SOME ASPECTS OF MINERAL CYCLING IN A MAQUIS (EVERGREEN SCLEROPHYLLOUS) ECOSYSTEM OF NORTHEASTERN GREECE

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ABSTRACT

Primary production and nutrient pools in the soil and vegetation of a maquis ecosystem of northeastern Greece are examined. The aboveground biomass of 43.5 t·ha^{-1} is similar to that of other Mediterranean-type ecosystems. Among the nutrients examined, the ecosystem seems to be deficient in phosphorus, since only 0.87 kg·ha^{-1} of it are incorporated into the soil annually, while plant uptake reaches 2.79 kg·ha^{-1}, resulting in a phosphorus deficit of about 1.9 kg·ha^{-1}.

INTRODUCTION

The circulation of nutrients in terrestrial ecosystems, and especially in forested ones, has received increasing attention over the last decades, mostly because of questions regarding management problems. Emphasis has been given to the nutrient return, and to the geological cycle of inputs to, and outputs from, the ecosystems (Ovington, 1965; Guthrie et al., 1978; Attiwill, 1980; Rapp and Lossaint, 1981; Schlesinger et al., 1982; Read and Mitchell, 1983; Swank, 1984; Schlesinger, 1985).

A series of studies by Arianoutsou and Mardiris (1987) and Arianoutsou (1989a,b, 1993) evaluated various aspects of nutrient cycling in a mature maquis ecosystem of northeastern Greece. Maquis ecosystems are characterized by evergreen sclerophyllous shrubs and constitute approximately 25% of the terrestrial ecosystems of Greece. Until recently, maquis ecosystems were considered rather unproductive marginal lands and were mostly used as rangelands. Typical Mediterranean-type maquis ecosystems are often threatened by fire (Arianoutsou-Faraggitaki and Margaris, 1981, 1982) that, together with overgrazing, causes considerable erosion and nutrient loss (Arianoutsou-Faraggitaki, 1985). For evaluating the impact of these perturbations, knowledge of mineral cycling is very important. This paper assesses the nutrient pools in the maquis ecosystem and indicates nutrient budgeting strategies that evergreen sclerophyllous ecosystems have possibly evolved in response to a habitat of limited mineral resources.

MATERIALS AND METHODS

The study was conducted at Stavros experimental site (40° 39' N, 23° 43' E, ca. 20 m above sea level, 60 km NE of Thessaloniki, Greece), from 1981 to 1983. The soil, down to 1 m deep, is overlying biotitic-gneiss amphibolitic metamorphic rocks. Data on soil characteristics are given in Table 1.

The vegetation consists of evergreen sclerophyllous shrubs, 23 years old (authors' unpublished data), and the climate is typical Mediterranean (Fig. 1).

Net primary production was estimated in 6 plots of 30 m² each by harvesting the above--ground biomass at the end of the plant-growing period (May 1982) (Arianoutsou and Mardiris, 1987). The fresh weight of the harvested material was measured in the field.

Table 1
Soil characteristics

Soil depth	Organic matter	C	N	P	K	C/N
cm	< ---------------------------------- kg·m⁻³ ---------------------------------- >					
0–30	31.07	18.07	1.19	0.0004	0.242	15.13

Nitrogen value refers to total nitrogen, while values for P and K are for their available forms.
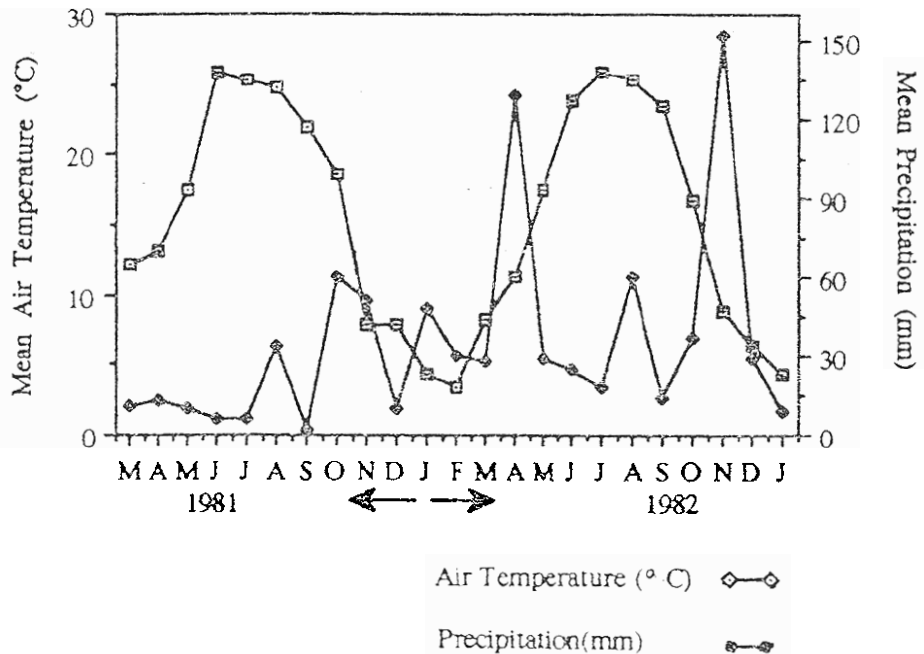

