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Calibration of charcoal production from trees biomass for soil charcoal analyses in subalpine ecosystems

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ABSTRACT

Subalpine ecosystems are mainly affected by surface fires of low to medium intensity. Charcoal production from trees is limited by the duration and the intensity of fires and, thus, by the wood combustibility. Because the combustibility properties of species differ, the functional traits that determine the wood combustibility could explain in part the taxonomic differences of charcoal abundance within the paleo-soil charcoal (pedoanthracological) assemblages. Eight subalpine broadleaf and needleleaf tree species were considered. Wood combustibility was studied by experimental burning on barked-wood samples exposed to constant heat. Two combustibility parameters are estimated (i) the rate of mass loss rate (MLR) and, (ii) the burning rate (BR). While BR describes the proportion of burned biomass per time unit assessing the potential conversion of wood biomass into charcoal, MLR reports the speed of fuel combustion that estimates the potential amount of charcoal produced. A hierarchy of species-specific potential production of charcoal by trees is developed by the use of biplot distribution of MLR and BR. Species were ranked from the worst to the best biomass for the charcoal conversion: *Larix decidua*, *Abies alba*, *Pinus uncinata*, *Picea abies*, *Betula pendula*, *Salix caprea*, *Pinus cembra*, *Sorbus aucuparia*. With thin smooth bark and dense wood, broadleaf trees are expected to produce more charcoal than needleleaves. Bark thickness and wood density explain half of combustibility variance. Thus, the production of charcoal tends to vary among species and among individuals of different diameter according to bark thickness. The amount of charcoal is a proxy of both (i) the abundance of understorey-tree (sapling) due to the high combustion susceptibility of small diameter stems (thin and smooth bark), and (ii) the abundance of woody debris on the ground produced by the canopy trees. The results are discussed in light of simulated data from Holocene soil charcoal assemblages for the western subalpine Alps. Among needleleaves, *L. decidua* is the least productive in terms of charcoal abundance due to its low MLR and BR values, whereas *P. cembra* and broadleaves should be better represented in the soil charcoal assemblages. This study provides rational elements for the quantitative calibration of soil charcoal through species-specific charcoal mass coefficients.

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1. Introduction

Fire is a key process that acts on the carbon budget (e.g. Seiler and Crutzen, 1980; Kasischke and Stocks, 2000), through release of carbonaceous gas toward the atmosphere or sequestration of black carbon within soils and sediments. Soil charcoal particles are analyzed for historical studies on past burned woody communities

(e.g. Jacquot et al., 1973; Albert and Minc, 1987; Hopkins et al., 1993; Favili et al., 2010) or carbon sequestration resulting from paleo-fires (Carcaillet and Talon, 2001; Clay and Worrall, 2011). The vegetation reconstruction inferred from soil charcoal are based on a strong implicit assumption that charcoal mass (charmass) is relative to the total biomass per species, and the combustibility properties of species are neutral. Unfortunately, no study has tackled the question of the species-specific conversion of wood biomass into charcoal. Very few have attempted to propose rate of biomass conversion into charcoal after experimental burning in forest in order to estimate the flux of carbon through soil (Fearnside et al., 2001; Eckmeier et al., 2007). It could be hypothesized that the combustibility properties of each species are different, which does

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not allow a strict comparison of charmass per species within an assemblage, or the charmass between different soils, if the botanical composition of charcoal co-varies with sites. The question is crucial because, depending on the rate of charcoal conversion according to the loss of mass in response to burning, highly combustible species could produce great amounts of burned biomass resulting in an important charmass, whereas some species would be less ignitable and consumable by fires and very little charcoal load could be produced. On the other hand, too high combustibility may lead to an inverse relationship for fine fuels, resulting in low charcoal load due to charcoal consumption into ashes and gases. Fig. 1 summarizes the theoretical framework of the present paper. The amount of charcoal load from trees is limited by both ignition and combustion ability of the outermost surface of trunks. Therefore, species that differ in terms of wood combustibility will produce different charmass from equal wood biomass. This process is able to affect the apparent structure of charcoal assemblages following wildfires and, could thus create distortions in the interpretation of relative representation of taxa in relative value (%) or in charmass (mg kg^{-1}). In this way, the assumption of a constant mass loss rate (MLR) value across species would be an important source of distortion and misleading interpretations in pediaanthracological studies.

