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HIGH FOLIAR NITROGEN IN DESERT SHRUBS: AN IMPORTANT ECOSYSTEM TRAIT OR DEFECTIVE DESERT DOCTRINE?[1]

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Abstract. Nitrogen concentrations in green and senesced leaves of perennial desert shrubs were compiled from a worldwide literature search to test the validity of the doctrine that desert shrubs produce foliage and leaf litter much richer in nitrogen than that in the foliage of plants from more mesic environments. Mean nitrogen concentration in the green leaves of 78 species of shrubs growing in 11 deserts on five continents (2.2%) was not different from that in 67 species of trees and shrubs growing in deciduous, and mixed deciduous forests (2.2%), and only slightly higher than that in overstory (2.0%) and understory (2.1%) plants growing in tropical wet forest. Mean nitrogen concentration in the green leaves of a ubiquitous shrub that dominates large areas of desert in the United States (*Larrea tridentata*, 2.1%), and in the green-stem tissues of leafless desert shrubs (2.1%) were also similar to that in plants from mesic environments. Mean green-leaf nitrogen was similar in shrubs growing in different deserts. Mean nitrogen concentration in leaf litter was 1.1% for 11 species of desert shrubs, and 1.0% for the 10 species of this group that were not capable of symbiotic nitrogen fixation. Both concentrations were lower than those routinely provided to describe nitrogen in the litter of desert shrubs (1.5–1.7%), and only slightly higher than the mean nitrogen concentration in 77 species of woody perennials growing in a wide variety of environments worldwide (0.9%). Nitrogen in the leaf litter of one desert shrub (0.4%, *Brickellia laciniata*) was nearly as low as the lowest leaf-litter nitrogen concentration known for any woody species (0.3%).

Because nitrogen concentrations in the foliage of desert shrubs are not higher than those in plants growing in more mesic environments, the tenet that desert shrubs support extraordinarily nitrogen-rich foliage can no longer be supported.

Key words: desert shrubs; ecosystem traits; green leaves; leaf litter; nitrogen in desert shrubs; nutrient cycling.

INTRODUCTION

Descriptions of desert ecosystems are infused with the notion that desert plants in general, and desert shrubs in particular, produce foliage and leaf litter that are abnormally rich in nitrogen (N). Consider the following observations and conclusions. "All desert plant tissues have higher concentrations of nitrogen . . . than plants of more mesic environments" (West 1981). "Nitrogen in desert plants is concentrated mostly in the new growth, and the N values are higher than in the plants of other biomes—often 3 to 4% N by dry weight" (Skujins 1981). "Highly active nitrogen accumulation is a characteristic feature of the litter fall in desert communities. The average nitrogen concentration in the litter fall is 1.7% . . . " (Rodin and Bazilevich 1967). "Desert shrubs are relatively high in . . . N content of leaves despite the low levels of N in most desert soils" (Whittaker et al. 1979).

The accuracy of these tenets came into question recently when their validity was not fully supported during an analysis of the relationships among green-leaf N, litter N, and resorption of N in desert shrubs (Killingbeck 1993*a*). For example, litter N in the seven species examined was much lower than the values published by Rodin and Bazilevich (1967) and West (1981) that are routinely cited as typical of litter N in desert shrubs. The realization that litter N might be lower than commonly thought piqued our interest and raised the question of whether green-leaf N might also be lower than desert doctrine dictates.

No comprehensive survey of N levels in the green foliage and litter of desert shrubs presently exists. This void prompted the assembly and synthesis of a collection of data documenting N concentrations in the green leaves and leaf litter of 78 species of shrubs growing in deserts worldwide. The primary questions we sought to answer are: (1) What are the concentrations of N in the green leaves and leaf litter of a wide variety of desert shrub species? and (2) How do these concentrations compare to those found in plants growing in more mesic ecosystems? Additional questions addressed include: (1) How do concentrations of N in the green-stem tissues and stem litter of leafless desert shrubs

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compare to N in the leaves and litter of desert and non-desert shrub species? and (2) To what degree do N concentrations differ in the foliage and litter of shrubs growing in different deserts?

