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Successional trends in Sonoran Desert abandoned agricultural fields in northern Mexico

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Abstract

Excessive ground-water use and saline intrusion to the aquifer led, in less than three decades, to an increase in abandoned agricultural fields at La Costa de Hermosillo, within the Sonoran Desert. Using a chronosequence from years since abandonment, patterns of field succession were developed. Contrary to most desert literature, species replacement was found, both in fields with and without saline intrusion. Seasonal photosynthetic capacity as well as water and nitrogen use efficiencies were different in dominant early and late successional plant species. These ecological findings provided a framework for a general explanation of species dominance and replacement within abandoned agricultural fields in the Sonoran Desert.
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1. Introduction

Land degradation due to human practices has been identified as a worldwide problem (Beaumont, 1989) that has ecological and socio-economic implications on the sustainability of ecosystems (Mouat and Hutchinson, 1995; Arnalds and Archer, 2000). Abandoned agricultural fields resulting from either economic or ecological causes such as depletion of available soil, nutrients, or water are becoming a major component of desert landscapes. Agricultural use of marginal lands is usually only a short-term benefit, yet is a widespread practice globally. Abandonment of such lands is expected to increase land degradation and desertification problems over the next few decades. In the arid regions of North America, agriculture was greatly expanded during the 1950s, with the help of large water and nitrogen inputs. Unsustainable agricultural practices were developed with cultivars requiring large amounts of limited resources to achieve increased productivity and short-term gain (García, 1987; Moreno, 1994). Ultimately such practices caused and continue to cause an increase in the number of abandoned agricultural fields (Halvorson et al., 2003).

Disturbed desert habitats are not well characterized or studied because there has been no "ecological services" assigned to desert vegetation and no social or ecological benefits have been determined by non-indigenous societies. Although agricultural productivity in desert agricultural lands has provided an important income to individuals and society, and has been a matter of regional pride, once abandoned, these lands represent no economic or societal value and their rehabilitation is generally not pursued. Only when economic or conservation perspectives have overcome the "wasteland" perceptions have restoration efforts been developed (Bainbridge and Virginia, 1990; Jackson et al., 1991).

It is important to study secondary succession on abandoned agricultural fields because of the increasingly large area they occupy and the large extent of transformation that takes place from the natural environment in which they are placed. In order to effectively manage these areas in the future, it is imperative that we better understand the causes underlying such ecological changes (Bazzaz, 1979; Tilman, 1987, 1988; Bazzaz, 1996). Given the extremely high rates of land conversion in most ecosystems (Beaumont, 1989), ecological succession is now a key component for restoration and ecological management (Glenn-Lewis et al., 1992; Landsberg and Gower, 1997). In defining restoration and ecological management as the management of succession (Luken, 1990) gives us a sense of the centrality of this ecological process at local, regional and global scales.

Structure, function and species diversity of plant communities established during ecological succession, are determined by life history characteristics, resource availability and differences in the ecological niche of different dominant species (Connell and Slatyer, 1977; Grubb, 1977; Grime, 1979, Noy-Meir and van der Maarel, 1987; Pickett et al., 1987; Tilman, 1988). Disturbance was incorporated as an important component in generalized models for secondary ecological succession by Connell and Slatyer (1977). Their three models are: facilitation, inhibition and tolerance, of these only the inhibition model has been proposed for desert plant communities. In desert habitats, facilitation or relay floristics has not been found

(Connell and Slatyer, 1977; Goldberg and Turner, 1986), however, secondary succession in these habitats has yet to be studied extensively. There is the generalized perception that vegetation changes within desert habitats take an extraordinarily long time with no species replacement during secondary succession (Shreve, 1929; Shreve and Hinckley, 1937; Goldberg and Turner, 1986). Long-term studies in the Sonoran Desert have found changes in population structure for certain species but no changes of dominant species composition (Shreve, 1929; Shreve and Hinckley, 1937; Goldberg and Turner, 1986), even after more than 60 years (Turner, 1990; Bowers and Turner, 2001, 2002). This was found to be true also during cyclic succession in the Chihuahuan Desert (Yeaton, 1978). In most studies, adaptation to the stressful physical conditions of the habitat is emphasized over biotic interactions, although facilitation and nurse–plant relationships are known to have an important role in desert habitats (Turner et al., 1966; Valiente-Banuet and Ezcurra, 1991; Suzán et al., 1997, Carrillo-Garcia et al., 1999, 2000). Some of the ecophysiological implications of these biotic interactions may be in response to heterogeneity in resource availability (Garcia-Moya and McKell, 1970; Schlesinger et al., 1990) which may promote facilitation rather than competition, among different species and growth forms (Pugnaire et al., 1996; Suzán et al., 1997; Tielbörger and Kadmon, 2000).

Individual ecophysiological response during successional stages is also a gap in studies in desert habitats. Bazzaz (1979, 1996) described the importance of species ecophysiological characteristics during secondary succession in a number of ecosystems and concluded that fast-growing, high photosynthetic capacity, sun-tolerant species are associated with early stages, while slow growing, low photosynthetic capacity and shade-tolerant species are more generally found in late successional stages. Tilman (1987, 1988) suggested that species replacement during secondary succession is determined by resource availability, in particular light and soil nitrogen. How species function in relation to the most limiting resource available may determine the sequence of ecological succession. Since light is not limiting in deserts, we may not expect these models to explain many of the trends and ecophysiological characteristics of species during secondary succession in desert habitats. Water has been suggested as the major limiting resources for plants in desert habitats, although more recently, the importance of nitrogen has been identified (Mooney et al., 1981; Whitford and Gutierrez, 1989; Gebauer and Ehleringer, 2000).

Water use efficiency is a physiological measure of plant adaptation to arid and stressful habitats. Higher plant water use efficiency allows plants to conserve water while still able to assimilate carbon through photosynthesis. This water-conserving trait has been found to be a characteristic of late but not of early successional species in most ecosystems (Grime, 1979; Bazzaz, 1996). Similar to water, early successional species are thought to thrive in habitats where nitrogen availability is higher, i.e., recently abandoned fields (Bazzaz, 1979). Nitrogen is then found to be decreasing through mid stages of succession and finally becoming a low availability and therefore a limiting resource at the latest stages (Tilman, 1988). However, no adaptive plant strategies have been studied for nitrogen in desert habitats.

In this paper our objective is to answer two main questions: Is there plant species substitution during succession on abandoned desert agricultural fields? How do individual traits and ecophysiological characteristics of dominant species differ between early and late successional species? In order to answer those questions, we characterized secondary successional stages within abandoned agricultural fields in desert habitats, using a chronosequence of up to 30 years since abandonment, and comparing two causes of abandonment. We also characterized some ecophysiological responses, in particular the potential use efficiencies of water and nitrogen of important early and late successional species.

2. Materials and methods

La Costa de Hermosillo is located in the western portion of the Central Region of Sonora, Mexico, between 28°30′ and 29° Lat. N and 111° and 112° Long. W. The area covers close to 833 km² and has been one of the most important irrigated agriculture districts in Mexico. It is located within the plains subdivision of the Sonoran Desert (Shreve and Wiggins, 1964). La Costa has a mean annual temperature of 22 °C and mean monthly maxima of 30 °C in July and August, with daily temperatures of up to 47 °C during summer months. Winter mean monthly temperatures are 12 °C (January and February), with no freezing. Annual rainfall varies from 100 to 225 mm with two distinctive rainy periods, summer (80–90%) and winter (up to 20%). The driest months are from the end of March to mid-June. The soils are extensive alluvial deposits with a mixed structure of clay, silt and sand (45%, 35%, 20%, respectively).

