Allelopathic effects of tree species on some soil microbial populations and herbaceous plants

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Abstract

The allelopathic potential of four tree species on soil microbial populations and some herbaceous plants (two understory species and one general biotest species) was investigated. Effects of three nonindigenous tree species, *Eucalyptus globulus* Labill, *Pinus radiata* D.Don and *Acacia melanoxylon* R.Br., on microorganisms participating in the cycle of nitrogen were evaluated, comparing them with those produced by the autochthonous *Quercus robur* L. Influence of the trees on *Lactuca sativa* L., *Dactylis glomerata* L. and *Trifolium repens* L. was also checked in bioassays. Cell numbers of *Nitrosomonas* sp. were negatively affected by *Acacia* and *Eucalyptus* stands, mainly during spring, when flowers are especially abundant on the ground. Proteolytic microorganisms were also negatively affected by *Eucalyptus* and *Pinus* stands, whilst *Quercus* stand did not show any toxicity. Soil bioassays showed clear inhibitory effects on germination and growth of understory plants, particularly soils from *Eucalyptus* and *Acacia* stands. The greatest effects had the soil from *Acacia* stand, which was phytotoxic during the whole period of germination and growth of understory plants. Allelopathic phenomena could be, at least partially, responsible of the low species diversity in the understory of the nonindigenous tree stands.

Additional key words: *Acacia melanoxylon*, *Dactylis glomerata*, *Eucalyptus globulus*, *Lactuca sativa*, nitrogen cycle, *Pinus radiata*, *Quercus robur*, *Trifolium repens*.

Introduction

Allelopathy is an important ecological factor in forest ecosystems. Rice (1984) has described many cases in which this competitive mechanism was a source of interferences between tree species and understory species. Other authors have reported its importance in forest ecology and management (Kuiters and Denneman 1987, Jobidon 1992, Melkania 1992).

Several studies have been focused on species which have not coevolved and which, therefore, seem unlikely to be adapted to the nature of chemical compounds in the surrounding environment. According to Rabotnov (1974) allelopathy is an effect principally possible between species from different areas or under conditions in which the soil microorganisms are not capable of destroying metabolic toxins. Therefore, in those places in which allochthonous forest species are grown, allelochemical agents could be, at least partially, responsible of the low number of understory species and scarcity of their cover (Chou and Leu 1992, Souto *et al.* 1994, Yamamoto 1995).

Allelopathic interactions are strongly related with microbial activity in the soil, and they are important in the action of allelopathic compounds released into the environment. This fact, pointed out by Vaughan *et al.* (1983) and Blum (1995), is particularly relevant in forest ecosystems, especially when phenolic compounds are considered (Kuiters 1990). Soil microorganisms can be both producers and degraders of chemicals and can be

Received 9 June 2000, *accepted* 18 September 2000.
Acknowledgements: We thank the Consellería de Educación e Ordenación Universitaria, Xunta de Galicia, for financial support of this work (XUGA 30104B94). We also thank Karen J. Duncan for her useful help in checking the manuscript.
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affected by plant secondary metabolites (Kaminsky 1980, Cheng 1992, Inderjit and Dakshini 1995, Pellissier and Souto 1999, Reigosa *et al.* 1999). Great attention has also been paid to phytotoxic microorganisms, especially soil and rhizosphere micromycetes which can negatively affect not only the growth of some plants, but also the microbial balance in the rhizosphere (Bunt and Mulder 1973, Čatská *et al.* 1982, Čatská 1994).

The aim of this work was to determine the role of allelopathic phenomenon in the plant community of this area. The allelopathic potential of four tree species on soil microbial populations and some understory species was investigated, and it was attempted to relate these effects to the low vegetation diversity in the understory of the nonindigenous trees (*Eucalyptus globulus*, *Pinus radiata*, and *Acacia melanoxylon*), always compared with the autochthonous *Quercus robur*. Also, *Lactuca sativa* was used as a general test species. The identification and quantification of phenolic compounds in soil was also studied, since they have been considered responsible for allelopathic effects by various authors (Pellissier 1993, Blum 1995).