Because the combustibility properties of tree species differ, the functional traits that determine the wood combustibility should explain in part the taxonomic differences in charcoal abundance

within the paleo-soil charcoal assemblages. The wood anatomical structure of species co-varies according to their phylogeny. Certain species display thick or rough bark whatever their life conditions. Additionally, the wood density that depends on the type of cells, the thickness of cell walls, and the chemical composition of cell wall is closely linked to the phylogeny.

Mountain ecosystems have been investigated using soil charcoal analyses, especially subalpine ecosystems (e.g. Tessier et al., 1993; Carcaillet and Brun, 2000; Touflan and Talon, 2009). Subalpine ecosystems experienced frequent fires during the Holocene (Carcaillet et al., 2009; Blarquez et al., 2010), whereas fires are rare today. These paleo-fires had effects on the plant communities (Blarquez and Carcaillet, 2010) and the ecosystem dynamics (Genries et al., 2009a; Mourier et al., 2010). The subalpine ecosystems are composed of species that are intuitively and traditionally distinguished according to their combustibility properties. Larch (*Larix decidua* Mill.) is used as firewood because its burning rate is low and the energy released high, whereas pines (*Pinus cembra* L., *Pinus uncinata* Mill.) are less appreciated, as they release energy too rapidly. Similarly, among broadleaf trees, beech (*Fagus sylvatica* L.) is greatly preferred as firewood to poplar (*Populus* sp.), willows (*Salix* sp.) or birches (*Betula* sp.). Furthermore, the firewood qualities of broadleaf and needleleaf species varies, including for their energy release and their MLR. Finally, knowing that larch and arolla pine (*P. cembra*) have different burning properties and, that Holocene charcoal assemblages are almost exclusively dominated by cembra pine in the northern Alps (e.g. Carcaillet and Brun, 2000) whereas larch co-abounds with cembra pine in the southern Alps (e.g. Talon, 2010), suggests that comparison of total soil charcoal mass should take into account wood combustibility for more solid interpretations. Consequently, the hypothesis of functional traits that determine the bark and wood properties and bark/wood ratios was tested on eight frequent subalpine broadleaf and needleleaf trees. Wood combustibility was measured by experimental burning on barked-wood samples exposed to constant heat. Two combustibility parameters are estimated: (i) the mass loss rate (MLR) and, (ii) the burning rate (BR). While BR describes the proportion of burned biomass per time unit assessing the potential conversion of wood biomass into charcoal, MLR reports the speed of fuel combustion that estimates the potential amount of charcoal produced.

2. Methods

2.1. Sampling

The eight tree species analyzed in this study constitute the main plant biomass in subalpine ecosystems in Europe. Plant communities in these ecosystems are dominated by needleleaf trees, e.g. larch (*L. decidua*), arolla pine (*P. cembra*), mountain pine (*P. uncinata*), spruce (*Picea abies* (L.) Karst.) and fir (*Abies alba* Mill.), with scattered broadleaf trees, e.g. *Betula* sp., *Populus tremula* L., *Salix* sp., and *Sorbus* sp., most genera being represented by several species. Here, the three most common broadleaves in terms of occurrence and biomass were selected, i.e. *Betula pendula* Roth. (silver birch), *Salix caprea* L. (goat willow) and *Sorbus aucuparia* L. (rowan). As *P. tremula* (aspen poplar) and *Salix* species display similar anatomy and wood properties (Schweingruber, 1990), goat willow was chosen as a representative for the erect willows and aspen poplar. These eight species were sampled in the Maurienne valley (Savoie, French Alps), from situations with similar ecological contexts, i.e. north-facing slopes at altitudes between 1900 and 2000 m a.s.l. Living trunks of ten individuals per species in the diameter-class 7–10 cm were sampled at ~50 cm height, where ground fires would be most likely to have an impact on trees.

