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Timing of litter production in a maquis ecosystem of North-Eastern Greece

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ABSTRACT

Seasonal litter fall was sampled throughout 2 years in an ecosystem of evergreen sclerophyllous shrubs of North-Eastern Greece. The annual total litter fall was 5,980 kg per hectare of which 70% was leaf fall. Litter fall was highest in late spring-early summer, the fall of each component (leaf, twigs, fruits, etc.) being markedly seasonal but not all in phase. Leaf litter fall maximum was in late spring-early summer, while fruit litter fall was in winter. The annual energy offer to the soil subsystem measures $1{,}824 \times 10^4$ kcal if leaf litter only is considered.

KEY WORDS: litter fall, nutrients, water stress, mediterranean ecosystems.

RÉSUMÉ

L'étude de la chute saisonnière de la litière a été effectuée pendant 2 années, dans un écosystème d'arbustes sclérophylles à feuillage persistant, du nord-est de la Grèce. La quantité de litière tombée au cours d'une année était de 5 980 kg par hectare, les feuilles représentaient 70 % de cette masse. Le maximum de chute de la litière est situé vers la fin du printemps et le début de l'été. La chute des différentes parties de la litière (feuilles, fruits, branches, etc.) est elle aussi, saisonnière. Le maximum de la chute des feuilles a lieu vers la fin du printemps et le commencement de l'été, alors que le maximum de la chute des fruits a lieu en hiver. En ne tenant compte que de la chute des feuilles, l'apport annuel d'énergie au sol atteint $1\,824 \times 10^4$ kcal.

INTRODUCTION

The formation of plant litter is a process associated with input of energy and nutrients to soil and it is the starting point of nutrient recyling (RODIN & BAZILEVICH, 1967; GRAY & SCHLESINGER, 1981). In consequence, in order to study the nutrient cycling in an ecosystem it is necessary to know the quantitative aspects of litter formation. The latter is a physiological process affecting not only the soil but also the growth patterns and nutrition of the plants.

In ecosystems where available nutrients are present in limited quantities only and the rate of decomposition is low the litter layer becomes increasingly important in the overall nutrient regime of the systems. Mediterranean type ecosystems (M.T.E.) belong to these nutrient-limited ecosystems, therefore the amount of plant material being returned to the soil is important. Moreover, current interest in the productivity of M.T.E. and their management problems requires knowledge of the litter production dynamics in terms of nutrient cycling (MARGARIS *et al.*, 1983). In the mediterranean type climate of Greece, maquis ecosystems (consisting of evergreen sclerophyllous tall shrubs) are predominately found at a precipitation regime of 600-1,000 mm per year approximately and they cover 25-30% of the forested land of the country. This paper deals with litter production and dynamics in a maquis ecosystem of North-Eastern Greece.

STUDY AREA

The study was carried out in a stand of sclerophyllous evergreen tall shrubs, 2 m in height approximately, near Stavros village in North-Eastern Greece, at an elevation of 20 m above sea level on metamorphic rocks of biotitic gneiss and amphibolites. The site has a north-east exposure and the slope is less than 5°.

The dominant plant species based on biomass are *Quercus coccifera* L. (32%) and *Arbutus unedo* L. (15%) (ARIANOUTSOU & MARDIRIS, 1987; ARIANOUTSOU & PARASKEVOPOULOS, 1989 submitted for publication). Other woody species which occur in the area are *Phillyrea media* L., *Erica arborea* L., *Quercus ilex* L. and *Cistus* sp. The site has not been burned for at least 20-25 years. The climate is mediterranean with mild and wet winters and hot dry summers (fig. 1).

METHODS

Preliminary estimations showed that 15 litter traps were enough to give representative data on the litter formation at the community level. Therefore, 15 traps, each of 32 cm in diameter and 50 cm high, were placed randomly over a sampling area of 0.1 ha, 0.5 m above the ground. The material fallen into the collectors was removed from the site at monthly intervals, transported to the laboratory and separated into five components: "leaf litter", "shoot litter", "flower litter", "fruit litter" and "miscellaneous" a component which included all that material which was not identifiable, mostly because it was damaged in some way (eaten by birds or insects). The material was dried at 60°C for 48 hours in an air-oven and weighed. Data for each sample period represent the mean value obtained from the 15 traps.

RESULTS AND DISCUSSION

The total amount of litter fall produced in the 2-year study period was 575.07 $g.m^{-2}$ and 502.28 $g.m^{-2}$ for the first and second year respectively (table I).

