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Adsorption of allelopathic compounds by wood-derived charcoal: the role of wood porosity

Olivier Keech[1,2,4], Christopher Carcaillet[3] & Marie-Charlotte Nilsson[1]
[1]*Department of Forest Vegetation Ecology, Swedish University of Agricultural Sciences, SE-901 83, Umeå, Sweden.* [2]*Present address: Department of Plant Physiology, Umeå Plant Science Centre, University of Umeå, SE-901 87, Umeå, Sweden.* [3]*Centre of Bio-Archaeology and Ecology (UMR 5059), CNRS/ Université Montpellier 2, EPHE, Institut de Botanique, 163 rue Broussonet, F-34090 Montpellier, France.* [4]*Corresponding author**

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Abstract

In Swedish boreal forests, areas dominated by the dwarf shrub *Empetrum hermaphroditum* Hagerup are known for their poor regeneration of trees and one of the causes of this poor regeneration has been attributed to allelopathy (i.e. chemical interferences) by *E. hermaphroditum*. Fire-produced charcoal is suggested to play an important role in rejuvenating those ecosystems by adsorbing allelopathic compounds, such as phenols, released by *E. hermaphroditum*. In this study, we firstly investigated whether the adsorption capacity of charcoal of different plant species varies according to the wood anatomical structures of these, and secondly we tried to relate the adsorption capacity to wood anatomical structure. Charcoal was produced from eight boreal and one temperate woody plant species and the adsorption capacity of charcoal was tested by bioassays technique. Seed germination was used as a measurement of the ability of charcoal to adsorb allelochemicals. The charcoal porosity was estimated and the pore size distribution was then calculated in order to relate the wood anatomical features to the adsorption capacity. The results showed that the adsorption capacity of charcoal was significantly different between plant species and that deciduous trees had a significantly higher adsorption capacity than conifers and ericaceous species. The presence of macro-pores rather than a high porosity appears to be the most important for the adsorption capacity. These results suggest that fire-produced charcoal has different ability to adsorb phenols in boreal forest soil, and therefore may have differing effects on the germination of seeds of establishing tree seedlings.

Introduction

Wildfire is the most important disturbance factor in boreal forests (Johnson, 1992; Payette, 1992) occurring with 50–100 years of intervals in Fennoscandia (e.g., Engelmark, 1984, 1999; Hellberg et al., 2004; Lehtonen and Huttunen, 1997; Niklasson and Granström, 2000; Zackrisson, 1977). In Northern Sweden, early post-fire successions are usually dominated by *Pinus sylvestris* L., *Populus tremula* L. and *Betula pubescens* Ehrh. in the overstorey and, *Vaccinium myrtillus* L. in the understorey. Long periods without fire favour the growth of *Picea abies* (L.) H. Karst and of the small fire sensitive dwarf shrub *Empetrum hermaphroditum* Hagerup (Haapasaari, 1988; Steijlen and Zackrisson, 1987). The fire suppression over the last 100 years in Swedish boreal forests has led to an intensive use of

* FAX No: +46-90-786-6676
E-mail: Olivier.Keech@plantphys.umu.se

mechanical soil scarification on clear-cuts and has triggered the expansion and the dominance of *E. hermaphroditum* (Zackrisson, 1977). *E. hermaphroditum* is today one of the most common species on northern inland clear-cuts (Data from the Swedish National Forest Survey) where it through chemical interference causes tree regeneration failures (Nilsson and Zackrisson, 1992).