Methods

Compilation of nitrogen values

Nitrogen concentrations in green and senesced leaves of perennial desert shrubs were extracted from the published literature to piece together a general view of N holdings in desert foliage. Litter data were only included if it was clear that the values were for senesced leaves and not mixed-tissue litter. Data for shrubs growing in non-desert ecosystems were excluded, as were data for plants growing in greenhouses, experimentally planted plots, or otherwise altered sites. The only taxonomic restriction imposed on our analysis was to exclude cacti and other leafless, stem-succulent plants. Data from both evergreen and deciduous species were tabulated, although data from leafless, evergreen species were segregated from other species. Unpublished data from Australia and North America were also used. An analysis such as this cannot uncover every appropriate N concentration value ever published, yet we are confident that a thorough search has yielded a data set representative of desert shrubs worldwide.

Because it was impossible to discern whether abnormally high or low values were legitimate or the artifact of measurement error, we included all values that met the criteria listed above. This strategy seems reasonable given the probability that faulty high and low values would counterbalance each other. Another concern arose from the realization that N concentrations vary seasonally. In most papers from which data were extracted, a single value was presented that represented N concentrations in mature green leaves. In papers that presented N concentrations in leaves of varying maturity, we always chose data for mature green leaves, thus eliminating values from young, expanding leaves and old, senescing leaves. Concentrations of litter N were always from fully senesced leaves. All concentrations are expressed as percentage N of dry leaf mass.

Assigning accepted names of deserts to specific sampling locations was problematic for specific data sets from Australia, Egypt, and Saudi Arabia. For all data from Australia, the name of the state in which the data were collected (Western Australia or New South Wales) was used in place of a proper name of a desert because there are no universally accepted "desert names" for many arid regions in Australia. For data sets from Egypt and Saudi Arabia, only names of the regions in which sampling took place were provided in the publications we cited. Regions were therefore substituted for desert names in Egypt (Omayed) and Saudi Arabia (Al-Jauf).

Plant nomenclature follows that reported in the cited literature with two exceptions. *Larrea divaricata* reported in Garcia-Moya and McKell (1970) was changed to *Larrea tridentata*, and *Prosopis juliflora* var. *velutina* reported in Klemmedson (1974) was changed to *Prosopis juliflora*.

Data synthesis and statistical analyses

Nitrogen data for many of the species of desert shrubs listed in Table 1 came from more than one study and/or more than one desert. Seventy-eight species are represented by 127 total entries. An additional three species of leafless shrubs are represented by eight entries in Table 2. Because the number of N concentration values representing each individual species varied from one (many of the listed species) to eight (*Larrea tridentata*), it was necessary to standardize the data sets in Tables 1 and 2 when calculating mean N concentrations. To equalize weighting among species, each species was assigned a single value each for green-leaf N, leaf-litter N (when available), green-stem N, and stem-litter N (when available). Each value was the mean of all values cited independently in different studies. Therefore, all species contributed equally to the calculation of the overall means.

Statistics were executed with SYSTAT software (Wilkinson 1992). The Lilliefors test was used to determine whether data were normally distributed. Because all data to which we applied statistics were normally distributed, parametric statistics were used for all analyses. One-way ANOVA was used to determine whether green-leaf N varied among deserts, or among continental locations.

Results

Green-leaf N concentrations were found for 78 species of shrubs in 48 genera growing in 11 deserts on five continents (Table 1). Nitrogen in the green leaves of these species (equally weighted among species, see *Methods*) was 2.2 ± 0.08% (mean ± 1 SE). Two species growing in Saudi Arabia shared the lowest N concentration (1.0%; *Amygdalus arabica, Salsola tetrandra*), and *Lycium andersonii* growing at one site in the Mojave Desert of Nevada had the highest recorded N concentration (4.8%). More than 85% of all species held green leaves containing mean N concentrations <3.0%.

Few data describing N concentrations in senesced leaves of individual species were available (Table 1). Mean N concentration in the leaf litter of 11 species (equally weighted among species) was 1.1 ± 0.17% (mean ± 1 SE). Leaf-litter N was lower in *Brickellia laciniata* growing in New Mexico (0.4%) than in any other combination of site and species, and litter N was highest in *Prosopis glandulosa* growing in New Mexico (2.6%).

Three leafless species of desert shrubs contained a mean (equally weighted among species) of 2.1% N in green stem tissues, and 0.8% N in stem litter (Table 2). *Ephedra nevadensis* had both the lowest green-stem

TABLE 1. Concentration of nitrogen (N) in the green leaves and/or leaf litter of 78 species of desert shrubs. For an explanation of desert names in Australia, Egypt, and Saudi Arabia, please see *Methods*.

