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Nitrogen immobilization in leaf litter at two Mediterranean ecosystems of SW Spain

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Abstract. Nitrogen immobilization in relation to the dynamics of lignin and tannins in nine different types of leaf litter was investigated during a 2-yr study at two Mediterranean ecosystems of SW Spain. Net nitrogen immobilization for all the species was higher in a forest than in the more nutrient-poor soil of a shrubland. Absolute amount of lignin increased in both ecosystems in the first 2–4 months whereas tannin rapidly decreased in the same time period. Increases in lignin were significantly correlated to losses of tannins during decomposition. Initial tannin content was the best predictor of the maximum amount of immobilized nitrogen in litter in both ecosystems. Mechanisms that could explain the immobilization of nitrogen in litter are discussed.

Introduction

Nitrogen often limits the rate of net primary production on land, partially because of positive feedbacks that exist between low nitrogen availability, low litter quality, and low rates of decomposition (Vitousek & Howarth 1991). Because most of the annual nitrogen requirements are supplied by the decomposition of dead materials in the soil (Schlesinger 1991), studies of the dynamics of this element in decomposing litter are essential to understand the possible causes of nitrogen limitation in terrestrial ecosystems. Most decomposer microorganisms have a higher nutrient concentration in their tissues than the source on which they feed (Swift et al. 1979). Under these circumstances, net immobilization tends to prevail until the nutrient occurs at non-living concentrations.

Most decomposition studies have found increases in relative nitrogen concentration in litter as decomposition proceeds. Aber & Melillo (1980) found an inverse-linear relationship between the remaining biomass and the nitrogen concentration in litter; this relationship has been validated for a large number of litter decomposition studies. Increases in the absolute amount of nitrogen in litter have also been found in numerous studies. In some materials, net nitrogen immobilization has been observed through ten years of decay (Fahey et al. 1991).

Fixation of atmospheric nitrogen, contamination by insect frass and throughfall, or importation from green litter have been proposed as possible explanations for this increase in nitrogen (Bocock 1963, 1964; Lousier & Parkinson 1978; McLean & Wein 1978; McClaugherty et al. 1985). Translocation from soil to litter by fungal hyphae is also possible (Gosz et al. 1973; Berg & Soderstrom 1979; Staff 1980; Berg & Staff 1981; Moore 1984; Fahey et al. 1985).

Net immobilization of nitrogen in litter has been related to the initial nitrogen concentration (Berg & Staff 1981), the initial carbon-to-nitrogen ratio (Berg & Ekbohm 1983), the lignin-to-nitrogen ratio, the initial lignin concentration (Aber & Melillo 1982; Melillo et al. 1982; Berg & McClaugherty 1987, 1989; Berg 1988) and the polyphenolic content (Palm & Sanchez 1991). The lignin fraction is a sink for nitrogen during decay, thereby producing the precursors of humus (Stevenson 1982; Berg & Theander 1984; Waring & Schlesinger 1985). Incorporation of soluble polyphenolic compounds into lignin has been postulated to explain increases in the absolute amount of lignin during decomposition (Suberkroppe et al. 1976, Schlesinger & Hasey 1981; Berg et al. 1982; Schlesinger 1985). Indeed, tannins form recalcitrant complexes with proteins and other substrates with electronegative moieties and, therefore, may form pre-humic substances (Basaraba & Starkey 1966).

The objective of this study was to investigate relationships between immobilized nitrogen and the dynamics of the lignin and tannin fractions during leaf litter decomposition in two contrasting Mediterranean ecosystems in SW Spain.

Methods

Area of study

The study was conducted in Doñana Biological Reserve, (37°7′N, 6°12′W) and in Monte La Sauceda (36°30′N, 5°35′W), Southwest Spain. Both areas have the typical winter-wet, summer-dry pattern of a Mediterranean-type climate.