Leaf litter constituted 58.23% and 84.50% of the total litter in the first and second year respectively, which gave a mean value of 70.51%. Shed flowers measured 4.56% of the total (mean value), while the fruits were 28.49 and 5.44% in the first and second year respectively, giving a mean value of 17.75%. Twigs constituted only 4.60% (mean valued) of the total litter fall.

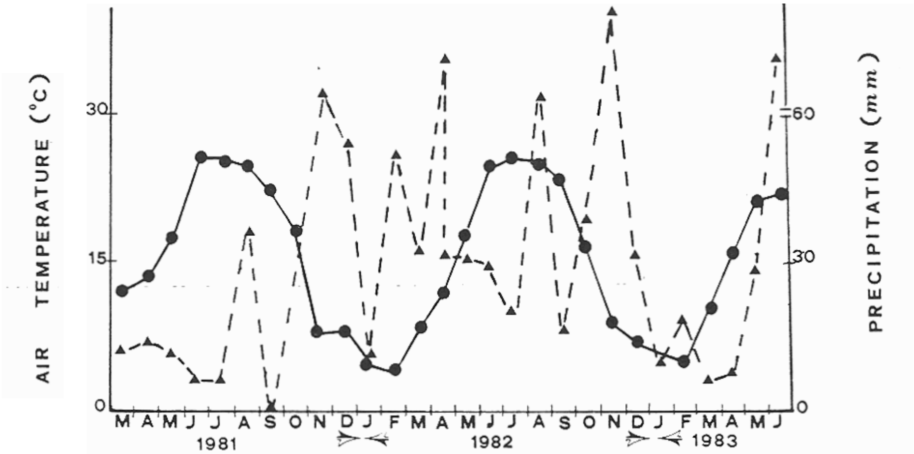

FIG. 1. – Climatic data of Stavros, NE Greece, experimental site.
●——● Air Temperature (°C), ▲- - - -▲ Rainfall (mm).

TABLE I. — *Litter produced in the 2-year study period at Stavros experimental site. Figures are in g.m*$^{-2}$. *The percent contribution of each component in the total litter is shown in parenthesis.*

Component									
Leaves	(%)	Twigs	(%)	Flowers	(%)	Fruits	(%)	Miscellaneous	Total
Year 1981-1982									
334.88	(58.23)	34.15	(5.94)	26.79	(4.66)	163.87	(28.49)	15.38	575.07
Year 1982-1983									
424.72	(84.50)	15.45	(3.07)	22.39	(4.46)	27.35	(5.44)	12.37	502.28
Mean									
379.80	(70.51)	24.80	(4.60)	24.59	(4.56)	95.61	(17.75)	13.87	538.67
±45.06	–	±9.38	–	±2.21	–	±68.46	–	±1.51	±36.50

There was a continuous litter fall throughout the year (fig. 2) although the majority took place in summer because of leaf abscission at that time. The peak value in litter fall observed in winter 1982 was due to sheding fruits.

The relative contribution of the two dominant species in the litter fall is shown in table II.

Leaves of both species fall in late spring-early summer, although a small portion of leaves are continuously shed. In the period between March 1981-April 1982, 68% of the leaf litter fall of *Quercus coccifera* took place in a period of only 3 months (April 4th-July 9th included), while the remaining 9 months contributed only by 32% of the total annual leaf litter fall. The same holds for *Arbutus unedo* leaft litter fall, where 82% of the total occurred in 3 months time (April 4th-July 9th included) and 18% in the other 9 months, during the first year of study.