2.1. Site conditions

Because of saline intrusion into the Costa de Hermosillo aquifer, a risk zone was determined by the federal government (CNA, 1992) and by decree all working deep wells were shut down and canceled to avoid further salinization of agricultural fields. All abandoned agricultural fields within this zone had already been irrigated with salty water. We called these fields, "saline" fields (Fig. 1). Some agricultural fields outside this zone, never irrigated with salty water, had been abandoned because of economic or other reasons. We called them "non-saline" fields. We sampled 30 abandoned fields, ten under non-saline and 20 in saline conditions. Most abandoned fields ranged between 500 to 2000 ha in size.

2.2. Vegetation sampling and floristics

Vegetation was sampled using the plotless point-centered quarter method. At each abandoned field, the number of points was determined by plotting the running mean of three points for the cumulative number of species (Mueller-Dumbois and Ellenberg, 1974). For each quadrant, absolute and relative values of mean density, dominance and frequency were obtained from formulas provided in Mueller-
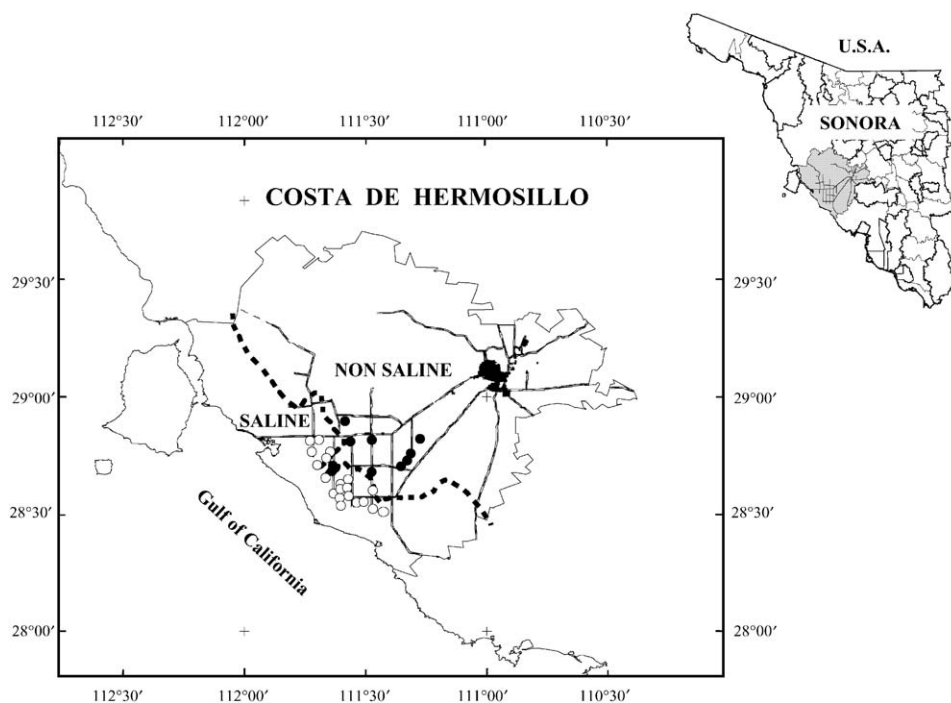
Fig. 1. Localization of La Costa de Hermosillo agricultural district within Hermosillo county (solid surrounding line) in Sonora, Mexico. Isoline (dashed) delimiting ground-water salt intrusion is shown. Abandoned agricultural study sites were located. Closed circles are non-saline, and open circles are saline study sites.

Dumbois and Ellenberg (1974). The same methodology was used to sample nearby natural vegetation patches when available. Plant species were identified following Shreve and Wiggins (1964).

2.3. Physiological measurements

Net photosynthesis was measured using a Portable Photosynthesis System (LICOR, 6200) for *Atriplex polycarpa*, *Baccharis sarathroides*, *Encelia farinosa* and *Prosopis glandulosa* in non-saline abandoned agricultural fields. *Atriplex canescens*, *Baccharis sarathroides*, *Encelia farinosa*, *Larrea tridentata* and *Cercidium microphyllum* were measured in saline-abandoned fields. Daily courses of net photosynthesis, stomatal conductance and transpiration were measured from February to November, except in April and October. Six leaves each of three individuals were measured at each date for both *Atriplex* species and *B. sarathroides*. For all other species at least two leaves were measured. Leaves were measured for area in the lab with a leaf area meter (LICOR, 3100), oven-dried for 48 h at 70 °C, and weighed.

Leaf nitrogen was determined by means of a total Kjeldahl rapid flow analyzer (RFA300, Alpkem), using the phenol method (EPA-600/4-79-020, Nitrogen Ammonia, Method 350.1. Colorimetric Automated Phenate) modified for the auto-analyzer (EPA, 1984). Dried leaves were ground using a mill with mesh 40. Up to 150 mg of sample per leaf were digested at 160 °C for an hour in a solution of sulfuric acid with potassium sulfite and oxide of mercury and at 290 °C for 3 additional hours. Leaf nitrogen was calculated on a per mass and a per area basis. Photosynthetic nitrogen use efficiency (PNUE) was calculated from the highest net photosynthetic rate determined during the morning and expressed on a per area nitrogen basis for the same measured leaf.

2.4. Environmental change history at La Costa

Environmental changes in La Costa de Hermosillo, including details of ground-water pumping, are discussed elsewhere (Halvorson et al., 2003) and only a brief overview is described here. In Mexico, about 51% of its territory is classified as arid or semi-arid (Rzedowski, 1978). Within these regions, many large irrigated agriculture projects have been developed with still more planned for the future. In some of these areas, a combination of high cost of water and nitrogen fertilizers, as well as a decreasing market value of crops, have led to the stoppage of agriculture on these lands; this is the case in large parts of La Laguna region in northeastern Mexico (García, 1987), and Northwestern Mexico, in Caborca and La Costa de Hermosillo in Sonora (Moreno, 1994; Halvorson et al., 2003), and Mexicali and San Quintín Valleys in Baja California.

Irrigated agriculture at La Costa de Hermosillo (LCH) was initiated in 1945 when river-bed agriculture was expanded through the use of well irrigation (Valenzuela, 1982). About 45% of agricultural fields at La Costa were larger than 20 ha and about an equal proportion were larger than 50 ha. Starting in the 1950s water extraction and hectares incorporated into cultivation increased at a fast rate into the 1970s (rising to $800 \, \mathrm{Mm^3 \, yr^{-1}}$ of water used to irrigate over 132,000 ha) when aquifer abatement and salinization of ground-water were recognized as serious problems. By 1990, the cultivated area had decreased to what it was during the 1950s (Halvorson et al., 2003), decreasing by half from the maximum during the 1970s. Most abandoned fields were between 1000 and 5500 ha in size.

3. Results

Saline-abandoned agricultural fields, those already irrigated with salty water, had an average electrical conductivity of $2.7 \pm 0.9 \, \mathrm{mmhos \, cm^{-1}}$. Fields outside this zone, either not previously irrigated with salty water or abandoned because of economic reasons, had an average electrical conductivity of $0.69 \pm 0.18 \, \mathrm{mmhos \, cm^{-1}}$ (Table 1). Percent organic matter in soils of saline fields (0.79 ± 0.09) was slightly higher, although not statistically different from soils of non-saline fields (data not shown).

