ISRAEL JOURNAL OF ECOLOGY & EVOLUTION, Vol. 55, 2009, pp. 63–76
DOI: 10.1560/IJEE.55.1.63

SOIL MOISTURE EFFECTS ON CELLULOSE DECOMPOSITION IN A MEDITERRANEAN ECOSYSTEM OF ATTICA, GREECE

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ABSTRACT

Water is the most critical limiting factor for decomposition processes in Mediterranean climate ecosystems. The aim of this study was to investigate the effects of increased soil moisture levels upon cellulose mass loss in an eastern Mediterranean ecosystem. We used a split plot experimental design to evaluate the effect of seasonality on the decomposition process by manipulating water availability in situ during different seasons. Nylon litterbags of mesh size 20 μm and 1 mm were filled with cellulose filter paper and placed on the plots during each season. The treatment consisted of a systematic uniform watering of the plots with 7 L/m^2/week. Litterbags were randomly removed from each plot on a monthly basis. Cellulose mass loss showed differences between treatment and control plots and between seasons but was significant only in the spring. Cellulose mass loss was significantly affected by irrigation treatment, season, and their interaction, while moisture seemed to be affected only by season. There was no significant difference in cellulose mass loss due to different mesh sizes.

Keywords: Mediterranean ecosystem, soil moisture manipulation, nylon mesh bags, mesh size, cellulose decomposition

INTRODUCTION

Considerable changes in precipitation patterns are predicted to occur during the present century (Arnell, 1999; McCarthy et al., 2001). For the Mediterranean Basin, air temperature is predicted to increase between 2 and 4 ºC over the next century (Palutikof and Wigley, 1996), while precipitation is expected to decrease in autumn and increase in winter (Déqué et al., 1998). Several authors have demonstrated the potential impact of these changes on soil organisms and biological processes in the soil (e.g., Briones et al., 1997; Wolters et al., 2000; Taylor et al., 2004).

Mediterranean ecosystems are characterized by dry, hot summers (lasting from two to three months on the French and Italian coasts in the Northern Mediterranean Rim to more than five or six months on the Libyan and Egyptian coasts to the south) and mild, wet winters.

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Received 16 September 2008, accepted 1 March 2009.

In these ecosystems, climatic conditions play an important role in the decomposition process, mainly because of predominantly quite low water availability, which usually coincides with high summer temperatures (Arianoutsou and Radea, 2000; Joffre et al., 2003). Soil moisture is usually the limiting factor for decomposition (Davidson et al., 2000). Increasing moisture activates soil processes up to a threshold beyond which it has negative effects on soil due to limited soil aeration (Cornejo et al., 1994; Chen et al., 2007).

Three different methods have been used to study the influence of soil moisture on decomposition: (i) the study of decomposition rates under controlled conditions in laboratory settings (e.g., Clein and Schimel, 1994; Fioretto et al., 1998; Buchmann, 2000, among others); (ii) comparative field studies along climatic gradients or areas with different moisture conditions (e.g., Steinberger et al., 1990; Wachendorf et al., 1997); and (iii) in situ manipulation of soil water availability. Soil moisture manipulations have been applied to several types of ecosystems, such as tropical forests (Cornejo et al., 1994), arctic tundra (Robinson et al., 1995), Alaskan taiga (Schimel et al., 1999), boreal forest understorey (Carrier and Krebs, 2002), and spruce forests (Taylor et al., 2004), but not to Mediterranean ecosystems. Most research on decomposition has focused on how litter quality and environmental factors affect this process. However, experimental work on the specific role of the soil biota—especially in the Mediterranean—is limited. Clearly, biotic and abiotic factors are not independent and together define the processes that operate during decomposition (Swift et al., 1979). For example, environmental conditions determine the levels of microbial activity (Arianoutsou and Margaris, 1982) and have a strong influence on soil macrofauna (David et al., 1999; Papatheodorou et al., 2004). As soil fungi have exoenzymes for soil organic matter breakdown and mineralization (Wardle and Lavelle, 1997), their specific activity in the decomposition process is often studied (Bloem et al., 1992; Clein and Schimel, 1994; Wardle and Lavelle, 1997; Schimel et al., 1999). Nevertheless, other soil organisms play an important role in promoting the breakdown of the plant material, thus multiplying the active area on which the microflora can act (Fragoso and Lavelle, 1992).

Here we investigate the potential influence of changing rainfall patterns, expressed as fluctuations in soil moisture, on the relationship between the soil community and decomposition. Litterbags containing pure cellulose filter paper were used to examine the response of decomposer activity with different levels of taxonomic and functional diversity (with and without mesofauna) to changes in rainfall and hence, soil moisture patterns. Cellulose filter paper was used rather than litter as the experimental material, to exclude the complexity that sclerophyllous litter might impose upon the experimental process. Decomposition rates of sclerophyllous litter in Mediterranean environments can be as low as 37% per year (Arianoutsou, 1993). Apart from the very low initial concentration in nitrogen that might play an important role in this process, re-absorption of this element before leaf abscission further decreases its availability to the decomposers and hence its decomposition (Arianoutsou, 1993).

Various experimental (e.g., Scholle et al., 1995) and modeling approaches (e.g., Schröter et al., 2003) have shown that mesofauna gains most of its functional importance

via numerous direct and indirect interactions with the decomposer microflora. In this study, the functional effects of mesofauna exclusion were investigated versus those of microbial origin, and cellulose mass loss was used as a measure of decomposition.

