BOREAL ENVIRONMENT RESEARCH 13: 113–120 © 2008
ISSN 1239-6095 (print) ISSN 1797-2469 (online) Helsinki 28 April 2008

Effect of dominant ground vegetation on soil organic matter quality in a declining mountain spruce forest of central Europe

Eleonora Bonifacio[1], Stefania Santoni[1], Pavel Cudlin[2]* & Ermanno Zanini[1]

[1] *Università degli Studi di Torino, Di.Va.P.R.A. — Chimica Agraria, Via L. da Vinci 44, I-10095 Grugliasco (TO), Italy*
[2] *Institute of Systems Biology and Ecology, Czech Academy of Sciences, Na Sádkách 7, CZ-370 05 České Budějovice, Czech Republic (corresponding author's e-mail: pavelcu@usbe.cas.cz)*

Received 20 Dec. 2006, accepted 7 May 2007 (Editor in charge of this article: Jaana Bäck)

Bonifacio, E., Santoni, S., Cudlin, P. & Zanini, E. 2008: Effect of dominant ground vegetation on soil organic matter quality in a declining mountain spruce forest of central Europe. *Boreal Env. Res.* 13: 113–120.

Grasses and shrubs constitute a high proportion of the total biomass in declining forest stands and may deeply affect soil organic matter. We fractionated the organic matter of 45 Oa horizons from the Krkonoše Mts. into humic and fulvic acids (HA and FA) and related the differences to the dominant ground vegetation *Vaccinium myrtillus*, *Deschampsia flexuosa* and *Molinia caerulea*. Organic C was higher under *M. caerulea* than under *Vaccinium myrtillus*, but the humification rate was similar at all sites. A higher proportion of HA was found under *M. caerulea*, indicating that differences in species lead to variations in the quality of humic substances, but not in the quantitative aspects of the humification process. Regarding the importance of HA and FA in soil development, the findings suggest that, upon forest decline, major changes may be expected not only in the O horizons, but also in the whole soil profile.

Introduction

The effect of vegetation on soil properties has been acknowledged since the development of the concept of the factors of soil formation (Jenny 1941). Vegetation influences soil evolution mainly through the addition of organic matter to the mineral soil phase. When in the soil, organic matter undergoes a complex sequence of transformations giving rise to organic substances that are different from the original plant material. The characteristics of soil organic matter (SOM) depend both on environmental conditions (e.g. soil water saturation, redox conditions, temperature) that influence soil microbial communities, and on the quality of the plant debris reaching the soil surface, thus on the type of vegetation (Rothe and Binkley 2001, Van Oijen *et al.* 2005). There is, however, a strong interaction between vegetation cover and site conditions (Drewnik 2006). A number of studies have compared broadleaf and conifer litter in relation to decomposition rate (e.g. Albers *et al.* 2004), N dynamics (e.g. McClaugherty *et al.* 1985, Ulbrichova *et al.* 2005), and the effects they have on the chemistry of the forest floor (e.g. Brandtberg *et al.* 2000). The differences are, however, not only limited to the organic horizons, but are also maintained in the mineral soil horizons and affect profile morphology. Nielsen *et al.* (1999) found that the original heathland podzols were transformed under oak into acid brown soils, while Sitka spruce induced an enhancement of podzolisation. Deforestation and grass invasion instead, decrease the podzolisation intensity, with changes in organic C and associated properties, such as pyrophosphate-extractable Fe and Al (Barrett and Schaetzl 1998). When humic substances are in fact characterised by the predominance of small molecules, with highly polar, acidic functional groups, the interaction with soil minerals is enhanced; Al and Fe released from minerals can be complexed and translocated as organic colloids through the profile, until they are immobilised in deeper horizons (e.g. Riise *et al.* 2000).