Fig. 1. Meteorological data for Stavros experimental site. Monthly precipitation, mean air temperature data are provided by the Meteorological Station at Vassilika, Thermi, for the period 1981–1982.

Representative samples were transported to the laboratory, oven-dried (80 °C for 48 h) and weighed, thus allowing the estimation of the total dry weight of the samples, sorted into green and non-green components.

The estimation of root biomass was based on mean value for root:shoot ratio of 0.57 for vegetative tissues, determined by others working on similar ecosystems (Kummerow et al., 1977; Miller and Ng, 1977; Mooney and Rundel, 1979).

Leaf and branch samples collected in May were oven-dried at 80 °C, weighed, and ground in a Wiley mill (40 mesh). For the analysis of Ca, Mg, and K, approximately 1 g of oven-dried ground plant material was weighed and ashed in a muffle furnace at 500 °C for 3 h. The ashed material was dissolved in 3–4 ml of a 1:1 solution of HCl:water in a water bath for 30 min until it was totally dissolved, then filtered through Whatman #41 filter paper, and brought to a final volume of 50 ml with distilled water. The minerals were determined in an atomic absorption spectrophotometer (Varian 775) (Allen et al., 1974).

Nitrogen in the plant material was determined in a Technicon Auto-Analyzer according to Varley (1966), after Kjeldahl digestion.

For the determination of phosphorus, plant samples were first heated in a muffle furnace for about 1 h at 250 °C and, after combustion smoke settled down, heated at 500 °C for an additional 4 h. The ash was then digested with 20% HNO_3 for 30 min, filtered through Whatman #1 filter paper, and brought to 100 ml volume. Phosphorus concentration was then determined in a Technicon Auto-Analyzer according to Varley (1966).

Values for soil nutrient storage are based on surface mineral soil (top 30 cm) and are calculated on the basis of a mean bulk density of 1.5. Soil nutrient data are mean values of 10 individually subsampled analyses randomly collected over the experimental site.

Soil nitrogen was estimated colorimetrically in 500-mg samples free of fine roots, after digestion with H_2SO_4 (Bremner, 1965) in a Technicon Auto-Analyzer (Varley, 1966). Soil phosphorus was estimated according to the method described by Olsen and Dean (1965).

Soil carbon was estimated in samples processed as for nitrogen. Determination of organic carbon was made by liquid oxidation with $K_2Cr_2O_7$ (Alexiadis, 1977).

Soil potassium was estimated in an atomic absorption spectrophotometer (Varian 775).

RESULTS

The flora at the study site is of typical Mediterranean composition, consisting mainly of the species shown in Table 2.

The photosynthetic biomass of the ecosystem is 14.0 t·ha⁻¹ and the non-green biomass is 29.5 t·ha⁻¹, while their ratio is 0.47. The annual average increment over a 23-year period in t·ha⁻¹ is 0.61, 1.28, and 1.89 for the green, non-green, and total aboveground biomass, respectively. These values were obtained by dividing the biomass by the age of the stand.

Nutrient pools in aboveground standing biomass are shown in Table 3. The annual increment of nutrients, estimated in the same way as for the annual increment of biomass, is 7.78, 2.17, 2.58, 0.64, and 2.4 kg·ha⁻¹ for N, P, Ca, Mg, and K, respectively.