MATERIALS AND METHODS

STUDY SITE

The site selected for the experiments is flat, having a well developed soil litter system with spatial uniformity and a homogenous vegetation structure, both horizontal and vertical. It is located in I. & A. Diomides Botanical Garden in Dafni, Attica, Greece (38º05′N, 23º40′W). The vegetation of the area is dominated by East Mediterranean pine (*Pinus brutia*) and cypress trees (*Cupressus sempervirens)* planted over 40 years ago, while the understory vegetation consists of sparse *Pistacia lentiscus* shrubs. The soil type of the study area is a calcareous loam and the organic horizon is a mor–moder type. Soil pH is 7.93 ± 0.6.

EXPERIMENTAL DESIGN

Nylon bags of 10 cm × 8 cm were filled with high quality filter paper made of pure cellulose. The mesh sizes of the bags were selected so as to distinguish cellulose mass loss due to microflora (20 μm, fine mesh) (Wachendorf et al., 1997) from that due to microflora and micro- and mesoarthropod (1 mm, coarse mesh) activity (Radea and Arianoutsou, 2000).

The experiment was carried out four times, each one starting in a different season of the year (Fig. 1). The duration of each cycle was 9 months, a period reported to be

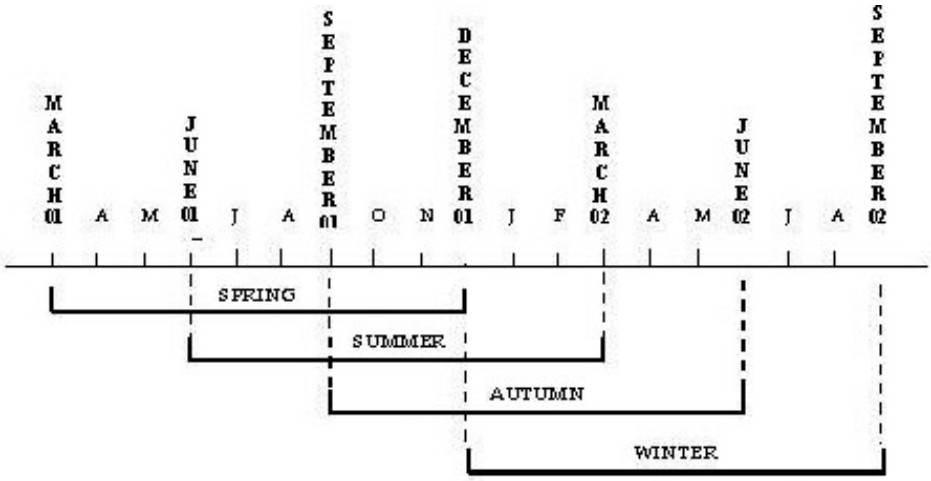

Fig. 1. The four seasonal cycles of the experimental design applied (from March 2001 to September 2002).

adequate for approximately 100% decomposition (Radea and Arianoutsou, 1998). Ten plots of 3 m × 1 m were delimited; five were used as controls (C) and the others were subjected to water treatments (T). The locations of all plots were randomly selected and dispersed throughout the site.

Treatment plots were systematically watered. An analysis of precipitation data of the last ten years provided by the nearest meteorological station (Elefsina—elevation 31 m asl, less than 5 km from the study plots) helped design the watering treatment schedule. Two basic criteria were set: (i) the treatment should be within the limits of the system defined by the average quantity of monthly precipitation (min: 1.87 ± 3.31 mm, max: 70.67 ± 46.54 mm) and the frequency of events (min: 1.18 ± 1.89 events, max: 13.60 ± 5.25 events), and (ii) it should make a significant difference during the dry months of the year. Plots were irrigated at a rate of 28 mm (28 L/m^2) per month, based on 7 mm (7 L/m^2) per week, and the water was evenly spread over the 5 treatment plots. The litterbags for each experimental (seasonal) cycle on each experimental plot were placed between the L (intact litter) and F (fermented litter) layers of the organic horizon.

Soil moisture was measured for all plots on a monthly basis using the oven-drying method. Soil cores of 5 cm in diameter, containing L, F, and H (humus) layers, were collected from each experimental plot on a monthly basis and oven-dried for 48 h (Memmert UL40, Schwabach, Germany) at 70 ºC.

One litterbag per seasonal cycle and per mesh size was removed from each plot on a monthly basis. After sampling, soil particles remaining on the bags were carefully removed. Retrieved cellulose strips were oven-dried (Memmert UL40 type) at 70 ºC for 48 h, weighed, and ignited at 500 ºC (Nabertherm model L3/S, West Germany), for 5.5 h. Results are expressed as ash-free cellulose mass loss.

Decay constant k and half-life time $T_{1/2}$ for each mesh size and experimental cycle were estimated according to the equations:

$$k = (\ln x_o - \ln x_t)/t \quad \text{and} \quad T_{1/2} = 0.693/t$$

where k = decay constant, corresponding to the daily decomposition rate; $T_{1/2}$ = half-life time of the material used (in this case pure cellulose); x_o = the initial mass of the decomposing material; x_t = the mass of the decomposing material remaining after time t.

