LITTER PRODUCTION AND DECOMPOSITION IN *PINUS HALEPENSIS* FORESTS

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Litter Production

Litter production is a process related to energy and nutrient input to the soil in all types of terrestrial ecosystems (Bray and Gorham 1964, Rodin and Bazilevich 1967). The amount of litter production depends mainly on climate, soil fertility, altitude, slope, aspect, stand age, vegetation type and time (Bray and Gorham 1964, Mangenot and Toutain 1980). Litterfall varies throughout the year, and its various fractions follow different patterns of shedding. The periodicity of litter production is determined by various external factors as well as by the physiological status of plant species (Rapp and Lossaint 1981).

In ecosystems where available nutrients in the soil are limited, as in the Mediterranean ecosystems, both litterfall and decomposition become crucial for nutrient recycling (Gray and Schlesinger 1981, Arianoutsou 1989).

Quantity, Composition and Phenology of Litterfall in Pinus halepensis Forests

The total annual mass of litter produced by *Pinus halepensis* (Aleppo pine) ranges from 150 to 530 g m^{-2}. These values are within the range recorded for other Mediterranean pine species, i.e., *Pinus brutia* and *P. pinea,* as well as for other coniferous species growing in colder climates (Table 1).

The understorey layer of an Aleppo pine forest normally consists of shrubs typical also to maquis stands. The amount of litter produced by these shrubs is of the same magnitude in both cases (Tables 2 and 3).

The amount of litter produced depends on the age of the stand, the morphology of the plants, the temperature regime prevailing and other abiotic factors (Bray and Gorham 1964). In the Mediterranean type ecosystems, leafy litter is a major constituent of the overall amount of litter produced on an annual basis. Rapp and Lossaint (1981) reported that 60% of the total litter fall produced by a garrigue in Southern France was leafy material. Poli *et al.* (1974) reported that 30% of the overall litterfall in a maquis stand in Aetna was between May and July, and it mainly consisted of leaves. Arianoutsou (1989) also reported that approximately 70% of the annually produced litter by a maquis stand in Northern Greece consisted of leaves. Leaf litter produced by Aleppo pine, as well as by other Mediterranean

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Table 1. Litter production ($g \cdot m^{-2} \cdot yr^{-1}$) and litter components (%) from pines and other coniferous species (range of values corresponds to series of years or stands).

Coniferous species	Locality	Litter production	Litter components			Authors
			Leaves	Wood	Reproductive units	
Juniperus phoenicea	Greece	199	80	8.5	11.5	Tsiourlis 1989
Pinus brutia	Lebanon	340	63-66	34-37		Dannaoui 1981
Pinus halepensis	France	410	69.6	21	9.3	Rapp 1967
Pinus halepensis	Spain	250-340	Not available			Garcia-Plc *et al.* 1995
Pinus halepensis	Greece	150	78.9	6.9	14.0	Radea 1989
Pinus halepensis	Greece	530	71.7	11.5	16.8	Marmari 1991
Pinus pinaster	Spain	170	96	3.0	1.0	Hernandez *et al.* 1992
Pinus pinea	France	790	77.4	11.2	11.4	Rapp 1984
Pinus pinea	Spain	240	89	10.4	0.6	Hernandez *et al.* 1992
Pinus pinea	Lebanon	400	74-85	15-26		Dannaoui 1981
Pinus ponderosa	USA	210	Not available			Jenny *et al.* 1949
Pinus sylvestris	England	480				Kendrick 1958
Pinus sylvestris	Spain	180				Pausas 1997

coniferous species, constitutes the main component of litter production. Its contribution ranges from 63 to 97% (Rapp 1967, 1984, Radea 1989, Marmari 1991). The percentage of wood and cones is comparatively low (Table 1). Tsiourlis (1989), working on a maritime juniper stand, found that leaf litter contributed up to 80% of the total litter produced. Leaves contain relatively high amounts of nutrients, therefore, their accumulation in the litter layer as well as their decomposition are important processes affecting stand productivity.

The seasonal pattern of litterfall is an important component for the stand productivity, too. Litter falls normally in small quantities throughout the year, but it is strongly seasonal with peak values in spring and early summer. This is a typical phenological event of sclerophyllous evergreen shrubs of Mediterranean ecosystems (Rapp 1969, Specht 1973, Schlesinger and Hasey 1981, Tsiourlis 1989, Arianoutsou 1989).

It is known that probably the most important factor limiting productivity in the Mediterranean ecosystems is water availability. In coping with this, evergreen sclerophyllous plants get rid of some of their structures as a means of conserving energy (Arianoutsou, 1989). This is the reason why the majority of leaf fall and litter pro-

Table 2. Litter production ($g \cdot m^{-2} \cdot yr^{-1}$) and litter components (%) from understorey shrub species in two Aleppo pine forests of Greece.