Species	Location: State and/or country	Location: Desert name or region	N (%): Green leaves	N (%): Leaf litter	Source of data
Acacia Gregii†	California, USA	Mojave	1.9	···	Garcia-Moya and McKell 1970
Acacia kempeana‡	Australia	Western Australia	1.7	···	Keay and Bettenay 1969
Acacia pruinocarpa†	Australia	Western Australia	1.9	···	Keay and Bettenay 1969
Acacia tetragonaphylla‡	Australia	Western Australia	1.5	···	Keay and Bettenay 1969
Acamptopappus shockleyi	Nevada, USA	Mojave	1.2	···	Romney et al. 1978
	Nevada, USA	Mojave	2.5	···	Wallace et al. 1978
	Nevada, USA	Mojave	3.0	···	Romney et al. 1980
Achillea fragrantissima	Iraq	Southern and Western	2.9	···	Thalen 1979
Ambrosia dumosa	Nevada, USA	Mojave	2.0	···	Romney et al. 1978
	Nevada, USA	Mojave	3.2	···	Wallace et al. 1978
	Nevada, USA	Mojave	3.7	···	Romney and Wallace 1980
	Nevada, USA	Mojave	4.2	···	Romney et al. 1980
	Nevada, USA§	Mojave	4.4	···	Wallace et al. 1980
Amygdalus arabica	Saudi Arabia	Al-Jauf	1.0	···	Al-Jaloud et al. 1994
Anvillea garcini	Iraq	Southern and Western	3.6	···	Thalen 1979
Artemisia herba-alba	Iraq	Southern and Western	4.1	···	Thalen 1979
Artemisia spinescens	Nevada, USA	Mojave	2.7	···	Wallace et al. 1978
Artemisia tridentata	Nevada, USA	Great Basin	1.3	0.6	Schlesinger et al. 1989
Astragalus spinosus†	Saudi Arabia	Al-Jauf	1.8	···	Al-Jaloud et al. 1994
Atriplex canescens	Nevada, USA	Mojave	2.5	···	Wallace et al. 1978
	Nevada, USA	Mojave	2.4	···	Romney and Wallace 1980
Atriplex confertifolia	Nevada, USA	Mojave	2.4	···	Wallace et al. 1978
	Nevada, USA	Mojave	3.0	···	Romney et al. 1980
	Nevada, USA	Mojave	1.8	1.1	Wallace et al. 1978
	Nevada, USA§	Mojave	3.8	···	Wallace et al. 1980
Atriplex hymenotheca	Australia	Western Australia	2.0	···	Keay and Bettenay 1969
Atriplex inflata	Australia	Western Australia	3.1	···	Keay and Bettenay 1969
Atriplex leucoclada	Saudi Arabia	Al-Jauf	2.8	···	Al-Jaloud et al. 1994
Atriplex nummularia	Australia	New South Wales	3.3	···	D. Tongway, *unpublished data*
Atriplex vesicaria	Australia	New South Wales	3.1	···	D. Tongway, *unpublished data*
	Australia	New South Wales	2.1	···	D. Tongway, *unpublished data*
Brickellia laciniata	New Mexico, USA	Chihuahuan	2.3	0.6	K. T. Killingbeck and W. G. Whitford, *unpublished data*
	New Mexico, USA	Chihuahuan	2.3	1.2	K. T. Killingbeck and W. G. Whitford, *unpublished data*
	New Mexico, USA	Chihuahuan	1.9	0.4	K. T. Killingbeck and W. G. Whitford, *unpublished data*
Brickellia incana	California, USA	Mojave	1.4	···	Garcia-Moya and McKell 1970
Calligonum comosum	Iraq	Southern and Western	3.7	···	Thalen 1979
Cassia sturtii‡	Australia	Western Australia	2.1	···	Keay and Bettenay 1969
Ceratoides lanata	Nevada, USA	Mojave	2.2	···	Romney et al. 1978
	Nevada, USA	Mojave	3.0	···	Wallace et al. 1978
	Nevada, USA	Mojave	2.8	···	Romney and Wallace 1980

TABLE 1. Continued.