Mean annual rainfall of Doñana Biological Reserve is around 500 mm with maxima in both winter and early spring. Summer drought is severe, with no precipitation during July and August, and little if any in June and September. Mean annual temperature is 16.7 °C. Winter temperatures are mild with a daily mean of 9.3 °C during the coldest months (December and January). Summer temperatures are high, with a daily mean of 23.9 °C for July, the warmest month. Matorral (scrub) is the predominant vegetation type. Species composition appears to be controlled by topography, which determines the depth to the water table (Gonzalez Bernaldez et al. 1975). Litterbags were incubated at about 20 m elevation above mean sea level in an open shrubland dominated by *Halimium halimifolium*, *Halimium commutatum*, *Cistus libanotis* and *Rosmarinus officinalis*. Biomass, productivity, and successional changes of the area are described by Merino & Martin Vicente (1981).

Average annual precipitation of Monte La Sauceda is around 1600 mm, with an annual mean temperature of 16.2 °C. The precipitation and temperature show the same seasonal pattern as they do in the Doñana Biological Reserve (Gallardo 1990). Litterbag incubation sites were located at 432-m elevation above mean sea level. This stand is mature edaphic climax forest, composed of a tree layer of *Quercus suber* and *Quercus canariensis*. Below this layer a shrub layer is formed mainly by *Teline monspessulana*, *Calicotome villosa*, *Crataegus monogyna*, *Smilax aspera* and *Rubus ulmifolius* (Gallardo & Pino 1988). Canopies are closed and ground vegetation is sparse.

Chemical and physical properties of Doñana and La Sauceda soils are given in Table 1.

Field methods

Leaf litter decomposition of five tree species, *Quercus suber*, *Quercus canariensis*, *Quercus pyrenaica*, *Salix atrocinerea* and *Fraxinus angustifolia*, and four shrub species, *Quercus lusitanica*, *Quercus coccifera*, *Halimium halimifolium* and *Cistus libanotis* was studied using the nylon mesh bag technique (Bocock & Gilbert 1957). Mesh size was 1 mm, small enough to prevent major losses of the smallest leaves, yet large enough to permit aerobic microbial activity and free entry of small soil animals.

Freshly abscised leaves of *Halimium halimifolium*, *Cistus libanotis*, *Quercus coccifera* and *Quercus suber* (evergreens) were collected in the Doñana Biological Reserve during June 1985, the peak period of litterfall. *Quercus canariensis*, *Quercus pyrenaica*, *Quercus lusitanica*, *Salix atrocinerea* and *Fraxinus angustifolia* (deciduous) were collected from Monte La Sauceda during October—December 1985 from the ground surface. Contaminant debris was carefully picked from each collection, which was thoroughly mixed to provide a uniform initial leaf litter for each species. The leaf litter samples were air-dried. The field moisture content was determined by oven-drying a subsample for 48 h at 80 °C.

For each species, approximately 2 g of air-dried leaf material was

Table 1. Some chemical and physical characteristics of Doñana and La Sauceda soils. Extractable P corresponds to the fraction soluble in dilute Acid-Fluoride; Ca and K values correspond to the extractable fraction (1N NH_4OAc). Samples are from 0—15 cm depth.

	O.M. (%)	C (%)	N (%)	C:N	P (ppm)	Ca (cmol/kg)	K (cmol/kg)	Sand (%)	Silt (%)	Clay (%)
DOÑANA	1.06	0.62	0.046	15.9	5.2	1.16	0.08	94.9	1.8	3.3
LA SAUCEDA	1.69	0.98	0.073	13.4	22.4	11.1	1.39	51.3	2.1	46.6

weighed to the nearest 0.01 g and placed in a litterbag. A total of 1372 10 × 15 cm litterbags were placed in the two ecosystems. Litterbags from the nine species were distributed randomly on the soil of Doñana Biological Reserve on 28 January 1986. Three days later, litterbags from eight species (all except *Q. coccifera*) were placed on the soil at Monte La Sauceda. At bimonthly intervals for two years between six to ten litterbags of each species were retrieved at each site. Litterbags were transported and stored in paper bags in order to minimize error through spillage (Suffling & Smith 1974).