Podzolisation is a process involving changes in humic and fulvic acids, which are separated according to their acid solubility. Soils developing under evergreen vegetation are normally richer in fulvic acids than those under broadleaves (e.g. McKeague *et al.* 1986), but there is a lack of information about the effect of forest herbaceous species. In forest ecosystems, because of natural succession events in vegetation communities, and drastic changes triggered by anthropogenic impacts, understory vegetation may constitute a high proportion of the total biomass.

In the Krkonoše National Park, the Czech Republic, the large dieback of Norway spruce forest, linked to the massive acid precipitation of the last decades, has created situations where actually grasses are the dominant species (Vacek *et al.* 1999). In that area, Bonifacio *et al.* (2006) found that, at the sites where grasses dominated, the quality of organic matter in the E horizons was different from that of the Bs; under Norway spruce, SOM was comparable in the two kinds of horizons.

The aim of this work was to evaluate how the presence of grass and shrub vegetation influences organic matter in the O horizons. By assessing the proportion of humic and fulvic acids, some considerations about the possibility for specific pedogenetic processes influencing the whole soil profile can be drawn.

Material and methods

The research was carried out in the Mumlavska Hora area (50°49´N, 15°08´E; 1185 m a.s.l.) in the Krkonoše National Park, situated in the northeastern part of the Czech Republic (Fig. 1), central Europe. The area is classified as having a severe forest decline (4th degree according to the Czech Forest Authority), which started more than 25 years ago and was caused mostly by the SO_2 pollution (Cudlín *et al.* 2003). Czech forest stand damage classification was based on the assessment of the percentage of tree defoliation and of dying and dead trees (Cudlín *et al.* 1995). Sampling plot was situated in the final stage of Norway spruce (*Picea abies*) forest decline, almost without natural regeneration, tree density 12 trees per ha, age 180 years (Cudlín *et al.* 2001). This forest stand was naturally established and minimally influenced by forestry management. The soil parent material is a fine grained granite; the annual average precipitation is 1500 mm, the average temperature is 2.5 °C. The soils of the area range from Typic and Humic Haplocryods, to Placic Cryaquods, to Typic Cryofibrists, according to the USDA Soil Taxonomy (Soil Survey Staff 1999). The pH is always acidic, ranging between 3.7 and 4.5 in the organic horizons, and between 4.0 and 4.4 in the mineral ones (Bonifacio *et al.* 2006).

We chose a 60 × 90-m sampling plot, as representative of the area: it has a gentle N-NW facing slope (8%–10%), with an average elevation of 1200 m a.s.l. Forty-five samples were taken from the plot, according to the sampling scheme shown in Fig. 1. At each sampling point, the prevailing species (> 50% of ground coverage in a 4 × 4-m square centred on the sampling point) of the herb layer were recorded; among the most common four at the site were blueberry (*Vaccinium myrtillus*), wavy hair-grass (*Deschampsia flexuosa*), purple moor-grass (*Molinia caerulea*) and *Sphagnum* sp.

The Oa horizon was collected after having discarded the fresh litter layer (Oi) and the fermentation organic horizon (Oe), where present. The average thickness of the Oi and Oe horizons was limited to about 1 cm, and they were found only at 18 (Oi), and 9 sites (Oe). The average