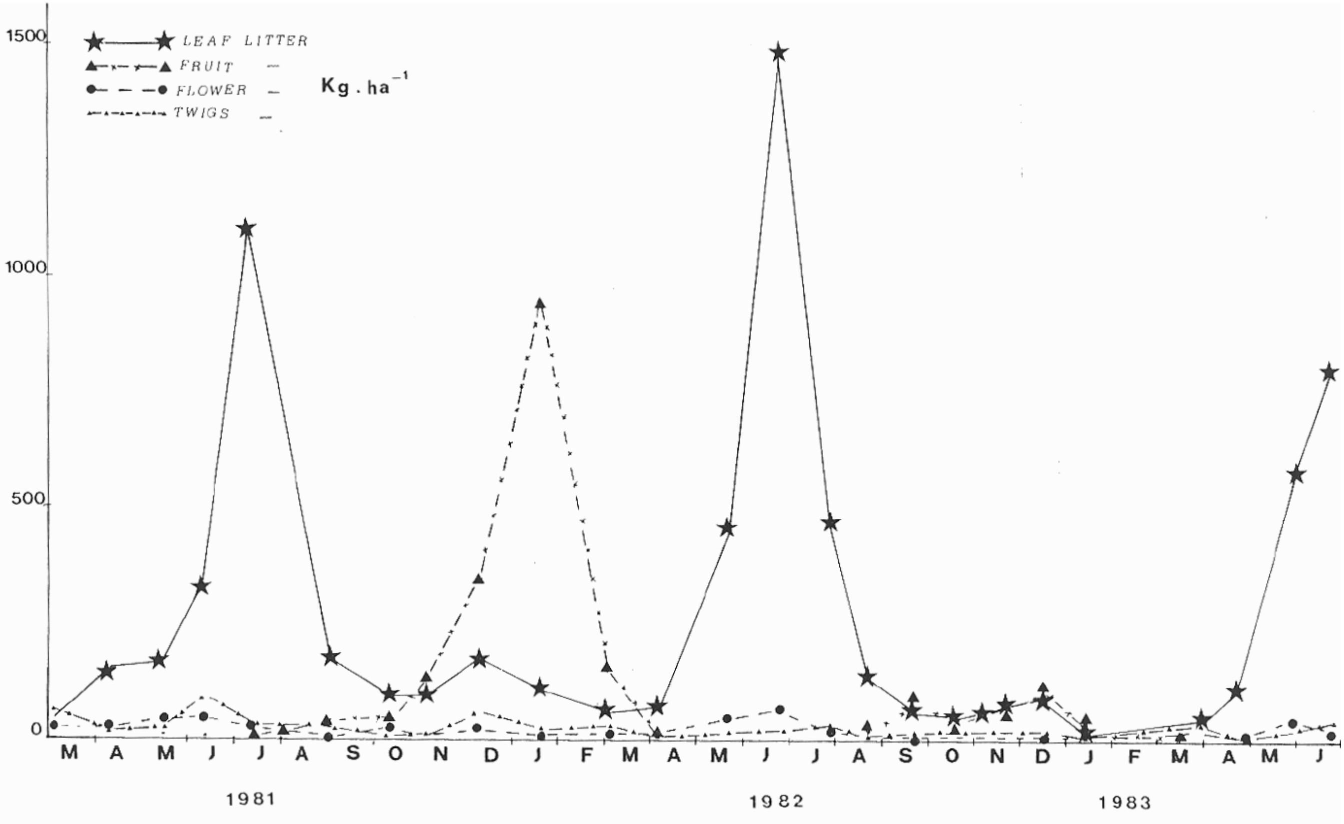

FIG. 2. — Litter fall at Stavros experimental site.

During the second year of study (April 1982-April 1983) leaf litter fall of *Quercus coccifera* took place—as was expected—between April 4th-August 23rd 1982 included (82% of the total annual leaf litter fall). The situation was quite similar for *Arbutus unedo* leaf litter fall where, in the period between May 20th-August 23rd 1982, 95% of the annual leaf litter fall occured, followed by a 5% for the intermediate months till the next summer, where leaf litter fall showed its maximum again.

TABLE II. — *Component of litter of the two dominant species* Arbutus unedo (*A.u.*) *and* Quercus coccifera (*Q.c.*) *at Stavros experimental site.*

