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Nutrient resorption in desert shrubs

La reabsorción de nutrientes en arbustos del desierto

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ABSTRACT

Nutrient resorption is the physiological process that acts to conserve plant nutrients by withdrawing them from tissues undergoing senescence and sequestering them for future use. Speculation about this process has suggested that desert shrubs may rely heavily on resorption to conserve specific nutrients that are often in short supply in arid lands. The objectives of this paper are to examine the efficiency of nitrogen and phosphorus resorption in desert shrubs and to comment on the potential interplay between resorption and desertification. Mean resorption efficiencies for nitrogen and phosphorus were 57% and 53%, respectively, in the seven species of desert shrubs for which resorption data were available. Corresponding efficiencies for non-desert woody perennials were 52% and 43%. Desert shrubs also had a higher proportion of resorption efficiencies in the upper extremes of recorded resorption values than did non-desert plants. These data suggest that resorption may be more important to the nutrient economy of desert shrubs than it is to woody perennials inhabiting more mesic environments. A detailed consideration of litter nutrient content in desert shrubs, placed in the context of functional resorption thresholds, provided further support for the hypothesis that resorption of nitrogen and phosphorus in desert shrubs is as efficient, or more efficient, than resorption of these nutrients in non-desert woody perennials. If the considerable transport of surface litter in deserts caused by wind and water erosion afford desert shrubs a reduced probability of recuperating nutrients from abscised litter, then differences in the availability of mineralizable organic litter could account for the disparity in resorption efficiencies between desert shrubs and non-desert woody perennials. The possibility that the regulation of resorption efficiencies in desert shrubs may be quite complex was supported by the high degree of intersite and interyear variation in resorption efficiency exhibited by *Fouquieria splendens*. Conclusions from previously published analyses suggesting that nitrogen in the litter of desert plants is substantially higher than in non-desert plants were not supported by the data assembled here on desert shrubs. Speculation on the potential interplay between resorption and desertification resulted in the conclusion that potential effects are reciprocal. Although high resorption efficiencies in the dominant plants of an area undergoing desertification could act to delay specific community-level effects of such a perturbation, environmental changes that often accompany the desertification process could also act to reduce resorption efficiencies.

Key words: Desertification, *Fouquieria splendens*, nitrogen, nutrient cycling, phosphorus.

RESUMEN

La reabsorción de nutrientes es el proceso biológico que actúa para conservar los nutrientes de las plantas a través de su remoción de tejidos sufriendo senescencia y secuestrándolos para uso futuro. La especulación acerca de este proceso ha sugerido que los arbustos xéricos pueden depender fuertemente de la reabsorción para conservar nutrientes específicos que a menudo están en bajas cantidades en suelos áridos. Los objetivos de este trabajo son examinar la eficiencia de la reabsorción del nitrógeno y el fósforo en arbustos xéricos y comentar la interacción potencial entre reabsorción y desertificación. Las eficiencias de reabsorción promedio para nitrógeno y fósforo fueron 57% y 53%, respectivamente, en las siete especies de arbustos xéricos para los cuales existen datos de reabsorción. Las eficiencias correspondientes para arbustos leñosos perennes no xéricos fueron 52% y 43%. Los arbustos xéricos tenían también una más alta proporción de eficiencias de reabsorción en los extremos superiores de valores de reabsorción registrada que las plantas no xéricas. Estos datos sugieren que la reabsorción puede ser más importante que la economía de nutrientes para los arbustos xéricos que para las perennes leñosas habitando ambientes más méxicos. Una consideración detallada del contenido de nutrientes en la hojarasca en arbustos xéricos, puesto en el contexto de umbrales de reabsorción funcional, proveyó más sustento a la hipótesis que la reabsorción de nitrógeno y fósforo en arbustos xéricos es tan eficiente o más eficiente que la reabsorción de estos nutrientes en perennes leñosas no xéricas. Si el considerable transporte de hojarasca superficial en desiertos, causado por erosión eólica y por agua, deja a los arbustos xéricos una reducida probabilidad de recuperar nutrientes de la hojarasca, luego las diferencias en la disponibilidad de hojarasca orgánica mineralizable podría dar cuenta para la disparidad en eficiencias de reabsorción entre arbustos xéricos y perennes leñosas no xéricas. La posibilidad que la regulación de eficiencias de reabsorción en arbustos xéricos puede ser bastante compleja fue confirmado por el alto grado de variación entre sitios y entre años en eficiencia de reabsorción exhibido por *Fouquieria splendens*. Las conclusiones de análisis previamente publicados sugiriendo que el nitrógeno en la hojarasca de plantas xéricas es sustancialmente más alto que en plantas no xéricas no fueron sustentado por los datos reunidos aquí sobre arbustos xéricos. La especulación sobre la interacción potencial entre reabsorción y desertificación resultó en la conclusión que los efectos potenciales son recíprocos. Aunque altas eficiencias de reabsorción en las plantas dominantes de un área sufriendo desertificación podrían actuar para retrasar efectos específicos al nivel comunitario de tal perturbación, los cambios medioambientales que a menudo acompañan el proceso de desertificación podrían también actuar para reducir las eficiencias de reabsorción.