Species	Location		N (%)		Source of data
	State and/or country	Desert name or region	Green leaves	Leaf litter	
	Nevada, USA§	Mojave	3.4	···	Wallace et al. 1980
	Nevada, USA	Mojave	3.6	···	Romney et al. 1980
Cericidium floridum‖	Arizona, USA	Sonoran	3.6	···	Klemmedson 1974
Chilopsis linearis	New Mexico, USA	Chihuahuan	2.1	0.7	K. T. Killingbeck and W. G. Whitford, *unpublished data*
	New Mexico, USA	Chihuahuan	1.8	1.0	K. T. Killingbeck and W. G. Whitford, *unpublished data*
	New Mexico, USA	Chihuahuan	2.0	0.8	K. T. Killingbeck and W. G. Whitford, *unpublished data*
Coleogyne ramosissima	Nevada, USA	Mojave	1.8	···	Wallace et al. 1978
	Nevada, USA§	Mojave	2.1	···	Wallace et al. 1980
Crotolaria cunninghamii‡	Australia	Western Australia	2.9	···	Keay and Bettenay 1969
Dalea fremontii†	Nevada, USA	Mojave	2.7	···	Wallace et al. 1978
Dodenea attenuata	Australia	Western Australia	1.8	···	Keay and Bettenay 1969
Eremophila foliosissima	Australia	Western Australia	2.3	···	Keay and Bettenay 1969
Eremophila fraseri	Australia	Western Australia	2.0	···	Keay and Bettenay 1969
Eremophila latrobei	Australia	Western Australia	2.3	···	Keay and Bettenay 1969
Eremophila leucophylla	Australia	Western Australia	2.0	···	Keay and Bettenay 1969
Eremophila longifolia	Australia	Western Australia	1.5	···	Keay and Bettenay 1969
Eremophila pterocarpa	Australia	Western Australia	2.5	···	Keay and Bettenay 1969
Eriogonum fasciculatum	California, USA	Mojave	1.1	···	Garcia-Moya and McKell 1970
Fallugia paradoxa	New Mexico, USA	Chihuahuan	1.7	1.0	K. T. Killingbeck and W. G. Whitford, *unpublished data*
Flourensia cernua	New Mexico, USA¶	Chihuahuan	2.8	···	R. E. Estell, E. L. Fredrickson, and K. M. Havstad, *unpublished manuscript*
	New Mexico, USA	Chihuahuan	2.7	1.1	K. T. Killingbeck and W. G. Whitford, *unpublished data*
	New Mexico, USA	Chihuahuan	3.0	···	King et al. 1996
Fouquieria splendens	New Mexico, USA	Chihuahuan	1.6	1.2	Killingbeck 1992
	New Mexico, USA#	Chihuahuan	1.9	···	Killingbeck 1992
	New Mexico, USA	Chihuahuan	1.1††	0.5	Killingbeck 1993*a*
	New Mexico, USA	Chihuahuan	2.1††	0.6	Killingbeck 1993*a*
Franseria dumosa	California, USA	Mojave	1.5	···	Garcia-Moya and McKell 1970
Grayia spinosa	Nevada, USA	Mojave	2.1	···	Romney et al. 1978
	Nevada, USA	Mojave	2.7	···	Wallace et al. 1978
	Nevada, USA	Mojave	2.2	···	Romney et al. 1980
	Nevada, USA	Mojave	1.7	1.5	Wallace et al. 1978
	Nevada, USA§	Mojave	2.5	···	Wallace et al. 1980
Halothamnus acutifolius	Saudi Arabia	Al-Jauf	2.4	···	Al-Jaloud et al. 1994
Heliotropium ramosissimum	Iraq	Southern and Western	1.9	···	Thalen 1979
Hymenoclea salsola	California, USA	Mojave	1.7	···	Garcia-Moya and McKell 1970
	Nevada, USA	Mojave	4.2	···	Wallace et al. 1978

TABLE 1. Continued.