The distribution and cycling of organic matter in the ecosystem is represented in Fig. 2. The above-ground standing biomass was estimated to be 43.5 t·ha⁻¹. From this

Table 2
Plant species dominating Stavros experimental site, northeastern Greece

Woody species	Herbaceous species
Arbutus unedo L.	*Trifolium* sp.
Quercus coccifera L.	*Linum* sp.
Phillyrea media L.	*Festuca* sp.
Erica arborea L.	*Medicago* sp.
Olea europea L.	*Campanula* sp.
ssp. *oleaster* (Hoffmans & Link)Negodi	*Petrorhagia prolifera* (L.)P.W. Ball & Heywood
Calicotome villosa (Poiret) Link	*Hymenocarpus circinatus* (L.) Savi
Cistus sp.	*Cynosurus echinatus* L.
	Muscari sp.
	Asphodelus aestivus Brot.

Table 3
Nutrients in aboveground standing biomass

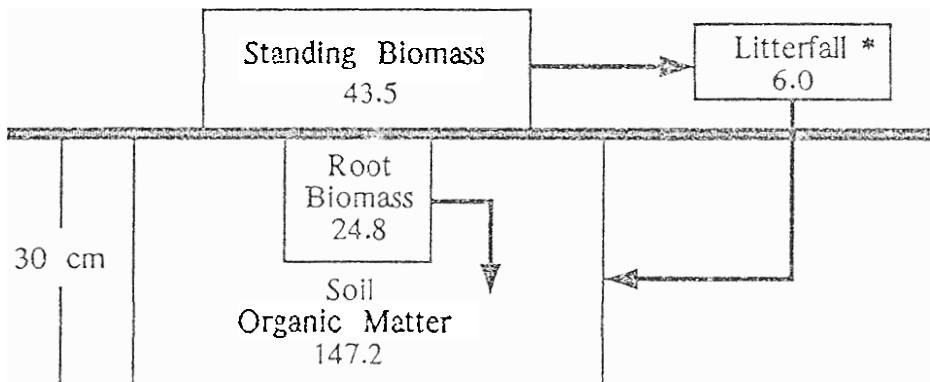| Ecosystem compartment	N	P	K	Ca	Mg	Biomass
	< ----------------------------- kg·ha^{-1} ---------------------------->					t·ha^{-1}
Leaves	66.5	22.6	19.1	19.6	5.8	14.0
Wood	112.5	27.3	36.1	39.7	8.9	29.5
Total	179.0	49.9	55.2	59.3	14.61	43.5
Leaves/Wood	0.59	0.83	0.53	0.49	0.65	0.47

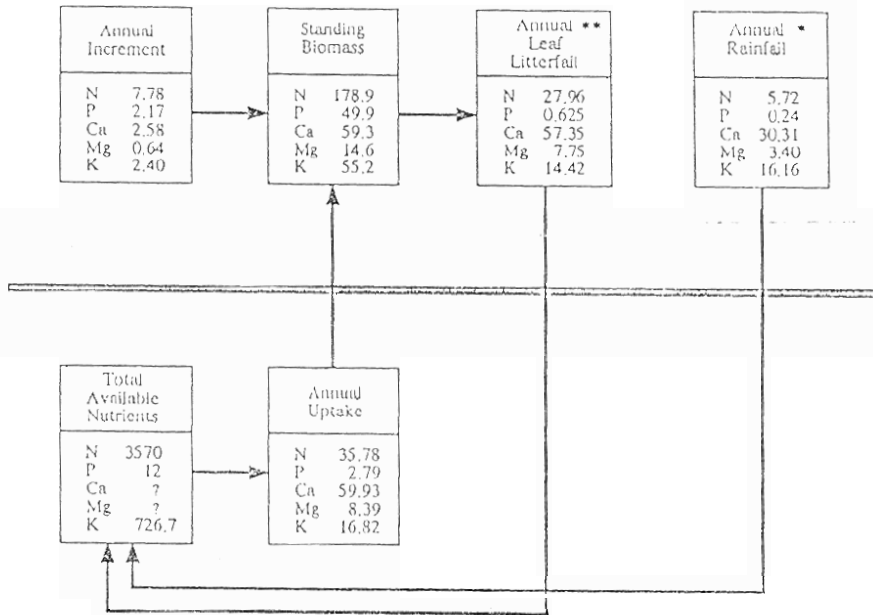Fig. 2. Distribution and cycling of organic matter of Stavros ecosystem (in kg·ha^{-1})
*Arianoutsou, 1989b.

