

Resource regulation by a twig-girdling beetle has implications for desertification

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Abstract. 1. Resource regulation by insects is the phenomenon by which herbivory enhances resources for the progeny of the herbivore. This report provides an example of resource regulation with implications for desertification in the Chihuahuan Desert of North America.

2. Female *Oncideres rhodosticta* beetles chew girdles around mesquite (*Prosopis glandulosa*) stems before ovipositing in those stems. The mesquite plants respond by producing compensatory stems below the girdle. Mesquite volume was significantly correlated with the total number of beetle girdles across a suite of low shrub density grassland and high shrub density dune sites, and plants in dune sites had more old and new girdles than mesquite in grasslands.

3. Smaller, younger shrubs in grassland responded more vigorously to girdling than did larger, older shrubs in dune landscapes. Stems on shrubs within grassland produced significantly more and longer compensatory stems per girdle than stems on shrubs in dunes. Soil capture by individual plants positively correlated with stem density, and stem density is increasing in the younger plants as a response to beetle damage.

4. This study suggests that the interaction between *O. rhodosticta* and mesquite is an example of resource regulation that increases the stem density and soil capture ability of mesquite. Because the conversion of productive grasslands to mesquite dune landscapes is one of the most important drivers of desertification in the Chihuahuan Desert, feedbacks between organisms that promote an increase in the size and soil capture ability of mesquite may exacerbate desertification.

Key words. Chihuahuan Desert, landscape conversion, *Oncideres rhodosticta*, plant–herbivore interactions, *Prosopis glandulosa*.

Introduction

A potential outcome of herbivore and plant interactions is that plant resource quality will increase following herbivory (Owen, 1980; Craig *et al.*, 1986). Plants may produce new shoots to compensate for photosynthetic area loss (Polk & Ueckert, 1973; McNaughton, 1983), which reduces the mean stem age of the affected plant and provides a younger more vigorous resource to herbivores (Craig *et al.*, 1986; Price, 1991). This phenomenon has been defined as *resource regulation* when the interaction between the plant and an insect herbivore maintains or promotes resources for the herbivore's offspring on an individual plant (Craig *et al.*, 1986).

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Mesquite (*Prosopis glandulosa*) is a deep-rooted legume that is extremely heterogeneous in its growth form. Mesquite can take the form of small shrubs, large trees, and any variation between. While mesquite is not known to produce secondary plant compounds discouraging herbivory, it has large thorns and exudes a thick sap when its parenchyma is disturbed (Whitford *et al.*, 1978).

Mesquite has greatly increased in local density in the Chihuahuan Desert of the southwestern United States and northern Mexico, and the conversion of grasslands to shrub-dune landscapes (Fig. 1a) in this region is a case study of anthropogenically driven desertification (Buffington & Herbel, 1965; Brown & Archer, 1989; Dick-Peddie, 1993; Whitford, 2002). Mesquite shrubs were historically constrained to riparian areas and arroyos, but have spread into former grasslands following the introduction of domestic cattle. Cattle overstocking in the



Fig. 1. (a) Intact Chihuahuan Desert grassland at the Jornada LTER, southern New Mexico, U.S.A. (b) Historic Chihuahuan Desert grassland that has been converted to a stable mesquite dune landscape due to cattle overstocking and drought, Jornada LTER, southern New Mexico, U.S.A. (c) Mesquite (*Prosopis glandulosa*) shrub girdled by a female *O. rhodosticta* (girdle in white oval), with four compensatory growth stems below the disturbance in incipient dune site, Jornada LTER, New Mexico. Mesquite twig girdler beetle, *Oncideres rhodosticta* (Cerambycidae) (inset).

1880s, concurrent with a severe drought, drastically reduced the cover and extent of grasses (Buffington & Herbel, 1965; Dick-Peddie, 1993). Livestock used mesquite seed pods as an alternate food source when grass forage was depleted, and shrub seeds that germinated from cattle dung would have faced reduced competition from drought-stressed, overgrazed grasses (Archer, 1989; Van Auken & Bush, 1990; Kramp *et al.*, 1998).