Collection time	Leaf litter		Flower litter ($g.m^{-2}+SE$)		Fruit litter	
	A.u	*Q.c.*	*A.u.*	*Q.c.*	*A.u.*	*Q.c.*
1981						
March 3	0.62± 0.35	2.77± 0.98	2.83±0.88	–	–	–
April 4	1.77± 0.78	12.43± 5.37	2.83±0.82	–	–	–
May 11	15.87± 5.92	61.47±16.83	4.19±1.74	5.62±1.28	–	–
June 6	32.21±10.52	20.18± 5.99	2.97±1.60	0.90±0.77	–	–
July 9	80.46±21.56	29.71± 9.86	0.13±0.13	0.74±0.74	1.37± 1.00	–
September 4	5.25± 1.24	10.88± 2.70	–	–	–	3.78± 1.71
October 13	2.45± 0.67	6.00± 1.12	–	–	0.30± 0.20	3.92± 2.97
November 11	6.64± 2.45	2.63± 0.76	–	–	0.51± 0.46	12.10± 8.58
December 9	6.89± 1.79	4.89± 1.82	2.12±1.13	–	14.98± 6.62	19.07±12.78
1982						
January 19	1.19± 0.71	4.42± 1.80	–	–	79.80±27.34	14.03±0.61
March 3	1.35± 0.61	3.84± 1.42	1.09±0.52	–	3.58± 3.58	11.19± 8.26
April 4	1.88± 0.97	4.26± 1.30	0.55±0.27	–	0.20± 0.15	–
May 20	9.53± 3.36	34.15±15.04	0.64±0.25	3.39±1.12	–	–
June 23	116.05±42.89	27.51±10.69	0.50±0.37	5.76±1.57	–	–
July 28	29.15± 8.95	15.11± 4.60	0.05±0.02	0.64±0.25	–	1.72± 0.87
August 23	2.49± 0.74	10.37± 3.23	–	–	–	1.67± 1.12
September 23	0.43± 0.25	5.37± 1.61	–	–	–	7.14± 5.12
October 10	0.88± 0.50	3.84± 1.12	–	–	0.34± 0.25	4.01± 3.35
December 20	0.47± 0.25	3.14± 1.12	0.11±0.07	–	8.65± 4.10	–
1983						
January 14	–	0.32± 0.12	0.42±0.25	–	0.35± 0.25	1.08± 0.99
March 30	1.18± 0.50	2.72± 0.99	1.09±0.74	–	0.27± 0.27	0.17± 0.11
April 20	0.65± 0.37	9.77± 3.98	0.04±0.04	–	–	0.36± 0.35
May 27	14.54± 5.84	41.99±18.40	0.64±0.50	3.59±1.61	–	1.25± 0.12
June 23	51.98±20.88	27.26± 9.45	0.05±0.05	1.14±0.62	–	0.34± 0.34

Concerning the fruit litter, for the first year of study, 91 and 97% of the total annual occurred in late autumn-early winter months for both species (November, December 1981 and January 1982 for *Quercus coccifera* and December 1981 and January 1982 for *Arbutus unedo*). During the second year of study the pattern was the same, that is 63 and 90% of the total annual fruit litter fall occurred in autumn and winter months for the *Quercus coccifera* and December 1982 for *Arbutus unedo*).

Similar data are reported by other scientists working on mediterranean-type ecosystems. Some of these data are compiled in table III.

RAPP and LOSSAINT (1981) reported that 60% of the total litter fall was leafy material while flowers and fruits were 30% and the wood material was only 10%. They observed maximal of litter fall in late spring. The same pattern is reported by the other workers as well. POLI *et al.* (1974) estimated that 30% of the total litterfall occurred in May-June and July and was mainly due to leaf litterfall. Litter in eucalupt forests falls throughout the year, but it is strongly seasonal with peak values in spring and early summer (MCCOLL, 1966; WEBB *et al.*, 1969; ASHTON, 1975; SPECHT & BROUWER, 1975; ROGERS & WESTMAN, 1977 among others).

Leaves are the predominate plant material in litterfall as most of the above scientists report. This is of major importance, since leaves contain 37% N, 46% P, 33% K, 40% Ca, 34% Mg of the above ground nutrient pools (ARIANOUTSOU & PARASKEVOPOULOS, 1989, submitted for publication). Although nutrient concentrations in leaves are relatively high (1) (9.5 mg $N.g^{-1}$ ldw, 0.20 mg $P.g^{-1}$ ldw, 6.5 mg $K.g^{-1}$ ldw, 7.89 mg $Ca.g^{-1}$ ldw, 1.33 mg $Mg.g^{-1}$ ldw) reabsorption before abscission partially reduces these concentrations in litterfall (ARIANOUTSOU, 1989, submitted for publication). In any case litterfall remains one of the major energy and nutrient inputs to the ecosystem unit through the soil system (ARIANOUTSOU, 1989, submitted for publication).

The seasonal pattern of litterfall is also important. It is known that one of the major environmental limitations to the mediterranean-type ecosystems is water availability; two distinct types of adaptations can be distinguished: (*a*) evergreeness which is usually combined with sclerophylly and (*b*) reduction of the total plant leaf tissue, depending on the intensity of the drought (ORSHAN, 1954). The actual productivity of the ecosystem is dependent only in part on the amount of carbon it fixes. Other important considerations are the efficiency by which carbon is fixed into dry matter and how much of the dry matter goes to produce new productive rather than supportive tissues. In this aspect conserving energy (fixed carbon) is very important. Evergreen sclerophyllous plants show their maximum activity in spring, coinciding with leaf emergence and expansion and shoot growth) (ARIANOUTSOU & MARDIRIS, 1987; PEREIRA *et al.*, 1987; KUMMEROW *et al.*, 1981), when the climatic conditions are favourable (fig. 1). Getting rid of their overmature structures at this time and before the onset of the dry season is therefore a very efficient means of saving energy.

