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K.T. Killingbeck · W.G. Whitford

Nutrient resorption in shrubs growing by design, and by default in Chihuahuan Desert arroyos

Abstract In the northern stretches of the Chihuahuan Desert, the margins of ephemeral stream channels called arroyos support a unique vegetation dominated by a guild of winter-deciduous shrubs. To explore the dynamics of nutrient conservation in this assemblage of arroyo shrubs, we measured nitrogen (N) and phosphorus (P) resorption efficiency and proficiency in six species of shrubs growing in arroyos in southern New Mexico, USA. Collectively, these six species were no more efficient or proficient at resorbing N and P from senescing leaves than shrubs growing in other environments. Resorption efficiency averaged 53% and 50% for N and P, respectively, and resorption proficiency averaged 0.80% and 0.06% for N and P, respectively. However, resorption varied significantly between species specifically restricted in their distribution to riparian habitats (obligate riparian species), and those that were not. The two obligate riparian species combined (*Brickellia laciniata*, *Chilopsis linearis*) were significantly more efficient and proficient at resorbing N than the non-obligate riparian species combined (*Fallugia paradoxa*, *Flourensia cernua*, *Prosopis glandulosa*, *Rhus microphylla*). Additionally, both *Brickellia* and *Chilopsis* were individually significantly more proficient at resorbing N than any of the other four species. The dichotomy in resorption between obligate riparian species and those that were not may have been the result of the interplay between hydrology, geomorphology, and biology. Because arroyos move in space as the movement of water erodes banks and changes channel location, some plants are found along arroyos only because the arroyos have moved to them. These plants (plants growing by default) may be less well adapted to arroyo margins than obligate riparian species (plants growing by design). Significant differences in resorption between obligate and non-obligate riparian species suggested that evolutionary history and habitat specificity may be added to the list of factors known to influence resorption. Selected life history traits of the six species did not appear to be related to any measure of resorption, but leaf surface area, specific leaf mass, and nutrient concentrations in green leaves were all correlated with resorption efficiency or proficiency in one or more species. The only species capable of symbiotic N fixation, *Prosopis glandulosa*, retained at least 2.3 times more N in its senesced leaves than any other species. Patterns of resorption in arroyo shrubs strongly indicated that efficiency and proficiency are fundamentally different, complementary measures of resorption.

Keywords Arroyo · Desert shrubs · Nutrients · Resorption · Riparian communities

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Introduction

Arroyos are ephemeral drainage channels in arid landscapes. They are normally dry, but are capable of transporting massive amounts of floodwater during intense storms (Goudie and Wilkinson 1977). Known also as creeks (Australia), sairs (Mongolia), wadis (North Africa and Arabia) and washes (USA; Petrov 1976; McGinnies 1979), these products of erosion "...are important features of all deserts..." (McGinnies 1979), yet almost nothing is known about the nutrient economy of the plants that dominate their borders.

In the northern stretches of the Chihuahuan Desert in southern New Mexico, USA, the margins of arroyos support vegetation dominated by a guild of completely, or predominately winter-deciduous shrubs. This unique assemblage of plants exists in an arid environment limited by water, yet has access to periodic pulses of water. Does this additional water influence the degree to which arroyo shrubs conserve nutrients through resorption (with-

drawal of nutrients from senescing leaves prior to abscission)? Selection for high nutrient conservation through efficient and proficient resorption may be the result of added water if the primary effect of the water is to elevate nutrient limitation as water limitation is diminished. However, water may also decrease selection for nutrient conservation because its presence increases rates of nutrient mineralization (e.g., Skujins 1981; Strogan et al. 1987). The general question posed above has never been answered. Even though there are published data on nutrient resorption in desert shrubs (Charley 1972; Wallace et al. 1978; Lajtha 1987; Schlesinger et al. 1989; Killingbeck 1992, 1993a), we are unaware of published data on resorption in shrubs growing along arroyos.

To address the fundamental question outlined above, and to explore the variability in resorption among species cohabiting arroyo margins, we measured nitrogen (N) and phosphorus (P) resorption efficiency (percentage of a nutrient withdrawn from leaves prior to abscission) and proficiency (concentration to which a nutrient is reduced in senesced leaves) in six winter-deciduous shrub species that grow in arroyos in southern New Mexico. The specific questions we sought to answer are: (1) Does nutrient resorption in shrubs growing along an arroyo differ from that in shrubs growing in other ecosystems, or in other landscape positions within arid ecosystems? (2) Does resorption differ between obligate and non-obligate riparian species? (3) Are interspecific differences in resorption prevalent, and if so, are these differences similar to patterns previously observed in more mesic environments? (4) Are differences in life history traits, physical characteristics of leaves, and nutrient contents of green leaves related to resorption? (5) Is N resorption exceptionally inefficient or unproficient in the single species (*Prosopis glandulosa*) that harbors a N-fixing symbiont? (6) Do efficiency and proficiency serve as fundamentally different measures of resorption that provide unique insights into questions of interspecies differences in nutrient resorption?