Once mesquite became established in grasslands, dune landscapes (Fig. 1b) formed when windblown soil became trapped in the stem matrix of individual shrubs (Van de ven *et al.*, 1989; Whitford, 2002). Mesquite is a winter deciduous shrub, and as high winds are typically more prevalent in the spring, soil capture by mesquite is a function of stem density rather than foliage presence or absence. Plant anchored dunes are physically stable, and dune interspaces are hostile sites for grass and forb recolonisation. Dune interspaces are unfavourable for grasses as they are characterised by higher albedo, less litter, and lower labile carbon and nitrogen compared with soils under mesquite plants or in undisturbed grasslands (Schlesinger *et al.*, 1990; Killgore, 2004). Although mesquite expansion into grasslands was probably instigated by the dispersal of seeds by cattle, processes increasing mesquite plant stem density are responsible for dune formation (*sensu* Van de ven *et al.*, 1989).

Oncideres rhodosticta (Cerambycidae) (Fig. 1c inset) is a twig girdling beetle that utilises mesquite stems for oviposition and larval development sites. Female beetles chew girdles around mesquite stems (Fig. 1c), severing the phloem and xylem, disrupting water and nutrient transport, and killing the affected stem above the girdle (Polk & Ueckert, 1973). The beetle then oviposits distally from the girdle, which protects its egg from being coated in sap flowing up the stem in response to the girdle (Whitford *et al.*, 1978; Dussourd & Eisner, 1987). Female beetles girdle and oviposit in only one branch, and have been reported to lay 8.1 eggs per stem (Ueckert *et al.*, 1971). In one of only three published reports on the ecology of *O. rhodosticta*,

Polk and Ueckert (1973) report a mean density of 4.7 beetles per mesquite plant in the Trans-Pecos region of Texas. Emergent adults kept in field cages lived only 20–30 days, and the longest living beetle survived 45 days (Polk & Ueckert, 1973). Eggs hatch within a month of oviposition and larvae over-winter by feeding on the dying mesquite stem (Ueckert *et al.*, 1971). The larvae pupate within the stem, and adults emerge in early autumn, mate, and oviposit in fresh mesquite stems prior to the winter frost (Ueckert *et al.*, 1971).

Early literature suggested that *O. rhodosticta* could be used as biocontrol agents for mesquite and aid in grassland restoration, because girdling kills impacted stems (Ueckert *et al.*, 1971; Polk & Ueckert, 1973). Mesquite responds to *O. rhodosticta* girdling behaviour, however, by producing new stems from nodes below the girdle, compensating for photosynthetic area loss on the dead girdled stem, and potentially increasing the stem density of individual plants (Whitford *et al.*, 1978). The response of mesquite to *O. rhodosticta* girdling suggests that this interaction is an example of resource regulation.

No biogeographic information exists by which to compare the distributions of mesquite and *O. rhodosticta*. Our extensive field surveys of beetles on impacted mesquite, in concert with the scant literature on this beetle suggest that these species co-occur at least from Big Bend National Park in Texas in the south, to the northern extent of the Chihuahuan Desert in New Mexico and west to the Chiricahua Mountains in Arizona, U.S.A. (Linsley *et al.*, 1961). This conservative estimate of the concurrent distribution of mesquite and *O. rhodosticta* represents an area of $\approx 25\,000\,000$ ha.

Hypotheses for resource regulation and desertification

The response of mesquite shrubs to *O. rhodosticta* disturbance is a potential resource regulation interaction structuring

mesquite dune landscapes and serves as a desertification feedback. *O. rhodosticta* herbivory may increase the stem density of mesquite and provide more resources for the next generation of beetles. Specifically, this research sought to investigate if there are differences in mesquite response to *O. rhodosticta* herbivory between stable dune landscapes and grassland landscapes. If a substantial number of new stems develop in response to beetle girdling in grassland areas, the stem density of individual mesquite shrubs will increase. This process may enable shrubs to more efficiently capture wind-blown soil and promote dune formation, a driver of desertification in the Chihuahuan Desert. This study reports that the interaction between the twig-girdling beetle *Oncideres rhodosticta* and mesquite is an example of resource regulation, and that the response of mesquite has implications for desertification in the Chihuahuan Desert.