Materials and methods

The stands under study were situated in the surroundings of Santiago de Compostela (NW Spain), with identic climatic conditions and parent material (granite with mica) for all of them. They were located between 250 and 290 m a.s.l. The distance between stands was approximately 300 m. The microbial analyses were made monthly throughout a year (from September 1995 to August 1996). Nine soil samples were taken in each stand at three randomly chosen locations (at least 4 m from the nearest tree). Not decomposed litter was removed and soil cores were taken up to 10 cm depth. Soil samples were immediately taken to the laboratory, sieved (2 mm) and homogenised. Aliquots were saved for determining pH in distilled water (Guitian and Carballas 1976), soil moisture, microbial populations densities and for performing soil bioassays.

Microbial quantifications were made using the most probable number method (MPN) (Alexander 1982). Twenty g of each soil were shaken in 180 cm^3 of water for 25 min (10^{-1} dilution) and consecutive 10-fold serial dilutions were obtained (until 10^{-8} dilution). Four replicates were prepared of each dilution for each soil. The following microbial groups were determined: dinitrogen fixers (Clark 1965), proteolytic micro-organisms (Pochon and Tardieux 1962), ammonifiers (Pochon and Tardieux 1962), denitrifying bacteria (Focht and Joseph 1973), *Nitrosomonas* (Alexander and Clark 1965), and *Nitrobacter* (Alexander and Clark 1965).

This investigation was focused to find whether allelopathic effects were present. As the most important differences among forest sites were soil pH, soil moisture and kind of vegetation, the effects produced by the first two parameters were removed using analysis of covariance (*ANCOVA*) in order to detect differences attributable to the trees. Since both parameters significantly affected microbial growth rate, multiple regression analyses were performed for each microbial group each month, taking soil pH and soil moisture as independent variables. A new variable was then created, in which effects produced by soil pH or soil moisture were removed. Oneway analysis of variance (*ANOVA*) and LSD test were then applied with the new variable to determine differences in microbial growth due exclusively to stand characteristics (kind of vegetation) once pH and soil moisture effects were statistically eliminated.

From February to July 1996 bioassays with soil of each stand were made, in order to determine the toxicity of the soil solutions. This period coincides with germination and early growth of most of the understory species in this part of the Iberian Peninsula.

Germination and growth of three species were measured: *Lactuca sativa* L. cv. Great Lakes, commonly used in allelopathic studies (Chou 1989, Molina *et al.* 1991, González *et al.* 1995), *Dactylis glomerata* L. and *Trifolium repens* L. (both as understory species in climax forests). Petri dishes were filled with soil of approximately 0.5 cm high, with *Whatman 3MM* filter paper and 50 seeds of each one of the receptor species, with five replicates. If necessary, soils were watered until field capacity with distilled water one h before sowing. Since seeds were not in contact with soil but with moistened paper, soil solutions were tested. A water control was also prepared, just made without soil, only distilled water, *Whatman* paper and seeds in Petri dishes.

Plates were placed in an incubator at 28 °C and constant humidity of 80 %. After 60 h (*L. sativa*), 72 h (*T. repens*) or 120 h (*D. glomerata*) dishes were transferred to a cold chamber at -20 °C for at least one day to stop radicle growth. Germination percentage and emergent radicle length were then determined.

Results

Statistically significant differences in microbial populations among stands for every microbial group in each month were observed (Tables 1 - 4). The most noteworthy results are those of *Nitrosomonas* and proteolytic microorganisms. Both pH and soil moisture were significantly correlated with *Nitrosomonas* growth (Table 1). During February to July there were significant differences between stands of *Quercus* and both *Eucalyptus* and *Acacia* stands with respect to *Nitrosomonas*. *Quercus* stand showed higher values than the other stands in some of these months (Table 2). All these differences were not due to pH or soil moisture (they were removed in the statistical analyses), so they must be considered as produced by characteristics of each stand (planted trees). Probably the kind of dominant vegetation in each case is related to the observed differences.