STATISTICAL ANALYSIS

One-way ANOVA was used to compare effects of experimental (seasonal) cycles on cellulose decomposition. Control and treatment plot parameters were compared by an ANOVA *F*-test. Correlation between cellulose mass loss and soil moisture content was explored using a Spearman correlation coefficient. The effects of mesh size, irrigation treatment, and seasonal cycle on decomposition rates were examined with a three-way ANOVA and the effects of irrigation treatment and seasonal cycle on soil moisture were examined using a two-way ANOVA.

RESULTS

The total amount of water received by each experimental plot corresponds to the actual precipitation plus the added water on the treated plots. The difference in soil moisture between experimental and control plots was greater during the 1st experimental cycle (March–December), when the prevailing climatic conditions matched the typical pattern of the Mediterranean climate. During the next period, corresponding to the last month of the 1st experimental cycle, and the entire period of the other three experimental cycles, differences were minimized because of unexpectedly high rainfall. Soil moisture levels were constantly higher on the treated plots throughout the 1st experimental period, but revealed no clear pattern afterwards.

Results on the decay constant and half-life time for both mesh sizes used and for all experimental cycles provide important information about the evolution of the decomposition process (Tables 1 and 2). The lag phase for all experimental cycles and for both mesh size bags have low k ($k_{0–30}$) values, but these are always higher in the winter experimental cycle (cycle number 4). Overall decay constant values ($k_{0–270}$) obtained for both mesh size bags are lower during the 1st experimental cycle (spring), while they increase during the following cycles, with the highest value observed during the 4th experimental cycle that started and completed under particularly wet conditions both in the control and treated plots. Differences in the decay constant k (between control and treated plots) have been observed during the 1st experimental cycle only. As expected, the half-life time follows exactly the opposite pattern, being higher in the cases where k is low.

Table 1
Cellulose decay, constant k, and half-life time ($T_{1/2}$) obtained from 20-μm-mesh-size nylon bags

	20-μm-mesh bags Experimental cycles							
Time in the soil (days)	1 k × 100		2 k × 100		3 k × 100		4 k × 100	
	Control plots	Treatment plots	Control plots	Treatment plots	Control plots	Treatment plots	Control plots	Treatment plots
30	0.03	0.08	0.03	0.07	0.04	0.06	1.82	1.29
60	0.11	0.56	0.02	0.04	0.04	0.28	3.62	3.48
90	0.06	0.18	0.02	0.07	1.19	1.30	3.50	4.86
120	0.05	0.32	0.01	0.14	1.90	1.53	1.76	3.68
150	0.13	0.19	0.06	0.18	1.58	1.22	3.19	3.62
180	0.04	0.31	0.55	0.34	1.60	1.26	2.34	3.05
210	0.03	0.24	0.85	0.59	1.50	2.06	1.76	2.85
240	0.10	0.38	0.75	0.98	2.07	1.42	1.79	2.53
270	0.37	0.40	0.82	0.79	0.34	1.35	2.59	2.31
	$T_{1/2}$		$T_{1/2}$		$T_{1/2}$		$T_{1/2}$	
	Control plots	Treatment plots	Control plots	Treatment plots	Control plots	Treatment plots	Control plots	Treatment plots
	187	173	117	88	204	51	27	30

Table 2
Cellulose decay constant k and half-life time ($T_{1/2}$) obtained from 1-mm-mesh-size nylon bags

	1-µm-mesh bags Experimental cycles							
Time in the soil (days)	1 k × 100		2 k × 100		3 k × 100		4 k × 100	
	Control plots	Treatment plots	Control plots	Treatment plots	Control plots	Treatment plots	Control plots	Treatment plots
30	0.02	0.07	0.09	0.11	0.05	0.10	1.94	1.69
60	0.13	0.55	0.05	0.08	0.07	0.27	3.68	6.20
90	0.04	0.19	0.03	0.14	0.64	2.07	4.50	7.24
120	0.06	0.24	0.02	0.17	3.34	4.53	2.31	4.13
150	0.10	0.24	0.04	0.26	2.86	3.01	3.52	4.07
180	0.07	0.29	0.43	0.41	2.74	2.86	2.05	3.86
210	0.04	0.55	0.94	0.95	1.25	2.63	2.30	2.66
240	0.09	0.56	1.52	1.55	3.10	2.98	3.04	3.33
270	0.55	0.49	1.06	1.36	1.92	2.59	2.73	2.57
	$T_{1/2}$		$T_{1/2}$		$T_{1/2}$		$T_{1/2}$	
	Control plots	Treatment plots	Control plots	Treatment plots	Control plots	Treatment plots	Control plots	Treatment plots
	126	141	65	51	36	27	25	27

Soil moisture content was strongly correlated ($p < 0.05$) to cellulose mass loss for both control and treatment plots, in both mesh sizes over the first experimental cycle.