Allelopathy, which involves the release of secondary plant metabolites, is a key process regulating plant regeneration in many world ecosystems (e.g., Fisher, 1987; Keeley et al., 1985; Li and Romane, 1997; Pellissier, 1993; Rice, 1979; Richardson and Williamson, 1988; Waller, 1987; Wardle et al., 1998a). In the boreal forests of northern Sweden, *E. hermaphroditum* releases phenolic compounds, and in particularly the dihydrostilbene Batatasin-III, from green leaves and litter (Nilsson et al., 1998; Odén et al., 1992; Wardle et al., 1998b; Zackrisson and Nilsson, 1992) which inhibits seed germination and seedling emergence, disturbs the plasmalemma integrity of target roots' cells (Wallstedt et al., 2001) and negatively affects mycorrhizal symbiosis of coniferous trees (Nilsson et al., 1993). Further, Batatasin-III impairs soil microbial activity and slows down decomposition which both contribute to an increased accumulation of soil organic material with time since last fire disturbance (DeLuca et al., 2002; Zackrisson et al., 1996). Many phenolic compounds also form recalcitrant complexes with soil organic nitrogen reducing the nitrogen accessibility to vascular plants (Bending and Read, 1996; Gallet and Lebreton, 1995; Wardle et al., 1998b). Therefore, the phenol-regulated accumulation of humus and the reduction of nitrogen available for plants inhibit tree seedling establishment and growth of *P. sylvestris* (Nilsson and Zackrisson 1992; Zackrisson et al., 1996), one of the most commonly occurring tree species in the European and the Asian boreal forests and one of the most important species for the forest industry.

In field experiments, activated carbon has been shown to adsorb phenols released by *E. hermaphroditum* vegetation and to eliminate the inhibitory effects of *E. hermaphroditum* on tree seedlings establishment and growth (DeLuca et al., 2002; Nilsson, 1994; Thoss et al., 2004; Zackrisson and Nilsson 1992). When added to field plots, activated carbon also increases humus nitrogen mineralization and stimulates soil microbial activity (Zackrisson et al., 1996). After a forest fire, up to 2000 kg ha^{-1} of wood charcoal is produced (Zackrisson et al., 1996) and wood charcoal produced by wild fire has similar properties as commercially manufactured activated carbon (Bansal et al., 1988; Chereminisoff and Ellerbusch, 1978). Fire-produced charcoal is thus able to adsorb phenolic compounds released by ericoid plants (Zackrisson et al., 1996). However, the possible differential phenolic adsorption capacities of charcoal produced by different woody species have not been investigated before whereas the wood anatomy varies between species (e.g., Hellberg and Carcaillet, 2003; Schweingruber, 1990).

The aim of the present study is (1) to determine whether the charcoal from different plant species differs in its ability to adsorb allelopathic compounds produced by *E. hermaphroditum* and (2) to investigate whether this adsorption can be related to the wood charcoal anatomy of individual plant species. The ultimate aim of this study is to contribute to a better understanding of the functional role of fire-produced charcoal in the boreal forest ecosystem.

Materials and methods

Plant species and production of charcoal

Twigs of eight plant species abundant in the north European boreal forest were collected close to Umeå, northern Sweden (63°49′N; 20°18′E). The species consisted of five angiosperms (*Betula pubescens* Ehrh., *Empetrum hermaphroditum* Hagerup, *Ledum palustre* L., *Populus tremula* L. and *Vaccinium myrtillus* L.) and three gymnosperms (*Juniperus communis* L., *Picea abies* (L.) H. Karst and *Pinus sylvestris* L.). In addition, twigs of *Ulmus minor* Mill. were collected in southern France (42°26′N; 3°10′E). *Ulmus minor* has been selected for its very large vessels (Jacquiot et al., 1973) and therefore provides a better possibility to test the effects of vessels size on the adsorption capacity of charcoal.

Twigs of 3–4 mm in diameter from each species were cut into segments of approximately 30 mm of length and were then left to dry at room temperature for 1 month. Charcoal was produced in a "muffle furnace" (Nabertherm, L9/S27) according to the following protocol: wood fragments of each species were put in an iron pan. Wood fragments from one species were separated from the others by vertically inserting a glass slide into the pan. The position of wood samples was randomized in the pan and samples were covered with sand to reduce the exposure to oxygen during the burning process. This procedure facilitates production of charcoal and avoids total combustion of organic material and production of ashes. The pan was put in the muffle furnace for 35 min to reach 450 °C and then for an additional 15 min at 450 °C after which the charcoal samples were removed from the muffle furnace. The selected temperature mimics the temperature at the ground surface during wildfire (Chandler et al., 1983; Wiedemann et al., 1988). Then, charcoal samples were sieved to retain material of 0.8–1.6 mm in size that corresponds to the main size of soil charcoal (Carcaillet and Talon, 2001). The burning procedure was replicated three times for each species.