Shrub species	Locality	Litter production	Litter components			Authors
			Leaves	Wood	Fruits	
Arbutus unedo	Greece	83.5	95.3	4.7	0	Radea 1989
Pistacia lentiscus	Greece	76.7	78.6	21.4	0	Radea 1989
Pistacia lentiscus	Greece	35.4	95.8	4.2	0	Marmari 1991

Table 3. Litter production ($g \cdot m^{-2} \cdot yr^{-1}$) in Mediterranean shrublands (range of values corresponds to series of years or stands).

Ecosystem type	Locality	Litter production	Authors
Chaparral			
Adenostoma fasciculatum	USA	83-213	Mooney and Rundell 1979
Garrigue			
Quercus coccifera	France	230	Rapp 1969
Maquis			
Juniperus phoenicea	Greece	199	Tsiourlis 1989
Quercus coccifera	Greece	726	Tsiourlis 1989
Quercus coccifera	Greece	300-324	Arianoutsou 1989
Pistacia lentiscus	Greece	170	Tsiourlis 1989
Olea europaea	Greece	127	Tsiourlis 1989
Arbutus unedo	Greece	179-274	Arianoutsou 1989
Fynbos			
Leucospermum parile, Thamnochortus punctatus	South Africa	72-84	Mitchell *et al.* 1986

duction occurs during late spring and early summer (Fig.1), periods characterised by long days, high air temperatures and limited water availability (Rapp 1967, Arianoutsou 1989). Aleppo pine shows a distinct seasonal pattern of litter production, which is defined mainly by the timing of needles' shedding. These patterns express the phenology of the species, and they are controlled by the seasonality of the Mediterranean climate, especially the onset and the duration of the summer drought.

Litter Decomposition

The decomposition rates of organic matter under various plant species in some Mediterranean-type ecosystems are shown in Table 4.

The rate of decomposition of litter is controlled by various factors. The decomposability of substrate depends greatly upon its physical structure and chemical composition. A strong negative correlation exists between the decomposition rate and the thickness, toughness (Anderson 1973a, King and Heath 1967), lignin content (Fogel and Cromack 1977, Meentemeyer 1978, Melillo *et al.* 1982, Horner *et al.* 1988, Taylor *et al.* 1989, Berg *et al.* 1993, among others), tannin content (Basarada and Starkey 1966, Benoit and Starkey 1968a,b) and the total polyphenolic content of the litter (King and Heath 1967, Anderson 1973b).

A close relationship exists between the composition and population density of saprophagous arthropods and the decomposition processes (Ghilarov 1971). Petersen and Luxton (1982), Hassall *et al.* (1987), Anderson (1988), and Shaefer and Shaumerman (1990) consider the abundance and the activity of the macrofauna saprophagous groups as "key factors" in the decomposition process.

Climate has a direct effect on litter decomposition due to the effects of temperature and moisture and indirect effects through the climatic impact on the chemical properties of litter (Aerts 1997) as well as the regulation of decomposers' activity (Virzo de Santo *et al.* 1993).