Table 1
Soil characteristics for saline and non-saline field conditions. Saline fields refer to those where cultivars had been irrigated with water from saline-intruded wells

	Conductivity (mmhos cm^{-1}) Mean ± s.e.		Sand % Mean ± s.e.		Clay % Mean ± s.e.		Nitrogen % Mean ± s.e.		Carbon % Mean ± s.e.		Potassium % Mean ± s.e.		Phosphorous % Mean ± s.e.	
Non-saline	0.696	0.186	38.5	8.15	21.48	5.21	0.072	0.014	0.568	0.152	0.44	0.04	0.768	0.038
Saline	2.738	0.901	34.2	13.83	20.36	8.59	0.067	0.027	0.583	0.275	0.47	0.06	0.757	0.089

3.1. Species establishment

Plant density decreases with time since abandonment in both saline and non-saline sites, as a consequence of changes in the growth form of dominant species, from herbaceous annuals to shrubs and trees in the oldest fields. Plant density of saline fields was higher and cover was lower compared to that of non-saline fields, however, natural stands of vegetation had higher density and cover than any abandoned fields (data not shown).

By recording the most common species, a floristic relay process was found in our sites. Changes in species composition in non-saline fields were recognized at four main periods (Fig. 2). Within the first 2 years, a number of native and non-native herbaceous species were found. From year 2 to 10, the number of shrub and tree species increased, some of which are normally found in mature communities. Early within this period, *B. sarathroides* invades and can form a monospecific cover that self-thins with time, allowing other species to become established. After year 4, tree species like *P. glandulosa*, *C. floridum* and *C. microphyllum*, found as dominant components in natural non-farmed plant communities, become established. During years 10–18, *L. tridentata*, *A. canescens* and *E. farinosa*, tend to become established. These shrub species are found as important components within natural undisturbed plant communities. During this period, most annual species are native.

No fields with less than 2 years of abandonment were found under saline conditions, nevertheless there is circumstantial evidence that a number of herbaceous species are present during those initial stages, although with lower abundance compared to non-saline fields. After year 2, highly invasive species such as *B. sarathroides* and *S. kali*, become the dominant species in these landscapes (Fig. 2). Species that are also found in undisturbed natural plant communities such as *E. farinosa*, *P. glandulosa*, *A. polycarpa* and *L. tridentata*, will become established after the fourth year.

After 18 years, shrubs and trees become the dominant species, while annuals and herbaceous perennials diminish in their importance (Fig. 2). At this stage, the species assemblage begins to mimic natural communities. At each site, characteristic species show after all dominant species have become established, species like *Croton wigginsii* on non-saline fields, and *Opuntia fulgida* on saline fields.

Non-saline

Plant Species	Growth form	Years since abandonment
		0É.2 >2É..4 >4É.10 >10É18 >18ÉÉ
Amaranthus fimbriatus	H	
Argemone intermedia	H	
Boerhavia coccinea	H	
Convolvulus arvensis	HP	
Helianthus annus	HP	
Salsola kali	H	
Taraxacum officinale	H	
Tidestromia lanuginosa	H	
Ambrosia confertiflora	H	
Acacia constricta	SH	
Baccharis sarathroides	SH	
Cercidium microphyllum	T	
Prosopis glandulosa	T	
Cercidium floridum	T	
Abutilon reventum	H	
Chenopodium leptophyllum	H	
Cryptantha grayi	H	
Haplopappus sonorensis	H	
Nicotiana trigonophylla	HP	
Ricinus communis	HP	
Sphaeralcea coulteri	H	
Atriplex canescens	SH	
Encelia farinosa	SH	
Larrea tridentata	SH	
Croton wigginsii	SH	

Saline

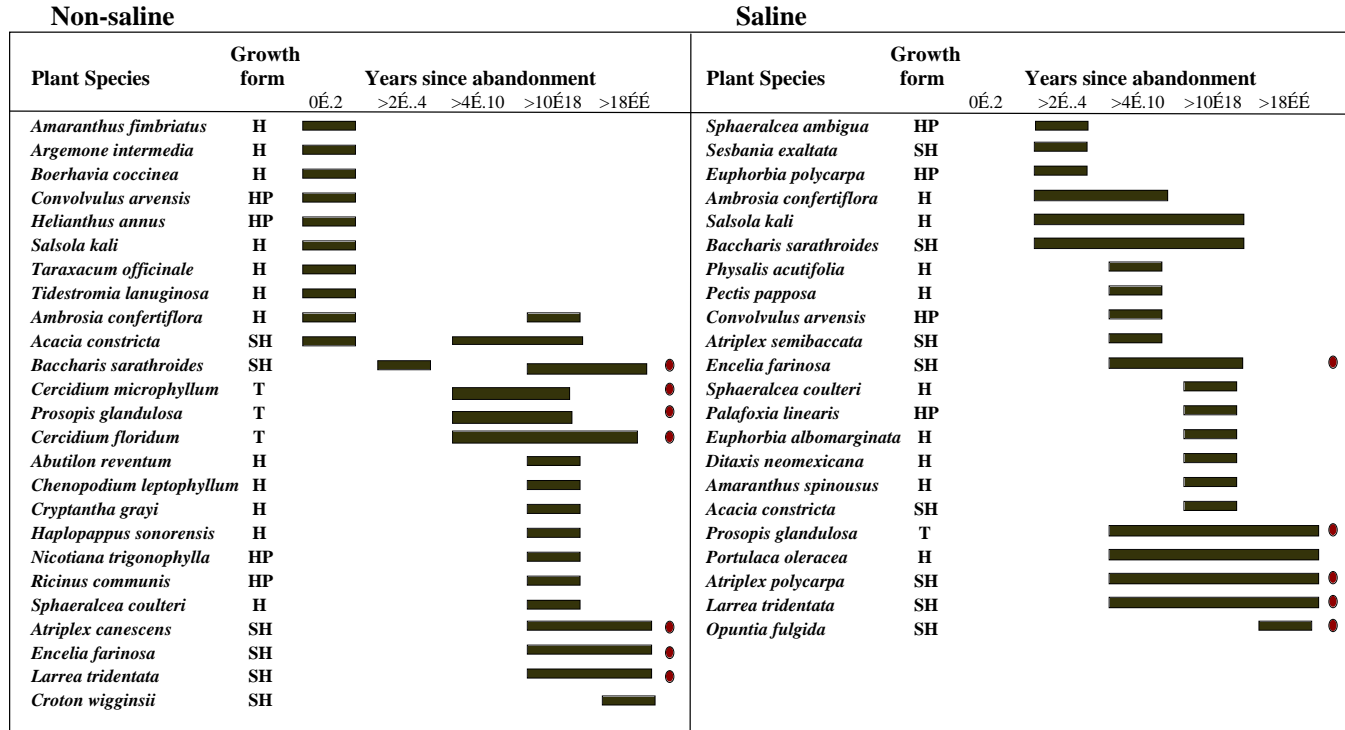| Plant Species	Growth form	Years since abandonment
		0É.2 >2É..4 >4É.10 >10É18 >18ÉÉ
Sphaeralcea ambigua	HP	
Sesbania exaltata	SH	
Euphorbia polycarpa	HP	
Ambrosia confertiflora	H	
Salsola kali	H	
Baccharis sarathroides	SH	
Physalis acutifolia	H	
Pectis papposa	H	
Convolvulus arvensis	HP	
Atriplex semibaccata	SH	
Encelia farinosa	SH	
Sphaeralcea coulteri	H	
Palafoxia linearis	HP	
Euphorbia albomarginata	H	
Ditaxis neomexicana	H	
Amaranthus spinousus	H	
Acacia constricta	SH	
Prosopis glandulosa	T	
Portulaca oleracea	H	
Atriplex polycarpa	SH	
Larrea tridentata	SH	
Opuntia fulgida	SH	

Fig. 2. Chronosequence of species successional changes in non-saline and saline-abandoned agricultural fields. Species growth form are H = herbaceous; HP = herbaceous perennials; SH = shrubs and T = trees. Filled circles represent species found as components of natural communities.