Species	Location		N (%)		Source of data
	State and/or country	Desert name or region	Green leaves	Leaf litter	
Indigofera brevidens†	Australia	Western Australia	2.4	···	Keay and Bettenay 1969
Krameria grayi	California, USA	Mojave	1.6	···	Garcia-Moya and McKell 1970
Krameria parvifolia	Nevada, USA	Mojave	2.0	···	Romney et al. 1978
	Nevada, USA	Mojave	2.2	···	Wallace et al. 1978
	Nevada, USA	Mojave	2.1	···	Romney et al. 1980
Larrea cuneifolia	Argentina	Monte	2.2	···	Rhodes 1977
Larrea tridentata	California, USA	Mojave	2.2	···	Garcia-Moya and McKell 1970
	New Mexico, USA§	Chihuahuan	1.5‡‡	0.7§§	Lajtha 1987
	Nevada, USA	Mojave	2.4	···	Romney and Wallace 1980
	Nevada, USA	Mojave	1.8	···	Romney et al. 1978
	Nevada, USA	Mojave	2.4	···	Wallace et al. 1978
	Nevada, USA	Mojave	2.6	···	Romney et al. 1980
	Nevada, USA	Mojave	1.9	0.9	Wallace et al. 1978
	Nevada, USA§	Mojave	2.1	···	Wallace et al. 1980
Lycium andersonii	Nevada, USA	Mojave	2.3	···	Romney and Wallace 1980
	Nevada, USA	Mojave	3.3	···	Wallace et al. 1978
	Nevada, USA	Mojave	4.8	···	Romney et al. 1978
	Nevada, USA	Mojave	3.3	···	Romney et al. 1980
	Nevada, USA§	Mojave	3.2	···	Wallace et al. 1980
Lycium pallidum	Nevada, USA	Mojave	2.8	···	Wallace et al. 1978
	Nevada, USA	Mojave	3.5	···	Wallace et al. 1980
Lycium shockleyi	Nevada, USA	Mojave	3.1	···	Wallace et al. 1978
Maireana carnosa	Australia	Western Australia	2.3	···	Keay and Bettenay 1969
Maireana pyramidata	Australia	Western Australia	2.8	···	Keay and Bettenay 1969
	Australia	New South Wales	3.0	···	D. Tongway, *unpublished data*
Maireana sedifolia	Australia	New South Wales	2.9	···	D. Tongway, *unpublished data*
Menodora spinescens	Nevada, USA	Mojave	2.4	···	Wallace et al. 1978
Prosopis glandulosa‡	New Mexico, USA	Chihuahuan	3.5	2.6	K. T. Killingbeck and W. G. Whitford, *unpublished data*
	California, USA	Sonoran	2.8‡‡	···	Rundel et al. 1982
Prosopis juliflora‡	Arizona, USA	Sonoran	2.8	···	Klemmedson 1974
Rhagodia gaudichaudiana	Australia	Western Australia	3.2	···	Keay and Bettenay 1969
Rhus microphylla	New Mexico, USA	Chihuahuan	2.3	1.1	K. T. Killingbeck and W. G. Whitford, *unpublished data*
	New Mexico, USA	Chihuahuan	2.8	1.6	K. T. Killingbeck and W. G. Whitford, *unpublished data*
	New Mexico, USA	Chihuahuan	2.6	1.4	K. T. Killingbeck and W. G. Whitford, *unpublished data*
Salsola chaudharyi	Saudi Arabia	Al-Jauf	1.2	···	Al-Jaloud et al. 1994
Salsola cyclophylla	Saudi Arabia	Al-Jauf	1.3	···	Al-Jaloud et al. 1994
Salsola tetrandra	Saudi Arabia	Al-Jauf	1.0	···	Al-Jaloud et al. 1994
Santalum acuminatum	Australia	Western Australia	2.0	···	Keay and Bettenay 1969
Santalum lanceolatum	Australia	Western Australia	2.1	···	Keay and Bettenay 1969
Scleroleana drummondii	Australia	Western Australia	1.9	···	Keay and Bettenay 1969

TABLE 1. Continued.

Species	Location		N (%)		Source of data
	State and/or country	Desert name or region	Green leaves	Leaf litter	
Scleroleana gardneri	Australia	Western Australia	1.9	···	Keay and Bettenay 1969
Scleroleana obliquicuspis	Australia	Western Australia	1.9	···	Keay and Bettenay 1969
Scleroleana paradoxa	Australia	Western Australia	1.8	···	Keay and Bettenay 1969
Sphaeralcea ambigua	Nevada, USA	Mojave	2.1	···	Romney and Wallace 1980
	Nevada, USA	Mojave	2.5	···	Wallace et al. 1978
Tetradymia glabrata	Nevada, USA	Mojave	1.4	···	Wallace et al. 1978
Teucrium polium	Iraq	Southern and Western	1.6	···	Thalen 1979
Thymelaea hirsuta	Egypt	Omayed	1.3	···	Shaltout 1992
Traganum nudatum	Saudi Arabia	Al-Jauf	1.1	···	Al-Jaloud et al. 1994
Zilla spinosa	Saudi Arabia	Al-Jauf	1.9	···	Al-Jaloud et al. 1994
Zygophyllum coccineum	Iraq	Southern and Western	1.1	···	Thalen 1979