Different patterns of cellulose decomposition were observed in the 20-µm-mesh-size bags for the four seasonal cycles (Fig. 3). These differences are attributed to the moisture conditions of the initial phase of the experiment (Fig. 2). The initial decomposition rate

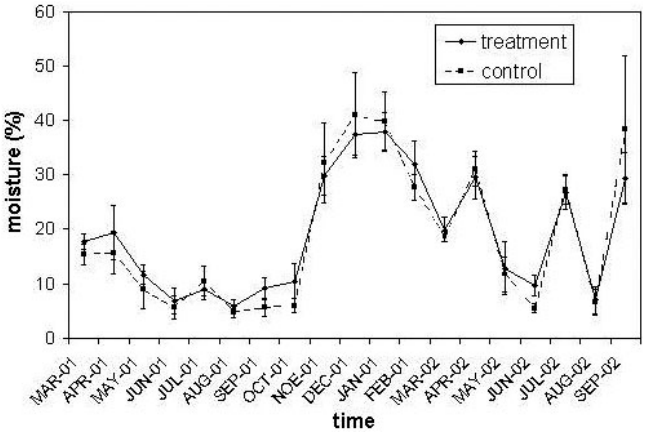

Fig. 2. Soil moisture levels in treatment and control plots (mean value ± SD).

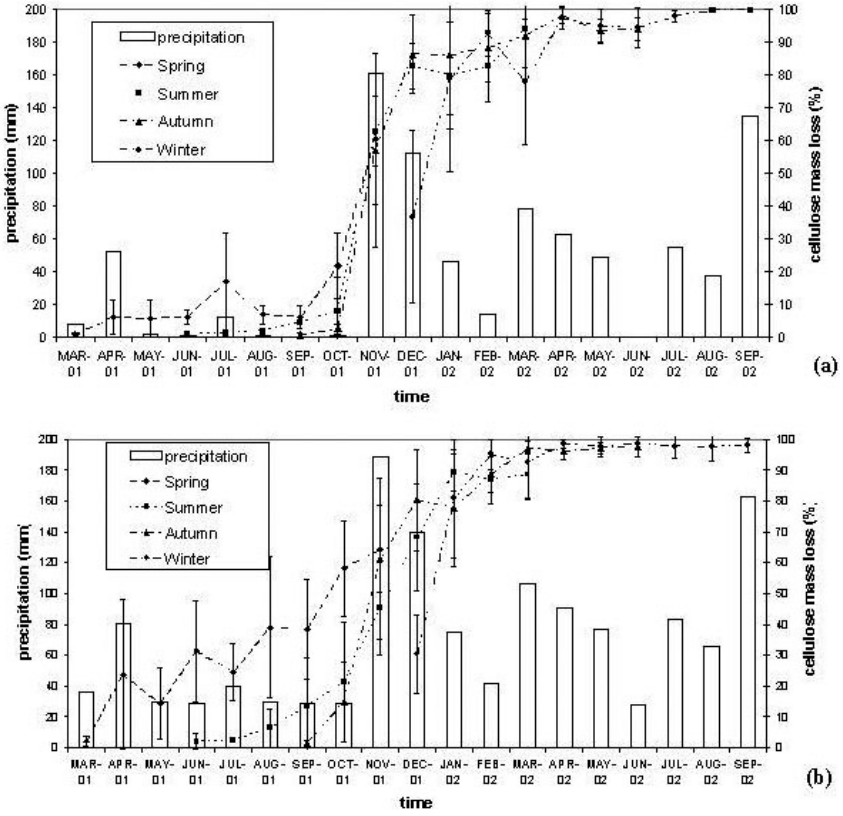

Fig. 3. Cellulose mass loss (%) for all seasonal cycles in the 20-μm-mesh-size nylon bags placed on the control (a) and on the treatment plots (b) (mean value ± SD).

was high and remained high whenever the experiment began in a wet period: approximately 80% after 4 months in the field, for experimental cycle 3 (autumnal seasonal cycle), and only 2 months for experimental cycle 4 (initiated in winter). In contrast, when the experimental cycle began in a dry period, decomposition was initially very slow and accelerated during the following months (less than 30% after 4 months in the field for seasonal cycles 1 (spring) and 2 (summer)).

Watering caused a statistically significant increase in cellulose decomposition rates ($p < 0.05$), during the first (dry) cycle only.

In a similar way, patterns of cellulose decomposition were different for the four experimental cycles in the 1-mm-mesh-size bags (Fig. 4), and this was related to the moisture condition of the initial phase of each cycle. Experimental cycle 1, started in spring, had higher cellulose mass loss ($p < 0.05$) on the treated plots. Differences between control and treated plots in the other 3 experimental cycles were also significant, but less than the first cycle. There were no significant differences in cellulose mass