Table 1. Analysis of covariance for *Nitrosomonas* and proteolytic microorganisms.

Source of variation	*Nitrosomonas*					Proteolytic microorganisms				
	Sum of squares	DF	Mean square	F	Sig. of F	Sum of squares	DF	Mean square	F	Sig. of F
Covariates	2.795	2	1.398	15.077	0.000	0.459	2	0.230	2.178	0.117
pH (H_2O)	1.842	1	1.842	19.865	0.000	0.041	1	0.041	0.393	0.532
Soil moisture	1.631	1	1.631	17.596	0.000	0.332	1	0.332	3.149	0.078
Main effects	18.947	14	1.353	14.599	0.000	16.226	14	1.159	10.991	0.000
Soil	1.516	3	0.505	5.450	0.001	6.017	3	2.006	19.021	0.000
Time	15.239	11	1.385	14.944	0.000	4.864	11	0.442	4.193	0.000
Interactions	27.049	31	0.873	9.412	0.000	7.544	31	0.243	2.308	0.000
Soil-time	27.049	31	0.873	9.412	0.000	7.544	31	0.243	2.308	0.000
Explained	48.791	47	1.038	11.198	0.000	24.229	47	0.516	4.889	0.000
Residual	12.886	139	0.093			15.185	144	0.105		
Total	61.677	186	0.332			39.414	191	0.206		
Covariate	Raw regression coefficient					Raw regression coefficient				
pH (H_2O)	0.341					0.050				
Soil moisture	0.009					0.004				

Table 2. Growth of *Nitrosomonas* and proteolytic microorganisms of four different forest stands throughout one year (September 1995 - August 1996), expressed as logarithm (n+1). Values reflect significant differences in each month (see rows) when letters are different ($P < 0.05$), once effects produced by pH and soil moisture were statistically removed.

Month	*Nitrosomonas*				Proteolytic microorganisms			
	Q. robur	*E. globulus*	*P. radiata*	*A. melanoxylon*	*Q. robur*	*E. globulus*	*P. radiata*	*A. melanoxylon*
September	1.33 a	1.91 a	1.86 a	1.67 a	6.30 a	5.31 b	5.76 ab	5.99 ab
October	1.51 a	1.72 a	1.72 a	1.57 a	5.69 ab	5.33 b	5.47 ab	5.84 a
November	1.57 a	1.59 a	1.53 a	1.63 a	5.98 a	5.84 a	5.49 ab	5.25 b
December	0.68 a	1.30 a	0.71 a	1.19 a	6.07 a	6.01 a	6.08 a	5.92 a
January	0.77 a	0.85 a	0.74 a	0.94 a	6.41 a	5.80 b	6.04 ab	6.09 ab
February	1.49 a	1.52 a	1.59 a	0.51 b	6.30 a	5.71 b	5.67 b	5.85 b
March	1.41 a	1.06 a	1.28 a	0.96 a	5.70 a	5.80 a	5.69 a	5.85 a
April	1.41 a	1.03 b	1.13 b	1.19 a	5.76 a	5.64 a	5.81 a	5.98 a
May	1.59 a	1.21 ab	1.52 a	1.04 b	5.77 ab	6.00 a	5.45 b	6.17 a
June	1.24 a	0.41 c	1.37 a	0.76 b	6.14 a	5.93 a	5.98 a	5.89 a
July	1.58 a	1.56 a	1.54 a	1.47 a	6.36 a	6.10 ab	5.63 b	6.18 ab
Aug	0.80 a	0.53 a	0.77 a	0.69 a	6.28 a	5.92 bc	5.65 b	6.17 ac

Neither pH nor soil moisture were statistically significant in the case of proteolytic microorganisms (Table 1). Statistically significant differences appeared between *Quercus* stand and both *Eucalyptus* and *Pinus* stands (Table 2). These differences were again not due to pH or soil moisture but to stand characteristics (mainly

vegetation). They were more important in winter, probably due to the presence of decomposing leaves and barks of dominant species (leaves and bark fall is very important in winter for nonindigenous species, while oak leaves fall in autumn).