Fig. 3. Nutrient pools and nutrient cycling of Stavros ecosystem (in kg·ha^{-1}).
* Arianoutsou, 1989a. **Arianoutsou, 1993.

standing biomass, 5.98 t·ha^{-1} is shed yearly as litterfall (Arianoutsou, 1989b). The organic matter stored in the top 30 cm of the soil is estimated to be 147 t·ha^{-1}. This soil organic matter is thought to be an intermediate result of litter decomposition plus the products of root decay.

The sizes of nutrient pools and their cycling are presented in Fig. 3. The rate of calcium cycling seems to be faster than that of the other nutrients. Approximately 88 kg·ha^{-1} of calcium reaches the soil annually, originating from rainfall and litterfall (Arianoutsou, 1989a, 1993). Calcium uptake by plants, estimated by adding the annual increment of nutrients in standing biomass plus the litter nutrient content, measures 59.93 kg·ha^{-1}. It appears that 27.73 kg·ha^{-1} is stored in the soil sink.

Nitrogen cycling is also relatively fast. Approximately 34 kg·ha^{-1} of nitrogen reaches the soil annually, originating from rainfall and litterfall (Arianoutsou, 1989a, 1993). Nitrogen uptake by plants was estimated to be 35.78 kg·ha^{-1}. It seems that there is a lack of 2.08 kg·ha^{-1} nitrogen, but additional nitrogen enters the system through nitrogen atmospheric fixation. This nitrogen fixation performed by the symbiotic nitrogen-fixing

plants of the ecosystem, mainly *Trifolium* sp., *Vicia* sp., and *Medicago* sp. among the herbaceous legumes and *Calicotome villosa* of the woody ones, can reach 32 kg·ha^{-1} when the ecosystem is still very young (1 year old), and 7 kg·ha^{-1} in its later stages (Margaris et al., 1983).

It seems that there is an excess of potassium in the soil since 31 kg·ha^{-1} of the element reaches the soil annually, while its uptake by plants accounts for not more than 16.8 kg·ha^{-1}. The same is true for magnesium, 11.45 kg·ha^{-1} of which returns to the soil on an annual basis, while only 8.39 kg·ha^{-1} is used by plants.

The ecosystem appears to be deficient in phosphorus since only 0.87 kg·ha^{-1} of it is incorporated into the soil annually, while plant uptake reaches 2.79 kg·ha^{-1}, thus resulting in a phosphorus deficit of about 1.9 kg·ha^{-1}.

DISCUSSION

The distribution of biomass among different plant compartments for the maquis ecosystem is similar to that reported for other Mediterranean-type ecosystems. Mooney and Rundel (1979), working on *Adenostoma* chaparral, give an aboveground biomass of 21 t·ha^{-1}, with photosynthetic tissues comprising 17.3% of this total. Mooney et al. (1977) report a mean of 28 t·ha^{-1} for a Chilean matorral. Rapp and Lossaint (1981) give 23 t·ha^{-1} for a 17-year-old *Quercus coccifera* garrigue in southern France. Standing crop values for *Calluna* heaths in England are also comparable, ranging from 11 to 29 t·ha^{-1} (Robertson and Davies, 1965; Chapman, 1967). These biomass levels are considerably lower than values for woodland and most savannah ecosystems, but comparable to those of semi-desert scrub formation and temperate grasslands (Rodin and Bazilevich, 1967; Whittaker, 1975).

The annual increment of 1.9 t·ha^{-1} is comparable to the 1.1 t·ha^{-1} given by Rapp and Lossaint (1981) for the *Quercus coccifera* garrigue in southern France. Specht (1969) reports increments in aboveground plant biomass for analogous ecosystems of Californian chaparral and Australian mallee varying from 0.88 to 1.5 t·ha^{-1} annually for the first 10 years. Mooney (1981), using data from Kittredge (1955), gives values ranging from 1.1 to 2.02 t·ha^{-1} annually for Californian chaparral.

Data on nutrient pool sizes and fluxes within the ecosystem are comparable to those reported by Specht (1969) and Mooney (1981) for *Adenostoma* chaparral, and by Rapp and Lossaint (1981) for the *Quercus coccifera* garrigue in southern France.