Considering that approximately 3,800 $kg.ha^{-1}$ (table I) of leaf litter is produced annually, we can estimate that $1{,}824 \times 10^4$ kcal of energy (2) and 36.10 kg $N.ha^{-1}$, 0.76 kg $P.ha^{-1}$, 24.7 kg $K.ha^{-1}$, 30.0 kg $Ca.ha^{-1}$, 50.0 kg $Mg.ha^{-1}$, are offered to the soil subsystem (ARIANOUTSOU, 1989, submitted for publication) (3). An additional nutrient input to the soil is that of fruit shedding during winter. Most of the fruits that fall, however are eaten by birds or small mammals (mostly rodents) and sometimes even ants (pers. observ.). Therefore, part

(1) Mean value of nutrient concentration in *Quercus coccifera* and *Arbutus unedo* leaves.

(2) Conversion based on the equation 1 kg dry material = 4,800 kcal = 700 l CO_2, after MACFADYEN, 1971.

(3) The amount of nutrients in leaf litterfall per hectare was estimated by multiplying the mean concentration of each element in the leaves of *Quercus coccifera* and *Arbutus unedo*, main component of the leaf litterfall (see footnote 1) by the amount of litter produced annually.

TABLE III. — *Litter fall in several mediterranean-type ecosystems of the world.*

Ecosystem, locale and reference	Litter fall ($kg.ha^{-1}.year^{-1}$)
Maquis, Italy, Poli *et al.*, 1974	3,414
Phrygana, Greece, Margaris, 1976	2,100
Coastal scrub, Australia, Maggs & Pearson, 1977	4,900
Dry eucalypt forest, Australia, Lee & Correll, 1978	2,333
Garrigue, France, Rapp & Lossaint, 1981	2,278-2,608
Coastal sage, California, Gray & Schlesinger, 1981	1,940
Ceanothus chaparral, California, Schlesinger cf. Gray & Schlesinger, 1981	5,980
Maquis, Greece, Present study	5,389

of their nutrients are input to the soil subsystem after passage through the animals digestive system.

The mean annual litterfall for mediterranean-type ecosystems (table III) is lower than the range given by BRAY and GORHAM (1964) and RODIN and BAZILEVICH (1967) for temperate deciduous and coniferous forest, 4,000 to 7,000 $kg.ha^{-1}.year^{-1}$. In typical mature deciduous forests 8 to 10% of above-ground nutrient pools are returned to the soil by annual litterfall (RODIN & BAZILEVICH, 1967). In older forests and in coniferous forests, the percentages decrease to 3-5% (RODIN & BAZILEVICH, 1967). Although available data are limited, the relatively high return of nutrients to the soil by litterfall in several mediterranean-type ecosystems might characterize them as still young, developing systems.

REFERENCES

ARIANOUTSOU M. & MARDIRIS Th. A., 1987. — Observations on the phenology of two dominant plants of the Greek maquis. *In: Plant Response to Stress. Functional Analysis in Mediterranean Ecosystems*, TENHUNEN J. D., CATARINO F. M., LANGE O. L. & OECHEL W. C., (Eds). NATO ASI Series, Series G. Ecological Sciences, Vol. 15, Springer-Verlag, Berlin/Heidelberg/New York/London/Paris/Tokyo, 515-521.

ARIANOUTSOU M., 1989. — Leaf litter decomposition and nutrient release in a maquis (evergreen sclerophyllous) ecosystem of North-Eastern Greece. Submitted to *Pedobiologia*.

ARIANOUTSOU M. & PARASKEVOPOULOS S., 1989. — Some aspect of mineral cycling in a maquis (evergreen sclerophyllous) ecosystem of North-Eastern Greece. Submitted to *For. Ecol. and Manage.*

ASHTON D. H., 1975. — Studies of litter in *Eucalyptus regnans* forest. *Austr. J. Bot.*, **23**, 413-433.

BRAY J. R. & GORHAM E., 1964. — Litter production in forest of the world. *Adv. Ecol. Res.*, **2**, 101-157.