Results of dinitrogen fixers and ammonifiers (Table 3) indicate few differences among stands, which appeared mainly between *Quercus* stand and *Eucalyptus* and *Acacia* stands. In the case of denitrifying bacteria differences appeared only in June between the *Quercus* and *Eucalyptus* stands and in February between the former and the *Pinus* stand. With respect to *Nitrobacter*

Table 3. Growth of dinitrogen fixers and ammonifiers of four different forest stands throughout one year (September 1995 - August 1996), expressed as logarithm (n + 1). Values reflect significant differences in each month (see rows) when letters are different ($P < 0.05$), once effects produced by pH and soil moisture were statistically removed.

Month	Dinitrogen fixers				Ammonifiers			
	Q. robur	*E. globulus*	*P. radiata*	*A. melanoxylon*	*Q. robur*	*E. globulus*	*P. radiata*	*A. melanoxylon*
September	2.71 a	2.73 a	2.53 a	2.80 a	6.74 a	5.84 b	6.13 ab	6.12 ab
October	2.77 a	2.84 a	2.67 a	2.60 a	6.41 a	6.26 a	6.25 a	6.61 a
November	2.89 a	2.95 a	2.55 a	3.11 a	5.91 a	6.00 a	5.61 a	6.03 a
December	2.67 a	2.69 a	2.61 a	2.76 a	5.83 a	5.68 a	5.79 a	6.07 a
January	2.77 a	2.84 a	2.74 a	2.92 a	6.18 ab	6.29 a	5.95 ab	5.71 b
February	2.73 a	3.12 a	2.67 a	2.99 a	5.91 a	6.02 a	6.19 a	5.87 a
March	2.85 a	3.07 a	2.87 a	3.08 a	5.77 b	5.97 ab	6.27 a	5.45 c
April	2.98 a	3.11 a	2.85 a	3.07 a	5.85 a	5.92 a	5.79 a	5.90 a
May	3.31 b	3.39 b	3.33 b	3.56 a	5.97 a	5.82 a	5.73 a	5.84 a
June	3.57 a	3.51 a	3.42 a	3.50 a	5.82 a	5.67 a	5.89 a	5.73 a
July	3.10 a	3.18 a	2.96 a	3.10 a	5.72 a	5.80 a	5.60 a	5.77 a
Aug	3.03 ab	3.16 ab	2.84 b	3.26 a	6.04 a	5.54 b	5.46 b	5.77 ab

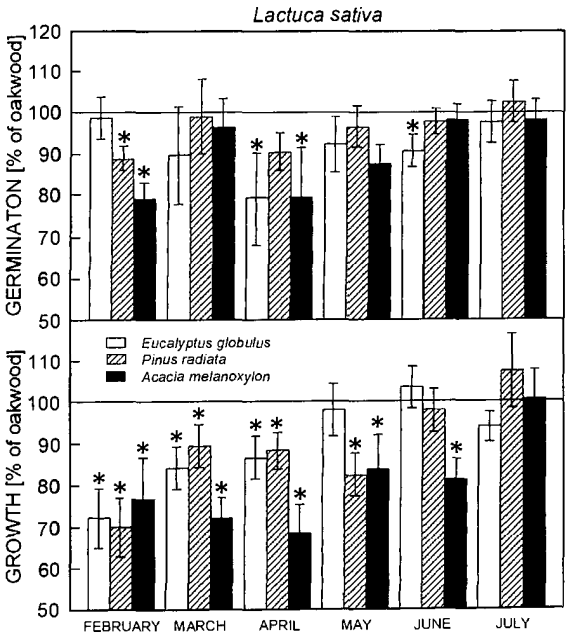

Fig. 1. Phytotoxic effects produced by soils of three different forest stands on *Lactuca sativa*. Values are given as a percentage with respect to control (oakwood stand soil). * - significant differences between stands with respect to the control ($P < 0.05$).