† Genus known to be nodulate, but nodulation in this species not confirmed.
‡ Species known to be nodulate (nitrogen-fixing symbiont = *Rhizobium*).
§ Mean of multiple sites.
|| Genus in family Fabaceae, but not known to be nodulate.
¶ Mean of multiple years.
# Different site and year from *Fouquieria* data above.
†† Percentage N in green leaves calculated from litter and percentage resorption data.
‡‡ Interpolated from figure.
§§ Litter N calculated from green-leaf N and percentage resorption.

N recorded (1.0%; California) and the highest (3.9%; Nevada).

Mean green-leaf N was similar in shrubs growing in different deserts worldwide (ANOVA; $P > 0.05$). Shrub species in Australia (2.2% N), the Middle East (2.0% N), North America (2.3% N), and South America (2.2% N) all produced green leaves that held similar concentrations of N. In the one case where data were available for at least eight shrub species in each of two distinct deserts on the same continent (North America), mean N concentrations in green leaves were nearly identical (Chihuahuan Desert, 2.26% N; Mojave Desert, 2.33% N).

In the only cold-desert species represented in Table 1 (*Artemisia tridentata*, Great Basin), both green-leaf N (1.3%) and litter N (0.6%) were lower than most of the remaining species, all of which were from hot deserts. Our synthesis does not contain enough species from cold deserts to make an adequate comparison between cold and hot deserts, but the possibility that green-leaf N and litter N may differ between shrub species inhabiting cold and hot deserts is intriguing.

DISCUSSION

Nitrogen in the green leaves of desert shrubs

The claim that " . . . desert shrubs contain about 3% N in their leaves . . . " (Skujins 1981) appears to be unfounded (Table 1). Mean N in the green leaves of 78 species of desert shrubs growing in a wide variety of deserts on five continents (2.2% N) was substantially less than the 3% value projected by Skujins (1981).

TABLE 2. Concentration of nitrogen (N) in the photosynthetic green-stem tissue and/or stem litter of three species of desert shrubs that do not produce leaves.

Species	Location		N (%)		Source of data
	State and/or country	Desert name	Stem tissue	Stem litter	
Acanthosicyos horridus	Namibia	Namib	1.2	0.8	Klopatek and Stock 1994
Ephedra funera	Nevada, USA	Mojave	2.8	···	Wallace et al. 1978
	Nevada, USA	Mojave	2.3	···	Romney et al. 1980
Ephedra nevadensis	California, USA	Mojave	1.0	···	Garcia-Moya and McKell 1970
	Nevada, USA	Mojave	2.4	···	Wallace et al. 1978
	Nevada, USA	Mojave	2.9	···	Romney et al. 1980
	Nevada, USA	Mojave	1.7	0.8	Wallace et al. 1978
	Nevada, USA	Mojave	3.9†	···	Wallace et al. 1980

† Mean of multiple sites.

TABLE 3. Mean concentration of nitrogen (N) in the green leaves of 67 species of perennial trees and shrubs growing in deciduous, and mixed deciduous forests (the number of species is not 71 because the same four species were included in each of two of the publications cited).

	Sample			
Type of plants	No. of species	Location	N (%)	Source of data
Deciduous and evergeen trees and shrubs	26	United Kingdom	2.1	Allen 1974
Deciduous trees	6	Belgium	2.3	Duvigneaud and Denaeyer-De Smet 1970
Deciduous trees and shrubs	34	Southeast Ontario, Canada	2.3	Ricklefs and Matthew 1982
Deciduous and evergreen trees	5	New Hampshire, USA	2.2	Whittaker et al. 1979

Similar claims of extraordinarily high N concentrations in the leaves of desert shrubs (e.g., Whittaker et al. 1979) are equally faulty. Even when data in Table 1 were segregated by geographical region (Australia, Middle East, North America, South America), no region supported desert shrubs with mean green-leaf N higher than 2.3%. Of the deserts in North America with more than two entries in Table 1, the shrubs in the Mojave Desert had the highest green-leaf N (2.3%). For this same desert, mean N concentration in the green leaves of 20 species of perennial forbs, grasses, and shrubs was 2.0% (El-Ghonemy et al. 1978). Photosynthetic stem tissues of leafless desert shrubs also contained much less than 3% N (2.1%; Table 2).