Palabras claves: Desertificación, *Fouquieria splendens*, nitrógeno, ciclos de nutrientes, fósforo.

INTRODUCTION

In wrestling with the onerous task of defining the word desert, noted ecologist and former director of the Carnegie Institution's Desert Laboratory, Forrest Shreve (1934), asserted that "low and irregular rainfall" was the single most essential physical feature of land forms considered to be deserts. Such a paucity of water has long been assumed to be the primary driving force behind the evolution of desert biota. Walter & Stadelmann (1974) provided evidence to suggest that maintaining sufficient levels of hydration is "the fundamental problem for plants in arid zones" and Evenari *et al.* (1982) concluded that "The principle adaptation that desert plants have to make is to the scarcity of water."

While the universality of the tenet that water relations play a major role in the evolution of desert plants is not in jeopardy, plant ecologists are becoming increasingly aware of the extent to which nutrients limit the growth rate and reproductive capacity of desert plants. In the Chihuahuan Desert of North America, plants have responded to experimental additions of nitrogen (Ettershank *et al.* 1978, Gutiérrez & Whitford 1987) indicating the importance of nutrients in plants that were previously considered to be strictly water-limited. Results from other studies also suggest that water is not the sole limiting factor in desert ecosystems (Wallace *et al.* 1978, Floret *et al.* 1982). Given the fact that most soils in arid ecosystems have low levels of available nitrogen (Skujins 1981), natural selection in desert environments should favor both the evolution of plant adaptations that conserve nutrients such as nitrogen, and those that conserve water.

One such adaptation that acts to conserve a variety of macronutrients and trace metals is nutrient resorption. Stated simply, resorption is the "mobilization and removal of inorganic and/or organic substances from senescing plant tissues and the subsequent transportation of these substances to surviving tissues" (Killingbeck 1986). It is most often expressed as resorption efficiency, which is the percentage of a leaf's nutrient content that is recovered by a plant before that leaf is lost through abscission. The process itself plays a key role in conserving nutrients previously acquired by plants, and is responsible for adjusting

nutrient transfers between plants and the ecosystems in which they grow. Efficient resorption should be particularly important to desert shrubs because these plants are not only faced with obtaining nutrients from soil nutrient pools that are often low to begin with, but they are also constrained by windows of time when nutrient uptake deteriorates because of drought conditions that severely limit nutrient availability.

The intent of this paper is to explore the processes of nitrogen (N) and phosphorus (P) resorption as they are implemented by shrub species growing in desert ecosystems. Although resorption has been credited with being one of the most important ecophysiological strategies used by desert plants to meet their demands for N (Wallace *et al.* 1978), there are few published data that adequately characterize resorption of N, P, or any other element in desert shrubs. Specific objectives of this paper are to; 1) determine the magnitude of N and P resorption in desert shrubs, 2) compare resorption in desert shrubs to that in non-desert woody perennials, 3) consider the relative importance and potential plasticity of resorption in desert shrubs, 4) address the paradox of reported high nutrient content in desert shrub litter as it relates to resorption thresholds, 5) speculate on the role of resorption in shrubs inhabiting Chilean deserts, and 6) consider the potential interrelationships between desertification and resorption through a brief analysis of regulatory factors that influence resorption efficiencies.

MAGNITUDE AND RELATIVE IMPORTANCE OF N AND P RESORPTION IN DESERT SHRUBS

Resorption of N and P have been measured in a variety of deciduous plants worldwide (Chapin & Kedrowski 1983), yet very few data have appeared in the literature that specifically document resorption in desert shrubs. Of the species of shrubs that have been the focus of nutrient cycling studies in desert ecosystems, seven appear in Table 1 along with measured resorption values. By design, data from studies conducted on shrubs growing in ecosystems other than deserts (such as mediterranean-type semi-arid ecosystems) were excluded.