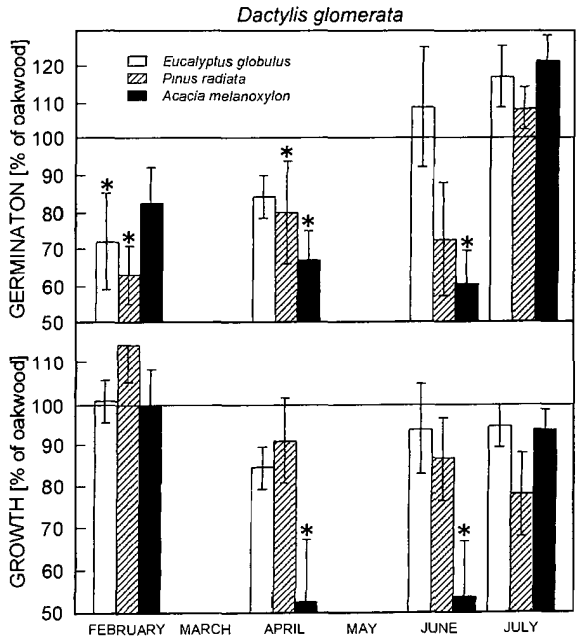

Fig. 2. Phytotoxic effects produced by soils of three different forest stands on *Dactylis glomerata*. See Fig. 1 for symbols.

no differences appeared once the effects of pH and soil moisture were removed, so results are not shown.

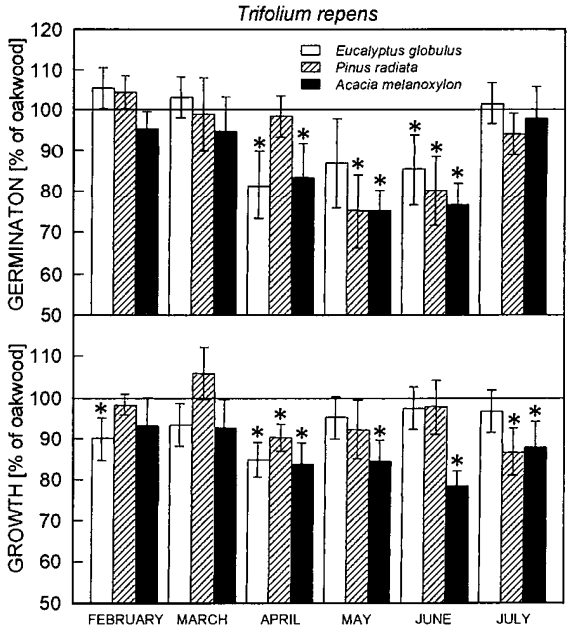

Fig. 3. Phytotoxic effects produced by soils of three different forest stands on *Trifolium repens*. See Fig. 1 for symbols.

In general, growth of tested plants was affected more than germination (Figs. 1 to 3). There were no statistically significant differences between oak forest soil treatment and water control, so the first was taken as a control because oak forest is the climax ecosystem.

L. sativa germination was affected essentially by soil extracts from *Eucalyptus* and *Acacia* stands (Fig. 1). The most important inhibitions were found, however, in growth. The soil samples of almost all months showed significant inhibitions, the most notable being those produced by *Acacia* soil. This soil was inhibitory from February up to June. Similar results were found with *Eucalyptus* and *Pinus* soils, but with less intensity and duration.

With respect to *D. glomerata*, it can be seen that phytotoxic effects are less important (Fig. 2). The most notable result is the inhibitory capacity of the soil from *Acacia* stand on both germination and growth, and also of soils from *Eucalyptus* and *Pinus* on germination.