Analytical and laboratory methods

Litter was dried at 80 °C for 24 h, weighed, and ground to pass through a 1-mm mesh screen. Samples were analyzed individually for N, tannins, and lignin. These data are expressed in concentrations as a percentage of oven-dry biomass. Total nitrogen was determined on 0.2-g subsamples using standard Kjeldahl procedures. Total phenolics were sequentially extracted with 100% methanol (low molecular weight) and 50% methanol (high molecular weight; Glyphis & Puttick 1988). These fractions were combined and colorimetrically measured using the Folin-Ciocalteu reagent with tannic acid as standard (Singlenton & Rosi 1965). The lignin fraction was analyzed by sequential analysis of fiber (Robertson & Van Soest 1981). About 1 g of sample was extracted with neutral detergent, followed by acid detergent and 72% sulfuric acid. Carbon content was taken as 50% of ash-free dry mass (Schlesinger 1977). Several replicate samples were analyzed during each procedure of chemical analysis.

Statistical methods

The maximum amount of nitrogen immobilized before net mineralization occurs (the "nitrogen factor") has been calculated following Aber & Melillo (1982). They found a linear relationship between the percent of remaining biomass and the nitrogen concentration in the residue. This relationship was validated for a wide range of litter types and ecosystems.

From this relationship:

$$[\text{REMAINING BIOMASS } (\%)] = a + b(X),$$

where X is the nitrogen concentration in the residue, Aber & Melillo (1982) deduced that the percent of original nitrogen remaining is:

$$Y = (a + b(X))\,(X/N),$$

where N is the original nitrogen concentration. The amount of nitrogen immobilized before net mineralization begins is the maximum value of this equation and will occur when its first derivative is equal to zero. Solving this equation they deduced the maximum nitrogen immobilized or "the nitrogen factor" as:

$$((a^2/-4b) - 100 \text{ NITROGEN CONCENTRATION})/10,^*$$

where "the nitrogen factor" is expressed in mg of immobilized nitrogen per g of litter, and the percent of original weight remaining at this point is:

$$Y = a/2$$

For more details on these equations, see Aber & Melillo (1982).

We determined the relationship between maximum immobilized nitrogen and the initial content of lignin, tannin, nitrogen and the C:N ratio by linear regression and stepwise multiple regression.

Results

In Doñana, net immobilization of nitrogen was found in the leaf litter of *Halimium halimifolium* after more than 1 yr of decay. No net immobilization of nitrogen was seen in the other species after the first four months of decay (Fig. 1). In La Sauceda, most species showed a net immobilization phase that lasted over 16 months, except for *F. angustifolia* and *Q. pyrenaica*, the species with the lowest tannin content and highest mass loss. Changes in leaf litter nitrogen in La Sauceda were more intense than those in Doñana, with La Sauceda having higher net nitrogen immobilization but also faster net mineralization when it appeared (see *F. angustifolia* and *H. halimifolium*).

A linear relationship between % remaining biomass and nitrogen content in the residue as decomposition proceeds was highly significant for all species in both ecosystems ($p < 0.01$; Fig. 2). The maximum amount of immobilized nitrogen in litter could have been estimated from the maximum increase of nitrogen showed in Fig. 1. However, owing to the relatively high degree of error inherent to these points, the equation of Aber & Melillo (1982) was used to calculate immobilized nitrogen (Table 2). Values from direct extrapolation from curves tend to be slightly higher for most species than those calculated using the equations of Aber &

* Error corrected from the original equations in Aber & Melillo (1982).