TABLE 1

Resorption of nitrogen (N) and phosphorus (P) in seven species of desert shrubs. In all cases, resorption represents the percent difference in N and P between green and senesced leaves. However, units of measure varied widely among studies. Resorption of N and P were calculated from temporal changes in foliar nutrient concentration (% of leaf mass; *Artemisia tridentata*), foliar nutrient mass per leaf ($\mu\text{g}/\text{leaf}$; *Atriplex confertifolia*, *Ephedra nevadensis*, *Grayia spinosa*), foliar nutrient mass per unit area of soil surface (g/m^2 , *Atriplex vesicaria*), and foliar nutrient mass per unit area of leaf surface (mg/cm^2 , *Fouquieria splendens*, *Larrea tridentata*). For *Fouquieria splendens* and *Larrea tridentata*, values are ranges of yearly means (F.s.) or monthly means (L.t.).

Reabsorción de nitrógeno (N) y fósforo (P) en siete especies de arbustos xéricos. En todos los casos la reabsorción representa la diferencia porcentual en N y P entre hojas verdes y senescentes. Sin embargo, las unidades de medición variaron ampliamente entre estudios. La reabsorción de N y P se calcularon desde cambios temporales en concentración foliar de nutrientes (% de masa foliar; *Artemisia tridentata*), masa de nutriente foliar por hoja ($\mu\text{g}/\text{hoja}$; *Atriplex confertifolia*, *Ephedra nevadensis*, *Grayia spinosa*), masa de nutriente foliar por unidad de área de superficie del suelo (g/m^2 ; *Atriplex vesicaria*) y masa de nutriente foliar por unidad de área de superficie foliar (mg/cm^2 ; *Fouquieria splendens*, *Larrea tridentata*). Para *Fouquieria splendens* y *Larrea tridentata*, los valores son rangos de promedios anuales (F.s.) o promedios mensuales (L.t.).

Species	Location	Nitrogen resorption (%)	Phosphorus resorption (%)	Reference
<i>Artemisia tridentata</i>	USA - Nevada	53	26	Schlesinger <i>et al.</i> 1989
<i>Atriplex confertifolia</i>	USA - Nevada	45	71	Wallace <i>et al.</i> 1978
<i>Ephedra nevadensis</i>		82	89	
<i>Grayia spinosa</i>		55	0	
<i>Atriplex vesicaria</i>	Australia - New South Wales	73	57	Charley 1972
<i>Fouquieria splendens</i>	USA - New Mexico	11-72	8-85	Killingbeck 1992 and Unpublished Data
<i>Larrea tridentata</i>	USA - New Mexico	42-61	72-86	Lajtha 1987

Resorption of the two elements in question was extremely variable (Table 1). Resorption of N and P ranged from 11-82%, and 0-89%, respectively. The highest and lowest P resorption efficiencies were recorded in different species at the same site, and a single species, *Fouquieria splendens*, accounted for nearly the entire range of N resorption efficiencies. Mean resorption efficiencies of N and P in all species combined were 57% and 53%, respectively (utilizing the mid-point of the ranges given for *Fouquieria* and *Larrea*).

Although there are currently no universally accepted ranges of N and P resorption efficiencies designed for the purpose of describing "typical" resorption efficiencies for plants in general, let alone desert plants in particular, resorption efficiencies in the range of 40-60% are thought to be normal. Chapin (1980) suggested that "half or more of the maximum nitrogen and phosphorus content of a

deciduous leaf is translocated to other plant parts before leaf abscission...". This "50% rule" was generated for non-agricultural wild plants and was intended to be used only as a very general guideline. In the most extensive published comparison of resorption values to date, Chapin & Kedrowski (1983) recorded a mean N resorption of 52% for 38 species of non-desert woody perennials, and a mean P resorption of 43% for 36 species of non-desert woody perennials. Speculating specifically on desert plants, Wallace *et al.* (1978) suggested that N resorption should be 30-60% or more.

Means of N and P resorption in desert shrubs were higher than the corresponding means reported by Chapin & Kedrowski (1983). It is unclear whether these differences are biologically important, or whether the differences have any ecological significance given the fact mean N and P resorption in desert shrubs falls within the general range of resorption values expected for most plants. What may be more

important than a comparison of central tendencies, however, is a comparison of the extremes.

There were considerable differences between the highest mean resorption values recorded by Chapin & Kedrowski (1983) for non-desert species and those found for desert shrubs (Table 1). Resorption of N reached 60% or higher in over half of the desert shrub species, yet only 30% of the species listed by Chapin & Kedrowski had mean resorption values of 60% or higher. Similarly, resorption of P reached 70% or higher in over half of the desert shrub species, yet only 21% of the species listed by Chapin & Kedrowski resorbed 70% or more of their foliar P. Therefore, not only were overall mean resorption efficiencies somewhat higher in desert than non-desert shrubs, but a higher percentage of desert shrubs than non-desert species had resorption efficiencies in the upper extremes of recorded resorption values.