Soil from the *Acacia* stand was the most inhibitory on *T. repens* (Fig. 3). The most critical months seem to be spring ones, from April to June, probably due to the presence of toxic substances released from flower residues on the stand ground. This effect can also be observed on growth, in which soil from *Acacia* stand was still the most inhibitory.

Discussion

In a previous work, Souto *et al.* (1994) showed that decomposition of aerial plant parts from *Eucalyptus globulus* and *Acacia melanoxylon* released phytotoxic compounds, inhibiting the germination and growth of *Lactuca sativa*. They also showed the importance of soil microorganisms in detoxifying such compounds, particularly in the *Quercus robur* forest soil.

The results indicate the existence of differences among the four soil samples caused by the planted trees with respect to some kinds of microorganisms, but also the importance of soil and climatic parameters (pH and moisture). In this sense, some groups did not show differences due to characteristics other than pH and moisture. However, it is noteworthy to mention the narrow relationship between pH and allelopathic phenomena. Soil pH depends, in part, on chemical substances (toxic or not) released into the soil, so a decrease or increase of pH could be directly related with the release rate of chemicals. Besides, activity of some substances is very much influenced by the soil pH (Kuiters 1990, Appel 1993). Differences found in our experiment that statistically would be explained by pH may really be due to differences in the activity of allelochemicals. The fact that a soil parameter such as pH can explain differences in microbial densities in soils of the stands under study could be related with allelopathic phenomena on those microorganisms due to changes in the activity of chemical compounds.

It has been recognised that soil community can have a dramatic impact on plant populations and communities. Westover *et al.* (1997) found that the rhizosphere populations of free-living bacteria and fungi can be influenced by the plants as well as *vice versa*. Bever *et al.* (1997) have provided a framework for the interrelations between the composition of plant and soil communities, in which a feedback process is involved. The model proposes two possibilities: a positive feedback leading to the loss of species diversity at a local scale, and a negative feedback leading to its maintenance. Under the first one the relative rate of population growth of a plant species in association with its local soil community increases over time. In this sense, Pellissier (1998) and Bever *et al.* (1998) pointed out that allelopathic interactions should be added to the model as a competitive mechanism that may affect the plant population dynamics. In our work significant interrelations between soil microorganisms and plants have been found. *Nitrosomonas* and proteolytic microorganisms were negatively affected by the *Acacia* stand, leading to a different composition of soil microbial populations with respect to the natural forest. Since all soil characteristics of the four stands were identical

except for vegetation, we suspect that plants growing in that stand (almost exclusively *Acacia melanoxylon*) affected soil populations. However, not only plants affect microbial populations, but soil microorganisms change soil conditions, such as nutrient availability (Wardle *et al.* 1998), and therefore plant populations dynamics. The observed differences in microbial growth of *Nitrosomonas* and proteolytic microorganisms have a seasonal pattern, in which the lowest number of microbes was found during spring. This period coincides with the presence of flower debris on the ground, and with the germination and early growth period for most of autochthonous understory species. This could help to explain the inhibitory capacity of the soil under *Acacia melanoxylon* just after the beginning of flowering. In this sense, another related species, *Acacia dealbata*, has been demonstrated to have important quantities of inhibiting compounds in its flowers (Casal *et al.* 1985, Reigosa *et al.* 1996). However, once spring finishes, cell numbers come back to normal values (meaning values not statistically different from the *Quercus robur* stand). These short-term effects can be of importance in the populations dynamics because of the period of the year in which it happens, just when understory species are germinating and growing. Small changes in soil properties derived from releasing of chemical substances and from changes in the microbial community may have dramatic effects on the success of understory species.

Bioassays with soils made from February to July derived from the need to approach field conditions in allelopathic studies (Inderjit and Dakshini 1995). Results indicate the possible occurrence of allelopathic phenomena, essentially by *Eucalyptus* and *Acacia* soils. Noteworthy are the highest inhibitory effects in spring. We suggest the same explanation as previously commented, that is, the presence of high amounts of flowers on the ground when understory plants are germinating and growing.