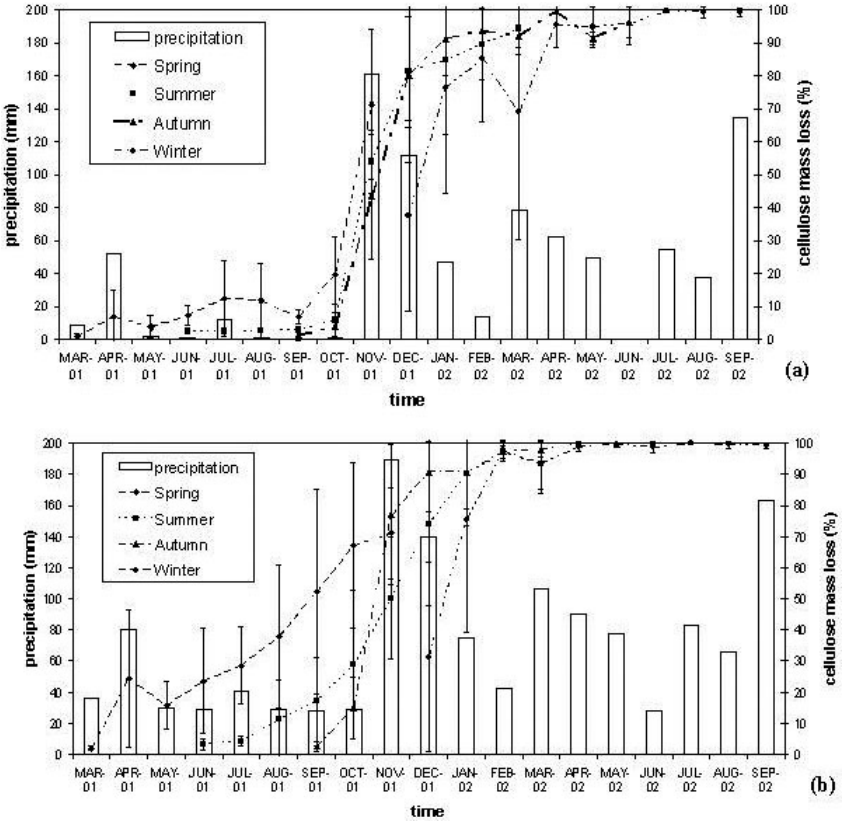

Fig. 4. Cellulose decomposition (%) for all seasonal cycles in the 1-mm-mesh-size nylon bags placed on the control plots (a) and on the treatment plots (b) (mean value ± SD).

loss for mesh sizes (20 μm and 1 mm) for any experimental cycle on control or treated plots. Cellulose mass loss for mesh size 20 μm differed significantly for all cycles in the control plots (Fig. 5a). In the treated plots, cycles 1 and 2 are grouped together, showing lower levels of cellulose mass loss, and differ significantly from cycles 3 and 4, which also form another group with higher cellulose mass loss levels (Fig. 5b). Exactly the same pattern was observed for the fine mesh bags (Fig. 5c,d).

Both the two- and three-way ANOVAs showed that cellulose mass loss is significantly affected by irrigation treatment, season, and their interaction, while moisture seems to be affected only by season (Table 3).

DISCUSSION

Decomposition rates in Mediterranean ecosystems are rather low compared to other terrestrial ecosystems (see for example Arianoutsou, 1993; Pausas, 1997; Arianoutsou and

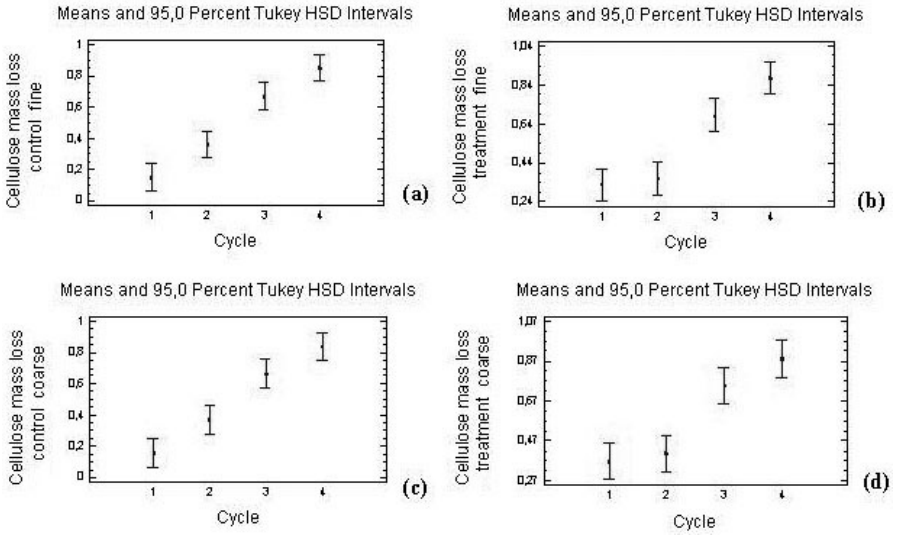

Fig. 5. Comparison of cellulose mass loss between all seasonal cycles in the 20-μm-mesh-size nylon bags placed on the control plots (a) and on the treatment plots (b). The same occurs for 1-mm-mesh-size bags placed on the control plots (c) and on the treatment plots (d).

Table 3

Summary of a three-way and a two-way ANOVA statistical analysis applied on cellulose mass loss from litterbags and moisture, respectively. The three main effects in the model were mesh size of litterbag (20 μm, 1 mm), irrigation treatment (yes, no), and season of the experiment (winter, spring, summer, autumn)

Dependent variable	Mesh size (MS)	Irrigation (I)	Season (S)	MS × I	MS × S	I × S
Cellulose mass loss	0.6295 NS	8.796**	137.488***	0.733 NS	0.111 NS	2.878*
Moisture	–	2.352 NS	11.223***	–	–	0.105 NS

F-values of main effects and first-order interactions on each of the dependent variables are presented. *$p < 0.05$. **$p < 0.01$. ***$p < 0.0001$. $p \geq 0.05$ = NS (not significant).

Radea, 2000; Kurz et al., 2000; Fioretto et al., 2007). This is mainly due to the water deficit prevailing during the hot summer periods, and also to the physical and chemical composition of the litter (Arianoutsou, 1993; Arianoutsou and Radea, 2000). Results from the current study confirm this, indicating low cellulose mass loss for all periods when water was limited, and accelerating when water became more abundant.

