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THE PARADOX OF MESQUITES (Prosopis spp.):
INVADING SPECIES OR BIODIVERSITY ENHANCERS?

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Resumen: Las zonas áridas y semiáridas presentan una gran diversidad de especies y están sujetas a un uso intenso, principalmente de ganadería extensiva. La expansión de las especies leñosas hacia los pastizales, conlleva un decrecimiento en el valor de las tierras para ganadería pues se presenta la necesidad de controlar arbustos, lo que en el largo plazo no tiene buenos resultados. En este artículo se presenta una revisión bibliográfica de la importancia ecológica de las especies del género Prosopis (mesquites); se recopiló información de todas las especies asociadas a mesquite (ca. 208 géneros y alrededor de 660 especies de diversos táxones) y se propone la conservación de éstos para mantener la diversidad de las especies asociadas. Además, se resalta la importancia del mesquite como una especie clave para mantener el balance de nitrogéne como y carbono en los suelos de las zonas áridas y semiáridas. Concluimos que la conservación de los mesquites debe tomarse en cuenta especialmente en las áreas en las que se pretende erradicarlo para introducir pastizales.

Palabras Clave: Zonas áridas, mesquites, manejo de pastizales, hábitat de fauna, incremento de leñosas.

Abstract. Arid and semi-arid environments contain relatively high species diversity and are subject to intense use, in particular extensive cattle grazing. The expansion of perennial species into the grasslands decreases the value of the rangeland, because it makes necessary to control the shrubs, which is not practical in the long term. This paper is a bibliographic review of the ecological importance of the Prosopis (mesquite) genus. We compiled information on all of the species associated with mesquite (ca. 208 genera and 660 species from different taxa) and we propose that it is important to conserve the mesquites in order to maintain the diversity of the other associated species. We also stress the importance of mesquite as a keystone species in the balance of nitrogen and carbon in the arid and semiarid environments soils. We conclude that the conservation of the mesquites is very relevant, in particular in areas where people want to remove them and convert the environment to grasslands.

Key words: Arid environments, mesquites, rangeland management, wildlife habitat, encroachment of woody species.

Arid and semi-arid environments contain relatively high species diversity (Redford et al., 1990) that decreases with increasing aridity (Huenneke and Noble, 1996). For example, the richest apiflora in the world is along the Mexico-USA border, with close to 900 species of solitary bees (Ayala et al., 1993). Mexican xerophilous scrub and grasslands contain ca. 6 000 plant species (20% of total Mexican flora; Reddowski, 1988) and Mexican desert scrub alone contains ca. 206 bird species (Escalante et al., 1979). Biotic and abiotic resources in these environments are scarce and patchily distributed during most of the year, largely depending on variable rainy periods (Noy-Meir, 1973). Spatial and temporal variation in rainfall, coupled with high average temperatures and differing soil textures, give rise to increased environmental heterogeneity which influences species diversity (Pianka, 1967; Rosenzweig and Winakur, 1969). Since environmental conditions are largely variable, net primary productivity are low (6 000-40 000 kg ha'') and the distribution and abundance of higher trophic levels are limited (Noy-Meir, 1973; Huenneke and Noble, 1996). Because of this relatively high species diversity, there is increasing concern on the conversion of
the arid environments that, for instance, may lead to desertification with a consequent loss of species diversity (Huenneke and Noble, 1996).

In particular, semi-arid grasslands and savannas of North America have recently undergone considerable change in structure and species composition (Buffington and Herbel, 1965). Especially, mesquite (Prosopis spp. L.) and juniper (Juniperus occidentalis Hook.) increase into southwestern savannas have had consequences on rangeland management. As a result, a wide array of research into the ecological impacts and control of encroaching species is being done. The increasing expansion of invading species has been attributed to a set of factors that range from drought, fire suppression, livestock grazing, and elevated atmospheric CO₂ concentrations (Archer et al., 1988). Habitat fragmentation and livestock grazing of arid environments have had ecological costs, including disruption of ecosystem function, alteration of ecosystem structure and loss of species diversity (Aizen and Feinsinger, 1994a; 1994b; Fleischner, 1994; but see Brown, and MacDonald, 1995). We must therefore assess the relative importance of species interactions in these environments in order to quantify the ecological costs of fragmentation and conversion in order to propose management and conservation strategies. In this sense, we compile information on species that are associated with Prosopis spp. (mesquite) and point out its role in ecosystem functioning. We highlight the importance of mesquite for many species, and propose its conservation as a means of maintaining species diversity in arid environments.