GRAY J. T. & SCHLESINGER W. H., 1981. — Nutrient Cycling in Mediterranean Type Ecosystems. *In: Resource use by chaparral and matorral. A comparison of vegetation function in two Mediterranean*

Type Ecosystems, MILLER P. C. (Ed.), Ecological Studies, Vol. 39. Springer-Verlag, New York/Heidelberg/Berlin, 259-286.

KUMMEROW J., MONTENEGRO G. & KRAUSE D., 1981. — Biomass, Phenology and Growth. *In: Resource use by chaparral and matorral. A comparison of vegetation function in two Mediterranean type ecosystems*, MILLER P. C. (Ed.), Ecological Studies, Vol. 39, Springer-Verlag, New York/Heidelberg/Berlin, 69-97.

LEE K. E. & CORRELL R. L., 1978. — Litter fall and its relationship to nutrient cycling in a South Australian dry sclerophyll forest. *Aust. J. Ecol.*, 3, 243-252.

MACFADYEN A., 1971. — The soil and its total metabolism. *In: Methods of study in quantitative soil ecology*, PHILIPSON J. (Ed.), IBP Handbook, No. 18, Blackwell, Oxford, 1-13.

MCCOLL J. C., 1966. — Accession and decomposition of litter in spotted gum forests. *Aust. For.*, 30, 191-198.

MAGGS J. & PEARSON C. J., 1977. — Litter fall and litter layer decay in coastal scrub at Sydney, Australia. *Oecologia* (Berlin), 31, 239-250.

MARGARIS N. S., 1976. — Structure and dynamics in a phryganic (East Mediterranen) ecosystem. *J. Biogeogr.*, 3, 249-259.

MARGARIS N. S., ARIANOUTSOU M. & PARASKEVOPOULOS S., 1983. — Harvesting before the fire for energy mediterranean-type ecosystems in Greece. Costs and benefits. *In: Energy from Biomass*, PALZ W. & PIRWITZ D. (Eds.), Series E, Vol. 5, D. Reidel Publishing Company, Dordrecht/Boston/Lancaster, 142-148.

MOONEY H. A. & DUNN P., 1970. — Convergent evolution of mediterranean-climate evergreen sclerophyllous shrubs. *Evolution*, 24, 292-303.

ORSHAN G., 1954. — Surface reduction and its significance as a hydroecological factor. *J. Ecol.*, 42, 442-444.

PEREIRA J. S., BEYSCHLAG G., LANGE O. L., BEYSCHLAG W. & TENHUNEN J. D., 1987. — Comparative phenology of four mediterranean shrub species growing in Portugal. *In: Plant Response to Stress. Functional Analysis in Mediterranean Ecosystems*, TENHUNEN J. D., CATARINO F. M., LANGE O. L. & OECHEL W. C. (Eds.), NATO ASI Series, Series G, Ecological Sciences, Vol. 15, Springer-Verlag, Berlin/Heidelberg/New York/London/Paris/Tokyo, 503-515.

POLI E., LEONARDI S. & BELLA R., 1974. — Produzione di lettiera nella lecceta del M. Minardo (Etna) nel periodo Settembre 1970-Giugno 1974. *Archivio Botanico e Biogeographico Italiano*, Vol. L, 4th Serie, Vol. XIX-Fasc. III-IV, 87-115.

RAPP M. & LOSSAINT P., 1981. — Some aspects of mineral cycling in the garrigue of Southern France. *In: Ecosystems of the World. Mediterranean-Type Shrublands* (Vol. 11), DI CASTRI F., GOODALL D. W. & SPECHT R. L. (Eds.). Elsevier Scientific Publishing Company, Amsterdam/Oxford/New York, 289-302.

RODIN L. E. & BAZILEVICH N. I., 1967. — *Production and Mineral Cycling in Terrestrial Vegetation* (transl. by G. E. Fogg, Oliver and Boyd, Edinburg).

ROGERS R. W. & WESTMAN W. E., 1977. — Seasonal nutrient dynamics of litter in a subtropical eucalypt forest, North Stradbroke Island. *Aust. J. Bot.*, 25, 47-58.

SPECHT R. L. & BROUWER Y. M., 1975. — Seasonal shoot growth of *Eucalyptus* spp. in the Brisbane area of Queensland (with notes on shoot growth and litter fall in other areas of Australia). *Aust. J. Bot.*, 23, 459-474.

WEBB L. J., TRACEY J. G., WILLIAMS W. T. & LANCE G. N., 1969. — The pattern of mineral return in leaf litter of three subtropical Australian forest. *Aust. For.*, 33, 99-110.