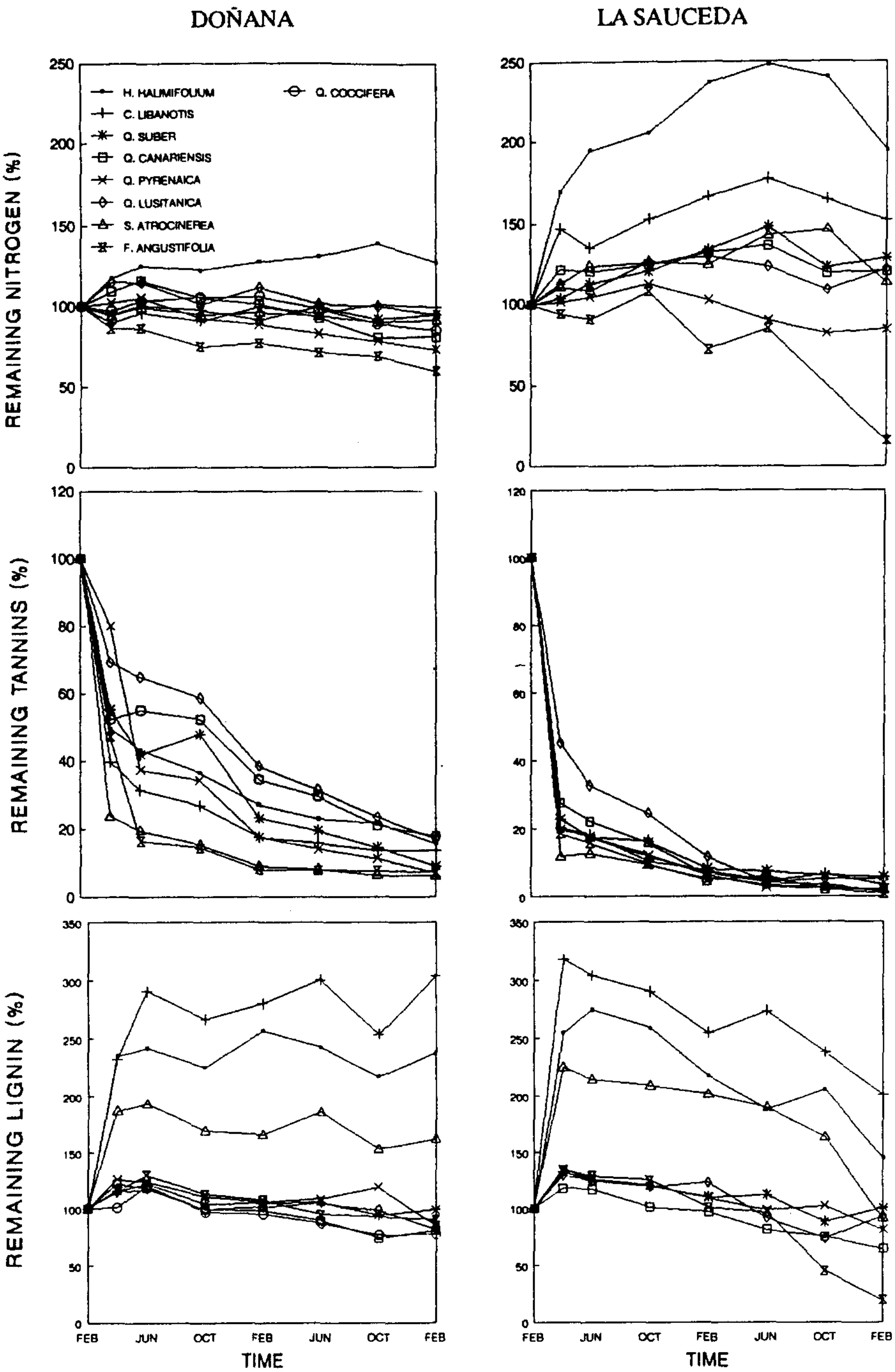

Fig. 1. Changes in the absolute amounts of nitrogen, tannins and lignin in several types of litter at Doñana and La Sauceda ecosystems during a 2-yr study. All data expressed as % of original content.