Mesquite Biology

All species of mesquite (the genus Prosopis), comprising 10 species in North America (Rzedowski, 1988) and 28 species in South America (Burkhart, 1976), should be regarded as important ecologically for arid environments in the Americas. Mesquite are aggressive invaders (Glendening, 1952), due to the production of long-lived seeds that germinate in a wide range of edaphic conditions, rapid root growth and a high potential for N, fixation (Glendening, 1952; Polley et al., 1994). However, mesquites have only recently expanded into grasslands from their characteristic mesic drainages and upland slopes, where they had been confined prior to livestock introductions during the Holocene (Polley et al., 1994). Mesquites are common and often the dominant species of these arid and semi-arid ecosystems, providing abundant resources at very specific times of the year (Simpson and Solbrig, 1977; Nilsen et al., 1991). In South America and western USA, mesquites always bloom in spring before the main rainy season (Simpson and Solbrig, 1977). In the southern Chihuahuan desert, during a three year period with widely varying precipitation (1984-1992; 138, 198.4 and 204.3 mm total annual rainfall, respectively), peak flowering periods in Prosopis glandulosa var. torreyana differed by less than ten days (Golubov, unpub. data). The phenological constancy of Prosopis species is in part due to a variety of adaptations to avoid water stress (e.g. phreatophytic root system, glabrous leaf surface, uncoupling of transpiration with atmospheric conditions, leaf size; Nilsen et al., 1989), which permit an escape from temporal and spatial unpredictability of rainfall. This buffers mesquites against environmental stochasticity, allowing them to grow and to reproduce in the driest seasons, providing resources for organisms that feed on their nectar, pollen, leaves, bark and fruits (Simpson et al., 1977).

Prosopis as a resource for animal and plant populations

Mesquites are used as a food, shelter and breeding area of a large number of invertebrate and vertebrate species (Table 1) having specific mutualistic interactions, such as those with solitary bees (e.g. Perdita spp.; Simpson et al., 1977). In the southern Chihuahuan desert in March, Prosopis glandulosa and Opuntia spp. are the only dominant plants producing abundant flowers, pollen and nectar. While only 7 bee genera visit Opuntia spp. flowers (mostly oligolectic bees; Mandujano et al., 1996), at least 20 genera visit P. glandulosa flowers (Lopez-Portillo et al., 1993; Golubov et al., 1999). Bird diversity has been shown to be higher in a Prosopis juliflora scrubland than in oak forests in western Mexico (Coe and Butler, 1999) and over 70 bird species are associated with mesquite scrublands in Mexico (Escalante et al., 1979). Few examples have addressed the change in avian communities after mesquite removal (Soutiere and Bouken, 1976; Reitzel, 1982; Smith et al., 1996; Nolte and Fulbright, 1997), but they all showed an increase in species diversity when mesquites were present when compared to grassland with no mesquites present. Reptile diversity and abundance has also shown to be higher in mesquite scrublands than in grasslands (Germano and Hungerford, 1981). Furthermore, mesquites are known to be visited by at least 200 species of herbivorous invertebrates (Cates and Rhaoades, 1977; Wisdom, 1991) and by over 150 species of solitary bees (Simpson et al., 1977). The habitat structure provided by areas with mesquites has been shown to influence arthropod diversity, mainly by providing architectural diversity (Gardner et al., 1995). In addition, mes-
Mesquite: invaders of biodiversity enhancers

Mesquites have important and often overlooked associations with nematodes (Freckman and Virginia, 1989) and symbiotic bacteria (Jenkins et al., 1987).

Besides the animals that feed directly or indirectly on mesquites, a diverse flora can be found growing beneath them, including many cacti and grasses (Cornejo-Oviedo et al., 1992; Suzan et al., 1994; Mandujano et al., 1998). Thus, mesquites, as other perennial species of arid and semi-arid environments, may function as potential nurse plants by passive facilitation, providing nutrients such as carbon (C) and nitrogen (N), lower temperatures, higher humidity, and different microtopographies under their canopies (Tiedeman and Klemmedson, 1973; Steenbergh and Lowe, 1977, Fulbright et al., 1995). All of the above mentioned characteristics are pivotal in successional processes from savannas to mesquite thorn woodlands (Archer et al., 1988). Given the high amount of interactions associated with Prosopis species, mesquites become ecologically important, especially providing a large amount of resources for many species.