The reason that consideration of resorption extremes may be significant in this attempt to compare resorption in desert shrubs to that in other woody perennials centers around the concept of "potential resorption". Potential resorption is the resorption efficiency biologically attainable by a plant (Killingbeck *et al.* 1990). It is a measure of the physiological capacity of a plant to withdraw and sequester nutrients from senescing foliage (or other tissues), and differs from "realized resorption" (actual measured resorption at a given point in time) in that it is not directly affected in the short term by proximate environmental constraints.

Since it appears that a considerable number of environmental factors are capable of influencing the processes of foliar senescence and resorption (*e.g.*, Addicot 1968, Hill 1980, Killingbeck 1988, Nooden & Leopold, 1988, Killingbeck *et al.* 1990, Chapin & Moilanen 1991, Del Arco *et al.* 1991), it is highly likely that measured resorption efficiencies are often less than potential resorption efficiencies. In an extreme example, resorption of N was reduced to zero (Killingbeck 1988) in a species whose potential N resorption is 60% or more (Killingbeck *et al.* 1990). It follows then that the values that comprise any list of resorption efficiencies may or may not include estimates of potential resorption. This fact, along with

the realization that the ultimate effects of natural selection are more inextricably tied to potential resorption, suggest that what is critical in our assessment of the differences in resorption between desert shrubs and non-desert woody perennials is a comparison of potential resorption, not realized resorption.

The disproportionate abundance of high resorption efficiencies in desert shrubs noted earlier suggests that potential resorption may be higher in these plants than in non-desert woody perennials. If this is true, then one can argue that desert shrubs rely more heavily on nutrient resorption as a strategy to conserve previously acquired nutrients than do other woody perennials. In light of recent evidence directly linking resorption to natural selection by demonstrating that artificially imposed reductions in nutrient resorption can cause concomitant losses in plant fitness (May & Killingbeck 1992), differences in the ability of classes of plants (*i.e.*, desert versus non-desert shrubs) to resorb nutrients are probably a function of evolutionary selection processes. Consequently, the observed differences in resorption between desert and non-desert woody plants are likely to be subject to evolutionary control and therefore reflect differences in ecosystem-imposed selection pressures.

Evidence for the hypothesis that desert shrubs rely more heavily than other plants on the process of resorption to conserve foliar N and P is suggestive, not conclusive. The existing data describing resorption in desert shrubs are too sparse to enable the formulation of incontrovertible conclusions regarding the relationship between woody desert perennials and their non-desert counterparts. There does seem to be, however, additional ecological evidence that supports the evolutionary plausibility of this hypothesis (see next section).

SURFACE TRANSPORT OF LITTER AND ITS POTENTIAL IMPACT ON THE NUTRIENT ECONOMY OF DESERT SHRUBS

One universal characteristic of semi-arid environments in general, and deserts in particular, is their paucity of surface litter compared to plant communities growing in

more mesic environments. Litter may accumulate to help form "islands of fertility" around the base of desert shrubs (García-Moya & McKell 1970, Whitford 1986), yet many individuals of shrub species such as *Fouquieria splendens* often do not retain large amounts of litter below their canopy (Killingbeck *personal observation*).

The "...absence of litter mats in most desert contexts..." may be due to rapid decomposition when water is present, and to the "...redistribution of litter by wind and overland flow of water" (West 1981). The extreme importance of the movement of surface litter and soil in deserts led West (1981) to further conclude that "Whereas most ecosystems lose the bulk of their nutrients through leaching, desert systems lose minerals largely through surface erosion or annual export". This last point may be critical in determining an evolutionary basis for the hypothesis that resorption might be more important to the nutrient economy of desert shrubs than it is to woody perennials growing in more mesic environments.

Plants can "reuse" nutrients that have already been translocated into leaves in two ways. First, they can resorb foliar nutrients before leaf abscission. Second, they can regain nutrients lost in foliar litterfall through subsequent uptake of nutrients from litter that was deposited and mineralized above their root system. In environments where one or more nutrients may be limiting, severe abiotic restrictions in the second reuse pathway would be expected to result in evolutionary selection for increased efficiency in the first reuse pathway. Therefore, if desert environments afford plants less of a chance to recuperate nutrients lost in litter than other environments, then it seems reasonable to expect desert shrubs to rely more heavily than non-desert plants on nutrient conservation strategies such as resorption.