The use of varying mesh size decomposition bags has been previously applied under dry Mediterranean conditions (Radea and Arianoutsou, 2000) and under wetter condi-

tions, namely in Amazonia (e.g., Anderson et al., 1983; Beck et al., 1998; Kurzatkowski et al., 2004), showing a clear difference in the activity of soil biota groups that is attributed to fine and coarse mesh bags. We show here that microarthropods were largely unaffected by the irrigation treatment, supporting previous results that showed them to be tolerant of a wide range of moisture conditions, including temporary flooding and drought (Taylor et al., 2004). It is reasonable to assume that under very dry or very wet conditions, the activity of all groups of soil biota is minimized and that in both situations water is the critical factor due either to its shortage or to its excess. In intermediate situations, the exclusion of micro- and mesoarthropod groups had adverse effects on the cellulose mass loss. It is thus concluded that the unexpectedly high rainfall received by the site during the last 3 experimental cycles masked all potential differences that could otherwise be detected.

Our results indicate that the watering treatment applied had a significant effect on the decomposition rate during the first experimental cycle only, which happened to be very dry—for both bag mesh sizes—and a minimum effect during the three following seasonal cycles, which were extremely wet. Although soil moisture greatly affects the decomposition process, other parameters may also affect soil moisture, e.g., the climatic conditions prevailing on the site (Lundquist et al., 1999) and the levels of soil moisture before and after the beginning of the decomposition process (Wachendorf et al., 1997; Schimel et al., 1999).

Although the amount of water used for the treatment was decided after studying the precipitation regime prevailing over the experimental area during the previous ten years, the experimental cycles covering periods 2–4 were among the wettest that the study site had experienced over the past years. Nevertheless, our experimental design provided the opportunity to study decomposition under very different climatic conditions, thus testing the limits of the treatment applied. More specifically, data covering the first dry seasonal cycle, where the treatment induced a significant difference in the decomposition rate, revealed the relationship between soil moisture availability, decomposition rate, and related soil microbiota responses. Clearly, the results of the following three experimental cycles indicated that soil moisture should be kept under a threshold limit because otherwise it could give rise to anoxic conditions.

Soil microorganisms are sensitive to soil moisture conditions; their activity is more intense after sudden rainfall events (Arianoutsou and Margaris, 1982). However, these organisms as well as other soil biota, such as microarthropods, are known to tolerate a wide range of moisture conditions, including flooding and drought (Walter and Proctor, 1999), apparently under the conditions of the current experiment. Monitoring of soil microbiota (acarina and collembolan) populations in all seasonal cycles, performed in parallel with the current experiment (Sotiriou and Arianoutsou, in review), revealed that they were statistically affected by season, steadily increasing from spring to winter experimental cycles. The same was also the case for total soil respiration. However, none of the above biological (soil biota) or functional (soil respiration) parameters was significantly affected by the watering treatment.

In addition to the direct effect on microbial activity, several physical processes that

can influence microbial and soil fauna activity vary with soil water content, particularly water movement and gas and solute diffusion. Consequently, the relationship between soil water content and decomposition processes is quite complex, depending on parameters such as the soil moisture retention curve, porosity, pH, and soil depth (Goncalves and Carlyle, 1994; Rodrigo et al., 1997; Leiros et al., 1999).

Several attempts to create multi-parametric ecological models have been made (Badre et al., 1998; Moncrief and Fang, 1999; Chen et al., 2000; Mielnick and Dugas, 2000; Paul, 2001), aiming to reveal details underlying the potential influence of various biotic and abiotic factors acting upon soil biological activity. However, the great difficulties in validating their results prevent them from being widely applied.

Decomposition and subsequent nutrient mobilization are complex phenomena involving the structure of soil microbial communities, their nutritional requirements, and seasonal activity, as well as the chemistry of plant tissues, occurring within the constraints of climatic factors. Although not many studies have been carried out on the interactions between these factors under Mediterranean climate conditions, especially under field conditions, future research may reveal new synergetic or antagonistic effects on decomposition and nutrient cycling. Our findings confirm the importance of seasonality in the study of soil biological processes in the Mediterranean environments. In addition, in situ experimentation proved to be a very powerful tool in the investigation of such working hypotheses despite the uncertainties that the unpredictability of the Mediterranean climate may create.

ACKNOWLEDGMENTS

The authors wish to thank the authorities at I. & A. Diomides Botanical Garden at Dafni, Attica, for permission to work on the study site. They are also grateful to Dr. Daniel Danielidis and Mrs. Maria Pantazi for their advice on the statistics. Mrs. Peny Marinou and Dr. Daniel Danielidis are also acknowledged for their support in the linguistic improvement of the manuscript. The field editor of the journal and the two anonymous referees are gratefully acknowledged for their valuable comments on an earlier version of the manuscript. This work was partially supported by the State Scholarships Foundation and EU project ModMED (ENV4-CT97-0680) funds.

REFERENCES

Anderson, J.M., Proctor, J., Vallack, H. 1983. Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak III. Decomposition processes and nutrient losses from leaf litter. J. Ecol. 71: 503–527.

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

Arianoutsou, M., Margaris, N.S. 1982. Decomposers and the fire cycle in a phryganic (East Mediterranean) Ecosystem. Microb. Ecol. 8: 91–98.