**Prosopis as a key element in ecosystems**

At an ecosystem level, mesquites have been shown to have high net primary productivities (3,650 kg h⁻¹; Table 1. Order, number of families, genera and species (in parenthesis) that use different resources of *Prosopis* spp. in arid environments. B = branches, BA = bark, F = fruits, L = leaves, N = nectar, P = pollen, M = microenvironment. Country abbreviations ARG= Argentina (Monte Desert and Chaco) MEX= Mexico (Chihuahuan and Sonoran Deserts), IND= India, USA= United States (Texas Plains, Sonoran and Chihuahuan Desert), AFR= Africa, MAG= Madagascar, IR= Iran, EG= Egypt.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Fam</th>
<th>Genera</th>
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<th>Source</th>
<th>Country where was study conducted</th>
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<td>24(?)</td>
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<td></td>
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<td>Simpson and Solbrig, 1977</td>
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<td>L, N</td>
<td>Glendening, 1952; Mares et al., 1977;</td>
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<td>Wisdom, 1991; Rivera-Garcia and</td>
<td>USA, MEX, IND</td>
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<td>Nematoda</td>
<td>5</td>
<td>5(7)</td>
<td>R</td>
<td>Freckman and Virginia, 1989</td>
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<td>Orthoptera</td>
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<td>16(21)</td>
<td>L</td>
<td>Wisdom, 1991</td>
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<td>Reptilia</td>
<td>1</td>
<td>4(4)</td>
<td>M</td>
<td>Germano and Hungerford, 1981</td>
<td>USA</td>
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<td>Rodentia</td>
<td>7</td>
<td>16(28)</td>
<td>S, B</td>
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<td>L, P, N</td>
<td>Wisdom, 1991</td>
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Sharifi et al., 1982) and, as other Leguminosae, are able to fix atmospheric nitrogen. This Nfixation is by means of nodulating rhizobia, that improve soil fertility at different depths (Jenkins et al., 1987) and increases microbial diversity. Large amounts of N (2.500 kg N ha⁻¹) associated to litter decomposition outweighs denitrification processes under mesquite canopies (0.5 kg N ha⁻¹; Virginia et al., 1982, 1983). Given the scarcity of N in arid and semi-arid environments, the large amount of N fixed by Prosopis (45-150 kg N ha⁻¹ yr⁻¹) makes it a large contributor to the N budget of these environments (Johnson and Mayeux, 1990). The large amount of N found in mesquite “fertility islands” would suggest increases in shrub species growth associated to them. Barnes and Archer (1996) did not find a significant effect of a Prosopis glandulosa Torr. overstory on physiological characteristics and growth of 7 associated shrub species. In contrast, Tiedeman and Klemmedson (1973) showed that the Arizona cotontop (Trichachne californica) had 15 times greater N yields in mesquite soil although there was only a 3 fold difference in N between soils. Furthermore, there seems to exist some passive facilitation of Prosopis species towards other shrubs such as Celtis (Franco-Pizana et al., 1995). Apparently, conditions for conversion of organic N to available forms are more favorable in soil under mesquite than in adjacent soil. Even compared to other leguminous shrubs of arid and semi-arid environments such as ironwood (Olneya tesota) Nfixation was higher under mesquite individuals (Shearer et al., 1983).

In general, soil properties beneath mesquites have been shown to favor water infiltration, avoiding soil sealing after heavy rainfall (Virginia and Jarell, 1989) and their association with nematodes seems to be an important component of deep soil nutrient cycling (Freckman and Virginia, 1989). In addition, high annual litter to soil coupled with subsequent decomposition and a low leaching environment found under mesquite canopies provides an accumulation of CAand Mg (Virginia and Jarell, 1983). Shrub communities such as those associated to mesquite enhance spatial heterogeneity of soil resources and biomass (Connin et al., in press) creating "islands of fertility." The change from surface to deep C storage by shrubs leads to a greater long-term C storage in soils. However, not all shrubs act similarly, in particular, mesquite communities maintain total C levels while other shrubs such as the creosote bush (Larrea tridentata) have a net loss of soil C (Connin et al., in press). The increase of atmospheric CO2 concentration since the early 1800's has been said to have favored C3 over C4 plants, however, the loss of productive grasslands to shrublands appears to be unrelated to climatic fluctuations, and the conversion of grasslands to scrublands is largely attributed to anthropogenic disturbances (Connin et al., in press). At an ecosystem level mesquite dominated communities, by creating "islands of fertility" and enhancing environmental heterogeneity, provides an increase in species richness.