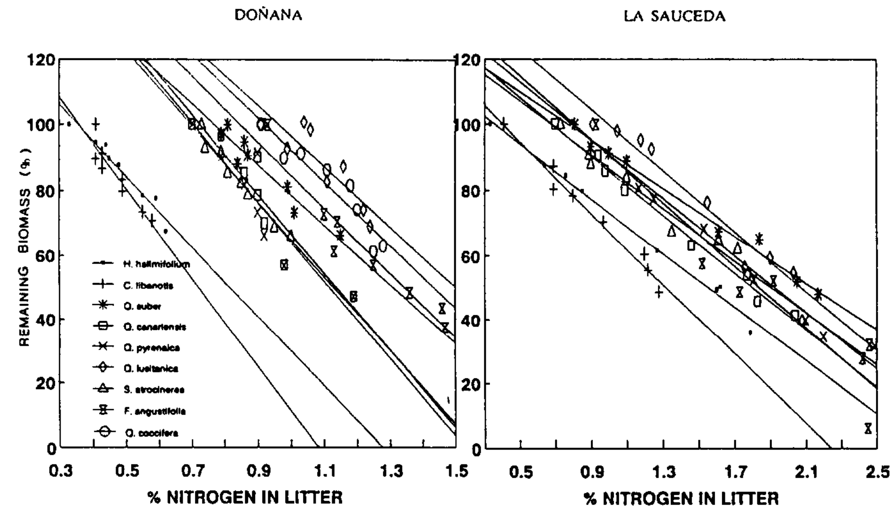

Fig. 2. Percentage of original biomass remaining as a function of the nitrogen concentration in the residual material of leaf litter at Doñana and La Sauceda ecosystems.

Melillo (1982). For example, immobilization in *H. halimifolium* was 1.13 and 1.3 mg g^{-1} in Doñana, and 4.61 and 4.9 mg g^{-1} in La Sauceda, using extrapolation from equations and from the curves, respectively. Only four species showed net nitrogen immobilization in Doñana with the highest value (1.13 mg g^{-1}) found in the litter of *H. halimifolium.* In La Sauceda all the species showed net immobilization, which ranged between 0.7 and 4.61 mg g^{-1}. In all cases, biomass remaining after 2 yr was higher in Doñana than in La Sauceda (Table 2).

Tannins were apparently leached from leaf litter during the first months in both ecosystems (Fig. 1), but they were lost more quickly from litter incubated in La Sauceda, the ecosystem with higher precipitation.

The lignin fraction increased in litter of all the species over a period of about for months in Doñana and two months in La Sauceda. The pattern of lignin accumulation was very similar in Doñana and La Sauceda, with maximum increments for *H. halimifolium*, *C. libanotis*, and *S. atrocinerea* (between 200 and 300% of the original weight) and lower increases for the remaining species (approximately 125% of original weight). Following maximum accumulation, lignin fractions of litter in La Sauceda began to lose mass; losses of lignin were not seen in litter at Doñana.

For the nine species, nitrogen content at the beginning of the experiment ranged between 0.33% and 0.93% of the leaf mass, whereas lignin and tannin content ranged between 8.91% and 20.1% and 4.5% and 23.9%, respectively. The initial C:N ratio varied between 53.7 and 151.5

Table 2. Maximum amount of immobilized nitrogen, biomass remaining at this point, and initial nitrogen, lignin, and tannin content in the leaf litter incubated in Doñana and La Sauceda soils. Negative values indicated that no immobilization occurred (mineralization from the beginning). (*) Collected at Doñana site. (#) Collected at La Sauceda site.

	Immobilized Nitrogen (mg/g litter)		Biomass Remaining (%)		Initial content				
					Nitrogen (%)	Lignin (%)	Tannin (%)	C:N	Lignin:N
	Doñana	La Sauceda	Doñana	La Sauceda					
H. halimifolium (*)	1.13	4.61	69.3	57.4	0.33	8.9	23.9	151.5	27.0
C. libanotis (*)	−0.04	2.74	100.0	61.1	0.41	8.9	19.3	121.9	21.6
Q. suber (*)	−0.19	3.15	100.0	64.0	0.81	18.1	10.6	61.7	22.4
Q. coccifera (*)	0.15		94.9		0.91	18.8	14.0	54.9	20.6
Q. canariensis (#)	0.28	2.54	93.9	65.2	0.70	15.5	13.3	71.4	22.2
Q. pyrenaica (#)	−0.07	1.04	100.0	67.6	0.93	18.3	8.2	53.8	19.7
Q. lusitanica (#)	0.56	2.46	94.5	73.2	0.91	20.2	14.9	54.9	22.1
S. atrocinerea (#)	−0.22	2.69	100.0	63.7	0.73	18.0	11.8	68.5	24.7
F. angustifolia (#)	−0.77	0.70	100.0	69.4	0.93	10.5	4.5	53.7	11.3

(Table 2). The minimum values of nitrogen and lignin content and the maximum values of C:N ratio and tannin content corresponded to the leaves of *Halimium halimifolium* and *Cistus libanotis*, both collected at Doñana. The leaves of *Quercus suber* and *Quercus coccifera*, also collected in Doñana site, were not significantly different from those of the remaining species collected at La Sauceda site.