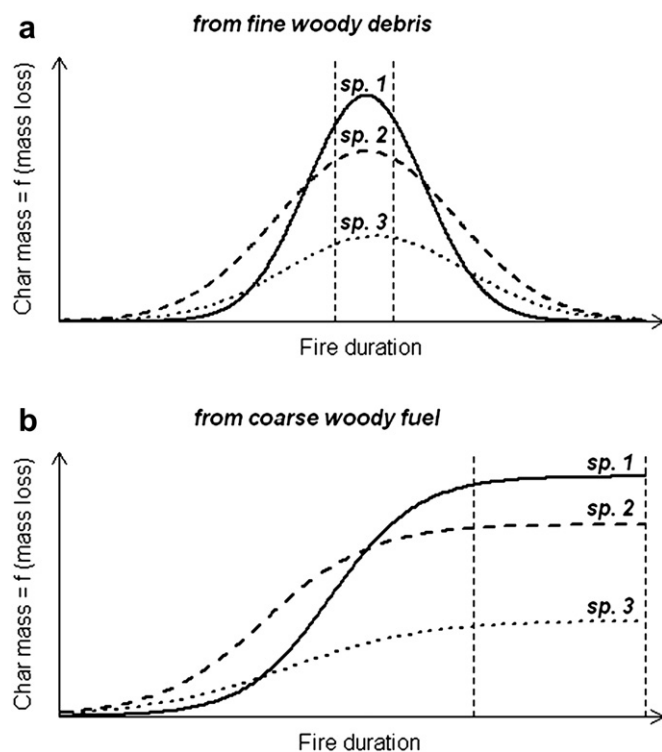


Fig. 1. Conceptual model of specific potential of charcoal production according to specific combustibility. The specific charcoal mass produced from fine woody debris (a) or coarse woody fuels (b, like large dead twigs on soil, live stems and trunks) is dependant of the fire duration of a given intensity and of fuel combustibility (ignition and combustion ability). The charmass is a function of the mass loss of woody fuels. Significant charmass differences between species (within vertical dotted lines) owing to the expression of specific combustibility are reached after a certain fire duration (a, b) and disappeared for fine woody debris when fire duration is too long due to complete charcoal consumption, i.e., when fuel is the limiting factor (a, right side), contrary to coarse woody fuels where the limiting factor is the fire duration or intensity (b, right side). Under a neutral hypothesis of biomass equitability between species, the charmass following a fire is expected to be greater for the most combustible species, i.e., greater for sp. 1 than sp. 2 and lower for sp. 3.

Combustibility analyses were conducted on dried samples of standing trees (i.e., unweathered) to maximize standardization (i.e., unbiased comparisons between species) and because time required to sample preparation for burning did not allow retaining *in situ* moisture content. The samples were stored for ~6 months away from moisture, to allow natural air-drying without altering the physico-chemical properties of bark and wood. The experiment does not take into account the environmental stressors (e.g. water variability) and test only the function of biological traits on the biomass conversion into charcoal.

Samples for burning in the combustion experiments were extracted from the peripheral parts of trunks (bark and first millimeters of sapwood) to obtain barked-wood samples. One sample from each of 10 different individuals per species was randomly selected, to produce a set of 10 experimental samples by species, i.e., 80 experimental burnings. Samples were cut to obtain a constant volume of wood (3×2 cm area of bark and 1.5 cm in radial section). Sample standardization was also based on a constant surface-to-volume ratio, as this is a major factor in combustibility (Papio and Trabaud, 1990). Differences in dry mass between samples reflect differences in wood density (WD). Supplementary wood samples were cut from under the bark ($3 \times 2 \times 1.5$ cm of wood) to measure the wood density.