Comparing both sequences, a distinct pattern arises in which herbs are predominant immediately after abandonment, aggressive colonizers come after the second year to self-thin and give way to late dominant species that become established after 4 years and then slowly take over. Site-characteristic species become established after other dominant species have already done so. The outcome is that natural community species richness is re-established after 10 to 18 years. As to when structure and function will become similar to pristine conditions, that will be the subject of continuing studies for years to come.

3.2. Comparative species functioning

We compared seasonal and diurnal ecophysiological characteristics of *B. sarathroides* (an early-succession species), with dominant late-succession species *A. canescens* (non-saline) and *A. polycarpa* (saline). Some comparisons included to a lesser extent, other late-succession dominant species such as *P. glandulosa*, *L. tridentata*, *E. farinosa* and *C. microphyllum*.

In non-saline fields, leaf water potential was −1 to −1.5 MPa significantly lower for *A. canescens* during August and November compared to *B. sarathroides*. Similar patterns were found in saline fields but with lower water potentials in *A. polycarpa* (−5 MPa) and up to −2.5 MPa difference with *B. sarathroides* during August (Fig. 3).

When comparing leaf photosynthetic capacity for three different periods during the year, spring, summer and autumn, maximum rates were present in the sub-shrub *E. farinosa* (28.1 μmol CO_2 m^{-2} s^{-1}) during the summer. During most periods, lower
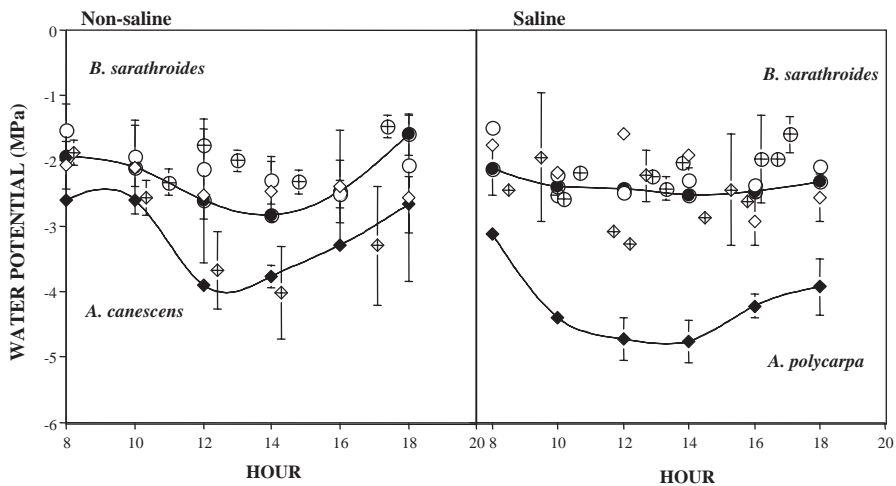

Fig. 3. Water potential in species from saline and non-saline-abandoned agricultural fields. Symbols represent daily courses in different months for *Atriplex* species (diamonds) and *B. saratrhoides* (circles). Open symbols represent data collected in July, symbols with crosses represent data collected in November, and closed symbols and lines represent data collected in August.

Table 2
Photosynthetic capacity and gas exchange characteristics for early and late successional species at La Costa de Hermosillo, Sonora

Plant species		Non-saline fields				Saline fields			
		Net photosynthesis ($\mu mol\,CO_2\,m^{-2}\,s^{-1}$)	PNUE ($\mu mol\,CO_2\,mol^{-1}\,N^{-1}\,s^{-1}$)	Leaf N ($mol\,N\,m^{-2}$)	WUE ($\mu mol\,CO_2\,mmol\,H_2O^{-1}$)	Net photosynthesis ($\mu mol\,CO_2\,m^{-2}\,s^{-1}$)	PNUE ($\mu mol\,CO_2\,mol^{-1}\,N^{-1}\,s^{-1}$)	Leaf N ($mol\,Nm^{-2}$)	WUE ($\mu mol\,CO_2\,mmol\,H_2O^{-1}$)
Atriplex polycarpa	Mar					7.12 (0.85)	17.88 (1.85)	0.40 (0.04)	n.d.
	Jul					16.21	25.95	0.62	3.74
	Sep					18.88	53.08	0.36	3.17
	Nov								
Atriplex canescens	Mar	17.74 (3.96)	42.98 (10.29)	0.42 (0.03)	3.18 (0.02)	6.85 (0.65)	23.90 (1.99)	0.29 (0.03)	0.91 (1.68)
	Jul	12.13 (2.38)	59.35 (7.30)	0.21 (0.06)	0.42 (0.10)	10.49 (2.87)	34.84 (7.50)	0.29 (0.04)	2.09 (0.43)
	Sep	10.78 (1.77)	43.71 (10.88)	0.27 (0.03)	0.96 (0.17)	7.76 (0.99)	37.52 (4.28)	0.21 (0.01)	0.74 (0.23)
	Nov	6.06 (2.08)	22.99 (11.93)	0.30 (0.06)	3.29 (1.25)	4.15	36.61	0.11	0.41
Baccharis sarathroides	Mar	10.60 (2.53)	31.28 (3.38)	0.33 (0.04)	1.23 (0.20)				
	Jul	7.37 (1.10)	30.00 (2.80)	0.25 (0.04)	1.69 (0.37)				
	Sep	8.50 (4.75)	27.86 (16.48)	0.31 (0.01)	1.19 (0.29)				
	Nov	6.25 (2.01)	22.78 (5.33)	0.29 (0.15)	2.18 (1.87)				
Cercidium microphyllum	Mar	12.23	39.88	0.31	1.83				
	Jul	12.53 (2.78)	26.10 (5.43)	0.48 (0.01)	0.53 (0.33)				
	Sep	11.43	65.70	0.17	1.13				
	Nov								
Encelia farinosa	Mar								
	Jul	22.50 (1.02)	75.09 (5.75)	0.30 (0.01)	3.40 (0.85)	28.13 (0.98)	n.d.	n.d.	3.97 (0.55)
	Sep	21.10 (3.37)	97.81 (8.67)	0.22 (0.02)	0.93 (0.01)	17.65 (2.59)	n.d.	n.d.	0.84 (0.05)
	Nov					15.45 (1.76)	58.43 (0.64)	0.27 (0.03)	1.36 (0.25)
Larrea tridentata	Mar								
	Jul	7.65 (0.58)	25.17 (1.58)	0.30 (0.01)	2.46 (0.31)				
	Sep	7.75 (1.45)	n.d.	n.d.	0.87 (0.58)				
	Nov	8.37 (1.28)	38.55 (6.64)	0.22 (0.01)	2.39 (0.45)				
Prosopis glandulosa	Mar					9.91	22.77	0.44	n.d.
	Jul								
	Sep					11.51 (0.23)	41.31 (1.26)	0.28 (0.01)	0.52
	Nov					6.70 (2.50)	24.65 (5.80)	0.27 (0.04)	0.87 (0.20)

Unique values do not show ± s.e. Blank spaces indicate either the species is not present or values not measured at specific dates.

photosynthetic rates were consistently found in *B. sarathroides* and *L. tridentata* (Table 2). *B. sarathroides* had higher rates early in the season and a downward trend through November in both non- and saline fields.