Materials and methods

Field sites

The interaction between *O. rhodosticta* and *P. glandulosa* was studied at four sites in the Chihuahuan Desert of southern New Mexico (Table 1). Sites were selected on the basis that they supported native Chihuahuan Desert grassland with low mesquite density (grassland) and high density mesquite dune landscapes (dune). Grassland plots were all intact, Chihuahuan Desert grassland, characterised by alkali sacaton (*Sporobolus airoides*), burro grass (*Scleropogon brevifolius*), black-grama (*Bouteloua eriopoda*), and tabosa (*Hilaria mutica*) grasses, a variety of herbaceous annuals, cacti and mesquite. Dune plots were dominated by large mesquite-anchored dunes with few grasses or forbs in the interspaces between mesquite.

At each site, mesquite were sampled along random 10 m wide band-transects. Within each transect, at least 15 shrubs were sampled per plot, with the exception of the Jornada-LTER dune site, which fell below this number due to changes in terrain that would have compromised sampling plants from a consistent dune landscape (Table 1). Each mesquite was sampled for total number of new (<1 year) and old (>1 year) girdles per plant, density of stems per plant, and plant volume. Stem density was

Table 1. Study sites within the Chihuahuan Desert of southern New Mexico where *O. rhodosticta* girdling on mesquite was characterised. Plots at the Jornada-LTER were utilised in an experiment to compare the compensatory growth response of mesquite shrubs with girdling between grassland and dune landscapes.

Study site	Plot	<i>n</i> plants	Shrub density (mesquite ha ⁻¹)
Armendaris Ranch	Dune	15	300.0
	Grassland	15	40.0
Corralitos Ranch	Dune	15	361.9
	Grassland	15	9.3
Jornada-LTER	Dune	12	600.0
	Grassland	27	333.3
Nutt Grassland	Dune	30	478.0
	Grassland	30	3.9

determined by counting the number of stems protruding at the soil surface within a 0.5 m² frame over each plant (Daubenmire, 1968). Volume (m³) of mesquite shrubs was calculated by measuring the height and two perpendicular diameters of each shrub. Because the shape of mesquite plants is highly variable, plant and soil-dune volume was determined by calculating the volume of an oblate spheroid. The formula used is as follows:

$$\frac{4}{3}\pi\left[\frac{(d_1+d_2)}{2}\right]^2 ht$$

where d_1 and d_2 represent the two perpendicular diameter measurements and ht is the height of the mesquite plant.

Fate of individual girdles

The response of individual mesquite stems to *O. rhodosticta* girdling was monitored at the stem-dense dune (mean 29.2 ± 3.2 SE stems m⁻²) and stem-sparse grassland (mean 17.2 ± 2.2 SE stems m⁻²) plots within the USDA-ARS Jornada Experimental Range-LTER (Table 1). The two plots are ≈3 km from each other and were selected to ensure that differences in mesquite response to *O. rhodosticta* disturbance were not attributable to landform or precipitation differences between sites. The Jornada grassland plot had the highest mesquite density of any grassland in the study, but the shrubs were younger and smaller than the shrubs in the Jornada dune plot, implicating this area as an incipient dune landscape. By comparing the response of mesquite to girdling in a stable dune area to mesquite in an incipient dune area (high density of smaller, younger mesquite), the results presented from this aspect of the study may speak to the importance of this plant/insect interaction as a desertification feedback.

Mesquite stems with fresh girdles were marked with pipe cleaners and aluminium tags below the beetle disturbance in September 2003 to coincide with the girdler's oviposition behaviour (Polk & Ueckert, 1973). Three *O. rhodosticta* oviposited stems were marked (Fig. 1c) on each of 10 mesquite shrubs in the dune plot and 10 shrubs in the grassland plot ($n = 3$ stems × 10 shrubs per site). Shrubs were selected by marking the first plants encountered along randomly generated transects. Marked stems were re-censused 14 months later in November 2004 for the number and length of new stems produced from the nodes below, and closest to, the marked girdles.