Materials and methods

Resorption was measured in three arroyos in late summer and fall of 1994 in the northern reaches of the Chihuahuan Desert. All three arroyos were located in southern New Mexico, within 40 km of the city of Las Cruces. Arroyo J-1 (32°29′ N, 106° 47′ W) was the primary focus of the study and was originally chosen because its hydrology had been partially characterized (Atchley and Whitford, unpublished data). All of the interspecies guild comparisons were made in this arroyo which is located in the Jornada Long Term Ecological Research (LTER) Area which, in turn, lies within the New Mexico State University Jornada Experiment Range. A second arroyo immediately north of Tortugas Mountain (32°18′ N, 106° 40′ W; Arroyo TMNTN) and a third arroyo within the Jornada LTER Area (32°28′ N, 106° 46′ W; Arroyo J-2) were sampled to better capture variability in resorption in the obligate riparian species.

The sampled segments of all three arroyos varied in width from approximately 4–15 m, had coarse, sandy substrates, and were bounded by a plant community dominated by winter-deciduous shrubs. Arroyo channels were devoid of shrubs because the scouring effects of periodic floods restricted plant growth to the perimeter of the arroyo channel, or to "islands" in braided sections of the arroyos. Climatic conditions include: (1) maximum summer temperatures frequently exceeding 37°C; (2) minimum December and January nighttime temperatures often less than 0°C; (3) a mean annual precipitation of 200–250 mm (West and Klemmedson 1978, 213 mm for the Jornada Experiment Station; unpublished data, 250 mm for the Jornada LTER Area); and (4) maximum precipitation during July–September, often from intense convectional storms. Desert communities surrounding the arroyos are presently dominated by *Larrea tridentata* (Sesse & Moçiño ex DC.) Coville (creosotebush), a ubiquitous C_3 shrub that has supplanted native grasses in this area during the past century (Buffington and Herbel 1965; Schlesinger et al. 1990).

Relative abundances of all shrub species growing on the margins of Arroyo J-1 were determined on 29 June 1996. Shrubs growing immediately adjacent to the channel along both sides of a 335-m arroyo segment were identified and counted. Relative abundances of all shrub species growing in the desert outside of the immediate influence of Arroyo J-1 were determined on 25 May 1998. All individual shrubs within two 4-m-wide belt transects, one on either side of the arroyo, were identified and counted. Each transect was centered 10 m from the nearest edge of the arroyo channel and encompassed the entire length of the 335-m arroyo segment.

In September 1994, eight individuals of each of the six most abundant winter-deciduous shrub species lining the 335-m segment of Arroyo J-1 (Table 1) were tagged. Only mature plants that were spatially separate from one another and that were immediately adjacent to the arroyo channel were chosen. The six species varied in (1) pattern of leaf retention, (2) degree of fidelity to riparian habitats, and (3) phenology of flowering (Table 1). *Brickellia laciniata* A. Gray, *Chilopsis linearis* (Cav.) Sweet., *Prosopis glandulosa* Torr., and *Rhus microphylla* Engelm. were completely winter-deciduous during the study, while *Fallugia paradoxa* (Don) Endl. and *Flourensia cernua* DC. held some leaves throughout the winter of 1994–1995. *Prosopis* was the only species associated with symbiotic N fixers. All species will be identified throughout by their genus name.

The degree to which these six species are restricted in their distribution to riparian habitats was addressed by Dick-Peddie (1993; see Table 9.1). *Brickellia* and *Chilopsis* were classified as obligate riparian species, *Fallugia*, *Prosopis*, and *Rhus* were classified as semiriparian species (i.e., facultative riparian species), and *Flourensia* was considered to be non-riparian. In the northern Chihuahuan Desert, *Brickellia* and *Chilopsis* were the only species we studied that were exclusively restricted to riparian ecosytems (personal observation).

Five other species of shrubs grew along the arroyo but were excluded from the study because they were evergreen (*Larrea*) or had a relative abundance of <2.5% (four other species). The six deciduous arroyo species studied accounted for 70% of all shrubs along the arroyo, while *Larrea* alone accounted for more than 90% of all shrubs growing outside of the immediate influence of Arroyo J-1 (Table 1). The two species of obligate riparian shrubs, *Brickellia* and *Chilopsis*, accounted for 43% of all shrub individuals growing along the arroyo, and 61% of all individuals of the six species studied.

Green leaves from each of the 48 tagged individuals were collected on 28 and 29 September 1994. Leaves were collected from all areas of the canopy on the side of each plant facing the arroyo. The dates on which senesced leaves were collected varied because the rate and timing of leaf senescence and abscission varied widely among the six species. All individuals were monitored frequently, and fully senesced leaves were collected in a large plastic-lined container only when shaking a plant resulted in leaf-fall. Senesced leaves were collected on 7 October (*Fallugia*), 18 October (*Brickellia*; additional senesced leaves from three individuals were collected on 7 November), 1 November (*Chilopsis*), 22 November (*Rhus*), 28 November (*Prosopis*), and 7 December (*Flourensia*; additional senesced leaves from two individuals were collected on 29 December).