Adsorption of allelopathic compounds

The ability of charcoal to adsorb phenolic compounds from an aqueous solution produced from green leaves of *E. hermaphroditum* was determined by the use of a bioassay method following Zackrisson and Nilsson (1992). In short, this method involved collecting green leaves of *E. hermaphroditum* (At Rovågern, N. Sweden, 63°50′N; 20°15′E), which were allowed to air-dry for 2 weeks. Deionized water was added to 50 g of dry leaves per litre and the solution was agitated during 48 h on a rotary shaker, and producing in this way a 5% weight/volume water extract. This solution was then filtered through a Munktell No. 3 filter paper and diluted with deionized water to produce a 2% solution *E. hermaphroditum* extract. This extract had a total inhibitory effect on seed germination of *Populus tremula* seeds (see below). For each species of charcoal, 0.4 g of charcoal fragments were added to 20 mL of the 2% solution *E. hermaphroditum* and placed on a rotary shaker for 12 h. Charcoal fragments were then removed from the solution by filtration through a filter paper (Munktell No. 3) and 2 mL of the remaining solution was added to each of five Petri dishes (50 mm in diameter). This latter procedure is reiterated for the three replicates of burning. To each dish, 25 *P. tremula* seeds (99.6% viability, stored at −18 °C) are added on a Munktell No. 3 filter paper. The inhibitory effect of the solution on *P. tremula* seeds was monitored and the number of germinated seeds was used as a measure of charcoal adsorption capacity (Zackrisson et al., 1996). To verify whether the charcoal itself might influence on *P. tremula* germination, five dishes were set up with 2 mL of deionized water that was soaked with 0.4 g of charcoal for 12 h; this experiment is performed for all species. The Petri dishes is placed in a climate chamber at 20 °C during 20 h per day of artificial illumination. The total seed germination in each dish was recorded after 7 days.

Charcoal porosity: estimation and size of pores

In this study, pores were defined as all longitudinal cells that represent more than 95% of the total wood composition in the selected species, i.e. the vessels, the fibres and the parenchyma in angiosperms and most of the tracheids in gymnosperms (Figure 1). The porosity of charcoal is defined as a ratio between the total volume of all pores and the total volume of wood. A transversal section of each fragment of charcoal was used to estimate the charcoal porosity. The total area covered by pores was measured within an observation surface of 5250–5500 μm^2. The ratio between the total area of all pores and the observation surface is performed for each species of charcoal to obtain a two-dimensional measurement of porosity called 'transversal porosity'. This ratio serves to investigate whether the adsorption capacity of charcoal is related to the porosity of charcoal. A high value of this ratio corresponds to a high charcoal porosity and conversely, a low value to a low charcoal porosity. The charcoal porosity was measured on 10 transversal sections for each species of charcoal. The final ratio is thus based on the average of the 10 measurements by species of charcoal. All measurements were performed under an episcopic-analysing microscope (magnification: ×500). Values of surface were obtained with the image analysing software 'OPTIMAS 5.2'. The pore area from each observation surface was used to test whether the pores size might be related to