Arianoutsou, M., Radea, C. 2000. Litter production and decomposition in *Pinus halepensis* forests. In: Ne'eman, G., Trabaud, L., eds. Ecology, biogeography and management of *Pinus*

halepensis and *Pinus brutia* forest ecosystems in the Mediterranean Basin. Backhuys Publishers, pp. 183–190.

Arnell, N.W. 1999. The effect of climate change on hydrological regimes in Europe: a continental perspective. Global Environ. Change 9: 5–23.

Badre, B., Nobelis, P., Trémolières, M. 1998. Quantitative study and modelling of the litter decomposition in European alluvial forest. Is there an influence of overstorey tree species on the decomposition of ivy litter (*Hedera helix* L.)? Acta Oecol. 19(6): 491–500.

Beck, L., Gasparotto, L., Förster, B., Franklin, E., Garcia, M., Harada, A., Höfer, H., Luizão, F., Luizão, R., Martius, C., de Morais, J. W., Oliveira, E., Römbke, J. 1998. The role of soil fauna in litter decomposition in primary forests, secondary forests and a polyculture plantation in Amazonia (SHIFT Project ENV 52): methodological considerations. Proceedings of the 3rd SHIFT Workshop, Bonn, Germany, pp. 471–481.

Bloem, J., de Ruiter, P.C., Koopman, G.J., Lebbink, G., Brussaard, L. 1992. Microbial numbers and activity in dried and rewetted arable soil under integrated and conventional management. Soil Biol. Biochem. 24(7): 655–665.

Briones, M.J.I., Ineson, P., Pierce, T.G. 1997. Effects of climate change on soil fauna: responses of enchytraeids, Diptera larvae and tardigrades in a transplant experiment. Appl. Soil Ecol. 6: 117–134.

Buchmann, N. 2000. Biotic and abiotic factors controlling soil respiration rates in *Picea abies* stands. Soil Biol. Biochem. 32: 1625–1635.

Carrier, P., Krebs, C.J. 2002. Trophic effects of rainfall on *Clethrionomys rutilus* voles: an experimental test in a xeric boreal forest in the Yukon Territory. Can. J. Zool. 80: 821–829.

Chen, H., Harmon, M.E., Griffiths, R.P., Hicks, W. 2000. Effects of temperature and moisture on carbon respired from decomposing woody roots. For. Ecol. Manage. 138: 51–64.

Chen, M.M., Zhu, Y.G., Su, Y.H., Chen, B.J., Marschner, P. 2007. Effects of soil moisture and plant interactions on the soil microbial community structure. Eur. J. Soil Biol. 43: 31–38.

Clein, J.S., Schimel, J.P. 1994. Reduction in microbial activity in birch litter due to drying and rewetting events. Soil Biol. Biochem. 26(3): 403–406.

Cornejo, F.H., Varela, A., Wright, S.J. 1994. Tropical forest litter decomposition under seasonal drought: nutrient release, fungi and bacteria. OIKOS 70: 183–190.

David, J.F., Devernay, S., Loucougaray, G., Le Floc'h, E. 1999. Belowground diversity in a Mediterranean landscape: relationships between saprophagous macroarthropod communities and vegetation structure. Biodiver. Conser. 8: 753–767.

Davidson, E.A., Verchot, L.V., Cattanio, J.H., Ackerman, I.L. and Carvalho, J.E.M. 2000. Effects of soil water content on soil respiration in forests and cattle pastures of eastern Amazonia. Biogeochemistry 48: 53–69.

Déqué, M., Marquet, P., Jones, R. 1998. Simulation of climate change over Europe using a global variable resolution general circulation model. Climate Dynamics 14: 173–189.

Fioretto, A., Musacchio, A., Andolfi, G., Virzo de Santo, A. 1998. Decomposition dynamics of litters of various pine species in a Corsican pine forest. Soil Biol. Biochem. 33(6): 721–727.

Fioretto, A., Papa, S., Pellegrino, A., Fuggi, A. 2007. Decomposition dynamics of *Myrtus communis* and *Quercus ilex* leaf litter: mass loss, microbial activity and quality change. Appl. Soil Ecol. 36: 32–40.

Fragoso, C., Lavelle, P. 1992. Earthworm communities of tropical rainforests. Soil Biol. Biochem. 24: 1397–1408.

Goncalves, J.L.M., Carlyle, J.C. 1994. Modelling the influence of moisture and temperature on net nitrogen mineralization in a forested sandy soil. Soil Biol. Biochem. 26: 1557–1564.

Joffre, R., Ourcival, J.M, Rambal, S., Rocheteau, A. 2003. The key-role of topsoil moisture on CO_2 efflux from a Mediterranean *Quercus ilex* forest. Ann. For. Sci. 60: 519–526.

Kurz, C., Couteaux, M.M., Tiery, J.M. 2000. Residence time and decomposition rate of *Pinus pinaster* needles in a forest floor from direct measurements under a Mediterranean climate. Soil Biol. Biochem. 32: 1197–1206.

Kurzatkowski, D., Martius, C., Höfer, H., Garcia M., Föster, B., Beck, L., Vlek, P. 2004. Litter decomposition, microbial biomass and activity of soil organisms in three agroforestry sites in central Amazonia. Nutrition Cycles in Agroecosys. 69: 257–267.