Eight additional individuals of *Chilopsis* were tagged on 1 October in a 90-m segment of Arroyo TMNTN. Green leaves from

Table 1 Degree of fidelity to riparian habitats, selected life history characteristics, and relative abundance of shrubs inhabiting the margins of Arroyo J-1 and the surrounding desert. Degree of fidelity is adapted from Dick-Peddie (1993); *OBL*=obligate riparian, *FAC*=facultative riparian, *N-R*=non-riparian (not listed as a riparian species in Dick-Peddie). Leaf retention (*Leaves*) is character- ized as winter-deciduous (*WD*), partially winter-deciduous (*PWD*; some leaves held in winter), or evergreen (*E*). Flower production (*Flowers*) is characterized as the seasons in which flowers are typically produced. Relative abundance is the number of stems of a species compared to the number of stems of all shrub species expressed as a percentage

Species	Fidelity	Leaves	Flowers	Relative abundance (%)	
				Arroyo	Desert
Species studied					
Brickellia laciniata	OBL	WD	F	38	0
Chilopsis linearis	OBL	WD	S,SU	5	0
Fallugia paradoxa	FAC	PWD	S,SU,F	14	0
Flourensia cernua	N-R	PWD	F	3	<1
Prosopis glandulosa	FAC	WD	S	4	6
Rhus microphylla	FAC	WD	S	7	<1
Remaining species					
Larrea tridentata	N-R	E	S,SU,F,W	22	93
Other (four species)	– – –	– – –	– – –	8	0

all sections of the canopy of these plants were collected the same day. *Chilopsis* leaves did not completely senesce until late November, and were collected on 24 November. On 5 October, four individuals of *Brickellia* were tagged. Because each of these individuals held both fully green, and fully senesced leaves on this date, both types of leaves were collected and segregated accordingly.

Leaves from *Chilopsis* and *Brickellia* were also collected in a 140-m segment of Arroyo J-2. The number of replicates and sampling format was the same as in Arroyo TMNTN. Green leaves of *Chilopsis* and *Brickellia* were collected on 2 October and 6 October, respectively, and senesced leaves of both species were collected on 1 November and 6 October, respectively.

Surface areas of leaves from each individual on each sampling date were measured in the laboratory immediately after collection with a LI-COR 3000 area meter. All leaves were dried at 70°C to constant mass, weighed, and ground in a Wiley mill to pass a 40-mesh screen. Nutrient analyses were carried out in the New Mexico State University Soil, Plant, and Water Testing Laboratory. N and P were chosen for measurement because of their preeminent importance to plant growth (Chapin 1980). Total Kjeldahl N was extracted from 0.2 g plant samples and measured with a Technicon AutoAnalyzer. P was extracted from 0.5 g plant samples with a microwave-assisted acid digestion technique utilizing concentrated nitric acid and 30% hydrogen peroxide, and measured with a Technicon AutoAnalyzer.

Resorption is expressed throughout the manuscript as either resorption efficiency or proficiency. Efficiency is the percentage of an element removed from senescing leaves and was calculated as the difference in nutrient content (μg/cm^2) between green and senesced leaves, divided by green-leaf nutrient content, and multiplied by 100. Proficiency is the level to which a nutrient has been reduced in senesced leaves and was calculated as the concentration (%) of a given nutrient in senesced leaves. Because a low nutrient concentration in senesced leaves is evidence of high proficiency, and vice versa, references to high resorption proficiency imply low proficiency concentrations.

Statistical analyses were performed with SYSTAT software (Wilkinson 1992). The Lilliefors test was used to determine whether data were normally distributed. Probabilities of differences among multiple means were generated with ANOVA when the assumption of normality was met, and with the Kruskal-Wallis distribution-free statistic when data were not normally distributed. The degree to which specific pairs of variables varied was measured with Fisher's LSD multiple means comparison when the assumption of normality was met, and with the Mann-Whitney U-test when data were not normally distributed.

Table 2 Mean surface area (cm^2), specific leaf mass (mg/cm^2), nitrogen concentration (%), and phosphorus concentration (%) in green leaves of the six shrub species studied in Arroyo J-1. $n=8$ for each species; numbers in parentheses are standard error of the mean; means in vertical columns with different letters are statistically different (Kruskal-Wallis, $P<0.001$, surface area and phosphorus; ANOVA, $P<0.001$, SLM and nitrogen). *Brickellia=B. laciniata, Chilopsis=C. linearis, Fallugia=F. paradoxa, Flourensia=F. cernua, Prosopis=P. glandulosa, Rhus=R. microphylla*