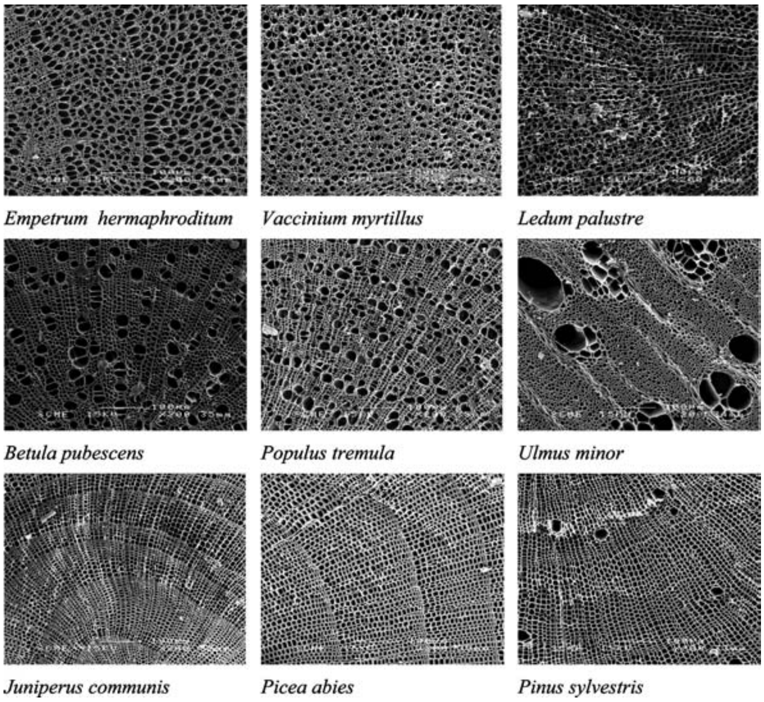

Figure 1. Scanning electronic microscope (SEM) pictures of transversal sections of wood charcoal. All pictures are at the same scale and magnification (×200). The top three pictures (ericoids) show small diameter vessels and fibres. *Betula pubescens* and *Populus tremula* have larger but less abundant vessels. Elm (*Ulmus minor*) has little but very large vessels. The porosity of the three gymnosperms (*Juniperus communis*, *Picea abies* and *Pinus sylvestris*) is mostly composed of tracheids with thin wall in the early wood and thick wall in the late wood.

the adsorption capacity. The pores are classified according to the size of their area into micro-pores ($<50\ \mu m^2$), meso-pores (from 50 to 250 μm^2) and macro-pores ($>250\ \mu m^2$). This classification is based on the frequency of pores area per species (Figure 2). A ratio between the total area occupied by each class of pores and the transversal porosity was calculated. The transversal porosity is thus defined as the sum of three areas i.e. micro-, meso- and macro-pores. Only charcoal produced from wood of ericoïd plants (*E. hermaphroditum*, *L. palustre* and *V. myrtillus*) and broad-leaved deciduous trees (*B. pubescens*, *P. tremula* and *U. minor*) were selected because conifers (gymnosperms) are mostly composed of tracheids that do not show such a distinction between micro-, meso- and macro-pores.

Statistical analysis of data

Homogeneity of variances (Levene test) of data was tested in accordance with the assumptions of ANOVA. Firstly, data relative to adsorption capacity of charcoal (Figure 3) was arsine square root transformed prior to analysis. ANOVA were performed to determine whether the adsorption capacity of different species of charcoal was significantly different from each other. Significant differences between species ($P \leq 0.05$) were $\log_{10}$ transformed and further analyzed by LSD test (least significant difference). Secondly, ANOVA used to determine whether the transversal porosity of each species of charcoal was significantly different between species of charcoal (Figure 4). Significant differences ($P \leq 0.05$) between species are analyzed by Tukey test (honestly significant difference). All statistics are computed with the statistical package 'SPSS 10.0'.