Maximum net photosynthetic rates in late successional *Atriplex* species showed decreasing rates from March to November for *A. canescens*, the dominant species in non-saline fields, but increasing rates for *A. polycarpa* in saline fields. In both species, peak photosynthesis occurred for only a short period near mid-morning, afternoon rates remained low after a mid-day depression.

Positive relationships between leaf photosynthetic capacity and leaf nitrogen had a large dispersion associated with it, although some differences among species are shown. *Atriplex* species had higher net photosynthetic capacity per unit leaf area nitrogen, photosynthetic nitrogen use efficiency, as well as higher overall leaf nitrogen concentration, compared to *B.sarathroides* in non-saline fields (Fig. 4).

Within desert habitats, water and nitrogen are the two most important and selective resources for plants. A relationship between photosynthetic nitrogen (PNUE) and water use efficiencies (WUE), allowed us to predict how net photosynthetic capacity is optimized per unit of water and nitrogen in leaves, and as a consequence to obtain the relationship of leaf nitrogen per unit of water transpired. We obtained these relationships from the mean maximum photosynthetic capacity per unit resource utilized (water or nitrogen per unit area) at each month, so points will represent resource use efficiencies for each species at different times of the year.

When related, water and nitrogen resource use efficiencies differed between early and late successional species. In both saline and non-saline fields, *Baccharis sarathroides*, the early successional dominant shrub, had an exponential increasing
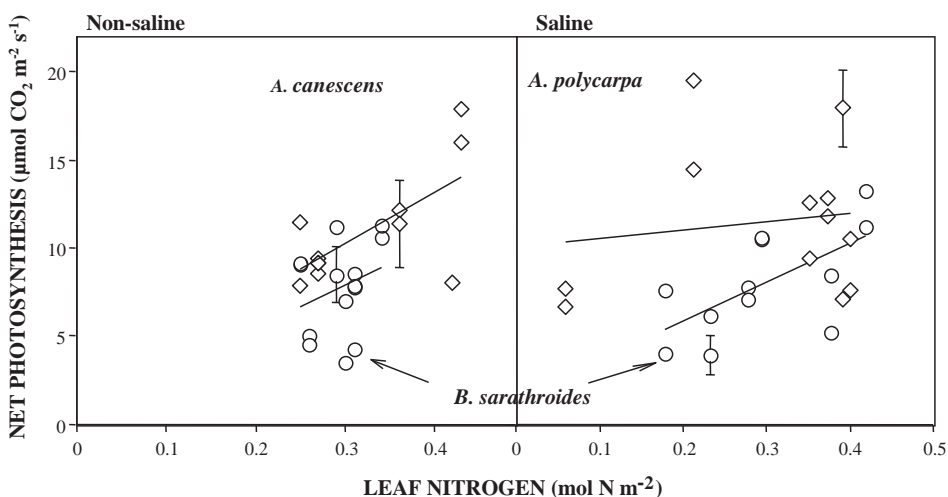

Fig. 4. Maximum diurnal photosynthetic rate to leaf nitrogen content for early and late successional species under non-saline and saline field conditions. Trends are shown for *Atriplex* species (diamond) and *B. sarathroides* (circles). Error line is the highest found for each species.
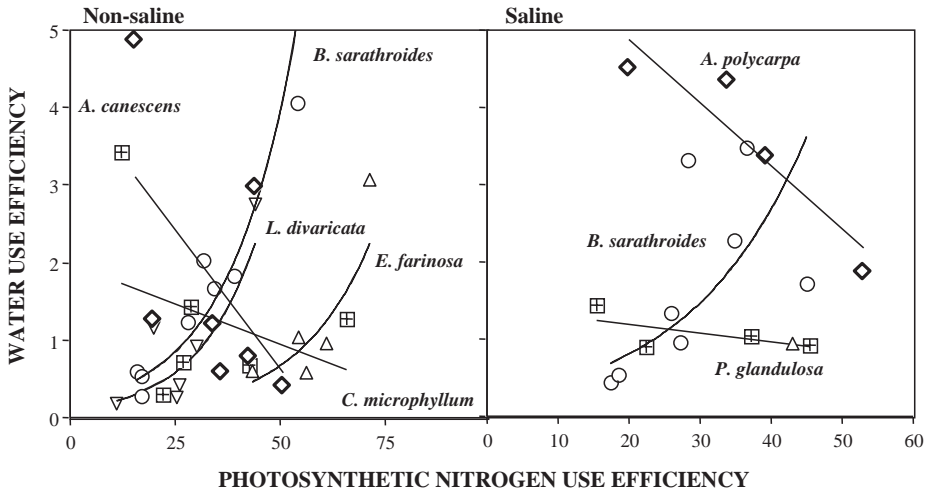
Fig. 5. Water and photosynthetic nitrogen use efficiencies for early and late successional species under non-saline and saline-abandoned field conditions. Early species represented by *B. sarathroides* (open circles) and *E. farinosa* (triangles); Late successional by *Atriplex* species (diamonds), *C. microphyllum* and *P. glandulosa* (crossed squares), and *L. divaricata* (inverted triangles). For each species, points represent the mean of gas exchange measurements made on three to six leaves at different times of the year.

trend where a small increase in PNUE resulted in a large increase in WUE (Fig. 5). Similar relationships were found for *Encelia farinosa* and *Larrea tridentata* under non-saline field conditions. A different pattern was found for late successional dominant shrubs and trees. In non- and saline-abandoned fields, increasing PNUE was related to decreasing WUE in shrub, *A. canescens* and *A. polycarpa*, and tree species, *C. microphyllum* and *P. glandulosa*. A higher intercept in the WUE axis was found for *Atriplex* compared to tree species (Fig. 5).

4. Discussion

Grazing, wood extraction and agriculture are three major ways in which plant cover has been used in desert habitats. Selective use of species during grazing and wood harvesting, when moderate pressure is exerted on plant communities, can trigger processes associated with niche regeneration and gap replacement responsible for the maintenance of species composition, structure and diversity within plant communities (Grubb, 1977; Pickett et al., 1987). Large-scale agriculture, as practiced in La Costa de Hermosillo, involves major disturbance to the soil, community structure and native species such that successional processes at different scales are required to restore natural conditions (Bazzaz, 1979, 1996). At this scale, interactions from different species lead to recognizable patterns of replacement in which pioneer species either facilitate, inhibit or tolerate colonization by other species (Connell and Slatyer, 1977; Peet and Christiensen, 1980). Within desert habitats, there is an

extremely poor literature in which these models of successional processes have been tested, in particular following agriculture abandonment (Bazzaz, 1996).

4.1. Changes in species composition during succession

Our study shows, that there is a species replacement pattern following agriculture abandonment in La Costa de Hermosillo desert region. Previously, plant species successional changes were thought not to be present in desert habitats, since changes in species composition or replacement had not been observed (Shreve, 1929; Connell and Slatyer, 1977). Most previous successional studies in warm desert environments, however, have been performed by following changes in permanent plots from non-disturbed habitats (Shreve and Hinckley, 1937; Goldberg and Turner, 1986; Turner, 1990).