Species	Surface area	SLM	Nitrogen	Phosphorus
Brickellia	1.1 (0.1)a	5.5 (0.2)a	2.3 (0.1)a	0.21 (0.01)a
Chilopsis	3.1 (0.2)b	12.5 (0.5)b	2.1 (0.1)a	0.18 (0.02)a
Fallugia	0.3 (0.1)c	13.4 (0.4)c	1.7 (0.1)b	0.20 (0.02)ab
Flourensia	2.0 (0.2)d	10.2 (0.3)d	2.7 (0.1)c	0.26 (0.03)ab
Prosopis	20.5 (2.6)e	17.4 (0.2)c	3.5 (0.1)d	0.12 (0.01)c
Rhus	2.4 (0.2)d	11.6 (0.3)b	2.3 (0.1)a	0.17 (0.02)ab

Results

Fundamental attributes of the green leaves of the six study species varied significantly [Table 2; $P<0.001$, ANOVA for specific leaf mass (SLM) and N; $P<0.001$, Kruskal-Wallis for surface area and P]. *Fallugia* leaves had three times less surface area than the species with the next largest leaves, and almost 70 times less surface area than the leaves of *Prosopis*. Specific leaf mass was lower in *Brickellia* than in all other species. *Prosopis* leaves had both the highest N concentration and the lowest P concentration.

In the three arroyos in which *Brickellia* and *Chilopsis* were sampled (J-1, J-2, and TMNTN), N and P resorption efficiencies of both species combined were approximately 50% (Table 3). The highest resorption efficiency measured in either species occurred in a single individual of *Brickellia* (78% P resorption efficiency). Mean resorption proficiencies for both species combined were 0.80% N
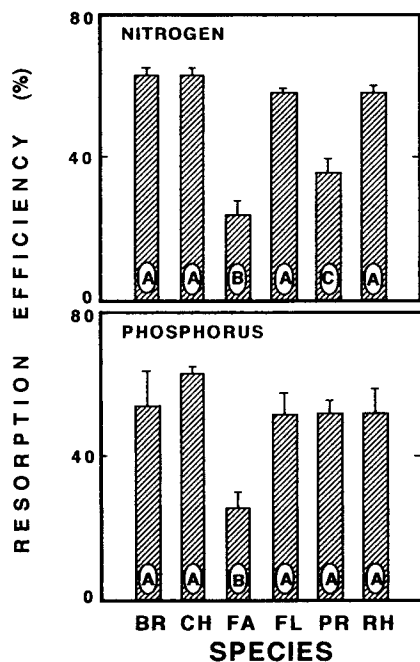
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Fig. 1 Mean resorption efficiencies (%) in the six deciduous shrub species that dominated the margins of Arroyo J-1. Differences among species were significant for both nitrogen (*P*<0.001, ANOVA) and phosphorus (*P*<0.01, ANOVA). For each nutrient, data bars housing the same letter are not significantly different (*P*>0.05; Fisher's LSD). (*n*=8; error bars = standard errors of the mean; *BR Brickellia laciniata*; *CH Chilopsis linearis*; *FA Fallugia paradoxa*; *FL Flourensia cernua*; *PR Prosopis glandulosa*; *RH Rhus microphylla*)
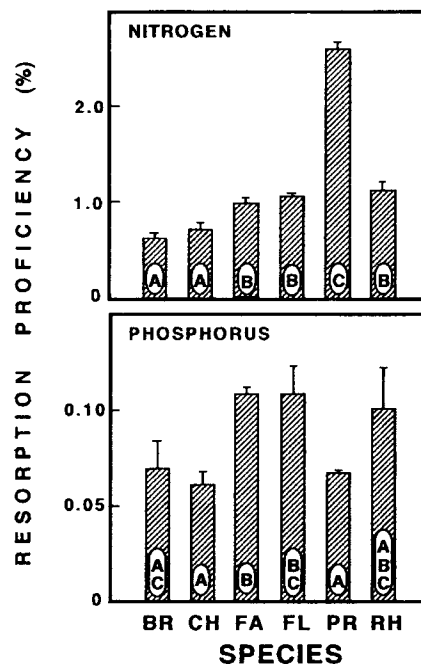
Fig. 2 Mean resorption proficiencies (%; concentration of each element in fully senesced leaves) in the six deciduous shrub species that dominated the margins of Arroyo J-1. Differences among species were significant for both nitrogen (*P*<0.001, Kruskal-Wallis) and phosphorus (*P*<0.01, Kruskal-Wallis). For each nutrient, data bars housing the same letter are not significantly different (*P*>0.05; Mann-Whitney U Test). (*n*=8; error bars = standard errors of the mean; *BR Brickellia laciniata*; *CH Chilopsis linearis*; *FA Fallugia paradoxa*; *FL Flourensia cernua*; *PR Prosopis glandulosa*; *RH Rhus microphylla*)

Table 3 Resorption efficiency (%) and proficiency (%) of two species of obligate riparian shrubs (*Brickellia laciniata* and *Chilopsis linearis*) growing in Arroyos J-1, J-2, and TMNTN. *n*=40; SE = standard error of the mean. Maximum proficiency = minimum concentration in senesced leaves

Nutrient	Mean	SE	Maximum
Resorption efficiency (%)			
Nitrogen	53	2	76
Phosphorus	50	3	78
Resorption proficiency (%)			
Nitrogen	0.80	0.05	0.37
Phosphorus	0.06	0.004	0.03

and 0.06% P. Resorption of N was most proficient in one individual of *Brickellia* in Arroyo J-2 (0.37%). Two other individuals of *Brickellia* (one each in Arroyos J-1 and J-2) reduced P in their senescing leaves to 0.03%.