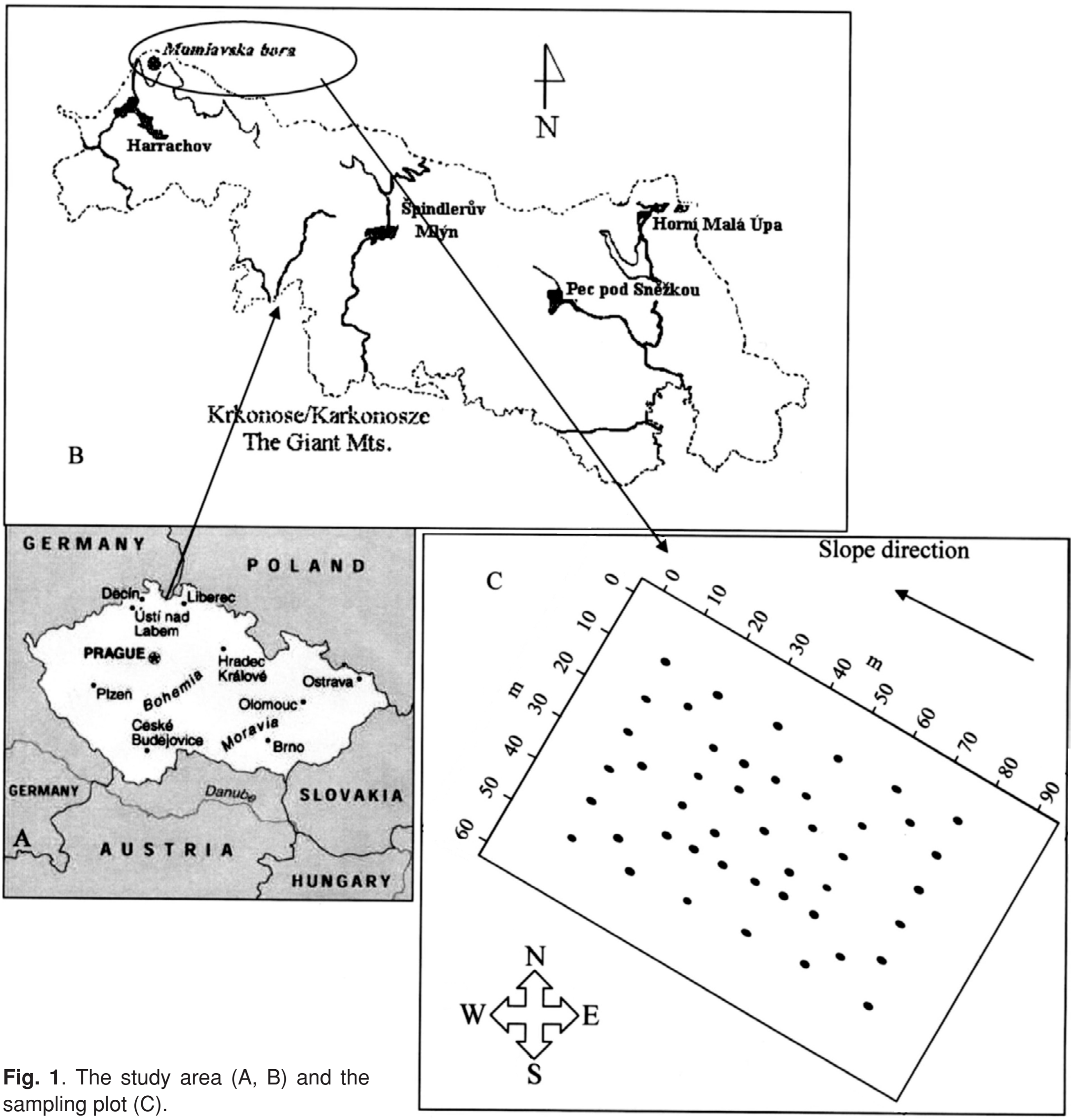

Fig. 1. The study area (A, B) and the sampling plot (C).

thickness of the Oa collected for the analyses was 14 cm, with a standard deviation of 7. The soils were air dried and sieved at 2 mm and the organic matter was fractionated. The organic carbon content (OC) was determined by combustion at 650 °C, the humic substances (TEC, total extractable carbon) were extracted using sodium hydroxide and sodium pyrophosphate 0.1 M solution (Sequi and De Nobili 2000). Humic (HA) and fulvic (FA) acids were separated from the extract by bringing the pH to 1 with HCl. FA were purified by PVP resins to separate the non-humic extracted material (NH). In all extracts, the C concentrations were determined using wet oxidation with $K_2Cr_2O_7$. The C contents of the NH fraction were obtained from the difference between TEC and (HA + FA). In all organic extracts, Fe and Al concentrations were measured with atomic absorption spectroscopy (AAS, Perkin Elmer 3030) to evaluate the quantity of metal associated with that organic fraction. We obtained, therefore, the amounts of Fe and Al associated with Total Extractable Carbon (Fe-TEC, Al-TEC), the humic acid fraction (Fe-HA