Differences in our results with those where no species replacement were found during succession in deserts, may point to important differences in habitat conditions following large disturbances in space and time, where some limiting resources may be freed and available for opportunistic species. Large disturbances are a common characteristic of our study with those where changes in vegetation structure and species composition have been found, such as in ghost towns in cold desert habitats (Webb and Wilshire, 1980), or abandoned agricultural fields (Karpiscak, 1980; Jackson et al., 1991). At la Costa abandoned fields, seed source availability as well as wood cutting or grazing do not seem to be issues that could influence regulating trends in plant succession.

In our study we found that species replacement and establishment of late successional species was relatively fast (after 4–10 years), at which time, most pioneer species were not present. Other studies using chronosequences of abandoned agricultural fields within the Northern edge of the Sonoran Desert, found very similar patterns of relatively fast species replacement (Karpiscak, 1980). Similarity of the patterns found between the two field conditions studied (Fig. 2) and a similar study in Arizona (Karpiscak, 1980), suggests a definite pattern within the Sonoran Desert. Although a chronosequence approach has been shown to be able to detect major trends in replacement processes (Foster and Tilman, 2000), this was somewhat surprising since we were expecting larger variability in the successional processes due to the environmental heterogeneity expected within desert habitats.

Soil salinity differences lead to changes in species characteristics of pioneer and late successional plant species. Our study showed that different species, both native and exotic, were present in non- and saline fields within the similar climatological conditions of La Costa de Hermosillo region. Both non- and saline fields had some pioneer and late dominant species in common, but also a number of species that were not shared. This resulted in different plant community structures for non- and saline fields (Fig. 2).

4.2. Ecophysiological differences

Changes in species composition may reflect selective pressures in the physiological characteristics of species, due to resource limitation or availability during establishment

and growth. Plant ecophysiological processes are known to be important within tropical and temperate forest succession, where light resource availability has been proposed as the main adaptive factor in the differentiation of incoming species (Bazzaz, 1996), although Bazzaz (1979) recognized that this may not be applicable to desert ecosystems. Light is generally not a limiting resource in most desert habitats, except for species which require "nurse" plants (Valiente-Banuet and Ezcurra, 1991; Suzán et al., 1997) and vines within tree canopies (Castellanos et al., 1999) for which too much light and heat is a problem. Because of this, other resources such as water (Noy-Meir, 1973; Schulze, 1982; Whitford and Gutierrez, 1989) and nitrogen (Whitford and Gutierrez, 1989; Hooper and Johnson, 1999; Gebauer and Ehleringer, 2000) may be of outmost importance within deserts and during secondary succession (Tilman, 1988).

Our study found similar general trends in photosynthetic capacity during secondary succession as a previous review (see Table 2 in Bazzaz, 1979), but no other study was found for desert systems where photosynthetic responses were compared among species during plant succession. *E. farinosa* a perennial sub-shrub, had larger photosynthetic capacity than *B. sarathroides*, *Atriplex* spp, and *L. tridentata* (shrubs), and trees like *C. microphyllum* and *P. glandulosa* (Table 2). However, *L. tridentata* and to a lesser extent *B. sarathroides* showed lower photosynthetic capacity than either tree species.

Some differences were not expected. An early successional species in both non- and saline fields, *B. sarathroides*, had higher (less negative) leaf water potentials during most of the growing and fall seasons, than *Atriplex* species. Since they were measured at the same site, early successional *Baccharis* either may have better uptake mechanisms, conserving strategies (lower conductance) or may be utilizing different sources of soil moisture. Better water relations may come with a cost, since lower photosynthetic rates and stomatal conductances (not shown), that may be related to the maintenance of higher leaf water potentials in *Baccharis*, may result in lower carbon assimilation and competitive ability in the long run (Schulze et al., 1986).

Other less well-known ecological interactions may also play an important role in the replacement of *B. sarathroides*. The species was an early successional species in both non- and saline fields conditions, and could be found during a long period in the chronosequence, with diminishing densities through time. It has been found, that abandoned fields, have initially large amounts of soil nitrogen, as a result of previous farming practices (Bazzaz, 1979; Tilman, 1988), although in some cases it has been found to parallel changes in biomass, diminishing during early stages and increasing during late succession. Nitrogen availability in arid and semi-arid plant communities plays an important role in the dynamics of successional processes (McLendon and Redente, 1992). Our data show lower photosynthetic capacity per leaf area nitrogen in *Baccharis* compared with the late successional species of *Atriplex* (Fig. 4), however, nonlimiting initial conditions and faster growth rates in the species (pers. obs.), allowed initial successful establishment of the former species. Differences in the response of these species may reflect contrasting photosynthetic pathways, with higher rates of photosynthesis per unit nitrogen in *Atriplex* (C_4) than *Baccharis* (C_3). Differences in the slope of the leaf photosynthesis-nitrogen relationship has been documented mostly for species with different photosynthetic pathway (Sage and

Pearcy, 1987; Evans, 1989), as a consequence of the lower amount of the enzyme Ribulose-bisphosphate carboxylase (RUBISCO) and concentrating activity of phosphoenol pyruvate carboxylase (PEP) during photosynthesis of C_4 species.

4.3. Use efficiencies

When daily maximum photosynthetic rates were plotted against leaf nitrogen per unit area a positive trend was present, although a large variability was associated with it (Fig. 4). A robust relationship has been found between maximum photosynthetic rate and leaf nitrogen on a weight basis (Field and Mooney, 1986; Peterson et al., 1999), but larger variability has been found when expressed on a per unit leaf area basis (Sobrado and Medina, 1980; Field and Mooney, 1986; Evans, 1989; Peterson et al., 1999). Differences in the intercept of the relationship photosynthesis—nitrogen have been found between early and late successional tropical species (Peterson et al., 1999).

Seasonal differences in resource use efficiency for different successional species, may represent adaptive responses of growth and carbon gain to the two most limiting resources in arid lands, water and nitrogen. Use efficiencies of these two most limiting resources in desert habitats followed two different trends when seasonal data were used. In general, late successional and tree species followed a linear trend of high water and low nitrogen use efficiency to higher nitrogen and low water use efficiency, while early successional species followed an exponential relationship from low nitrogen and water to high nitrogen and water use efficiencies (Fig. 5). During successional stages, early colonizers may find initial low nitrogen availability in the soil (Tilman, 1988). However, in abandoned agricultural fields, initial soil conditions may have higher nutrient availability, particularly in those fields abandoned not because decreasing productivity potential but saline soil or economic conditions, as in La Costa de Hermosillo. Those conditions may be advantageous for early colonizers with maximum water use when nitrogen use is high. This may also be an important strategy for L. tridentata, the only ''late'' successional species with a use efficiency pattern similar to ''early'' successional species. L.tridentata, a species considered a late colonizer, is at the same time, a successful invader within the most dry and hot desert plant communities in North America.

We may expect that as nitrogen becomes more limiting, after agricultural abandonment, and when water is not ''as'' limiting (lower water use efficiency), late successional species and particularly legume trees, will increase their dominance, as found in our field sites. Bigger changes in nitrogen use efficiencies with small changes in water use efficiencies in trees compared to shrubs, point to the relative importance of the two resources within these different functional types.