In the six species in Arroyo J-1, mean N and P resorption efficiencies were both 50%. Mean N and P resorption proficiencies were 1.18% and 0.09%, respectively. When *Prosopis* was excluded because of its N-fixing status, mean N resorption proficiency of the remaining five species in Arroyo J-1 was 0.90%.

Nitrogen and P resorption efficiency varied significantly among species in Arroyo J-1 (Fig. 1; *P*<0.001, ANOVA for N; *P*<0.01, ANOVA for P). *Fallugia* was significantly less efficient at resorbing N and P (23% and 26%, respectively) than any other species. *Brickellia* and *Chilopsis* had the highest mean N resorption efficiencies (each 63%), but they did not differ statistically from those of *Flourensia* and *Rhus* (each 58%). *Brickellia* and *Chilopsis* also had the highest mean P resorption efficiencies (54% and 62%, respectively), but they did not differ statistically from those of *Flourensia*, *Prosopis*, and *Rhus* (52% for all three species). Mean resorption efficiencies of the obligate riparian species combined (*Brickellia* and *Chilopsis*; N=63%, P=58%) were significantly higher than in the non-obligate riparian species combined (N=44%, P=45%; *P*<0.001, Mann-Whitney U test for N; *P*<0.05, Student's *t*-test for P).

Nitrogen and P resorption proficiency also varied significantly among species in Arroyo J-1 (Fig. 2; *P*<0.001, Kruskal-Wallis for N; *P*<0.01, Kruskal-Wallis for P). *Brickellia* and *Chilopsis* were most proficient at resorbing N (0.62% and 0.71%, respectively), and *Prosopis* was least proficient (2.60%). *Brickellia*, *Chilopsis*, and *Prosopis* were the most proficient species at resorbing P (0.07%, 0.06%, and 0.07%, respectively). Mean N and P resorption in the obligate riparian species combined

Table 4 Coefficients of determination (R^2) from linear regressions indicating relationships between resorption in Arroyo J-1 and leaf surface area, specific leaf mass, green-leaf nitrogen, and green-leaf phosphorus. For each measure of resorption, only variables that were significantly related to that measure in at least one species are presented. Regressions were performed on each species separately. *BR Brickellia laciniata; CH Chilopsis linearis; FA Fallugia paradoxa; FL Flourensia cernua; PR Prosopis glandulosa; RH Rhus microphylla*; * $P<0.05$, ** $P<0.01$, *** $P<0.001$; $n=8$ throughout. All significant relationships were positive except for those noted with a '-' after the probability asterisk(s)

Species	BR	CH	FA	FL	PR	RH
N resorption efficiency						
Leaf surface area	–	–	–	0.50*-	–	–
Specific leaf mass	0.60*	–	–	–	0.76**-	–
N resorption proficiency						
Green-leaf N	0.89***	0.80**	–	0.79**	0.69*	–
P resorption efficiency						
Green-leaf N	0.61*-	–	0.50*	0.56*	–	–
Specific leaf mass	–	–	–	–	0.68*-	–
P resorption proficiency						
Green-leaf P	–	–	–	–	–	0.66*
Leaf surface area	–	–	–	–	0.57*-	–
Specific leaf mass	–	–	–	–	–	0.61*

(0.66% N, 0.066% P) were also significantly more proficient than in the non-obligate riparian species combined (1.1% N, excluding the N-fixing *Prosopis*; 0.10% P; $P<0.001$, Mann-Whitney U test for N; $P<0.01$, Mann-Whitney U test for P).

All of the measured attributes of green leaves were significantly related to resorption efficiency or proficiency in one or more of the species in Arroyo J-1 (Table 4). Leaf surface area was related to N resorption efficiency in *Flourensia* and to P resorption proficiency in *Prosopis*. Specific leaf mass was related to both N and P resorption efficiency in *Prosopis*, and to N resorption efficiency in *Brickellia*, and P resorption proficiency in *Rhus*. Concentrations of N and P in green leaves were each significantly related to the proficiency of resorption of that element. Of all the combinations of attributes and measures of resorption, the linkage between green-leaf N and N resorption proficiency was the most evident. In four of the six species, green-leaf N accounted for 69–89% of the variance in N resorption proficiency. In *Brickellia*, *Chilopsis*, *Flourensia*, and *Prosopis*, increases in green-leaf N were consistently linked to decreases in N resorption proficiency.