2.2. Biological traits

For each tree, bark traits and WD were recorded from the barked-wood samples and supplementary wood samples respectively. WD (g cm^{-3}) is the ratio given by the oven-dried mass of a wood sample divided by its volume. Measurements of volume were obtained from the geometrical dimensions of the wood core (Chave et al., 2006). The bark traits: bark thickness (BT, mm), bark heterogeneity or bark roughness (BH, no unit), proportion of outer bark (rhytidome) over entire bark (OB), were measured on all dried barked-wood samples. Individual BT was estimated from the maximal value of 10 measurements per sample; BT sometimes varied considerably within a single sample. In order to obtain quantitative estimates of bark fissure-depth and degree of bark roughness for a given BT (i.e. the bark heterogeneity as proportion of the bark thickness), BH was estimated for a sample i as follows (Eq. (1)):

$$BH_i = \frac{BT_{i\max} - BT_{i\min}}{BT_{i\max}} \quad (1)$$

where $BT_{i\min}$ and $BT_{i\max}$ are the minimum and maximum bark thicknesses measured for the individual i . Standardized bark thickness, i.e. expressed as proportion of stem diameter, was estimated from the ratio between BT and diameter.

2.3. Burning experiments and combustibility variables

Barked-wood samples were placed in a drying oven for 72 h at 30 °C to ensure gentle and uniform drying and to prevent peeling of bark. It was assumed that experimentally revealed differences of trunk combustibility between species for a standard diameter-class are conserved in the field, although field moisture content can affect burning properties. Dried samples were submitted to constant heat (215 ± 6 °C) from an epiradiator (reference UNE 23729-90-IR). A burning experiment began when the sample was exposed to the heat source, and was considered complete when the flame self-extinguished. Sample mass and temperature were measured continuously at 2 s intervals using a digital scale (accuracy: ± 0.01 g) and a K-type thermocouple (accuracy: ± 0.1 °C) placed at 1 cm above the sample. Both datasets were digitized in real time

using the programs RsWeight 1.0 (©A&D Company) and AMR Control 5.13, respectively.

Two combustibility variables were computed to describe burning efficiency and potential conversion of wood into charcoal: i) the mass loss rate (MLR, g s^{-1}) which expresses the speed of wood combustion and reflects the potential quantity of biomass converted into charcoal; ii) the burning rate (BR, $\% \text{ s}^{-1}$), i.e., the mean proportion of burned biomass per time unit (Eq. (2)), which reproduce the potential proportion of biomass converted into charcoal. Ignition delay was also measured.

$$BR = \frac{1}{n \cdot dt} \left[\sum_{t=1}^n \frac{1}{dt} \left(1 - \frac{m_{t+1}}{m_t} \right) \right] \quad (2)$$

where dt is the time unit of calculations (2 s), m_t is the sample mass at time t , and $n \cdot dt$ is the duration of the burning experiment here, i.e. the time between sample exposition to heat and ignition end, expressed in number of time units. The standardization by the mass (m) at a given time instead of the initial mass allows describing the temporal dynamics of fuel combustion properties during burning. The ignitability was indirectly considered in the analyses because combustibility variables were computed from a time period that encompass pre- and post-ignition (i.e., since heating to combustion end). In this way, ignition ability of fuel can act on combustibility as the fuel ignites more quickly, more the combustion occurs early.

2.4. Data analysis

Multi comparisons of combustibility variables between species were performed using analysis of variance (ANOVA) followed by Duncan's multiple comparison tests. Variables were rescaled between 0 and 1 as follows:

$$Y' = \frac{Y_i - Y_{\min}}{Y_{\max} - Y_{\min}} \quad (3)$$

where Y_i is the value of a given individual; and Y_{\min} and Y_{\max} the minimum and maximum values over all individuals, respectively.