In the present work the negative effects of these tree species on some soil microbial groups could help to understand the low species diversity in the understory of the non-indigenous trees. Allelopathic phenomena could be, at least partially, responsible of that fact.

References

Alexander, M.: Most-probable number method for microbial populations. - In: Page, A.L. (ed.): Methods of Soil Analysis. Part 2. Chemical and Microbiological Properties, 2nd Edition. Pp. 815-820. American Society of Agronomy, Madison 1982.

Alexander, M., Clark, F.E.: Nitrifying bacteria. - In: Black, C.A., Evans, D.D., White, J.L., Ensminger, L.E., Clark, F.E. (ed.): Methods of Soil Analysis. Part 2. Pp. 1477-1483. American Society of Agronomy, Madison 1965.

Appel, H.M.: Phenolics in ecological interactions: the importance of oxidation. - J. chem. Ecol. **19**: 1521-1552, 1993.

Bever, J.D., Westover, K.M., Antonovics, J.: Incorporating the soil community into plant population dynamics: the utility of the feedback approach. - J. Ecol. **85**: 561-573, 1997.

Bever, J.D., Westover, K.M., Antonovics, J.: Reply correspondence. - Trends Ecol. Evol. **13**: 407-408, 1998.

Blum, U.: The value of model plant-microbe-soil systems for understanding processes associated with allelopathic interaction. One example. - In: Inderjit, K.M.M., Dakshini, Einhellig, F.A. (ed.): Allelopathy. Organisms, Processes and Applications. (Symposium Series 582.) Pp. 127-131. American Chemical Society, Washington 1995.

Bunt, J.A., Mulder, D.: The possible role of bacteria in relation to the apple replant disease. - Meded. Fac. Landbouwwet. Rijksuniv. Gent **38**: 1381-1385, 1973.

Casal, J.F., Reigosa, M.J., Carballeira, A.: Potentiel allelopathique de *Acacia dealbata* Link. - Rev. Ecol. Biol. Sol **22**: 1-12, 1985.

Čatská, V.: Interrelationships between vesicular-arbuscular mycorrhiza and rhizosphere microflora in apple replant disease. - Biol. Plant. **36**: 99-104, 1994.

Čatská, V., Vančura, V., Hudská, G., Přikryl, Z.: Rhizosphere micro-organisms in relation to the apple replant problem. - Plant Soil **69**: 187-197, 1982.

Clark, F.E.: Agar-plate method for total microbial count. - In: Black, C.A., Evans, D.D., White, J.L., Ensminger, L.E., Clark, F.E. (ed.): Methods of Soil Analysis. Part 2. Pp. 1460-1466. American Society of Agronomy, Madison 1965.

Cheng, H.H.: A conceptual framework for assessing allelochemicals in the soil environment. - In: Rizvi, S.J.H., Rizvi, V. (ed.): Allelopathy: Basic and Applied Aspects. Pp. 21-29. Chapman & Hall, London 1992.

Chou, C.H.: Allelopathic research of subtropical vegetation in Taiwan. IV. Comparative phytotoxic nature of leachate from four subtropical grasses. - J. chem. Ecol. **17**: 2149-2159, 1989.

Chou, C.H., Leu, L.L.: Allelopathic substances and interactions of *Delonix regia* (Boj) Raf. - J. chem. Ecol. **18**: 2285-2303, 1992.

Focht, D.D., Joseph, H.: An improved method for the enumeration of denitrifying bacteria. - Soil Sci. Soc. Amer. Proc. **37**: 698-699, 1973.

González, L., Souto, X.C., Reigosa, M.J.: Allelopathic effects of *Acacia melanoxylon* R.Br. phyllodes during their decomposition. - Forest Ecol. Manage. 77: 53-63, 1995.

Guitian, F., Carballas, I.: Técnicas de Análisis de Suelos. [Techniques in Soil Analysis]. 2ª Ed. - Pico Sacro, Santiago de Compostela 1976. [In Span.]