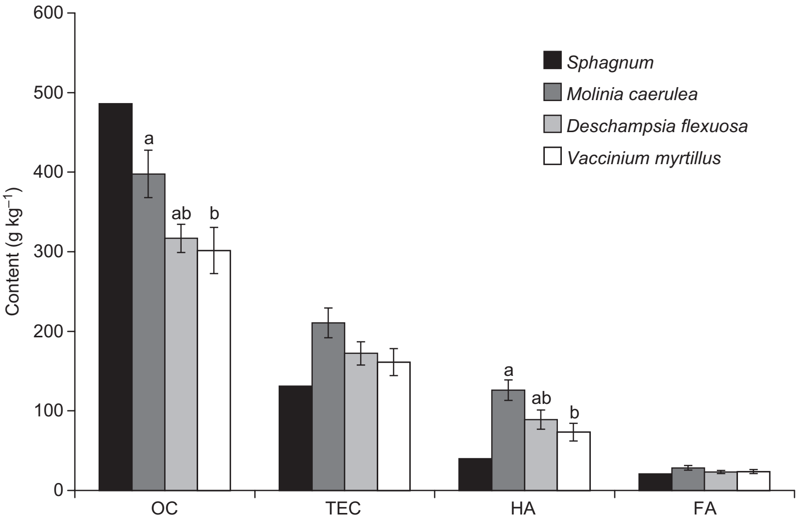

Fig. 2. Organic carbon (OC), total extractable carbon (TEC), humic (HA) and fulvic acid (FA) contents. Different letters indicate significant differences ($p < 0.05$, Scheffe test).

and Al-HA) and the fulvic acid fraction (Fe-FA and Al-FA).

The acid-extractable (AE) contents of Fe and Al were obtained after $HCl–HNO_3$ (3:1) treatment of previously ignited (to 650 °C) samples. The concentrations were measured with AAS.

The soil data were grouped according to the dominant vegetation type and compared with the one-way ANOVA (SPSS 12.0).

Results

Out of the 45 sampling points, *Molinia caerulea* was found dominant at 14 sites, *Deschampsia flexuosa* at 16 sites, while in 14 sites *Vaccinium myrtillus* was the main species. *Sphagnum* was found only at one site, at the bottom of the gentle slope, and therefore the related data are presented in the descriptive tables, but were not used for statistical evaluation. The OC contents (Fig. 2) varied from 96 to 492 g kg^{-1}. We found higher values under *M. caerulea* cover than under *V. myrtillus* ($p = 0.026$, $n = 44$): average values of 398 and 301 g kg^{-1}, respectively. The Oa horizons under *D. flexuosa* showed intermediate contents (317 g kg^{-1}) (Fig. 2). The TEC showed the same trend of the OC, but no significant differences were found. The content of humic acids (HA) was the highest under *M. caerulea* (126 g kg^{-1}), and different from that found in the Oa horizons of the blueberry sites ($p = 0.013$, $n = 44$), while we found no significant differences in the fulvic acid and non-humic substances contents.

The ratio between TEC and OC was constant for all vegetation types, with average values ranging from 0.54 to 0.56 (Table 1), independent of the amount of organic matter accumulated. The (HA + FA)/OC ratio, i.e. the degree of humification, showed the same trend as the TEC/OC ratio, without any significant differences, and ranged from 0.34 to 0.40. On average, 55% of OC was extractable, but only 36% of OC was humified. The ratio between the two humic fractions (FA/HA) ranged from 0.14 to 0.66 (Table 1), indicating the prevalence of humic acids to fulvic ones in all organic horizons. It showed, however, significantly higher values at the blueberry dominated sites ($p = 0.026$, $n = 44$) than at the sites dominated by *M. caerulea*; intermediate ratios were found for *D. flexuosa*. Under *M. caerulea*, HA were not only present in higher amounts, as indicated before, but also represented a higher proportion of the TEC than under the blueberry ($p = 0.026$, $n = 44$).