Results

The ability of charcoal to adsorb allelopathic compounds in *E. hermaphroditum* leaf water extract differs significantly (ANOVA: $F_{8,18} = 9.633$;

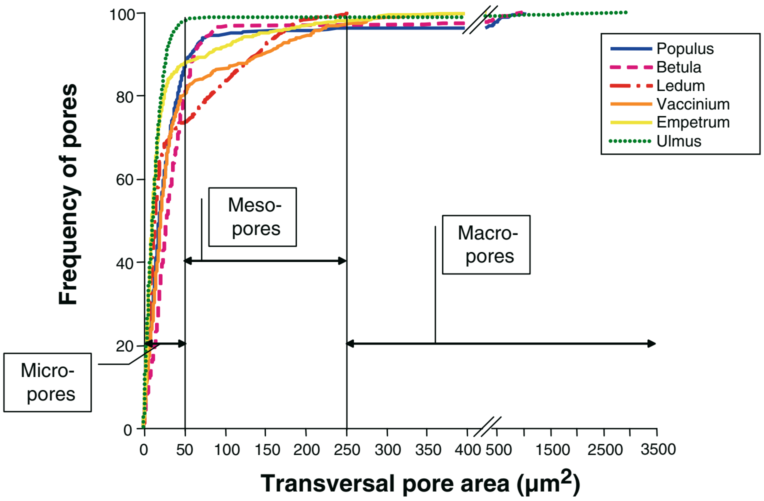

Figure 2. Frequency of pores per area of wood charcoal of different plant species.

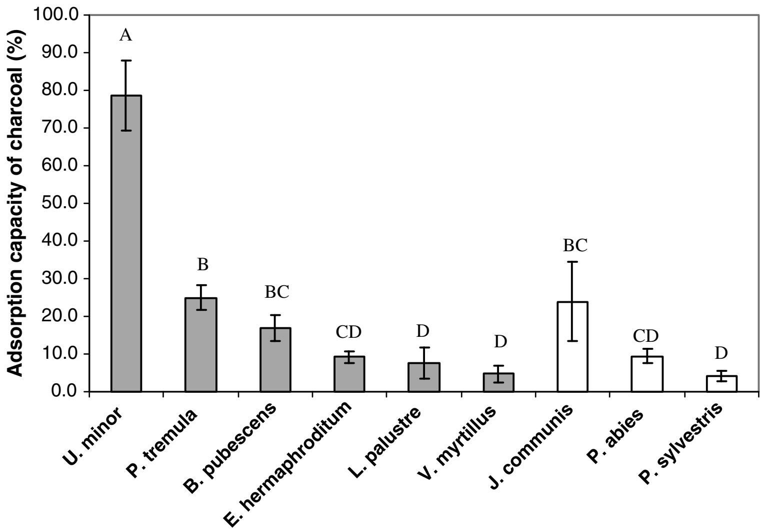

Figure 3. Adsorption capacity of charcoal from different plant species measured as the mean (±SE) number of germinated *Populus tremula* seeds. The shaded bars correspond to angiosperm and open bars to gymnosperms. Data are expressed as the percentage of seeds germinated in deionised water (control). Bars topped with different letters are significantly different from each other at $P \leq 0.05$ (LSD test following ANOVA).

$P \leq 0.001$) between species (Figure 3). With the exception of *Juniperus communis*, the adsorption of allelopathic compounds by charcoal produced from broad-leaved deciduous trees (*B. pubescens*, *P. tremula* and *U. minor*) are higher than the adsorption by charcoal from ericoid species (*E. hermaphroditum*, *L. palustre* and *V. myrtillus*) and conifers (*P. abies* and *P. sylvestris*) (Figure 3). Charcoal produced from *U. minor* wood shows the highest adsorbing capacity amongst the tested plant species, i.e. about three times higher than *P. tremula* and about 15 times higher than *P. sylvestris*. *Juniperus communis* adsorbs allelopathic compounds in the same range as *B. pubescens* and *P. tremula*. The overall lowest adsorption capacities are found for charcoal produced from *V. myrtillus* and *P. sylvestris* (<5% of germinated *P. tremula* seeds). Adsorption capacity of charcoal