The volume of soil captured per mesquite shrub was determined by measuring the height of the soil mound beneath each plant, and two perpendicular diameters of the soil mound beneath each shrub. The total volume of soil captured by individual plants was then determined using the formula for an oblate spheroid presented above.

Statistical analysis

Volume/girdle relationships were evaluated using Pearson's correlation coefficient (r) across the four landscapes. Spearman's rank correlation (r_s) was used to determine the relationship between plant volume and number of girdles when only considering the tagged plants at the Jornada landscape, and for analysis of

stem density versus captured soil at the Jornada due to smaller sample size ($n = 20$). One-way analysis of variance (ANOVA) was employed to compare means of dune and grassland plots when assumptions of variance equality were met. The number of compensatory stems per girdle, and the mean lengths of those stems were heteroskedastic, and were log transformed to meet the assumptions of ANOVA.

Results

Plant condition

Mesquite plants in dune plots were significantly larger in volume than plants in grassland plots (ANOVA, $F_{1,156} = 3.87$, $P = 0.05$) (Table 2). The stem density of mesquite plants in dune sites was also higher than grassland shrubs (Kruskal–Wallis, $\chi^2 = 24.79$, $P < 0.001$) (Table 2).

Mesquite shrub volume (m^3) positively correlated with the number of old *O. rhodosticta* girdles ($r = 0.49$, $P < 0.001$, $n = 173$) and new girdles per shrub ($r = 0.43$, $P < 0.001$, $n = 161$) (Fig. 2a,b). The same pattern was also observed when only the Jornada plots with tagged girdles were considered ($r_s = 0.69$, $P < 0.001$, $n = 20$).

Effect of beetles on mesquite

There were more old and new *O. rhodosticta* girdles on shrubs in the dune sites than the grassland sites (Table 2: old girdles, Kruskal–Wallis, $\chi^2 = 9.08$, $P < 0.003$; new girdles, $\chi^2 = 3.65$, $P = 0.056$). Additionally, the marked mesquite at the Jornada dune plot hosted more old and new girdles than mesquite at the Jornada grassland plot (ANOVA old girdles, $F_{1,18} = 3.34$, $P = 0.08$; new girdles, $F_{1,18} = 54.91$, $P < 0.001$).

The young mesquite in the Jornada grassland produced more new stems per girdle after 1 year than older shrubs in dunes (Fig. 3a, grassland, 2.30 ± 0.51 new stems per girdle per plant; dunes, 0.80 ± 0.19 dunes: $F_{1,58} = 6.91$, $P = 0.01$), and compensatory stems were longer in the grassland than in dunes (Fig. 3b, 19.75 ± 3.07 cm grassland; 6.57 ± 1.77 cm dunes: $F_{1,58} = 7.78$, $P = 0.007$). The volume of plant-captured soil was greater in the dune ($145.18 \pm 46.73 m^3$) than in the grassland ($2.74 \pm 0.94 m^3$), and the volume of plant-captured soil positively correlated with shrub stem density (Fig. 4, $r_s = 0.58$, $P < 0.01$).

Table 2. Characteristics of mesquite plants measured for *O. rhodosticta* girdling in the Chihuahuan Desert of southern New Mexico. Dune sites represent high density mesquite landscapes while grassland sites represent low mesquite density grassland.

Plant characteristic	Dune sites	Grassland sites
Volume ($m^3 \pm SE$)	$40.29 \pm 4.80^{***}$	27.20 ± 1.21
Stems m^{-2} ($\pm SE$)	$27.48 \pm 4.40^{**}$	17.07 ± 1.58
Old girdles (>1 year $\pm SE$)	$7.69 \pm 1.32^{***}$	4.09 ± 0.53
New girdles ($\pm SE$)	$3.35 \pm 1.16^*$	0.77 ± 0.18

* $P < 0.1$, ** $P = 0.05$, *** $P < 0.01$.

