, McCool DK, King LG, Gatto LW (2001) Soil compaction and over-winter changes to tracked-vehicle ruts, Yakima Training Center, Washington. Journal of Terramechanics 38:133–151

Haugen LB, Ayers PD, Anderson AB (2003) Vehicle movement patterns and vegetative impacts during military training exercises. Journal of Terramechanics 40:83–95

Hayden BP (1998) Regional climate and the distribution of tallgrass prairie. Pages 19–34 In: Knapp AK, Briggs JM, Hartnett DC, Collins SL (eds) Grassland dynamics: Long-term ecological research in tallgrass prairie. Oxford, New York

Hedges LV, Gurevitch J, Curtis PS (1999) The meta-analysis of response ratios in experimental ecology. Ecology 80:1150–1156

Hirst RA, Pywell RF, Marrs RH, Putwain PD (2003) The resistance of a chalk grassland to disturbance. Journal of Applied Ecology 40:368–379

Hirst RA, Pywell RF, Putwain PD (2000) Assessing habitat disturbance using an historical perspective: The case of Salisbury Plain military training area. Journal of Environmental Management 60:181–193

Hobbs NT, Baker DL, Ellis JE, Swift DM, Green RA (1982) Energy- and nitrogen-based estimates of elk winter-range carrying capacity. Journal of Wildlife Management 46:12–21

Johnson FL (1982) Effects of tank training activities on botanical features at Fort Hood, Texas. The Southwestern Naturalist 27:309–314

Kaiser HF (1960) The application of electronic computers to factor analysis. Educational and psychological measurement 20:141–151

Knapp AK, Seastedt TR (1998) Grasslands, Konza Prairie, and long-term ecological research. In: Knapp AK, Briggs JM, Hartnett DC, Collins SL (eds) Grassland dynamics: Long-term ecological research in tallgrass prairie. Oxford, New York, pp 3–15

Kockelman WJ (1983) Introduction. In: Webb RH, Wilshire HG (eds) Environmental effects of off-road vehicles. Springer-Verlag, New York, USA, pp 1–11

Lamba PS, Ahlgren HL, Muckenhirn RJ (1949) Root growth of alfalfa, medium red clover, bromegrass, and timothy under various soil conditions. Agronomy Journal 41:451–458

Leis SA, Engle DM, DML Jr, Fehmi JS (2005) Effects of short- and long-term disturbance resulting from military maneuvers on vegetation and soils in a mixed prairie area. Environmental Management 36:849–861

Li Q, Ayers PD, Anderson AB (2007) Prediction of impacts of wheeled vehicles on terrain. Journal of Terramechanics 44:205–215

Littell RC, Stroup WW, Freund RJ (2002) SAS for linear models, 4th edition. SAS Institue Inc., Cary, NC, USA

Milchunas DG, Schulz KA, Shaw RB (2000) Plant community structure in relation to long-term disturbance by mechanized military maneuvers in a semiarid region. Environmental Management 25:525–539

NCDC, NOAA (2005) April 2005 Kansas Climatological Data from National Climatic Data Center, Thomas R. Karl director. Volume 119 (4)

Palazzo AJ, Jensen KB, Waldron BL, Cary TJ (2005) Effects of tank tracking on range grasses. Journal of Terramechanics 42:177–191

Payne GF, Foster JW, Leininger WC (1983) Vehicle impacts on northern Great Plains range vegetation. Journal of Range Management 36:327–331

Philippi TE, Dixon PM, Taylor BE (1998) Detecting trends in species composition. Ecological Applications 8:300–308

Quist MC, Fay PA, Guy CS, Knapp AK, Rubenstein BN (2003) Military training effects on terrestrial and aquatic communities on a grassland military installation. Ecological Applications 13:432–442

Scheffer M, Carpenter S, Foley JA, Folkes C, Walker B (2001) Catastrophic shifts in ecosystems. Nature 413:591–596

Schläpfer F., Schmid B (1999) Ecosystem effects of biodiversity: A classification of hypotheses and exploration of empirical results. Ecological Applications 9:893–912

Shaw RB, Diersing VE (1990) Tracked vehicle impacts on vegetation at the Pinon Canyon Maneuver Site, Colorado. Journal of Environmental Quality 19:234–243

Smith B, Wilson JB (1996) A consumer's guide to evenness indices. Oikos 76:70–82

Sokal RR, Rohlf FJ (1995) Biometry, Third edition. W.H. Freeman and Company, New York

Stevens J (1996) Applied multivariate statistics for the social sciences. Lawrence Erlbaum Associates, Mahwah, NJ, USA

Suding KN, Gross KL (2006) The dynamic nature of ecological systems: Multiple states and restoration trajectories. In: Falk DA, Palmer MA, Zedler JB (eds) Foundations of restoration ecology. Island Press, USA pp. 190–209

Suding KN, Gross KL, Houseman GR (2004) Alternative states and positive feedbacks in restoration ecology. Trends in Ecology and Evolution 19:46–53

Tasser E, Mader M, Tappeiner U (2003) Effects of land use in alpine grasslands on the probability of landslides. Basic and Applied Ecology 4:271–280

Temperton VM, Hobbs RJ, Nuttle T, Halle S (eds) (2004) Assembly rules and restoration ecology: bridging the gap between theory and practice. Island Press, Washington, DC, USA

Vertegaal PJM (1989) Environmental impact of Dutch military activities. Environmental Conservation 16:54–64

Wang G, Gertner G, Anderson AB, Howard H, Gebhart D, Althoff D, Davis T, Woodford P (2007) Spatial variability and temporal dynamics analysis of soil erosion due to military land use activities: Uncertainty and implications for land management. Land Degradation and Development 18:519–542

Watts SE (1998) Short-term influence of tank tracks on vegetation and microphytic crusts in shrubsteppe habitat. Environmental Management 22:611–616

Weaver T, Dale D (1978) Trampling effects of hikers, motorcycles and horses in meadows and forests. Journal of Applied Ecology 15:451–457

Wilsey BJ, Polley HW (2006) Aboveground productivity and root-shoot allocation differ between native and introduced grass species. Oecologia 150:300–309

Wilson SD (1988) The effects of military tank traffic on prairie: A management model. Environmental Management 12:397–403

Yorks TP, West NE, Mueller RJ, Warren SD (1997) Toleration of traffic by vegetation: Life form conclusions and summary extracts from a comprehensive data base. Environmental Management 21:121–131