RESORPTION THRESHOLDS AND THE PARADOX OF HIGH NUTRIENT CONTENT IN THE LITTER OF DESERT SHRUBS

It is generally held that N is often deficient in desert soils (Dregne 1976, Skujins 1981) but that green leaf N in desert plants is high, higher even than in plants of other biomes (Skujins

1981). This apparent paradox is further complicated by the supposition that "A characteristic feature of the litter fall in desert communities is its high nitrogen content..." (West 1981). To maintain that desert plants have well-developed N conservation mechanisms (Skujins 1981) while retaining abnormally high amounts of N in their litter seems quite contradictory.

Resorption, which has been recognized as one of the most important adaptations responsible for conserving N in desert plants (Wallace *et al.* 1978), is considered to be efficient when the difference between green leaf N and litter N is high. Therefore, various combinations of leaf and litter N status can result in efficient resorption. For example, relatively high resorption efficiencies can be achieved in plants that shed foliar litter rich in N if those plants produced green foliage containing abnormally high amounts of N. This relationship would allow for the occurrence of both efficient resorption of N and N-rich foliar litter. However, it appears that this scenario is not representative of the desert shrub *Fouquieria splendens*, or many, if any, of the other shrubs listed in Table 1.

Based on data presented by Rodin & Bazilevich (1967), West (1981) argued that N in the litter of desert plants was higher than in plants of other ecosystem-types. The mean value used to represent desert litter N in this analysis was 1.5% (West 1981), although Rodin and Bazilevich (1967) stated that the mean N concentration was 1.7%. West (1981) was correct in using the value of 1.5%, however, since the mathematical mean of the desert litter N data presented by Rodin & Bazilevich (1967; Table 44) was in fact 1.5%. Either value appears to be inordinately high since of the shrub species listed in Table 1 for which there are accompanying data describing N concentrations in litter (all species except *Atriplex vesicaria*), only one produced litter that had a mean N concentration as high as 1.5%.

In 1989, litter from *Fouquieria splendens* growing at sites in the Organ Mountains of New Mexico (11 km east of Las Cruces, New Mexico, USA) and in the Jornada Long Term Ecological Research Area (40 km north northeast of Las Cruces) contained 0.6% and 0.5% N, respectively (Killingbeck *unpublished*

data). During the other studies cited in Table 1, mean litter N was 0.6% (*Artemisia tridentata*), 1.1% (*Atriplex confertifolia*), 0.8% (*Ephedra nevadensis*), 1.5% (*Grayia spinosa*), 1.2% (*Fouquieria splendens*, 1986 only) and 0.7% (*Larrea tridentata*). Mean litter N in these desert shrubs during all the above studies (0.9%) was considerably less than the value of 1.5% previously cited as the mean concentration of N in desert litter.

Regardless of the amount of N held in the green foliage of a shrub, it is the reduction of N during senescence, and the subsequent content of N in the deposited litter that determines whether or not resorption has been efficient. Killingbeck & Costigan (1988) proposed the existence of a "litter N threshold" which represents the lower limit of N in foliar litter. The implication is that further reductions below the threshold may not be biochemically possible. The N concentration that serves as the numerical value of this threshold is 0.6% and was derived from the finding that species in a guild of deciduous forest shrubs had significant differences in green leaf N and resorption of N, but did not differ in litter N (Killingbeck & Costigan 1988).

Since it is highly likely that resorption of N can not be 100% efficient and that some structural N will remain in leaves as they abscise, the expectation that maximum efficiency of N resorption should occur when litter N is reduced to approximately 0.4-0.8% appears to be realistic. The fact that mean litter N in the six species of desert shrubs considered above approaches this threshold range suggests a high degree of resorption efficiency in this group of plants. This conclusion becomes even more convincing when one considers that resorption values for *Fouquieria* in 1986 represented realized resorption that was much less than potential resorption. This is clearly the case since litter N in 1986 (1.2%) was double that of plants at the same site three years later (0.6%). Potential resorption was never reached in 1986. The removal of the litter N value for *Fouquieria* in 1986 further reduces the calculated mean N in desert shrub litter from 0.9% to 0.8%. By comparison, mean litter N calculated from data on 28 species of non-desert woody perennials (calculated from data in Chapin & Kedrowski 1983) was also 0.8%.

A threshold for resorption of P also emerged from the forest shrub guild study alluded to earlier (Killingbeck & Costigan 1988). This threshold was 0.06% P in foliar litter, an order of magnitude less than that of the N threshold. Utilizing the same data sources and species used above to calculate mean N in desert shrub litter, and excluding *Fouquieria* data from 1986, mean P in the litter of desert shrubs was 0.07%. Phosphorus concentrations in the litter of *Atriplex confertifolia* (0.03%), *Ephedra nevadensis* (0.02%), *Fouquieria splendens* (0.02%; Organ Mountains site in 1989, only), and *Larrea tridentata* (0.02%) were considerably less than the forest shrub P threshold indicating that 0.06% P does not represent an absolute biochemical minimum for P in litter. Mean P in the litter of 34 non-desert woody plants was 0.07% (calculated from data in Chapin & Kedrowski 1983). As with N, it appears that desert shrubs are entirely capable of withdrawing maximal amounts of P from senescing leaves.