The acid-extractable Al contents varied between 5.2 and 20.2 g kg^{-1} and the acid-extractable Fe concentration between 3.6 and 13.2 (Table 2). The values were scattered over the sampling area, and no significant differences were found according to vegetation. Aluminium and iron were present in the TEC extracts and their contents varied with vegetation ($p = 0.015$, $n = 44$). On average, 6.4 g of Al and 2.3 g of

Fe kg^{-1} soil were associated with extractable carbon in the case of *M. caerulea*, while significantly lower contents were found under *V. myrtillus* (4.3 and 0.8 g kg^{-1} for Al and Fe, respectively). The amounts of Al associated with HA were higher than the quantity associated with FA, but no significant differences were found. The amounts of Fe in the FA extracts were extremely low, often more than ten times lower than the corresponding amounts of Al. Low Fe contents were also found in the HA extracts, but the differences with the Al contents were less marked. Also in the case of Fe, no differences related to vegetation were found. The molar ratios between carbon and metals in the TEC extracts varied between 21 and 148 for Al and from 205 to 1452 for Fe, independent of vegetation (Table 2).

Discussion

The first difference we found between vegetation types was quantitative. The high accumulation of organic matter at the sites where *M. caerulea* was dominant may be related to the high productivity of this species in wet areas: up to 513 g m^{-2} annual aboveground production according to Berendse *et al*. (1987). The TEC data showed the same trend as OC, although no significant differences were found, and, as a consequence, we found no differences in the humification indexes, such as the ratio between extractable and total carbon or the ratio (HA + FA)/OC.

This lack of differences indicates that humification in the study area is independent of the vegetation type. The same proportion of organic

Table 1. Indexes of humification according to dominant understory vegetation.

	Sphagnum	*Molinia caerulea*		*Deschampsia flexuosa*		*Vaccinium myrtillus*	
		Mean	SD	Mean	SD	Mean	SD
TEC/OC	0.27	0.54	0.12	0.55	0.16	0.56	0.17
(HA + FA)/OC	0.12	0.40	0.11	0.35	0.13	0.34	0.16
HA/TEC	0.30	0.60 a	0.13	0.50 ab	0.17	0.44 b	0.15
FA/TEC	0.16	0.14	0.04	0.14	0.04	0.16	0.05
NH/TEC	0.54	0.26	0.14	0.36	0.18	0.40	0.17
FA/HA	0.52	0.24 b	0.10	0.31 ab	0.13	0.38 a	0.16

Different letters indicate significant differences (Scheffe test) at $p < 0.05$.
Abbreviations: TEC = Total Extractable Carbon; OC = Organic Carbon; FA = Fulvic Acids; HA = Humic Acids; NH = Non humic extracted substances.

Table 2. Aluminium and iron in the soils and in the humic fractions.

	Sphagnum	*Molinia caerulea*		*Deschampsia flexuosa*		*Vaccinium myrtillus*	
		Mean	SD	Mean	SD	Mean	SD
Al-AE (g kg^{-1})	8.0	11.0	2.0	11.4	3.4	12.3	3.7
Al-TEC (g kg^{-1})	5.7	6.4 a	1.6	4.6 b	1.5	4.3 b	2.1
Al-HA (mg kg^{-1})	350	880	270	740	330	830	330
Al-FA (mg kg^{-1})	50	40	30	40	30	30	30
C/Al (mol mol^{-1})	53	74	20	86	26	92	32
Fe-AE (g kg^{-1})	4.9	7.8	2.7	8.1	2.3	7.2	2.5
Fe-TEC (g kg^{-1})	3.6	2.3 a	1.0	1.9 ab	0.8	1.4 b	0.9
Fe-HA (mg kg^{-1})	120	320	120	260	110	250	120
Fe-FA (mg kg^{-1})	0	4	5	3	6	2	2
C/Fe (mol mol^{-1})	170	511	304	456	152	696	352