Concerning the phosphorus deficiency of the ecosystem, various forms of evidence suggest a limited availability of this element in evergreen sclerophyllous ecosystems (Margaris et al., 1984; Schlesinger, 1985; Arianoutsou, unpublished data). Schlesinger and Gill (1980) found foliar P to decline in an age sequence of *Ceanothus chaparral* stands. Gray (1983) found that among foliar nutrients, P was reabsorbed most strongly before leaf abscission. Arianoutsou (1993) also found that 16–19% of P was redrawn from the leaves of the dominant woody maquis species before their abscission, possibly as a conservation mechanism.

As far as the nutrient budget at the ecosystem level is concerned, there are several important points which must be stressed. Quantitative schemes like the one in Fig. 3 are fundamental and very useful for comparisons between ecosystems. However, their value may be relative, mainly for the following reasons, observed by other workers as well.

a. A considerable amount of nutrients is reabsorbed from the leaves before their shedding as litter. 23–25% of nitrogen, 16–19% of phosphorus, and 33–49% of potassium are redrawn from the leaves of the dominant woody maquis species before their abscission (Gray, 1983; Schlesinger, 1985; Arianoutsou, 1993). This holding back of nutrients by the standing biomass means that plants do not satisfy their nutrient needs exclusively through nutrient input with rainfall, of litter decomposition and uptake from soil, but also through an internal transfer within the plant body. This mechanism possibly enables the plants to save energy. Evergreenness is strongly correlated with nutrient saving in nutrient "deficit" habitats. The adaptive value of this character has been discussed by Monk (1966), Small (1972), and Schlesinger and Chabot (1977). In addition to the fact that evergreenness provides a potentially greater photosynthetic return-per-nutrient invested in leaf construction, it might also act as a sink for nutrient storage during nutrient uptake but non-growth periods. Therefore, studies of nutrient uptake by plants or even plant communities in nature which only consider nutrient contents in a single plant compartment at a single time, are giving static results which may be misleading and far from the actual, dynamic situation. Mooney and Rundel (1979) have also pointed out this aspect. In addition, static determinations do not take into account that plant communities do not use the same amount of nutrients at all stages of age-successional gradients. The amount of nutrients they use as they age diminishes continuously. Therefore, dividing the total amount of nutrients in the standing biomass by the stand may give data of limited value, although useful for comparisons between ecosystems.

b. The time needed for the litter to decompose and mineralize, or even its half-life time, has not been taken into consideration. In these studies, minerals of the freshly fallen litter are usually considered to be available to the plants. This is not necessarily so. Not only is half-life time decomposition of most of the evergreen sclerophyllous species longer than one year (Maggs and Pearson, 1977; Schlesinger and Hasey, 1981; Schlesinger, 1985; Radea, 1989; Arianoutsou, 1993, among others), but nutrient release through decomposition is also very slow (Gosz et al., 1973; Lossaint, 1973; Lousier and Parkinson, 1978; Schlesinger, 1985; Arianoutsou, 1993). At the experimental site studied, an annual leaf litterfall of 158 g·m^{-2} of *A. unedo* and 131 g·m^{-2} of *Q. coccifera*, the dominant woody shrubs of the ecosystem (Arianoutsou, 1989a) would stabilize N and P at a rate of 1536 and 27 mg·m^{-2} for the former and 1480 and 34 mg·m^{-2} for the latter, during the first year of their decomposition (Arianoutsou, 1993).

So, it could be stated that the maquis ecosystem is nitrogen- and, especially, phosphorus-deficient, if the mineral cycling is studied on an annual basis, without considering either (1) retention by plants before litter formation and shedding, or (2) the time necessary for the nutrients to be released through mineralization. Phosphorus deficiency, though, is a fact and must be studied further.

ACKNOWLEDGMENTS

REFERENCES

Alexiadis, A.K. 1977. Physical and chemical soil analysis. Thessaloniki, Greece, 383 pp. (Greek).

Allen, S.E., Grimshaw, H.M., Parkinson, J.A., and Quarmby, C. 1974. Chemical analysis of ecological materials. Blackwell, Oxford.

Arianoutsou, M. 1989a. Atmospheric deposition of nutrients in a coastal maquis ecosystem of North-Eastern Greece. Int. J. Biometeor. 33: 124–130.