These data challenge the idea that desert shrubs retain high levels of N in their senescing foliage. Further, they corroborate the earlier conclusion that resorption of N and P in desert shrubs appears to be as efficient, or more efficient, than resorption in plants growing in other ecosystem-types. The fact that this conclusion emerges from either 1) comparisons of resorption estimates between desert shrubs and non-desert woody perennials, or 2) comparisons of the levels to which desert shrubs and non-desert woody perennials can biochemically reduce N and P in their foliar litter, lends further support to the conclusion itself.

RESORPTION PLASTICITY:
FOUQUIERIA SPLENDENS
AS A CASE STUDY

Recent studies of *Fouquieria splendens* (ocotillo), a drought-deciduous perennial that grows from sea level to 1,066 m in the deserts of Mexico and the southwestern United States (Freeman *et al.* 1977), indicate that the process of nutrient resorption in desert shrubs may in fact be quite complex. Extreme variation in resorption between years and between sites (Figure 1) exemplifies the plasticity of this process.

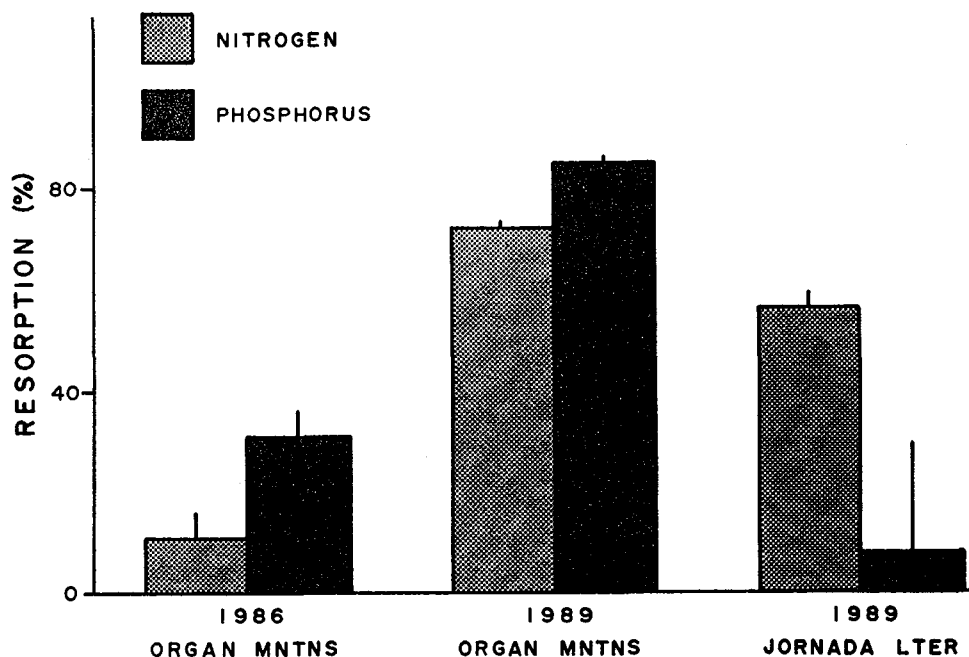


Fig. 1: Mean resorption of nitrogen and phosphorus in unfertilized individuals of *Fouquieria splendens* growing at two sites in New Mexico, USA (the foothills of the Organ Mountains and the Jornada Long Term Ecological Research area). Sample size was seven and six in 1986 and 1989, respectively, at the Organ Mountains site, and 12 at the Jornada LTER site. Vertical lines attached to bars depict one standard error of the mean.

Reabsorción promedio de nitrógeno y fósforo en individuos no fertilizados de *Fouquieria splendens* creciendo en dos sitios en Nuevo México, USA (a los pies de las Organ Mountains y en el área Jornada Long Term Ecological Research). El tamaño de la muestra fue siete y seis en 1986 y 1989, respectivamente, en el sitio de las Organ Mountains, y 12 en el sitio Jornada LTER. Las líneas verticales en las barras indican un error estándar del promedio.

In 1989, resorption of N was more than six times higher than it had been three years earlier in a single population of *Fouquieria splendens* growing in the foothills of the Organ Mountains of New Mexico (72% versus 11%; Figure 1). In the same population, resorption of P was more than two times higher in 1989 than in 1986 (85% versus 31%; Figure 1). Resorption estimates based solely on the 1986 data would appreciably underestimate potential resorption of N and P in this species.