Different letters indicate significant differences (Scheffe test) at the $p < 0.05$.
Abbreviations: AE = acid extractable; Al or Fe-TEC = metal in the NaOH–Na-pyrophosphate extract; Al or Fe-HA = metal in the humic acid extract; Al or Fe-FA = metal in the fulvic acid extract; C/Al and C/Fe = molar ratio between C and metal in the NaOH–Na-pyrophosphate extract.

matter was humified, even if the quantity of the deposited organic material was different. The humification rate depends on the vegetation, but also on environmental conditions, such as temperature and moisture, which influence the activity of soil organisms (e.g. Gennadiyev 1998). The litter produced by *M. caerulea* is reported to decompose easily, and has a weighted decomposition constant of 0.25 yr^{-1} (Berendse 1998), thus the lack of variation could be caused by the interaction between litter quality and site conditions, namely by the presence of unfavourable soil conditions for microbial communities at the sites where *M. caerulea* grows. As the temperature was homogeneous, with the sampling points located in a restricted area of about half a hectare, the differences could only be related to variable water saturation conditions of the soil; *M. caerulea* is more adapted to poorly-drained soils than *D. flexuosa* (Miles 1985). This hypothesis is supported by the spatial distribution of organic matter humification under the purple moor-grass at different sampling points. The humification index showed in fact a very large range for *M. caerulea*: from 0.25 to 0.56. A decrease of the (HA + FA)/OC ratio was observed when going downslope, towards the sites where the *Sphagnum* was found. The samples located at the bottom of the plot had a lower humification degree (mean = 0.33, $n = 5$). At the *Sphagnum* sampling site, a low humification index was found (0.12), despite the higher accumulation of organic matter. In the area, therefore, the humification of *M. caerulea* organic matter was probably lowered because of soil hydromorphic conditions that may limit the activity of soil organisms. This is also in agreement with the C/N ratio found in the Oa horizons of some profiles located at the bottom of the area of the present work: where *M. caerulea* dominated, the C/N ratio was 26–27, indicating low mineralisation; where *V. myrtillus* was present, at the well drained sites, the C/N was about 20 (Bonifacio *et al.* 2006).

Both quantitative and qualitative differences were found in the fractionation of humic substances. A higher content of HA under purple moor grass and a higher ratio between FA and HA under blueberry were found. While the higher HA contents may simply reflect the accumulation of organic matter under this more productive species, the differences in the FA to HA ratio indicate that the diversity in the transformation pathway of plant debris is subtle, being appreciable only in the quality of humic substances, but clearly visible even in the presence of a potential interaction between vegetation and site conditions. This difference in quality may have important consequences for soil development. In fact, the ratio between FA and HA is a good indicator for podzolisation, as FA enhance metal complexation and translocation because of their higher polarity (e.g. McKeague *et al.* 1986). The contents of these two humic fractions in soils may vary due to changes in vegetation. In Wisconsin, Quideau and Bockheim (1996) found that the afforestation of native prairie induced an increase in fulvic acids and Fe organic complexes, which were then preferentially leached leading to incipient podzolisation. In the Krkonoše Mts., Bonifacio *et al.* (2006) studied a transition between Podzols and Histosols which was, among other factors, also related to shifts in vegetation, and the changes in FA to HA ratios were evident. The results of the present study indicate that the situation is widespread over the Mumlavska Hora area, and suggest a tendency towards the formation of organic soils under *M. caerulea* not only because of the high OC contents, but also because of the lower migration capacity of humic substances.