Management Practices

Mesquite encroachment to desert grasslands is partially due to inadequate management of arid environments and rangelands. Historically, the Sonoran and Chihuahuan Deserts were covered by a dry tropical forest in the late Eocene that has experienced a drying trend, especially in the last 8,000 years (Smeins, 1983). The expansion of shrublands has thus created an "impoverished" system for livestock grazing, which in turn has reduced the income of many range land users. Mesquite is often associated to impoverished ranges as it gradually replaces desirable grasses, it increases soil erosion and higher water runoff, while it decreases soil nutrients, and increases environmental heterogeneity. The vast prairies observed by European settlers may in fact be remnants from previous favorable conditions for grasslands. These persisting grasslands in the already deteriorating environment have surely been accelerated with the intensity of livestock grazing. In relation to native Holocene fauna (rodents, peccary and coyote) livestock have become a much more effective disperser (Janzen, 1986; Brown and Archer, 1987), coupled with prolonged livestock grazing and high grazing intensities have caused the doubling of mesquite cover in grasslands (Glendenning, 1952; Buffington and Herbel, 1965). These ranges have frequently been cleared in favor of introduced grass species that often affect ecosystem structure and functioning (Fleischner, 1994; Pierson and McAlister, 1994). Furthermore, clearing of mesquites does not result in long-term favorable responses of forage grasses (Holechek et al., 1994) and does not seem to decrease water evaporation (Dugas and Mayeux, 1991). Studies on how mesquite influences vegetation, show little effects on perennial grasses and non-poisonous forbs at mesquite cover levels below 17% (Warren et al., 1996). Besides supporting a large number of animals, Prosopis spp. provide resources for a large variety of income producing game such as mule deer (Odocoileus hemionus), bobwhite quail (Colinus virginianus), collared peccary (Tayassu tajacu), mourning dove (Zenaida macroura) and wild turkey (Meleagris gallopavo; Maris et al., 1977; Germano et al., 1983; Scifres et al., 1988). Mesquites also provide favorable conditions for native herbaceous, ephemeral and perennial plants under their canopies that are palat-
able for both livestock and wildlife (such as the Texas wintergrass *Setaria texana*; Heitschmidt et al., 1986, and *Panicum mexicanum*; Cornejo-Oviedo et al., 1999; Nolte and Fulbright, 1997). In addition, mesquites are often used as multipurpose agroforestry species as they provide fodder, food, fuel, nitrogen fixation, dune stabilization, soil conservation and honey production (Nair et al., 1984; Fagg and Stewart, 1994), as well as for the recovery of salt lands (Singh, 1995). It is therefore important to take into account the way brush management is seen, from “eradication” to brush “management”. Mesquite problems arise in grassland areas and regions where they were introduced for agroforestry. Many indigenous cultures and local communities in Argentina and the southern semi-arid environments of Mexico depend on mesquite where *Prosopis* is used for livestock forage, food, shade and fuel (D’Antoni and Solbrig, 1977).

The question arises as to the proper balance between conservation and exploitation of rangelands. Studies in the South American Chaco have shown a negative effect of fragmentation on bee pollinators and on reproduction of several arid and semi-arid zone plant species (Aizen and Feinsinger, 1994a; 1994b). Bock et al. (1993) suggested the exclusion of livestock from 20% of current federal grazing lands and Scifres et al. (1989) suggested creating mosaics of mesquite-infested fields, which could enhance diversity (Whittaker et al., 1979), however mesquite stands will eventually coalesce into larger thorn woodlands (Archer et al., 1988). There is no clear-cut management practice. Some evidence points towards grazing intensities that do not exceed one third of current year annual growth on key forage species (Holecheck et al., 1994). This may, under favorable climatic conditions, actually improve ecological and perennial grass cover in short time periods (Holecheck et al., 1994). In addition, reduced light levels and competition with a herbaceous layer essentially stops growth of mesquite seedlings (Bush and Auken, 1990). Combined management practices could be the solution to land encroachment if they prove to be cost-effective (e.g. Integrated Brush Management Systems, IBMS; Scifres et al., 1983; 1988).

The Rangeland Paradox

The mesquite controversy does not stand alone, as similar management practices are affecting other community structures involving woody species such as the Chaco region of South America (D’Antonio and Solbrig, 1977, Morello, 1972) and large areas of Africa (Zimmermann, 1991). The controversies surrounding these species vary greatly, however a common denominator is the expansion of woody species towards grasslands, with a concomitant decrease in land value towards livestock grazing. The introduction of *Prosopis* into areas far from their original habitat have also affected natural vegetation and expanded rapidly. A clear example is South Africa were *Prosopis* was introduced as an agroforestry product in the 1800’s, now covering approximately 180,400 ha and is currently considered an invader under the Conservation of Natural Resources Act 43 of 1983 and under an intense biological control program (Zimmerman, 1991). However, given the characteristics outlined above, conservation and management programs in arid and semi-arid environments should place a priority on the management of mesquite populations in areas deple- ed through conversion and its control in areas of livestock grazing as well as in areas far from its original distribution. This would provide a compromise between livestock productivity on the one hand, and conservation of species diversity and maintenance of ecosystem structure on the other.

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MESQUITES: INVASORS OF BIODIVERSITY ENHANCERS


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