Leiros, M.C., Trasar-Cepeda, C., Seoane, S., Gil-Sotres, F. 1999. Dependence of mineralization of soil organic matter on temperature and moisture. Soil Biol. Biochem. 31: 327–335.

Lundquist, E.J., Jackson, L.E., Scow, K.M. 1999. Wet–dry cycles affect dissolved organic carbon in two California agricultural soils. Soil Biol. Biochem. 31: 1031–1038.

McCarthy, J.J., Canziani, O..F, Leary, N.A., Dokken, D.J., White, K.S. 2001. Climate change 2001: impacts, adaptations, and vulnerability. Contribution of the Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Mielnick, P.C., Dugas, W.A. 2000. Soil CO_2 flux in a tallgrass prairie. Soil Biol. Biochem. 32: 221–228.

Moncrief, J.B., Fang, C. 1999. A model for soil CO_2 production and transport 2: application to a Florida *Pinus elliotte* plantation. Agric. For. Meteorol. 95: 237–256.

Palutikof, J., Wigley, T. 1996. Developing climate change scenarios for the Mediterranean region. In: Jeftic, L., Keckes S., Pernetta, J.C., eds., Climate change and the Mediterranean, Vol. 2. Arnold, London, pp. 27–56.

Papatheodorou, E.M., Argyropoulou, M.D., Stamou, G.P. 2004. The effects of large- and small-scale differences in soil temperature and moisture on bacterial functional diversity and the community of bacterivorous nematodes. Appl. Soil Ecol. 25: 37–49.

Paul, K. 2001. Temperature and moisture effects on decomposition. NEE Workshop Proceedings, 18–20 April 2001, pp. 95–102.

Pausas, J.G. 1997. Litter fall and litter decomposition in *Pinus sylvestris* forests of the eastern Pyrenees. J. Veg. Sci. 8: 643–650.

Radea, C., Arianoutsou, M. 1998. Decomposition processes and soil mesofauna groups in post- fire successional *Pinus halepensis* forests of Greece. In: Trabaud, L., ed. Fire management and landscape ecology. International Association of Wildland Fire, Fairfield, WA, pp. 247–252.

Radea, C., Arianoutsou, M. 2000. Cellulose decomposition rates and soil arthropod community in a *Pinus halepensis* Mill. forest of Greece after a wildfire. Eur. J. Soil Biol. 36: 57–64.

Robinson, C.H., Wookey, P.A., Parsons, A.N., Potter, J.A., Callaghan, T.V., Lee, J.A., Press, M.C., Welker, J.M. 1995. Responses of plant litter decomposition and nitrogen mineralisation to stimulated environmental change in a high arctic polar semi-desert and subarctic dwarf shrub heath. Oikos 74: 503–512.

Rodrigo, A., Recous, S., Neel, C., Mary, B. 1997. Modelling temperature and moisture effects on C–N transformations in soils: comparison of nine models. Ecol. Model. 102: 325–339.

Scholle, G., Wolters, V., Schaefer, M. 1995. Mesofauna reaction to microbial growth conditions during the early stage of leaf litter decomposition. Acta Zool. Fenn. 196: 171–175.

Schröter D., Wolters, V., De Ruiter, P.C. 2003. C and N mineralisation in the decomposer food webs of a European forest transect. Oikos 102: 294–308.

Shimel, J.P., Gelledge, J.M., Clein-Curley, J.S., Lindstrom, J.E., Braddock, J.F. 1999. Moisture effects on microbial activity and community structure in decomposing birch litter in the Alaskan taiga. Soil Biol. Biochem. 31: 831–838.

Steinberger, Y., Shmida, A., Whitford, W.G. 1990. Decomposition along a rainfall gradient in the Judean desert, Israel. Oecologia 82: 322–324.

Swift, M.J., Heal, M.W., Anderson, J.M. 1979. Decomposition in terrestrial ecosystems. Studies in ecology, Vol. 5. Blackwell Scientific Publication, Oxford, UK.

Taylor, A.R., Schröter, D., Pflug, A., Wolters, V. 2004. Response of different decomposer communities to the manipulation of moisture availability: potential effects of changing precipitation patterns. Global Change Biol. 10: 1313–1324.

Wachendorf, C., Irmler, U., Blume, H.-P. 1997. Relationships between litter fauna and chemical changes of litter during decomposition under different moisture conditions. In: Cadish, G., Giller, K.E., eds. Driven by nature: plant litter quality and decomposition. CAB International, pp. 135–144.

Walter, D.E., Proctor, H.C. 1999. Mites: ecology, evolution and behaviour. University of New South Wales Press and CAB International Publishing.

Wardle, D.A., Lavelle, P. 1997. Linkages between soil biota, plant litter quality and decomposition. In: Cadish, G., Giller, K.E., eds. Driven by nature: plant litter quality and decomposition. CAB International, pp.107–124.

Wolters V., Silver W.L., Bignell, D.E., Coleman, D.C., Lavelle, P., van der Putten, W.H., de Ruiter, P.C., Rusek, J., Wall, D.H., Wardle, D.A., Brussaard, L., Dangerfield, JM., Brown, V.K., Giller, K.E., Hooper, D.U., Sala, O., Tiedje, J.M., van Veen, J.A. 2000. Effects of global changes on above and belowground biodiversity in terrestrial ecosystems: implications for ecosystem functioning. BioScience 50: 1089–1098.