Desert shrubs clearly have less N in their green leaves than previously thought, but that bears only indirectly on the assertion that all tissues of desert plants have higher N concentrations than tissues of plants from more mesic environments (Rodin and Bazilevich 1967, West 1981). To judge the merits of this speculation, data from our analysis were compared to green-leaf N concentrations in 67 species of trees and shrubs growing in deciduous, and mixed deciduous forests (Table 3). Mean N concentrations in the four studies cited varied from 2.1 to 2.3%. The mean of the four values, 2.2%, coincided exactly with the mean of green-leaf N in desert shrubs.

To extend the comparison between desert shrubs and plants from more mesic environments, we examined N concentrations in the leaves of plants growing at six sites in the tropical wet forests of Panama (Golley et al. 1975). We reasoned that tropical wet forests would occupy a position at the opposite end of the moisture continuum from deserts. Mean concentrations of N in green leaves of the overstory and understory at these six tropical wet forest sites were 2.0% and 2.1%, respectively (Golley et al. 1975).

The answer to the question of whether green-leaf N concentrations are appreciably higher in desert shrubs than in plants from more mesic environments is evident; they are not. The consistent convergence of means (2.0–2.3% N) clearly indicates the high similarity in green-leaf N concentrations among species growing in strikingly dissimilar environments. This convergence and its implications are thought provoking, and consistent with the estimate that the average N concentration in the green leaves of land plants is 2% (Barbour et al. 1980).

Finally, it is possible that N concentrations in the green leaves of desert shrubs might still be considered abnormally high from an ecosystem perspective. For example, if N concentrations are particularly high in the leaves of the few shrub species that dominate desert ecosystems, then the N sequestered in the shrub foliage of those ecosystems might be extraordinarily high even though green-leaf N concentrations in most desert shrub species is typical of all plants. *Larrea tridentata* was chosen to evaluate this possibility because it is the most ubiquitous, dominant shrub of the southwest United States (Shreve 1951, Mabry et al. 1977) and probably produces more biomass than any other shrub species growing within its range of occurrence. The mean concentration of N in the green leaves of *Larrea tridentata* growing in the Chihuahuan and Mojave Deserts of the U.S. was 2.1% (Table 1), thus dispelling the possibility that green-leaf N is disproportionately high in the shrub species that dominate desert ecosystems.

Nitrogen in the leaf litter of desert shrubs

Data describing N in the leaf litter of desert shrub species are scarce (Table 1). Furthermore, much of what is available is not segregated by species and tissue type and is often displayed on a per-unit-area basis (e.g., Charley 1972) rather than as a percentage of dry leaf mass. While the scarcity of data limits a comprehensive comparison between N concentrations in the leaf litter of desert shrubs and species growing in more mesic environments, several observations appear to be in order.

Mean leaf-litter N in 11 species was 1.1%, a value considerably lower than the one offered for desert communities in Syria and the former USSR by Rodin and Bazilevich (1967; 1.7% N). West (1981) correctly reported mean litter N to be 1.5% rather than 1.7% in the data presented by Rodin and Bazilevich (Killingbeck 1993*a*), yet even the lower value was high enough to prompt West (1981) to conclude that "A characteristic feature of the litter fall in desert communities is its high nitrogen content . . . ."

Our data strongly suggest that this view is unfounded. First, N concentrations reported in Table 1 are for leaf litter only, whereas N concentrations reported by Rodin and Bazilevich (1967) and West (1981) appear to be for total litter. Because the leaf tissues contain more N than non-leaf tissues (e.g., Allen 1974, Likens et al. 1977), the difference between N in the leaf litter reported in Table 1 and N in the leaf component of the total litter reported by Rodin and Bazilevich (1967) and West (1981) is likely to be higher than the actual data initially suggest.

Second, 45% of all values for leaf-litter N in Table 1 were <1.0%, and the value for *Brickellia laciniata* growing in the Chihuahuan Desert (0.4 ± 0.04% N, [mean ± 1 SE], $n = 4$, Jornada Experiment Range) approaches what appears to be the lowest leaf-litter N concentration known for any woody perennial (0.3% N; Killingbeck 1996).