The maximum amount of immobilized nitrogen in Doñana was significantly correlated with the initial tannin content of the leaves ($r = 0.83$, $p < 0.01$; Fig. 3), but not with initial percent of nitrogen, lignin, or with the ratios of lignin:N or C:N. In La Sauceda, initial tannin content also was a significant predictor of the maximum nitrogen immobilization ($r = 0.86$,

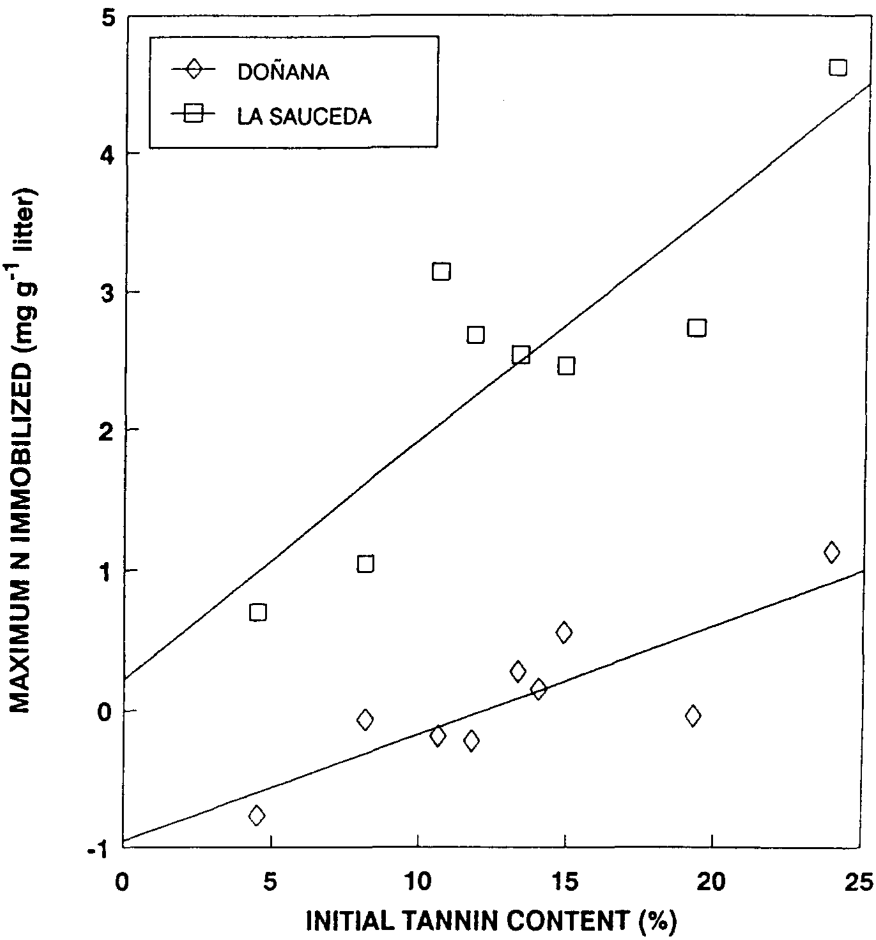

Fig. 3. Relationship between the maximum amount of immobilized nitrogen and the initial tannin content of leaf litter at Doñana and La Sauceda ecosystems.

$p < 0.01$, Fig. 3); but the relationships with nitrogen, lignin:N, and C:N were also statistically significant ($r = -0.77$, $p < 0.05$; $r = 0.86$, $p < 0.01$ and $r = 0.74$, $p < 0.05$ respectively). Using a stepwise forward multiple regression with initial nitrogen, lignin, and tannin contents and C:N ratio as independent variables, only tannin content was included as predictor of the immobilized nitrogen in both ecosystems. The same amount of initial tannin content was related to a higher amount of immobilized nitrogen in La Sauceda than in Doñana (Fig. 3).