Inderjit, Dakshini, K.M.M.: On laboratory bioassays in allelopathy. - Bot. Rev. **61**: 28-44, 1995.

Jobidon, R.: Allelopathy in Quebec forestry - case studies in natural and managed ecosystems. - In: Rizvi, S.J.H., Rizvi, V. (ed.): Allelopathy: Basic and Applied Aspects. Pp. 341-356. Chapman & Hall, London 1992.

Kaminsky, R.: The determination and extraction of available

soil organic compounds. - Soil Sci. **130**: 118-123, 1980.

Kuiters, A.T.: Role of phenolic substances from decomposing forest litter in plant-soil interactions. - Acta bot. neerl. **39**: 329-348, 1990.

Kuiters, A.T., Denneman, C.A.J.: Water-soluble phenolic substances in soils under several coniferous and deciduous tree species. - Soil Biol. Biochem. **19**: 765-769, 1987.

Melkania, N.P.: Allelopathy in forest and agroecosystems in the Himalayan region. - In: Rizvi, S.J.H., Rizvi, V. (ed.): Allelopathy: Basic and Applied Aspects. Pp. 371-388. Chapman & Hall, London 1992.

Molina, A., Reigosa, M.J., Carballeira, A.: Release of allelochemical agents from litter, throughfall, and topsoil in plantations of *Eucalyptus globulus* Labill in Spain. - J. chem. Ecol. **17**: 147-160, 1991.

Pellissier, F.: Allelopathic effect of phenolic acids from humic solutions on two spruce mycorrhizal fungi: *Cenococcum graniforme* and *Laccaria laccata*. - J. chem. Ecol. **19**: 2105-2114, 1993.

Pellissier, F.: The role of soil community in plant population dynamics: is allelopathy a key component? - Trends Ecol. Evolut. **13**: 407, 1998.

Pellissier, F., Souto, X.C.: Allelopathy in northern temperate and boreal semi-natural woodland. - Crit. Rev. Plant Sci. **18**: 637-652, 1999.

Pochon, J., Tardieux, P.: Techniques d'Analyse en Microbiologie du Sol. - La Tourelle, St. Mandé 1962.

Rabotnov, T.A.: [On the allelopathy in the phytocenoses.] - Izv. Akad Nauk SSSR Ser. Biol. **1974** (6): 811-820, 1974. [In Russ.]

Reigosa, M.J., Sánchez-Moreiras, A.M., González, L.: Ecophysiological approach to allelopathy. - Crit. Rev. Plant Sci. **18**: 577-608, 1999.

Reigosa, M.J., Souto, X.C., González, L.: Allelopathic research: methodological, ecological and evolutionary aspects. - In: Narwal, S.S., Tauro, P. (ed.): Allelopathy: Field Observations and Methodology. Pp. 213-231. Scientific Publishers, Jodhpur 1996.

Rice, E.L.: Allelopathy. 2nd Ed. - Academic Press, Orlando 1984.

Souto, X.C., González, L., Reigosa, M.J.: Comparative analysis of allelopathic effects produced by four forestry species during decomposition process in their soils in Galicia (NW Spain). - J. chem. Ecol. **20**: 3005-3015, 1994.

Vaughan, D., Sparling, G.P., Ord, B.G.: Amelioration of the phytotoxicity of phenolic acid by some soil microbes. - Soil Biol. Biochem. **15**: 613-614, 1983.

Wardle, D.A., Nilsson, M., Gallet, C., Zackrisson, O.: An ecosystem-level perspective of allelopathy. - Biol. Rev. **73**: 305-319, 1998.

Westover, K.M., Kennedy, A.C., Kelley, S.E.: Patterns of rhizosphere microbial community structure associated with co-occurring plant species. - J. Ecol. **85**: 863-873, 1997.

Yamamoto, Y.: Allelopathic potential of *Anthoxanthum odoratum* for invading *Zoysia*-grassland in Japan. - J. chem. Ecol. **21**: 1365-1373, 1995.