This study shows that early and late successional species have different ecophysiological characteristics within desert habitats, and differences in resource limitations may result from ecophysiological or biophysical adaptive strategies. Increased water availability may be achieved, by roots tapping deep water (*Prosopis*) or by partitioning soil moisture or seasonal changes in their gas exchange activity (*Atriplex*). Several mechanisms, biochemical and biophysical, may be responsible for

the nitrogen use efficiency within a species (Field and Mooney, 1986; Evans, 1989; Grindlay, 1997; Peterson et al., 1999), and throughout the growing cycle. Allocation of resources for growth while maximizing photosynthetic nitrogen use efficiency and water use efficiency has been found in invasive species (McDowell, 2002).

The mechanistic basis of the relationship between photosynthetic water and nitrogen use efficiencies is not completely understood, however it has been shown to differ for leaf age, species (Fredeen et al., 1991; Reich et al., 1998; Gerdol et al., 2000), functional types (Reich et al., 1998), sites (Reich et al., 1998, 1999; Wright et al., 2001) and successional stages (Abrams and Mostoller, 1995; Ellsworth and Reich, 1996; Peterson et al., 1999). Increased water use efficiency (WUE) can be related to either high or low photosynthetic rates due to stomatal limitations, although WUE has been inversely related to biomass (Pereira, 1995). These studies found an inverse relationship between water and nitrogen use efficiencies as proposed here for late successional species. McDowell (2002) on the other hand, found that the most important predictive factor for invasiveness of *Rubus* species was WUE, and her data showed a positive relationship for water and nitrogen use efficiencies, similar to the trend described for early successional species in our study. She proposes that high photosynthetic rate is possible even with lower stomatal conductance at high WUE, due to a larger C_i/C_a CO_2 gradient between the leaf mesophyll and the external surrounding air. Positive relationships for NUE and WUE between evergreen and deciduous species have also been found for *Vaccinium* in stressful subalpine habitats (Gerdol et al., 2000).

Land-use and cover change impacts at regional and global scales are now widespread. Further studies on the ecophysiological resource-use strategies of early and late successional species should provide important insights to the general adaptive traits of such species. This will lead to better understanding of the mechanistic basis for plant species diversity, replacement and structure within natural, degraded, and recovering ecosystems.

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References

Abrams, M.D., Mostoller, S.A., 1995. Gas exchange, leaf structure and nitrogen in contrasting successional tree species growing in open and understory sites during a drought. Tree Physiology 15, 361–370.

Arnalds, O., Archer, S., 2000. Rangeland Desertification. Kluwer Academic Publishers, Dordrecht, 209pp.

Bainbridge, D.A., Virginia, R.A., 1990. Restoration in the Sonoran Desert of California. Restoration and Management Notes 8, 3–13.

Bazzaz, F.A., 1979. The physiological ecology of plant succession. Annual Review of Ecology and Systematics 10, 351–371.

Bazzaz, F.A., 1996. Plants in Changing Environments. Linking Physiological, Population, and Community Ecology. Cambridge University Press, Cambridge, 320pp.

Beaumont, P., 1989. Drylands, Environmental Management and Development. Routledge, London, 536pp.

Bowers, J.E., Turner, R.M., 2001. Dieback and episodic mortality of *Cercidium microphyllum* (foothill paloverde), a dominant Sonoran Desert tree. Bulletin Torrey Botanical Club 128, 128–140.

Bowers, J.E., Turner, R.M., 2002. The influence of climatic variability on local population dynamics of *Cercidium microphyllum* (foothill paloverde). Oecologia 130, 105–113.

Carrillo-Garcia, A., Bashan, Y., Diaz Rivera, E., Bethlfenfavay, G.J., 2000. Effects of resource-island soils, competition, and inoculation with *Azospirillum* on survival and growth of *Pachycereus pringlei*, the giant cactus of the Sonoran Desert. Restoration Ecology 8, 65–73.

Carrillo-Garcia, A., León de la Luz, J.-L., Bashan, Y., Bethlenfalvay, G.J., 1999. Nurse plants, mycorrhizae and plant establishment in a disturbed area of the Sonoran Desert. Restoration Ecology 7, 321–335.

Castellanos, A.E., Tinoco-Ojanguren, C., Molina-Freaner, F.E., 1999. Microenvironmental heterogeneity and space utilization by desert vines within their host trees. Annals of Botany 84, 145–153.

CNA, 1992. Programa Estatal Hidráulico (Sonora). Comisión Nacional del Agua, Hermosillo.

Connell, J.H., Slatyer, R.O., 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist 111, 1119–1144.

Ellsworth, D.S., Reich, P.B., 1996. Photosynthesis and leaf nitrogen in five Amazonian tree species during early secondary succession. Ecology 77, 581–594.

EPA, 1984. Methods for Chemical Analysis of Water and Wastes. Environmental Monitoring and Support Laboratory, Cincinnati, OH.

Evans, J.R., 1989. Photosynthesis and nitrogen relationships in leaves of C_3 plants. Oecologia 78, 9–19.

Field, C.B., Mooney, H.A., 1986. The photosynthesis–nitrogen relationship in wild plants. In: Givnish, T.J. (Ed.), On the Economy of Plant Form and Function. Cambridge University Press, Cambridge, pp. 25–55.

Foster, B.L., Tilman, D., 2000. Dynamic and static views of succession: testing the descriptive power of the chronosequence approach. Plant Ecology 146, 1–10.

Fredeen, A., Gamon, J.A., Field, C.B., 1991. Responses of photosynthesis and carbohydrate-partitioning to limitations in nitrogen and water availability in field-grown sunflower. Plant Cell and Environment 14, 963–970.

García, R., 1987. Deterioro Ambiental y Pobreza en la Abundancia Productiva: El Caso de la Comarca Lagunera, México. IFIAS-CINVESTAV, Guanajuato, 112pp.

Garcia-Moya, E., McKell, C.M., 1970. Contribution of shrubs to the nitrogen economy of a desert-wash plant community. Ecology 51, 81–88.

Gebauer, R.L.E., Ehleringer, J.R., 2000. Water and nitrogen uptake patterns following moisture pulses in a cold desert community. Ecology 81, 1415–1424.

Gerdol, R., Iacumin, P., Marchesini, R., Bragazza, L., 2000. Water- and nutrient-use efficiency of a deciduous species, *Vaccinium myrtillus*, and an evergreen species, *V. vitis-idaea*, in a subalpine dwarf shrub heath in the southern Alps, Italy. Oikos 88, 19–32.

Glenn-Lewis, D.C., Peet, R.K., Veblen, T.T., 1992. Plant Succession: Theory and Prediction. Chapman & Hall, London, 352pp.

Goldberg, D.E., Turner, R.M., 1986. Vegetation change and plant demography in permanent plots in the Sonoran Desert. Ecology 67, 695–712.

Grime, J.P., 1979. Plant Strategies and Vegetation Processes. John Wiley and Sons, New York, 222pp.

Grindlay, D.J.C., 1997. Towards and explanation of crop nitrogen demand based on the optimization of leaf nitrogen per unit leaf area. Journal of Agricultural Science 128, 377–396.

Grubb, P.J., 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biological Reviews 52, 107–145.

Halvorson, W.L., Castellanos, A.E., Murrieta, J., 2003. Sustainable land use requires attention to ecological signals. Environmental Management 32, 551–558.

Hooper, D.U., Johnson, L., 1999. Nitrogen limitation in dryland ecosystems: responses to geographical and temporal variation in precipitation. Biogeochemistry 46, 247–293.

Jackson, L., McAuliffe, J.R., Roundy, B.A., 1991. Desert restoration. Restoration and Management Notes 9, 71–80.