Disparate resorption efficiencies in the same year between individuals of *Fouquieria splendens* occupying neighboring sites also indicate a high degree of plasticity in this process (Figure 1). In 1989, resorption of N by *Fouquieria splendens* growing at the Organ Mountains site was substantially higher (72% versus 56%) than at the Jornada Long Term

Ecological Research site. Resorption of P was an order of magnitude higher at the Organ Mountains site (85% versus 8%). Plasticity in resorption of P was further indicated by extremely high variance within a single population of *Fouquieria splendens* at the Jornada site (Figure 1). The highest P resorption efficiency for an individual in this population was 85%, yet foliar P actually increased by more than 80% during senescence in several individuals.

RESORPTION IN CHILEAN DESERT SHRUBS

Although aspects of the vegetation dynamics and physiological ecology of shrub species growing in Chile have previously been considered (*e.g.*, Mooney & Dunn 1970,

Parsons & Moldenke 1975, Giliberto & Estay 1978, Montenegro *et al.* 1979, Torres *et al.* 1980, Kummerow *et al.* 1982, Rundel 1982, Gutiérrez *et al.* 1988, Rundel *et al.* 1991), there are no published data describing the process of nutrient resorption in shrub species growing in the Atacama Desert. The only published paper that I am aware of containing data on resorption efficiency in Chilean plants reports on mediterranean-climate shrub species growing west of Santiago (Rundel 1982). Nitrogen resorption ranged from 22-56% in the seven matorral species considered in this paper. Mean resorption was extremely low (35%, SE = 4.6), and elements other than N were not considered.

There is no reason to think that resorption in the desert shrubs which grow in the Atacama Desert would be as low as that measured in the matorral shrubs to the south. Rather, it seems reasonable to predict that resorption efficiencies should be as high as those measured in desert shrubs growing in North America and Australia (Table 1).

Evolutionary selection for efficient resorption should be strong given the fact that parts of the Atacama Desert have never received rainfall in modern times (Rumney 1968) and that the Atacama Desert, in its entirety, is considered to be the driest coastal desert in the world (McGinnies 1979). Significant restrictions in the duration of time plants have to absorb nutrients from the soil should serve to enhance the selection of adaptations, such as resorption, which conserve nutrients. The extreme paucity of precipitation and the great depth of the water table (Petrov 1976) throughout the Atacama Desert must drastically limit the window of time in which active uptake can occur, except in those plants occupying sites on the western slopes of the Cordillera de la Costa which obtain supplemental water from coastal fog.

Water deprivation might not constitute a strong selection pressure for increased efficiency in resorption if soil nutrients were abundant and readily available during the short periods of time when soil water was present. However, true soils that might harbor significant amounts of mineralized organic matter are limited to "a few scattered Entisols or Aridisols" and much of the surface of the Atacama Desert has been described as a

"...barren, rough land of rocks and stony colluvial debris and outwash gravels" (Fuller 1974). Therefore, if the soils of the Atacama Desert are as nutrient depauperate as these descriptions suggest, then nutrient resorption would be expected to increase fitness and undergo directional selection toward higher efficiency.

Geographical locations that are perpetually subjected to extremes in environmental conditions are often prized as research sites since they provide unequalled opportunities for the study of the limits of biotic evolution. The Atacama Desert falls into this category and harbors a wide variety of shrub species suitable for detailed resorption studies. *Oxalis gigantea*, for example, is a deciduous woody perennial that grows on rocky soils in the southern reaches of the Atacama Desert and appears to have at least several important life history traits similar to those exhibited by *Fouquieria splendens* in the United States. A comparative study of the resorption dynamics of these two desert shrubs could significantly contribute to our meager understanding of the intricacies of this important ecophysiological process.

INTERPLAY BETWEEN RESORPTION AND DESERTIFICATION

One of the many goals of the workshop held in La Serena was to place desertification in an ecological perspective and to fuse what we know about ecological relationships with what we know about desertification. It was hoped that such a fusion would provide valuable insights into the retardation, prevention, and reversibility of the degradative processes of desertification. In this context, a brief analysis of the relationship between desertification and resorption in perennial shrubs seems to be in order.

A credible discussion of the relationships between desertification and resorption must begin with a stated definition of the term desertification, since only the term resorption was defined earlier in this paper. According to Dregne (1983) "Desertification is the impoverishment of terrestrial ecosystems under the impact of man. It is the process of deterioration in these ecosystems that can be

measured by reduced productivity of desirable plants, undesirable alterations in the biomass and the diversity of the micro and macro fauna and flora, accelerated soil deterioration, and increased hazards for human occupancy". Pertinent to the discussion here is the fact that one of the certain outcomes of desertification is a diminution in soil nutrient reserves.