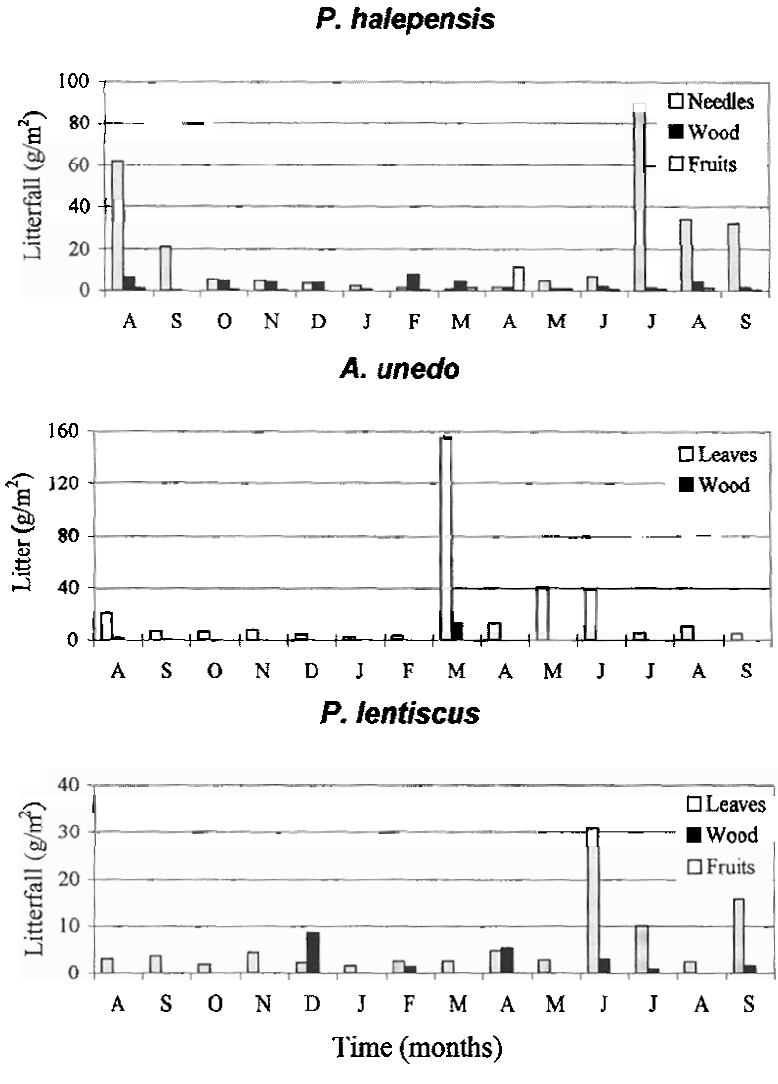

Fig. 1. Monthly litter production by *Pinus halepensis, Arbutus unedo* and *Pistacia lentiscus* in *Pinus halepensis* of Scopelos island, Central Greece.

Decomposition in Mediterranean ecosystems is expected to be a slow process because of the water deficit prevailing during summer and the physical structure as well as the chemical composition of litter. Shaefer (1973) and Virzo De Santo *et al.* (1991) have stated that in the dry Mediterranean climate, where the water availability is limited, the rate of litter mass loss is closely and positively correlated with the water content of litter. The structure and chemical composition of the leaves of Mediterranean plants seem to be important factors in decomposition. Gallardo and Merino (1993) and Gillon *et al.* (1994) have found that toughness of leaf and non-leaf material of Mediterranean plants could be used as a reliable index of substrate

Table 4. Annual decomposition constant (k' = L/L+A, where L= total annual litter input and A= total accumulated organic matter, Jenny *et al.* 1949) of the organic matter accumulated under coniferous trees and understorey shrubs in the Mediterranean basin and USA.

Plant species	Locality	k'	Authors
Overstorey pines			
Pinus sp.	USA	0.01-0.03	Jenny *et al.* 1949
Pinus pinea	France	0.19	Rapp 1984
Pinus sylvestris	Spain	0.13	Santa Regina and Gallardo 1995
Pinus halepensis	Greece	0.11	Radea 1989
Understorey shrubs			
Pistacia lentiscus	Greece	0.04	Radea 1989
Arbutus unedo	Greece	0.12	Radea 1989
Maquis			
Juniperus phoenicea	Greece	0.09	Tsiourlis 1989
Chaparral			
Adenostoma fasciculatum	USA	0.20	Mooney and Rundell 1979

quality and of its decomposability. Additionally, Gray and Schlesinger (1981) and Arianoutsou (1993) have noted the impact of chemical composition of the litter on its decomposition rate in Mediterranean ecosystems. Berg and Staaf (1980) have proposed a schematic model in which they suggested that early decay stages are regulated primarily by the concentrations of nitrogen and phosphorus, whereas lignin concentration controls mainly later stages.

A significant positive relationship between the initial concentration of N or P in the leaves and their loss in weight has also been reported for the evergreen sclerophyllous Mediterranean plants (Woods and Raison 1983, Arianoutsou 1993 among others).

The quantitative and qualitative composition of soil animal and microbial communities, as well as the duration and the intensity of their decomposing activities, depend greatly on climatic conditions. Although soil animals show high mortality and inactivity during the summer in Mediterranean ecosystems, their diversity and activity lead to high decomposition rates during the wet period of the year (Couteaux *et al.*, 1995). As saprophagous arthropods tend to have the greatest effect on decomposition and nutrient cycling in forest ecosystems with well-developed organic layers and strong fungal influence (Moore and Walter, 1988), their contribution in decomposition of accumulated organic matter in the Aleppo pine forest seems to be of great importance.

Conclusions

Considering that approximately 0.17 $kg \cdot m^{-2}$ of litter is produced annually by Aleppo pines, we can estimate that an amount of 816 Kcal (1 Kg litter equals 4,800 Kcal, MacFadyen 1971) is offered to the soil subsystem, and with the additional energy from the litter of the understorey shrubs (about 773 Kcal), we may presume that a relative significant amount of energy is offered to the decomposers subsystem annually. However, not this entire amount is simultaneously used by the soil biota,

as the k' indicates. This is due to the very slow decomposition rate of the sclerophyllous material in the litter of *P. halepensis* forests. The mobilisation of nutrients from the decomposing litter into the soil is very important and affects also stand productivity. However, the few studies that have been performed on this issue refer only to evergreen shrublands.

In conclusion, litter production and decomposition are complex phenomena, involving both abiotic and biotic factors of the ecosystem. Both phenomena critically affect stand productivity because they define the rate of nutrient cycling that it is mediated by the ecosystem's biota. Both litter production and litter decomposition follow the typical phenological pattern of the Mediterranean climate, which is primarily defined by summer water stress and by the limited nutrient availability.

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