Third, only 3 of the 20 entries for leaf-litter N in Table 1 were even as high as 1.5% N, and one of those entries was for a N-fixing species, *Prosopis glandulosa*. Because N-fixers typically have extraordinarily high concentrations of N in their leaf litter (Turner et al. 1976, Gorham et al. 1979, Killingbeck 1993*b*), it is doubtful that the elevated N concentration in *Prosopis* is a function of its life form (shrub) or environment (desert).

When *Prosopis* is removed from consideration, mean N concentration in the desert shrubs listed in Table 1 drops to 1.0%. This N concentration is equal to or lower than mean N concentrations reported for total litter in shrub tundra (2.1%), meadow steppe (1.2%), and tropical rain-forest (1.0%) communities (Charley 1972, as adapted from Rodin and Bazilevich 1967), and only marginally higher than N in the leaf litter of 77 species of woody plants growing at a wide variety of sites worldwide (0.9%; Killingbeck 1996). These comparisons suggest the likelihood that N concentrations in the leaf litter of desert shrubs are not substantially higher than N in the litter of species growing in more mesic environments. Further, application of the ecosystem-level argument provides more unequivocal evidence for the above speculation given the fact that mean leaf-litter N in the ubiquitous shrub *Larrea tridentata* was only 0.8%.

Conclusions

In desert ecosystems the co-occurrence of low soil N (Dregne 1976, Charley 1972, West 1981) and extraordinarily high shrub-foliage N (Skujins 1981, West 1981) was thought to be a recurring pattern (Whittaker et al. 1979) with significant ecosystem-level implications. This soil–plant paradox can no longer exist as once envisioned because N concentrations in the green leaves, and probably leaf litter, of desert shrubs are not substantially different from N concentrations in woody perennials growing in other ecosystems.

Instead, the relevant question now becomes how and why do desert ecosystems inherently low in soil N support shrub species that contain foliar N concentrations typical of species in more N-rich ecosystems? The answer to this question likely involves the high spatial and temporal heterogeneity common to desert ecosystems. Resources such as N are typically much more concentrated in the immediate vicinity of desert shrubs than in inter-shrub spaces (Garcia-Moya and McKell 1970, Charley and West 1975, Virginia and Jarrell 1983). An absence of these resource islands would result in a more homogeneous distribution of N, which in turn would result in widespread nitrogen deficiency (Romney et al. 1978). Therefore, spatially heterogeneous "islands of fertility" (Garcia-Moya and McKell 1970) effectively buffer their host plants from chronically low levels of resources.

Likewise, temporal heterogeneity promotes episodes of relatively high resource availability. During and immediately after the arrival of the infrequent rains that characterize desert ecosystems, decomposers are temporarily released from water limitations, mineralization rates increase (Strojan et al. 1987), and resources such as N become more readily available (Skujins 1981). Litter decomposition appears to be somewhat independent of short-term precipition patterns in the Chihuahuan Desert (Santos et al. 1984, Whitford et al. 1986), yet even in this desert, alternating periods of resource mobilization and immobilization (Fisher et al. 1987, Whitford et al. 1987) reflect a high degree of temporal heterogeneity in resource availability. Therefore, in a functional sense, desert shrubs are not subjected to the selection pressures of a constantly N-deficient environment.

Finally, the similarities in leaf N concentration observed in this analysis suggest that the "adaptive constancy" in leaf N displayed by individual genotypes of a single species growing in nutritionally distinct soils (*Polygonum persicaria*; Sultan and Bazzaz 1993) is not just an attribute of identical or closely related taxa, but may also exist in different species or groups of species growing in a wide assortment of ecosystems. The interplay between photosynthetic capacity and leaf N may provide insights into possible reasons for the relative constancy of average leaf N, yet because it is the ratio of leaf N to photosynthetic capacity that is "relatively insensitive to differences among species or growth conditions" (Field and Mooney 1983), and not photosynthetic capacity itself, the robust correlation between photosynthetic capacity and leaf N (Field and Mooney 1983) does not predict, and cannot explain, similarities among groups of plants growing in diverse environments. If photosynthetic capacity per unit N is in fact more variable than once thought (Evans 1989), then it is possible that woody perennials adjust photosynthetic capacity rather than leaf N to match the constraints of varying environments. In spite of the fact that specific reasons for constancy in leaf N are not obvious, trade-offs among foliar N, water-use efficiency, and rates of photosynthetic carbon fixation (e.g., Field et al. 1983) may be the mechanism by which this tendency can be maintained.

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