The lack of differences in the acid-extractable forms of Al and Fe indicates that these metals are scattered over the area, as expected, and not related to vegetation. The forms associated with humic substances were instead higher where *M. caerulea* was dominant. This was, however, not caused by a higher affinity of extractable carbon under *M. caerulea*, as the molar ratio between metals and carbon did not show any difference, and all values of the molar ratios were well below the threshold value for precipitation indicated by Buurman (1985), as expected. When the differences in the analysed fractions are taken into account, the molar ratios are also in agreement with those found by Titeux *et al.* (2002) in forest floor leachates: those authors found a C to (Al + Fe) ratio of 427 at sites showing incipient podzolisation, and lower values where this process was not effective. In the present study, the molar ratio C/(Al + Fe) showed the following order: *Spagnum* < *M. caerulea* < *D. flexuosa* < *V. myrtillus*, thus the low values which are present under *M. caerulea*, further indicate a lower podzolisation where this species dominates. The higher absolute amounts of metals associated with humic substances were probably only related to the different TEC amounts. This was confirmed by the correlation between TEC and metal contents in TEC: the correlation coefficient was 0.50 ($p < 0.01$, $n = 45$) for Al, and 0.43 for Fe ($p < 0.01$, $n = 45$).

Conclusions

The results of this study indicate that, quantitatively, sharp differences were present in the amounts of carbon in organic horizons depending on the kind of shrub or grasses dominating in the area. The differences in the transformation pathway of fresh litter were less visible, probably because of a strong interaction with site conditions, and appeared only in the quality of humic substances. The proportion of fulvic and humic acids was in fact different according to vegetation type and, given the importance that is often given to these organic fractions during soil genesis, this is likely to induce changes in soil processes in the medium to long term. When forest decline triggers a shift in vegetation towards grass species, major changes may therefore be expected not only in the organic horizons, but also in the whole soil profile.

Acknowledgements: Funding of this work by the European Union (contracts CT98-0111 and PL013388), research plan of the CAS AV0Z60870520 and by the project of the Ministry of the Environment of the Czech Republic OC E38.001 is gratefully acknowledged. We thank Angelo Caimi for his help in the vegetation survey.

References

Albers D., Migge S., Schaefer M. & Scheu S. 2004. Decomposition of beech leaves (*Fagus sylvatica*) and spruce needles (*Picea abies*) in pure and mixed stands of beech and spruce. *Soil Biol. Biochem.* 36: 155–64.

Barrett L.R. & Schaetzl R.J. 1998. Regressive pedogenesis following a century of deforestation: evidence for depodzolization. *Soil Science* 163: 482–497.

Berendse F. 1998. Effects of the dominant plant species on soils during succession in nutrient poor ecosystems. *Biogeochemistry* 42: 73–88.

Berendse F., Beltman B., Bobbink R., Kwant R. & Schmitz, M. 1987. Primary production and nutrient availability in wet heathland ecosystems. *Acta Oecologica, Oecologia Plantarum* 8: 265–279.

Bonifacio E., Santoni S., Celi L. & Zanini E. 2006. Spodosol–Histosol evolution in the Krkonoše National Park (CZ). *Geoderma* 131: 237–250.

Brandtberg P.O., Lundkvist H. & Bengtsson J. 2000. Changes in forest-floor chemistry caused by a birch admixture in Norway spruce stands. *For. Ecol. Manage.* 130: 253–264.

Buurman P. 1985. Carbon/sesquioxide ratios in organic complexes and the transition albic–spodic horizons. *J. Soil Sci.* 36: 255–260.

Cudlín P., Chmelíková E. & Rauch O. 1995. Monitoring of Norway spruce forest stand response to the stress impact in the Krkonoše Mts. In: Flousek J. & Roberts G.C.S. (eds.), *Mountain National Parks and biosphere reserves: monitoring and management*, Proc. Int. Conf. IUCN & MAB, Office of Krkonoše National Park, Vrchlabí, pp. 75–80.