Discussion

Larger mesquite shrubs in dune landscapes had more old and fresh *O. rhodosticta* girdles than mesquite in grasslands across the sites studied. The greater number of old girdles on mesquite in dunes, coincident with higher stem densities at these landscapes, suggests that historic herbivory by *O. rhodosticta* increased the stem density of mesquite. The observation that dune mesquite also experienced more new *O. rhodosticta* herbivory is probably due to greater oviposition site availability afforded by stem-dense shrubs. The positive correlations between mesquite volume with both old and new girdles also suggests a feedback loop where girdling increases stem density. Stem dense shrubs provide greater resources to emerging female *O. rhodosticta* the following year, and the plant responds by growing more new stems. There may be a threshold where this feedback breaks down, as the results of this study demonstrate that larger, older mesquite respond less vigorously to girdling than smaller, younger plants.

The strong response of mesquite at the grassland site to *O. rhodosticta* girdles supports the resource regulation hypothesis (Craig *et al.*, 1986). Beetles are directly contributing to the increase of resources (oviposition sites and food) for the next generation of beetles that will emerge on that same plant. This interaction has also been reported between a tropical tree and *O. albomarginata*, whereby the tree regenerates branches after damage by the beetle, demonstrating that resource regulation has been established within this genus (Uribe-Mu & Quesada, 2006). The historic evidence for intense girdling on dune mesquite supports the hypothesis that girdling leads to dune formation, because an incidental consequence of *O. rhodosticta* girdling is that mesquite stem density increases, enabling

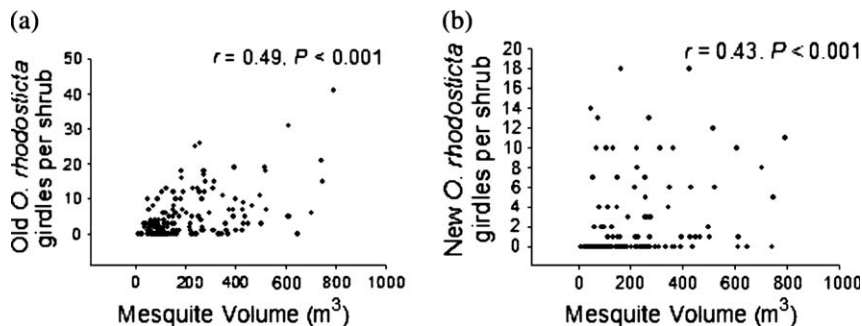
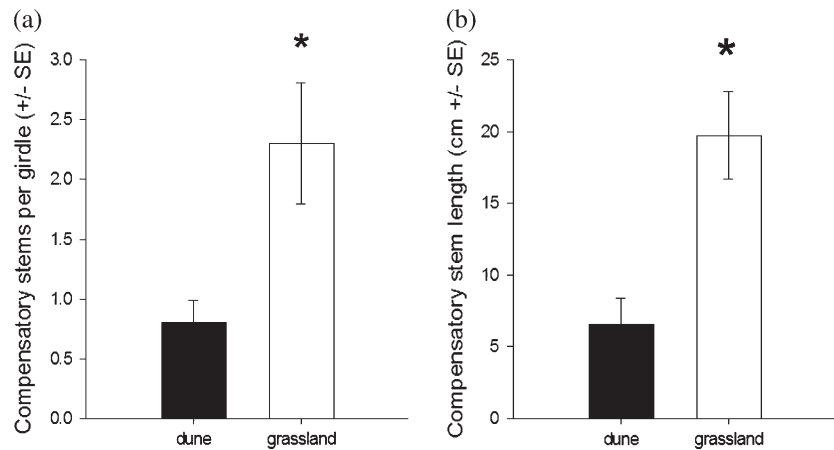


Fig. 2. (a) Correlation of mesquite shrub volume (m^3) with old (>1 year) beetle girdles ($r = 0.43$, $P < 0.001$, $n = 173$). (b) Correlation of mesquite shrub volume (m^3) with new (<1 year) beetle girdles ($r = 0.49$, $P < 0.001$, $n = 161$).