Arianoutsou, M. 1989b. Timing of litter production in a maquis ecosystem of North-Eastern Greece. Acta Oecologia (Oecol. Plant.) 10: 371–378.

Arianoutsou, M. 1993. Leaf litter decomposition and nutrient release in a maquis (evergreen sclerophyllous) ecosystem of North-Eastern Greece. Pedobiologia 37: 65–71.

Arianoutsou-Faraggitaki, M. 1985. Desertification in Greece: the case of Lesvos Island. J. Arid. Environ. 9: 237–242.

Arianoutsou-Faraggitaki, M. and Margaris, N.S. 1981. Fire-induced nutrient losses in a phryganic ecosystem. Int. J. Biometeor. 25(4): 341–347.

Arianoutsou-Faraggitaki, M. and Margaris, N.S.1982. Phryganic (East Mediterranean) ecosystems and fire. Ecol. Medit. 8: 473–480.

Arianoutsou-Faraggitaki, M. and Mardiris, Th.A. 1987. Observations on the phenology of two dominant plants of the Greek maquis. In: Tenhunen, J.D., Catarino, F.M., Lange, O.L., and Oechel, W.C., eds. Plant response to stress. Functional analysis in Mediterranean ecosystems. NATO ASI Series, Series G: Ecological Sciences.Vol. 15. Springer-Verlag, Berlin, pp. 515–521.

Attiwill, P.M. 1980. Nutrient cycling in a *Eucalyptus obliqua* (L'Herit.) Forest. IV. Nutrient uptake and nutrient return. Aust. J. Bot. 28: 199–222.

Bremner, J.M. 1965. Total nitrogen. In: Black, C.A., Evans, D.P., Ewshinger, L.E., White, J.L., and Clark, F.E., eds. Methods of soil analysis Part 2. Am. Soc. Agr. Inc., Madison, Wisconsin, pp. 1149–1176

Chapman, S.B. 1967. Nutrient budgets for a dry heath ecosystem in the south of England. J. Ecol. 55: 677–689.

Gosz, J.R., Likens, C.E., and Bormann, F.H. 1973. Nutrient release from decomposing leaf and branch litter in the Hubbard Brook forest, New Hampshire. Ecol. Monogr. 43: 173–191.

Gray, J.T. 1983. Nutrient use by evergreen and deciduous shrubs in southern California. I. Community nutrient cycling and nutrient-use efficiency. J. Ecol. 71: 21–41.

Guthrie, H.B., Attiwill, P.M., and Leuning, R. 1978. Nutrient cycling in a *Eucalyptus obliqua* (L'Herit.) Forest. Aust. J. Bot. 26: 189–201.

Kittredge, J. 1955. Litter and forest floor of the chaparral in parts of the San Dimas Experimental Forest, California. Hilgardia 23: 563–596.

Kummerow, J., Krause, D., and Jow, W. 1977. Root systems of chapparal shrubs. Oecologia 29: 163–177.

Lossaint, P. 1973. Soil vegetation relationships in Mediterranean ecosystems of Southern France. In: di Castri, F. and Mooney, H.A., eds. Mediterranean-type ecosystems. Springer, New York,

pp. 199–210.

Louvier, J.D. and Parkinson, D. 1978. Chemical element dynamics in decomposing leaf litter. Can. J. Bot. 56: 2795–2812.

Maggs, J. and Pearson, C.J. 1977. Litter fall and litter decay in coastal scrub at Sydney, Australia Oecologia 31: 239–250.

Margaris, N.S., Arianoutsou, M., and Paraskevopoulos, S. 1983. Harvesting before fire for energy Mediterranean-type ecosystems in Greece; costs and benefits. In: Palz, W. and Pirwitz, D., eds. Energy from Biomass. Series E. Vol. 5. Reidel, Dordrecht. pp. 142–147.

Margaris, N.S., Adamantiadou, S., Siafaca, L., and Diamantopoulos, J. 1984. Nitrogen and phosphorus content in plant species of Mediterranean ecosystems in Greece. Vegetatio 55: 29–35.

Miller, P.C. and Ng, E. 1977. Root:shoot biomass ratios in shrubs in southern California and central Chile. Madrono 24: 215–223.

Monk, C.D. 1966. An ecological significance of evergreeness. Ecology 47: 504–505.