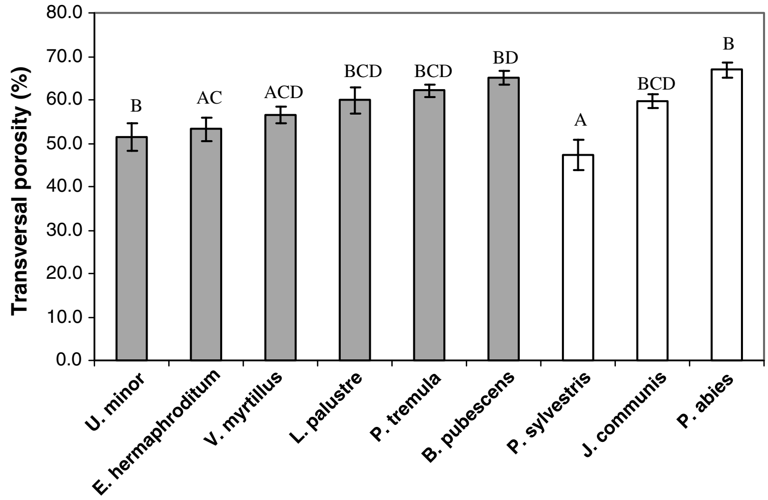

Figure 4. Mean (±SE) of transversal porosity of charcoal from different plant species expressed as percent of the relative total area of pores in the wood. Shaded bars correspond to angiosperms and open bars to gymnosperms. Bars topped with different letters are significantly different from each other at $P \leq 0.05$ (Tukey's HSD test following ANOVA).

produced from *J. communis*, *B. pubescens*, *P. abies* and *E. hermaphroditum* are not significantly different from each other at $P \leq 0.05$ (Figure 3).

The overall transversal porosity varies between 47 and 67% among the species (Figure 4). The highest transversal porosity is found for *P. abies* and the lowest for *P. sylvestris*. The values are significantly different from each other at $P \leq 0.05$ (ANOVA: $F_{8,81} = 7.986$; $P \leq 0.001$). The transversal porosity for *P. sylvestris* is significantly lower than the transversal porosity (<55%) of the other species (Figure 4). The transversal porosity of *U. minor* is also relatively low, but is only significantly different from *V. myrtillus, E. hermaphroditum* and *P. sylvestris*. When transversal porosity is tested against the adsorption capacity of charcoal, no correlation between the two is evidenced (Figure 5).

The frequency of pores per transversal pore areas displays three classes of pores that differ between species (Figure 2). For the broad-leaved deciduous trees, the surface corresponding to the sum of macro-pores represents more than 50% of the transversal porosity (i.e. *U. minor* and *P. tremula*) and almost 40% for *B. pubescens* (Figure 6). The species with the largest relative amount of macro-pores are also the species with highest adsorption capacity (Figure 3). Macro-pores are almost non-existent in *L. palustre*, which is mainly constituted of meso-pores representing more than 75% of the transversal porosity (Figure 6). For *E. hermaphroditum* and *V. myrtillus*, species with relatively low adsorption capacity, the surface of the sum of meso-pores ranges between 40 and 50% of the transversal porosity. The percentage of micro-pores does not differ between species and ranges between 20 and 40% (Figure 6). Examples of transversal wood pattern of selected species are displayed in Figure 1.

Discussion

The results of the present study show that charcoal of different plant species has differing capacity to adsorb phenolic compounds released by *E. hermaphroditum*. The adsorption capacity of charcoal from *U. minor*, deliberately selected for its large pores (vessels), is about double than all other species (Figure 3). Amongst the angiosperms, the adsorption capacity is higher for charcoal produced from broad-leaved deciduous trees than charcoal from ericoid species. Most Ericaceous species are characterized by small pores diameter, whereas broad-leaved trees have larger pores diameter (Figure 1). The adsorption capacity of gymnosperm charcoal differs significantly among the selected species. We expected, however wrongly, the total surface of adsorption