Increases in the lignin fraction in the first two months in La Sauceda and during the first four months in Doñana were significantly related to losses of tannins in the same period (Fig. 4). This relationship was statistically better in Doñana ($r = 0.82$, $p < 0.01$) than in La Sauceda ($r = 0.74$, $p < 0.05$), but the observed pattern was very similar in both sites. *H. halimifolium*, *C. libanotis*, and *S. atrocinerea* form a group with the highest increases in lignin and losses of tannins (Fig. 4).

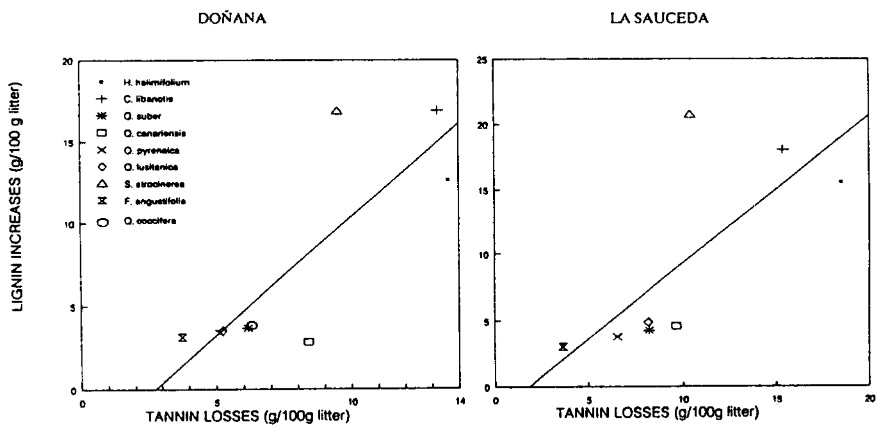

Fig. 4. Relationship between the maximum increases in the absolute amount of lignin and the losses of tannins in leaf litter at Doñana and La Sauceda ecosystems.

Discussion

The maximum amount of immobilized nitrogen was higher in La Sauceda, a forest with relatively high soil nutrient content, than in Doñana, a shrubland with nutrient-poor soil. For example, maximum net immobilization was four, five and nine times higher in the litter of *H. halimifolium*, *Q. lusitanica* and *Q. canariensis* (respectively) incubated in La Sauceda than in the same substrate in Doñana. Soil nitrogen content was only 1.6 times higher in La Sauceda than in Doñana, but phosphorus, calcium and potassium concentration at La Sauceda were four, ten and seventeen times (respectively) higher than in the Doñana soils (Table 1). These results could reflect the influence of site characteristics on the immobilization process and do not support the conclusion of McClaugherty et al. (1985) that, except for the most nitrogen-poor litter, nitrogen dynamics during initial stages of decay were essentially independent of the available nutrients in soil. Nitrogen content in leaf litter of this study was in the range of that used by McClaugherty et al. (1985); however, differences in precipitation between the two ecosystems are also important. Precipitation, rather than site fertility, may influence the immobilization processes by controlling the size and activity of microbial biomass in litter.

Maximum net immobilization was in the same range as that reported in other Mediterranean ecosystems. For example, Schlesinger (1985) reported between 0.63 and 4.8 mg/g for two species in the California chaparral at two different elevations. Lower increases in nitrogen were found by Mitchell et al. (1986) in a coastal fynbos of South Africa.

Evidence of rapid losses of tannin and absolute increases of the lignin fraction during initial stages of decay have led various investigators to postulate a direct relationship between their dynamics (Schlesinger & Hasey 1981; Berg et al. 1982; Yavitt & Fahey 1986). Suberkropp et al. (1976) suggest that polyphenolics may complex with proteins during the initial stages of decay and become isolated in the lignin fraction. In this study, this hypothesis is supported since those species that showed the greatest increases in lignin, exhibited the greatest losses of tannins (Fig. 4). However, the existence of two groups of species in Fig. 4 suggests that the chemical characteristics of tannins could be regulating its changes more than the absolute amount in each species. Net accumulations of lignin were fairly similar in both ecosystems; therefore, unlike nitrogen, the dynamics of this fraction appear to be strongly dependent on litter quality and only slightly affected by site characteristics.