Discussion

Resorption in arroyos compared to other environments

Shrubs growing along the margins of arroyos in the Chihuahuan Desert were no more efficient at resorbing N and P from senescing leaves than shrubs growing in other environments. Mean N and P resorption efficiencies in all species growing in Arroyo J-1 (50% for N and P), and in the obligate riparian species growing in all arroyos studied (53% and 50%, respectively), differed little from mean resorption efficiencies in the only other desert shrub species for which there are resorption data (57% and 53%, respectively; $n=7$ species; Killingbeck

1993a). Similarities were likewise high between N and P resorption efficiencies in the arroyo shrubs and more than 50 species of plants growing in a wide array of environments worldwide (52% and 43%, respectively, Chapin and Kedrowski 1983; 50% and 52%, respectively, Aerts 1996).

Resorption proficiencies in arroyo shrubs were also highly similar to those in other species. Mean N resorption proficiency in the five non-N-fixing species in Arroyo J-1 (0.90%) and in the obligate riparian species growing in all arroyos studied (0.80%) was virtually identical to that in woody plants worldwide (0.82%, Chapin and Kedrowski 1983; 0.87%; Killingbeck 1996) and to that in six other species of desert shrubs (0.80%; Killingbeck 1993a). Mean P resorption proficiency in the obligate riparian species growing in all arroyos studied (0.06%) was also very similar to that in woody plants worldwide (0.07%, Chapin and Kedrowski 1983; 0.06%, Killingbeck 1996) and to that in six other species of desert shrubs (0.07%, Killingbeck 1993a).

Plants growing by design, and by default

Two of the six guild species studied (*Brickellia* and *Chilopsis*) are restricted in their distribution to riparian habitats such as arroyos, yet the other four (*Fallugia*, *Flourensia*, *Prosopis*, and *Rhus*) are not (Dick-Peddie 1993). This dichotomy in distribution paralleled a dichotomy in resorption. In Arroyo J-1, *Brickellia* and *Chilopsis* combined were significantly more efficient and proficient at resorbing N and P than the non-obligate species combined. Additionally, both *Brickellia* and *Chilopsis* were individually significantly more proficient at resorbing N than any of the other four species ($P<0.001$, Kruskal-Wallis).

A comparison of maximum N and P resorption proficiencies further suggests a divergence between species that are, and are not restricted to riparian habitats
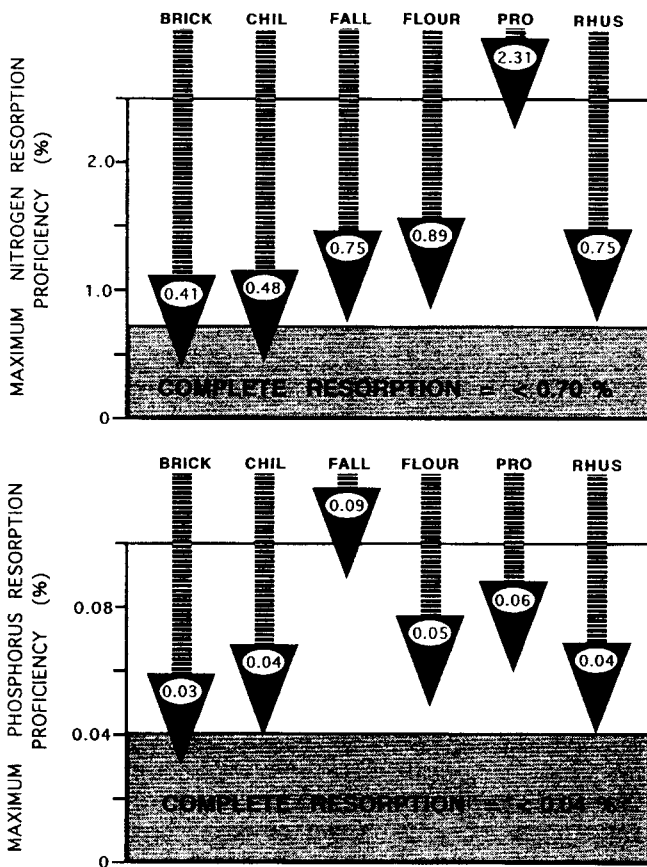
Fig. 3 Maximum nitrogen and phosphorus resorption proficiencies [nutrient concentration (%) in fully senesced leaves] in Arroyo J-1. The tip of each *arrow* represents the lowest concentration of nitrogen (*top panel*) or phosphorus (*bottom panel*) measured in the senesced leaves of each species. The *shaded boxes* at the bottom of each panel represent nutrient concentrations considered to represent highly proficient resorption (i.e., complete resorption; Killingbeck 1996). (*BRICK Brickellia laciniata, CHIL Chilopsis linearis, FALL Fallugia paradoxa, FLOUR Flourensia cernua, PRO Prosopis glandulosa, RHUS Rhus microphylla*)

(Fig. 3). Resorption is considered to be biochemically complete when nutrient concentrations are reduced below 0.70% N and 0.04% P in senescing leaves (Killingbeck 1996; in the original description of these estimates of complete resorption, limits for P resorption proficiency differed between deciduous (0.05%) and evergreen species (0.04%). We chose the 0.04% limit in the present analysis to make it as difficult as possible for resorption to be considered complete). Although species likely differ somewhat in their inherent resorption abilities, N and P resorption are considered to be less than complete when fully senesced leaves retain more than 0.70% N or 0.04% P. In Arroyo J-1, only individuals of obligate riparian species reduced N below 0.7%. The single most proficient individuals of *Brickellia* and *Chilopsis* reduced N in their senescing leaves to 0.41% and 0.48%, respectively. Twelve of the 16 individuals of *Brickellia* and *Chilopsis* had N resorption proficiencies <0.70%. By contrast, every individual of *Fallugia, Flourensia, Prosopis,* and *Rhus* had N resorption proficiencies >0.70%.