Karpiscak, M.M., 1980. Secondary succession of abandoned field vegetation in southern Arizona. Ph. D. Dissertation, University of Arizona, Tucson, AZ.

Landsberg, J.J., Gower, S.T., 1997. Applications of Physiological Ecology to Forest Management. Academic Press, San Diego, 354pp.

Luken, J.O., 1990. Directing Ecological Succession. Chapman & Hall, London, 251pp.

McDowell, S.C.L., 2002. Photosynthetic characteristics of invasive and noninvasive species of *Rubus* (Rosaceae). American Journal of Botany 89, 1431–1438.

McLendon, T., Redente, E.F., 1992. Effects of nitrogen limitation on species replacement dynamics during early secondary succession on a semiarid sagebrush site. Oecologia 91, 312–317.

Mooney, H.A., Field, C.B., Gulmon, S.L., Bazzaz, F.A., 1981. Photosynthetic capacity in relation to leaf position in desert versus old-field annuals. Oecologia 50, 109–112.

Moreno, J.L., 1994. El uso del agua en un distrito agrícola de riego por bombeo: El caso de la Costa de Hermosillo, Sonora, México, In: Shoko, D., Pérez, E.P. (Eds.), Sociedad, Economía y Cultura Alimentaria Centro de Investigación y Estudios Superiores en Antropología Social (CIESAS) y Centro de Investigación en Alimentación y Desarrollo (CIAD), Hermosillo, pp. 452.

Mouat, D.A., Hutchinson, C.F., 1995. Desertification in Developed Countries. Kluwer Academic Publishers, Dordrecht, 363pp.

Mueller-Dumbois, D., Ellenberg, H., 1974. Aims and Methods of Vegetation Ecology. Wiley, New York, 547pp.

Noy-Meir, I., 1973. Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics 4, 25–51.

Noy-Meir, I., Van der Maarel, E., 1987. Relations between community theory and community analysis in vegetation science: some historical perspectives. Vegetatio 69, 5–15.

Peet, R.K., Christiensen, N.L., 1980. Succession: a population process. Vegetatio 43, 131–140.

Pereira, J.S., 1995. Gas exchange and growth. In: Schulze, E.D., Caldwell, M.M. (Eds.), Ecophysiology of Photosynthesis. Springer-Verlag, Berlin, pp. 147–181.

Peterson, A.G., Ball, J.T., Luo, Y., Field, C.B., Reich, P.B., Curtis, P.S., Griffin, K.L., Gunderson, C.A., Norby, R.J., Tissue, D.T., Forstreuter, M., Rey, A., Vogel, C.S., and CMEAL participants, 1999. The photosynthesis—leaf nitrogen relationship at ambient and elevated atmospheric carbon dioxide: a meta-analysis. Global Change Biology 5, 331–346.

Pickett, S.T.A., Collins, S.L., Armesto, J.J., 1987. A hierarchical consideration of causes and mechanisms of succession. Vegetatio 69, 109–114.

Pugnaire, F.I., Haase, P., Puigdefábregas, J., Cueto, M., Clark, S.C., Incoll, L.D., 1996. Facilitation and succession under the canopy of a leguminous shrub, *Retama Sphaerocarpa*, in a semi-arid environment in south-east Spain. Oikos 76, 455–464.

Reich, P.B., Ellsworth, D.S., Walters, M.B., Vose, J.M., Greshman, C., Volin, J.C., Bowman, W.D., 1999. Generality of leaf trait relationships: a test across six biomes. Ecology 80, 1955–1969.

Reich, P.B., Walters, M.B., Ellsworth, D.S., Vose, J.M., Volin, J.C., Greshman, C., Bowman, W.D., 1998. Relationships of leaf dark respiration to leaf nitrogen, specific leaf area and leaf life-span: a test across biomes and functional groups. Oecologia 114, 471–482.

Rzedowski, J. 1978. Tipos de Vegetación de México. LIMUSA, México, 432pp.

Sage, R.F., Pearcy, R.W., 1987. The nitrogen use efficiency of C3 and C4 plants. I. Leaf nitrogen, growth and biomass partitioning in *Chenopodium album* (L) and *Amaranthus retroflexus* (L). Plant Physiology 84, 954–958.

Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrel, W.M., Virginia, R.A., Whitford, W.G., 1990. Biological feedbacks in global desertification. Science 247, 1043–1048.

Schulze, E.-D., 1982. Plant life forms and their carbon, water and nutrient relations. In: Lange, O., Nobel, P.S., Osmond, C.B., Ziegler, H.J. (Eds.), Encyclopedia of Plant Physiology. New Series. Springer-Verlag, Berlin.

Schulze, E.-D., Küppers, M., Matyssek, R., 1986. The roles of carbon balance and branching pattern in the growth of woody species. In: Givnish, T.J. (Ed.), On the Economy of Plant Growth and Function. Cambridge University Press, Cambridge, p. 717.

Shreve, F., 1929. Changes in desert vegetation. Ecology 10, 364–373.

Shreve, F., Hinckley, A.L., 1937. Thirty years of change in desert vegetation. Ecology 18, 463–478.

Shreve, F., Wiggins, I.L., 1964. Vegetation and Flora of the Sonoran Desert. Stanford University Press, Stanford.

Sobrado, M.A., Medina, E., 1980. General morphology, anatomical structure, and nutrient content of sclerophyllous leaves of the "Bana" vegetation of Amazonas. Oecologia 45, 341–345.

Suzán, H., Patten, D.T., Nabhan, G.P., 1997. Exploitation and conservation of ironwood (*Olneya tesota*) in the Sonoran Desert. Ecological Applications 7, 948–957.

Tielbörger, K., Kadmon, R., 2000. Temporal environmental variation tips the balance between facilitation and interference in desert plants. Ecology 81, 1544–1553.

Tilman, D., 1987. Secondary succession and pattern of dominance along experimental nitrogen gradients. Ecological Monographs 57, 189–214.

Tilman, D., 1988. Plant Strategies and the Dynamics and Structure of Plant Communities. Princeton University Press, NJ, 360pp.

Turner, R.M., 1990. Long-term vegetation change at a fully protected Sonoran Desert site. Ecology 71, 464–477.

Turner, R.M., Alcorn, S.M., Olin, G., Booth, J.A., 1966. The influence of shade, soil and water on saguaro seedlings establishment. Botanical Gazzete 127, 95–102.

Valenzuela, E., 1982. La costa de Hermosillo y necesidades de información técnica de los productores agrícolas, en relación a la escasez de agua. Ingeniero Agrónomo, Universidad de Sonora, Hermosillo.

Valiente-Banuet, A., Ezcurra, E., 1991. Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse plant *Mimosa luisana* in the Tehuacán Valley, Mexico. Journal of Ecology 79, 961–971.

Webb, R.H., Wilshire, H.G., 1980. Recovery of soils and vegetation in a Mojave desert ghost town, Nevada, USA. Journal of Arid Environments 3, 291–303.

Whitford, W.G., Gutierrez, J.R., 1989. Effects of water and nitrogen supplementation on phenology, plant size, tissue nitrogen, and seed yield of Chihuahuan desert annual plants. Southwestern Naturalist 34, 546–549.

Wright, I.J., Reich, P.B., Westoby, M., 2001. Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats. Functional Ecology 15, 423–434.

Yeaton, R.I., 1978. A cyclical relationship between *Larrea tridentata* and *Opuntia leptocaulis* in the northern Chihuahuan Desert. Journal of Ecology 66, 651–656.