Fig. 3. (a) Difference in mean number of compensatory growth stems per marked *O. rhodosticta* girdle \pm SE per mesquite shrub between dune site (filled bars) and grassland site (open bars), (Kruskal–Wallis, $\chi^2 = 5.51$, d.f. = 1, $P = 0.003$). (b) Difference between mesquite in dunes (filled bars) and mesquite in grassland (open bars) in mean length of compensatory growth stems (cm \pm SE) per marked *O. rhodosticta* girdle per mesquite shrub, (Kruskal–Wallis, $\chi^2 = 9.14$, d.f. = 1, $P < 0.02$). Asterisks denote statistical difference between bars.



older, larger plants to capture more soil and form stable dune landscapes (Archer *et al.*, 1988, Van de ven *et al.*, 1989). The ≈ 70 -fold difference in soil capture by plants in dunes versus incipient dunes, and the correlation of soil capture and stem density, provide evidence that increases in plant stem density increase the soil capture ability of individual plants (Van de ven *et al.*, 1989).

Implications for desertification

Desertification is the degradation of arid landscapes caused by anthropogenic influences and climatic variability (Williams & Balling, 1996). Desertified systems are characterised by less biodiversity, increased erosion, and limited agricultural productivity compared with undesertified ecosystems (Whitford, 2002). This ongoing global process is estimated to affect over 30% of terrestrial ecosystems and up to 750 million people (Williams & Balling, 1996).

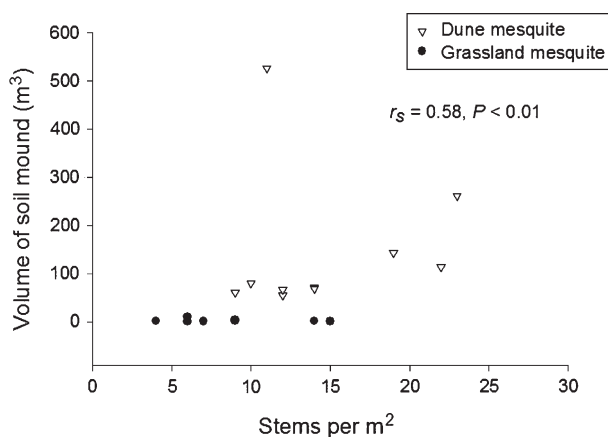


Fig. 4. Correlation of mesquite stem density (stems m⁻² shrub area) with the volume of soil captured by individual mesquite plants (soil mound). Black symbols represent mesquite shrubs in grassland; white symbols denote mesquite in dune landscape.

The conversion of grasslands to mesquite shrublands is one of the most important factors contributing to desertification in the Chihuahuan Desert. Cattle foraging reduced grass cover, which lessened competition between grasses and mesquite seeds (Van Auken & Bush, 1987, 1989). Mesquite seeds were also dispersed by cattle and deposited in their nutrient-rich dung (Kramp *et al.*, 1998). While these observations explain the spread of mesquite, the resource regulation behaviour of *O. rhodosticta* provides a mechanism by which individual mesquite plants could increase in stem density and form dunes faster than their normal growth pattern would allow, and underscores the importance of considering the role of native organisms in desertification and landscape change.

Acknowledgements

We thank V. Mathis and E. Druskat for field assistance and T. Turner and T. Waddell for access to the Armendaris Ranch. We sincerely thank Dr B.A. Hungate, Dr P.W. Price and Dr G.A. Sword as well as anonymous reviewers for valuable comments on previous drafts of the manuscript. Research was funded by grants to Dr W.G. Whitford from the International Arid Land Consortium and an interagency agreement between the United States Environmental Protection Agency Office of Research and Development and the USDA-ARS Jornada Experimental Range.

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Accepted 4 April 2007

First published online 24 January 2008