It appears that the primary effect of resorption on desertification may be to delay, or retard the rate of degradation. Since the resorption and subsequent reuse of nutrients by established shrubs reduces the requirement for uptake of soil nutrients, shrub species with well developed resorption capabilities may survive in nutritionally degraded environments for a period of time. Such survival can represent a form of successional inertia which delays wholesale changes in community structure and species composition. In the Chilean Espinal, for example, efficient resorption and reuse of nutrients by dominant woody perennials such as *Acacia caven* would be expected to delay the demise of this savanna ecosystem during a time when environmental conditions and anthropogenic practices act in concert to hasten desertification. Farther to the north in the heart of the Atacama Desert, resorption in the few plants that grow there is of little consequence to the rate of desertification since the hyperarid nature of the environment virtually precludes further desertification.

Resorption-mediated delays in desertification, however, would only constitute a brief respite in community change because ecological longevity is a function of fecundity and survival, not merely survival. Newly established seedlings in degraded environments are highly susceptible to mortality because they must rely almost exclusively on uptake from the soil to meet their nutrient demands. Because they do not already have internal reservoirs of nutrients that can be conserved, efficient resorption means little for their chances of survival. Therefore, it seems that the impact of resorption on desertification is limited to relatively short term delays. Even extraordinarily efficient resorption can not prevent or reverse the process of desertification.

The above hypothesis outlining the possibility of a delay in the full effects of desertification due to resorption-driven successional inertia is predicated upon the assumption that in the short term the efficiency of realized resorption is not severely diminished by desertification itself. Considering some of the factors that play major roles in regulating both realized and potential resorption (Table 2), it appears that the above assumption may be valid in some instances, but not others.

Episodes of desertification often produce changes in environmental parameters that bear directly on a number of the regulatory factors

TABLE 2

Factors that play major roles in determining the efficiency of nutrient resorption. Citations denote selected papers in which the regulatory factors are discussed.

Factores que juegan roles mayores en determinar la eficiencia de reabsorción de nutrientes. Las citas son publicaciones seleccionadas en las cuales se discuten los factores reguladores.

Regulatory Factor	Selected Citations
Availability of Water	Hill 1980, Hocking 1982, Del Arco <i>et al.</i> 1991
Long-Term Fertility on the Environment	Small 1972, Grubb 1977, Ralhan and Singh 1987
Nutrient Content in Unsensced Leaves	Loneragan <i>et al.</i> 1976, Chapin and Kedrowski 1983, Killingbeck and Costigan 1988
Source-Sink Relations	Nambiar and Fite 1987, Chapin and Wardlaw 1988, Chapin and Moilanen 1991
Timing and Duration of Leaf Abcission	Killingbeck 1988, Killingbeck <i>et al.</i> 1990, Del Arco <i>et al.</i> 1991

that govern resorption efficiency. One of the most obvious environmental changes to accompany desertification also may be one of the most important factors regulating resorption efficiency; that is, water availability. Del Arco *et al.* (1991) contend that water availability is "the determining factor" in the resorption efficiency of plants growing in semiarid climates and have shown that "...species that occupy the more xeric sites thus show lower retranslocation [resorption] rates". Another regulator of resorption, timing of abscission, is also linked to water availability. Early abscission can be induced by depleted plant tissue water reserves (Hocking 1982) and has also been directly linked to realized resorption efficiencies that were well below potential resorption efficiencies (Killingbeck *et al.* 1990). Therefore, desertification-induced reductions in water availability may initiate concomitant reductions in resorption efficiency. This type of induced inefficiency in resorption might well negate the resorption-induced delays in desertification outlined above.

The remaining regulatory factors listed in Table 2 can all potentially be influenced by desertification. However, the collective effects of their desertification-altered status on resorption are likely to be less unilateral than are the effects of water availability and timing of abscission. For example, it is possible that consistent decreases in site fertility could constitute a selection pressure that would act over long periods of time to increase the efficiency of resorption (*e.g.*, Small 1972, Ralhan & Singh 1987). The short term response to the same decreases in nutrient availability would probably be a decrease in resorption efficiency since resorption efficiency has been positively correlated with nutrient content in unsenesced leaves (Lone-ragan *et al.* 1976, Killingbeck & Costigan 1988).

While it seems reasonable to suggest that resorption may act to delay some community-level effects of desertification, and that desertification may act to reduce short term resorption efficiencies, it should also be evident that there are no clearly predictable, invariate outcomes of the interplay between desertification and resorption.

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