Differences in the resorption proficiencies of P between obligate and non-obligate riparian species were not quite as clear-cut as with N, but were still discernible. Four individuals of *Brickellia* and *Chilopsis* reduced P to 0.04% or lower in their senesced leaves, yet only one individual of all the non-obligate riparian species had a P resorption proficiency as low as 0.04% (one individual of *Rhus*). The remaining seven individuals of *Rhus* had a mean P resorption proficiency of 0.11%.

The divergence in resorption in these two groups of species may be the result of the interplay between hydrology, geomorphology, and biology. As fluvial erosion initiates new arroyo channels, or widens and changes the course of existing channels, individual plants that were growing in open desert away from arroyo margins may end up on the margin of an arroyo. The result is a unique assemblage of shrub species, some of which are adapted to grow along the margins of watercourses (obligate riparian species), some of which are adapted to grow in both riparian and non-riparian sites (facultative riparian species), and some of which are adapted to grow in open desert away from the influence of watercourses (non-riparian species). While many of the wide array of factors known to influence resorption (Killingbeck, in press) may also have influenced resorption in the species growing along Arroyo J-1, significant differences in resorption between obligate and non-obligate riparian species indicate the importance of evolutionary history and habitat specificity.

Following the advice that "the essential dynamics of ecosystems can be captured by grouping species into a restricted number of groups or functional types" (Smith et al. 1997), we suggest two new functional classes of plant species: species growing by design, and species growing by default. In Arroyo J-1, there can be both an evolutionary basis and a physical basis for this classification. *Brickellia* and *Chilopsis*, the obligate riparian species, evolved under the specific selection pressures imposed on them by desert riparian environments. They grow along arroyos "by design" because their adaptations more closely match the constraints associated with riparian ecosystems than species evolving elsewhere, and because their existence along Arroyo J-1 did not depend on previous movements of the arroyo channel.

The non-obligate riparian species evolved under different (non-riparian ecosystems), or less narrowly focused (riparian and non-riparian ecosystems) selection pressures than the obligate riparian species. However, while it is highly likely that individuals of the non-riparian *Flourensia* grew along Arroyo J-1 "by default" because of channel formation or channel movement, we do not know which individuals of the facultative riparian species (*Fallugia, Prosopis,* and *Rhus*) originated in open desert, and which originated along Arroyo J-1 itself. Even though the adaptations of these facultative riparian species are less narrowly focused than that of obligate riparian species, they have in fact evolved to successfully colonize riparian environments. Therefore, only the non-riparian *Flourensia* can be unequivocally clas-

sified as a species growing by default along arroyos in the Chihuahuan Desert.

Although the majority of plants inhabiting natural, undisturbed ecosystems grow there by design, a contingent of plants growing by default will likely be present in ecosystems where rapid, large-scale changes act to alter critical ecological conditions. Ecosystems shaped over short time spans by geological forces come to mind as the most obvious examples of systems that would likely harbor a combination of plants growing by design, and by default. Arroyo communities fit this description, as do communities impinged upon by shifting dunes and river channels. In communities confronted with rapid human-induced environmental change, plants growing by design may rapidly become plants growing by default.

Interspecific differences in a guild of arroyo shrubs

Does resorption differ among species within woody plant guilds? For a guild of understory shrub species growing in an oak-dominated forest in New England, N and P resorption efficiency differed among species, but resorption proficiency did not (Killingbeck and Costigan 1988). This inverse juxtaposition of efficiency and proficiency in the understory shrub guild did not hold in the shrub guild inhabiting the margins of Arroyo J-1. Not only did N and P resorption efficiency differ among species, but so did resorption proficiency of both elements. In the Okefenokee Swamp, neither efficiency or proficiency of N resorption differed among three species of deciduous shrubs, but both efficiency and proficiency of P resorption differed among the same species (DeLucia and Schlesinger 1995). Therefore, divergence in resorption efficiency coupled with convergence in resorption proficiency is not a constant feature of woody plant guilds.

When subsets of the shrub guild in Arroyo J-1 were considered independently, their patterns in resorption proficiency more closely matched the patterns found in the New England understory. In the two obligate riparian species, N and P resorption proficiency in *Brickellia* did not differ from that in *Chilopsis*, supporting the notion of a threshold beyond which further resorption does not occur. In the non-obligate riparian species (*Fallugia, Flourensia, Prosopis, Rhus*), both N and P resorption proficiency did vary among species, yet proficiency did not differ among the three non-N-fixing species. This again supports the possibility that functionally similar groups of plants coexisting in the same community have similar resorption proficiencies.