Most investigators have determined that the initial lignin content or the lignin:N ratio are the best predictors of maximum net immobilization of nitrogen (Aber & Melillo 1982; Melillo et al. 1982; Berg & McClaugherty 1987, 1989; Berg 1988). However, in this study, initial tannin content was the parameter that best explained the immobilization phase in both ecosystems. This difference may be explained by the high tannin content of some of the Mediterranean leaves. Palm & Sanchez (1991) found a significant negative relationship between net mineralization and initial polyphenolics content in tropical legumes, but they reported very low values of polyphenolics content as compared with our values.

The sources of nitrogen taken up by decomposing litter are not well established, with biological and non-biological processes having been proposed. Microbial biomass may be a major contributor to the absolute increase of nitrogen in litter. For example, Fouseki & Margaris (1981) found that increases in nitrogen were related to increases in aminoacids, and He et al. (1988) using ^{15}N found that a significant fraction of the recently immobilized nitrogen in soils occurred as insoluble components of microbial tissues, such as fungal melanins. Nitrogen in microbial biomass in litter estimated by the fumigation-extraction method in a warm-temperate forest gave values between 0.1 and 0.5 mg N g^{-1} litter (Gallardo & Schlesinger, unpublished data). This amount would explain a significant percentage of immobilized nitrogen in some species, at least in Doñana, but realistically, microbial biomass in Mediterranean ecosystems should be lower, particularly in the Doñana soil. Axelsson & Berg (1988) reported maximum values of fixation of ammonium in sterilized *Pinus sylvestris* needle litter were 0.02 mg g^{-1}, an amount that would explain only a low percentage of net immobilization. Part of the immobilized nitrogen in litter could be associated with proteins and other tissues from dead microbial biomass. Polyphenolic compounds could kill microbial biomass and precipitate its components with a subsequent incorporation in the lignin fraction. For example, *Quercus* species frequently contain quercitol gallates which have antibacterial activity by binding with the cell wall (Serit et al. 1991).

In La Sauceda, net disappearance of lignin began long before a net nitrogen release, which coincides with the results found by Berg & McClaugherty (1987) for several types of litter. However, in Doñana the net release of these two fractions began about the same time, which may indicate a larger proportion of the total nitrogen in the lignin fraction than at La Sauceda. Because the same litter was used in both ecosystems, differences in microbial biomass, as affected by different external nutrient supply and precipitation, may explain the different association between nitrogen and lignin fractions between sites, with immobilization of nitrogen in microbial biomass predominating La Sauceda. This conclusion is also supported by the significant relationship found at La Sauceda, but not at Doñana, between nitrogen immobilization and nitrogen content, lignin:N and carbon:N ratio, which would indicate a significant contribution of microbial biomass to the nitrogen immobilized in the high quality litter at La Sauceda.

Our results suggest that tannin may be responsible for nitrogen immobilization in leaf litter of Mediterranean species and its effect would be relatively more important in a nutrient-poor soil with less microbial biomass. In our model, nitrogen, would be imported to the litter by microbial biomass. In a second step, nitrogen would be precipitated by tannins and immobilized in the lignin fraction. The maximum amount of immobilized nitrogen would be limited by the size of microbial biomass (as dependent of site characteristics) and the amount and quality of tannins (as a factor of litter quality). However, the absolute increase in the lignin fraction would be independent of the site characteristics and only determined by litter quality (amount and quality of tannins).

This process may describe the first steps in the formation of humus compounds, with lignin, tannins and proteins as precursors. Humic substances are known to be nitrogen-rich substances forming part of the long-term mineralizable nitrogen in soil (Paul & Clark 1989). Species with high tannin content in leaves are frequently associated with nutrient-poor soils. These species would produce more nitrogen-rich humus than those with a low tannin content in leaves, which might be interpreted as a mechanism of nutrient conservation.

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