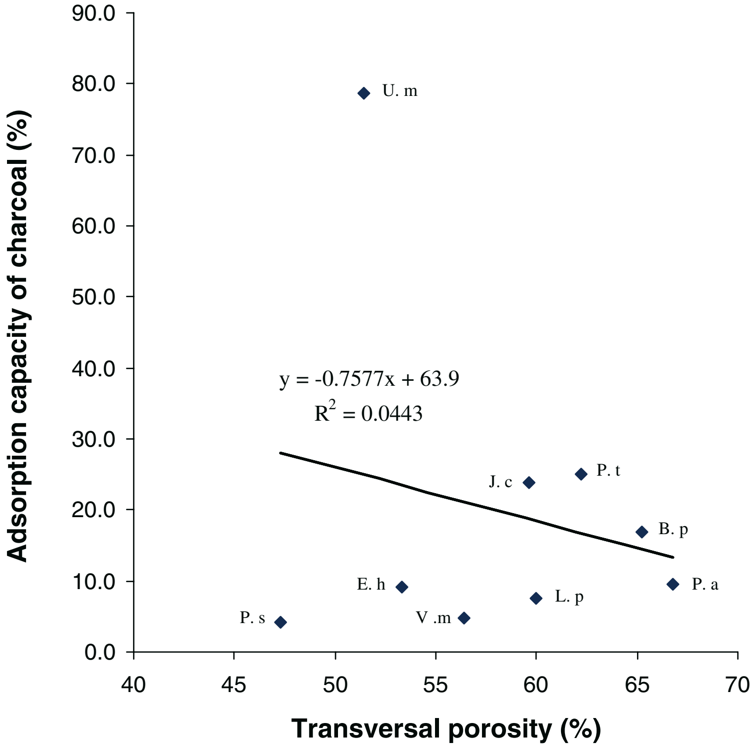

Figure 5. Adsorption capacity and transversal porosity of charcoal from different plant species. U. m: *Ulmus minor*; P. t: *Populus tremula*; B. p: *Betula pubescens*; E. h: *Empetrum hermaphroditum*; L. p: *Ledum palustre*; V. m: *Vaccinium myrtillus*; J. c: *Juniperus communis*; P. a: *Picea abies*; P. s: *Pinus sylvestris*.

to be higher for those charcoal containing small diameter pores than those charcoal having large diameter pores. This is because the relative porosity could have been lower when there was a higher abundance of cell wall material. However, although different species differ in adsorption capacity (presumably due to wood anatom ical differences), transversal porosity of the wood does not emerge as a driver of differences in adsorptive capacities among species because the process seems more complex and involves other factors such as pore size distribution. If the total porosity was a significant factor explaining the adsorption, we should expect charcoal of *P. abies* which had the largest transversal (Figure 4) to also have the largest adsorption capacity (Figure 3), whereas this is not the case (Figure 5). Furthermore, the transversal porosity of *P. abies* and of *P. tremula* are not significantly different from each other (Figure 4), while the adsorption capacity is significantly different (Figure 3).

The pore size distribution for each charcoal species shows that the surface represented by macro-pores is generally higher for broad-leaved deciduous trees than for ericoid species where macro-pores can be almost non-existent like in *L. palustre* (Figure 6). Charcoal species with a high density of macro-pores are also those with the highest adsorption capacity, e.g., *U. minor, B. pub- escens* and *P. tremula* (Figure 3 and 6). This observation suggests that a high adsorption capacity is linked with the total volume of macro-pores. This result is strengthened by the observations of Chereminisoff and Ellerbusch (1978) showing that adsorption capacities of charcoal were the results of both chemical and physical properties. Macro-pores may have a lower surface tension than meso- and micro-pores, which should in turn facilitate the penetration of water and dissolved compounds within charcoal.