Relationships between life history traits, leaf characteristics, and resorption

Because growth form (perennial shrubs of short stature), leaf form (broad as opposed to needle-type leaves), and site-specific location were similar in all guild species, we reasoned that other life history traits might be a source of interspecific differences in resorption. For example, resorption in fall-flowering plants or partially winter-deciduous plants might be expected to be higher than in spring-flowering plants or strictly winter-deciduous plants because source-sink relations influence resorption (Chapin and Moilanen 1991). Flowers of *Brickellia* and *Flourensia* developing in the fall might act as strong sinks for nutrients being moved out of senescing leaves (sources). Likewise, leaves retained into the winter in partially winter-deciduous species such as *Fallugia* and *Flourensia* might act as strong sinks. However, no clear patterns emerged between these life history traits and resorption efficiency or proficiency.

Regression models indicated that differences in leaf surface area, SLM, and foliar nutrient concentrations were related to resorption. Leaf surface area and/or SLM were related to one or more measures of resorption in all arroyo species except *Chilopsis*. Linkages between leaf surface area, per se, and resorption have not previously been explored, yet various ratios of leaf mass to area, such as specific leaf area (SLA; Reich et al. 1997) and tissue density (Ryser 1996), have been linked to a wide variety of plant processes. Because increases in leaf surface area and SLM were linked to both increases and decreases in measures of resorption, depending on species, neither factor exerted a consistent influence on resorption.

Nutrient concentrations in unsenesced green leaves have influenced resorption efficiency in plants growing in other environments (Chapin and Kedrowski 1983; Nordell and Karlsson 1995), and influenced both resorption efficiency and proficiency in Arroyo J-1. Increases in green-leaf N were linked to both increases (*Fallugia* and *Flourensia*) and decreases (*Brickellia*) in P resorption efficiency. By contrast, high green-leaf N was linked with low N resorption proficiency (i.e., high concentrations of N in senesced leaves) in four of the six species. This relationship further confirms the importance of green-leaf N to resorption, and suggests that terminal concentrations of N in senesced leaves may be, in part, a function of N concentrations in unsenesced leaves.

Inefficient and unproficient resorption in Prosopis

Extremely low resorption in woody species that harbor N-fixing symbionts (Rodriguez-Barrueco et al. 1984; Côté et al. 1989; Killingbeck 1993b) is evidence of the existence of a relationship between resorption and nutrient availability. Resorption patterns in *Prosopis* growing in Arroyo J-1 also support such a relationship. *Prosopis*, a woody legume harboring N-fixing symbionts (Shearer et al. 1983), had a lower N resorption efficiency than all other arroyo species except *Fallugia*, and held more than twice the N in its senesced leaves as the species with the next most proficient resorption. In the Sonoran Desert, autumnal N resorption in *Prosopis glandulosa* was virtually nonexistent (Rundel et al. 1982). Relatively efficient

and proficient resorption of P in *Prosopis* growing in Arroyo J-1 (P is a nutrient for which *Prosopis* has no source other than direct uptake) coupled with inefficient and unproficient resorption of N seem to corroborate the existence of a linkage between resorption and nutrient status.

Are efficiency and proficiency complementary or redundant measures of resorption?

Both efficiency and proficiency have value as measures of resorption (Killingbeck 1996), yet little evidence exists to indicate whether they are redundant, or whether they complement one another in providing insights into the process of resorption? Four examples from Arroyo J-1 suggest that they are not redundant. First, based on efficiency, resorption of N and P was much lower in *Fallugia* than in all other species. Based on proficiency, resorption in *Fallugia* was not different from the majority of the non-obligate riparian species. The likely reason for this pattern shift is that N and P may have been transported out of *Fallugia* leaves earlier in the growing season than in the other species (i.e., resorption began before the date on which green leaves were collected). Calculation of efficiency is susceptible to differences in time of transport. Calculation of proficiency is not.

Second, N resorption efficiency in *Prosopis* was relatively low, but not glaringly so. N resorption in *Prosopis* was 2.3 times less proficient than in the next most proficient non-obligate riparian species, and 4.2 times less proficient than the most proficient obligate riparian species. Third, green-leaf N was not linked to N resorption efficiency in any of the six arroyo species, but was highly related to N resorption proficiency in four species.

Finally, *Flourensia*, the only species unequivocally growing by default in Arroyo-J1, was significantly less proficient at resorbing N than either *Brickellia* or *Chilopsis*, the two species growing by design. However, N resorption efficiency in *Flourensia* was similar to that in *Brickellia* and *Chilopsis*. Therefore, even though efficiency and proficiency sometimes overlap in information content, the evidence suggests that they are fundamentally different measures of resorption that are often complementary.

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