Cudlin P., Godbold D.L., Bonifacio E., Egli S., Fritz H.W., Gonthier P., Chmelíková E., Kowalik P., Martinotti M.G., Moravec I., Nicolotti G. & Zanini E. 2003. Conditions of natural regeneration of Norway spruce ecosystems in the Krkonose Mountains. *Ekologia (Bratislava)* 22, Suppl. 1: 66–79.

Cudlín P., Novotný R., Moravec I. & Chmelíková E. 2001. Retrospective evaluation of the response of montane forest ecosystems to multiple stress. *Ekologia (Bratislava)* 20: 108–124.

Drewnik M. 2006. The effect of environmental conditions on the decomposition rate of cellulose in mountain soils. *Geoderma* 132: 116–130.

Gennadiyev A. 1998. Rate of humus (organic carbon) accumulation in soils of different ecosystems. In: Lal R., Kimble J.F., Follett R.F. & Stewart B.A. (eds.), *Soil processes and the carbon cycle*, CRC Press, Boca Raton, pp. 103–107.

Jenny H. 1941. *Factors of soil formation*. McGraw-Hill Publishers, New York.

McClaugherty C.A., Pastor J., Aber J.D. & Melillo J.M. 1985. Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. *Ecology* 66: 266–275.

McKeague J.A., Cheshire M.V., Andreux F. & Berthelin J. 1986. Organo-mineral complexes in relation to pedogenesis. In: Huang P.M. & Schnitzer M. (eds.), *Interactions of soil minerals with natural organics and microbes,* Soil Science Society of America Special Publication, Madison, pp. 549–592.

Miles J. 1985. The pedogenic effects of different species and vegetation types and the implications of succession. *J. Soil Sci.* 36: 571–584.

Nielsen K.E., Ladekarl U.L. & Nornberg P. 1999. Dynamic soil processes on heathland due to changes in vegetation to oak and Sitka spruce. *For. Ecol. Manage.* 114: 107–116.

Quideau S.A. & Bockheim J.G. 1996. Vegetation and cropping effects on pedogenic processes in a sandy prairie soil. *Soil Sci. Soc. Amer. J.* 60: 536–545.

Riise G., Van Hees P., Lundström U. & Tau Strand L. 2000. Mobility of different size fractions of organic carbon, Al, Fe, Mn and Si in podzols. *Geoderma* 94: 327–247.

Rothe A. & Binkley D. 2001. Nutritional interactions in mixed species forests: a synthesis. *Can. J. For. Res.* 31: 1855–1870.

Sequi P. & De Nobili M. 2000. Frazionamento del carbonio organico. In: Violante P. (eds.), *Metodi di analisi chimica del suolo*, Istituto Sperimentale per la Nutrizione delle Piante per conto del Ministero delle Politiche Agricole e Forestali, Roma, pp. 8.1–8.13.

Soil Survey Staff 1999. *Soil taxonomy, a basic system of soil classification for making and interpreting soil surveys,* 2nd ed. U.S. Dept. Agric., Natural Resources Conservation Service, Agriculture Handbook 436, U.S. Govt. Printing Office, Washington, D.C.

Titeux H., Brahy V. & Delvaux B. 2002. Metal complexing properties of forest floor leachates might promote incipient podzolization in a Camisol under deciduous forest. *Geoderma* 107: 93–107.

Ulbrichova I., Podrazsky V.V. & Slodičak M. 2005. Soil forming role of birch in the Ore Mts. *Journal of Forest Science* 51: 54–58.

Vacek S., Bastl M. & Lepš J. 1999. Vegetation changes in forests of the Krkonoše Mts. over a period of air pollution stress (1980–1995). *Plant Ecology* 143: 1–11.

Van Oijen D., Feijen M., Hommel P., Den Ouden J. & De Waal R. 2005. Effects of tree species composition on within-forest distribution of understorey species. *Appl. Veg. Sci.* 8: 155–166.