Mooney, H.A., Kummerow, J., Johnson, A.W., Parsons, D.J., Keeley, S., Hoffmann, A., Hays, R.I., Giliberto, J., and Chu, C. 1977. The producers, their resources and adaptive responses. In: Mooney, H.A., ed. Convergent evolution in Chile and California. Mediterranean climate ecosystems. Dowden, Hutchinson and Ross, Stroudsbourg, Pennsylvania.

Mooney, H.A. and Rundel, P.W. 1979. Nutrient relations of the evergreen shrub *Adenostoma fasciculatum* in the California chaparral. Bot. Gaz. 140: 109–113.

Mooney, H.A. 1981. Primary production in mediterranean climate. In: Di Castri, F., Goodall, D.W., and Specht, R.L., eds. Ecosystems of the world. Vol. II. Mediterranean-type shrublands. Elsevier, Amsterdam, pp. 249–257.

Olsen, S.E. and Dean, L.A. 1965. Phosphorus. In: Black, C.A., Evans, D.D., Ewshinger, L.E., White, J.L., and Clark, F.E., eds. Methods of soil analysis. Part 2. Am. Soc. Agr. Inc., Madison, Wisconsin, pp. 1035–1049.

Ovinngton, J.D. 1965. Organic production, turnover and mineral cycling in woodlands. Biol. Rev. 40: 295–336.

Radea, K. 1989. Study on the litter production, the decomposition rate of the organic horizon and the arthropod community in ecosystems with *Pinus halepensis* Mill. of the insular Greece. Ph.D. thesis, University of Athens (Greek, English summary and figure captions).

Rapp, M. and Lossaint, P. 1981. Some aspects of mineral cycling in the garrigue of Southern France. In: Di Castri, F., Goodall, D.W., and Specht, R.L., eds. Ecosystems of the World. Vol. II, Mediterranean-type shrublands. Elsevier, Amsterdam, pp. 289–302.

Read, D.J. and Mitchell, D.T. 1983. Decomposition and mineralization processes in Mediterranean-type ecosystems and in heathlands of similar structure. In: Kruger, F.J., Mitchell, D.T., and Jarvis, J.V.M., eds. Mediterranean-type ecosystems. The role of nutrients. Springer-Verlag, Berlin, pp. 208–232.

Robertson, R.A. and Davies, C.E. 1965. Quantities of plant nutrients in heather ecosystems. J. Appl. Ecol. 2: 211–220.

Rodin, L.E. and Bazilevich, M.I. 1967. Production and mineral cycling in terrestrial vegetation. Oliver and Boyd, Edinburgh.

Schlesinger, W.H 1985. Decomposition of chaparral shrub foliage. Ecology 66: 1353–1359.

Schlesinger, W.H. and Chabot, B.F. 1977. The use of water and minerals by evergreen and deciduous shrubs in Okefenokee Swamp. Bot. Gaz. 138: 490–497.

Schlesinger, W.H. and Gill, D.S. 1980. Biomass, production and changes in the availability of light, water and nutrient during development of pure stands of the chaparral shrubs *Ceanothus megacarpus*, after fire. Ecology 61: 781–789.

Schlesinger, W.H. and Hasey, M.M. 1981. Decomposition of chaparral shrub foliage: losses of organic and inorganic constituents from deciduous and evergreen leaves. Ecology 62 (3): 762–764.

Schlesinger, W.H., Gray, J.J., and Gilliam, F.S. 1982. Atmospheric deposition processes and their importance as sources of nutrients in a chaparral ecosystem of southern California. Water Resour. Res. 18 (3): 623–629.

Small, E. 1972. Photosynthetic rates in relation to nitrogen recycling as an adaptation to nutrient deficiency in a peat bog plants. Can. J. Bot. 50: 2227–2233.

Specht, R.L. 1969. A comparison of the sclerophyllous vegetation characteristic of mediterranean-type climates in France, California and southern Australia. II. Dry matter, energy and nutrient accumulation. Aust. J. Bot. 17: 293–308.

Swank, W.T. 1984. Atmospheric contributions to forest nutrient cycling. Water Resources Bulletin 20: 313–322.

Varley, J.A. 1966. Automatic method for the determination of nitrogen, phosphorus and potassium in plant material. Analyst 91: 119–126.

Whittaker, R.J. 1975. Communities and ecosystems. 2nd ed. Macmillan, New York.