Among the gymnosperms, *J. communis* and *P. abies* have a higher total porosity than *P. sylvestris* (Figure 4). SEM pictures (Figure 1) and literature on wood anatomy (Schweingruber, 1990) show that *Pinus* is generally characterized by thick late wood relatively to the thickness of

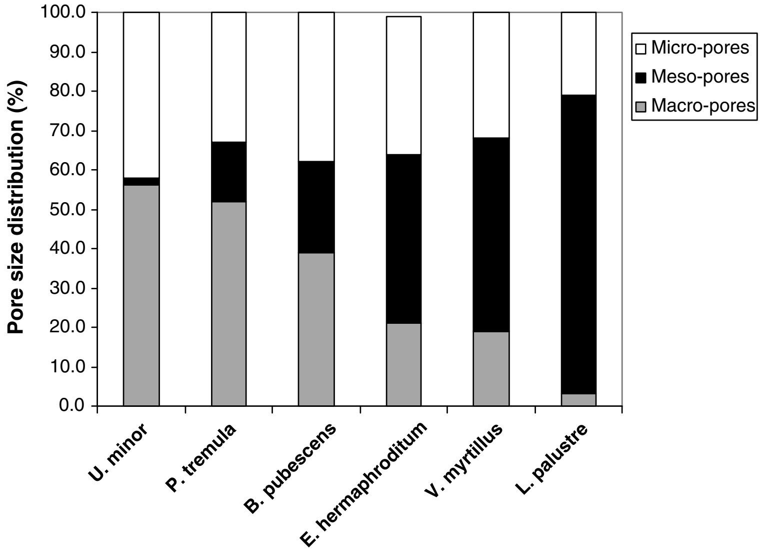

Figure 6. Pore size distribution in charcoal of six angiosperm species. Micro- (μm^2), meso- (50–250 μm^2) and macro-porosity (>250 μm^2) are expressed as percentage of the total number of transversal pores of each species.

early wood, whereas *Juniperus* and *Picea* generally have a narrow late wood. Although the diameter of conifer tracheids is relatively independent of the position within the tree ring, the wall thickness varies significantly which influences the volume of the porosity. Our data indicate that species with a high proportion of late wood material in their tree-rings appear to be linked to a lower adsorption capacity.

The differences in adsorption capacity between all species tested might also be influenced by the presence of wood tar. Tar is produced during the burning process and could block the pores reducing the adsorption capacity of charcoal (www.fao.org/docrep/X5328f/x5328f00.htm#Contents) but also modify the chemical properties of the charred surface. However, it is also likely that the different tree species do not produce the same amount of tar during the burning process, which also could explain why the adsorption capacity is not linked to porosity. The presence of resins within conifers trees might also influence the adsorption capacity of the charcoal produced, by modifying the internal chemical structure of the pores. One of the limitations of the present study relates to the two dimensional estimation of the porosity that we used. The adsorption by charcoal could be influenced by other physical properties such as the length of the pores (i.e. mostly length of vessels for angiosperms and length of tracheids for gymnosperms), the density and the diameter of pit orifices and the shape of the perforations that control the penetration of phenolic compounds into charred cells.

To conclude, the present study supports previous work showing that fire-produced charcoal is able to regulate soil phenolic compounds released by *E. hermaphroditum* in the European boreal forests (Pietikainen et al., 2000; Wardle et al., 1998b; Zackrisson et al., 1996). Obviously, the simple volumetric process of adsorption occurs during the first days, but we stress the need to understand the mechanism and kinetics of the physico-chemical process of adsorption. The identity of the plant producing the charcoal can be important for determining the adsorption capacity. Therefore, it is expected that variations in seed germination and success of establishing new trees seedlings are dependent on differences in charcoal properties. It is likely that the regeneration of trees is less important after a fire in areas dominated by ericoid species associated with conifers than in areas dominated by broad-leaved deciduous tree species notably those with large and abundant vessels, e.g., *Ulmus*, *Quercus*, *Fraxinus*, *Castanea* in temperate forests and, *Salix*, *Populus*, *Betula* and *Sorbus* in boreal forests. The present study highlights the need for conservation of broad-leaved deciduous trees in boreal forests.

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