Correlation analyses between combustibility variables and plant traits were carried out with Spearman's coefficient. Multiple linear regressions were conducted to evaluate the variance of combustibility variables explained by biological attributes. Interspecific differences in biological traits were analyzed using Kruskal–Wallis (KW) non-parametric tests, followed by Mann–Whitney pairwise tests (W) at significance level $p = 0.05$. Analyses were performed using the R program (stats and FactoMineR packages, Le et al., 2008) and Statgraphics Centurion XVI for Duncan tests.

3. Results

3.1. Burning efficiency

Interspecific comparisons of combustibility variables (Table 1) show significant differences in burning efficiency between trunk samples of angiosperms (broadleaf) and gymnosperms (needleleaf). Duncan's multiple range tests indicate that the broadleaf species (*S. aucuparia*, *B. pendula* and *S. caprea*) have a higher rate of mass loss, MLR ($p < 0.05$; Table 1) than the needleleaves (*P. cembra*, *P. abies*, *P. uncinata*, *A. alba* and *L. decidua*). *Larix* has the lowest MLR ($p < 0.05$) and the lowest burning rate (BR) with *Abies*. *P. cembra* has the highest BR with *S. aucuparia* ($p < 0.05$). Species ranking for burning efficiency changes according to the process taken into account (Fig. 2). If the mass loss is the focus (MLR), the burning efficiency of trunk samples is higher for broadleaf than needleleaf trees. However, burning efficiency of broadleaves is high but not

Table 1

Mass loss rate (MLR) and burning rate (BR) of some dominant European subalpine tree species on a 0–1 scale.

Species	MLR ^a		BR ^b	
	Mean ^c	s.d.	Mean ^c	s.d.
<i>Sorbus aucuparia</i> (Sa)	0.75 A	0.07	0.52 A	0.03
<i>Betula pendula</i> (Bp)	0.59 B	0.04	0.33 B	0.03
<i>Salix caprea</i> (Sc)	0.58 B	0.03	0.38 B	0.03
<i>Pinus cembra</i> (Pc)	0.47 C	0.05	0.61 A	0.12
<i>Picea abies</i> (Pa)	0.42 C	0.04	0.35 B	0.07
<i>Pinus uncinata</i> (Pu)	0.39 C	0.03	0.29 BC	0.06
<i>Abies alba</i> (Aa)	0.39 C	0.04	0.21 CD	0.04
<i>Larix decidua</i> (Ld)	0.28 D	0.05	0.16 D	0.03

^a MLR reports the speed of fuel combustion that illustrates the potential quantity of biomass converted into charcoal.

^b BR expresses the percentage of burned biomass per time unit that illustrates the potential wood conversion into charcoal.

^c Test of significance was performed by Duncan's multiple range test, at 95% confidence level. The means with the same letters are not significantly different.

significantly higher than needleleaves when the proportion of mass lost (BR) is the focus (Table 1; Fig. 2). Taking into account these complementary metrics of burning efficiency, species ranks in an ascending order of burning efficiency from *Larix* to broadleaf trees and *P. cembra* through other needleleaf trees (Fig. 2). On a 0 to 1 scale, cembra pine has $\sim 2\times$ mean MLR value than larch (0.47 ± 0.05 versus 0.28 ± 0.05 , respectively) indicating that this first species would produce twofold more charcoal than larch (Table 1). Furthermore, *Sorbus* has a mean MLR (0.75 ± 0.07 , Table 1) that is $\sim 3\times$ the larch value.

3.2. Relationships between combustibility and biological traits

Multiple regression analyses summarize the effects of bark and wood traits on combustibility variables since the sample exposition to heat to the end of ignition (Table 2). Bark thickness (BT) has a significant inhibiting effect on burning efficiency decreasing MLR and BR ($p < 0.001$). The other bark traits (outer bark, OB; bark heterogeneity, BH) are strongly correlated with BT (Spearman's $r > 0.52$, $p < 0.001$) and do not explain more variance of combustibility variables when they are added to the model. Concerning the general temporal patterns of these relationships calculated for all individuals taken together (Fig. 3), the inhibiting effect of bark traits on combustibility occurred mainly after the ignition period, i.e.,

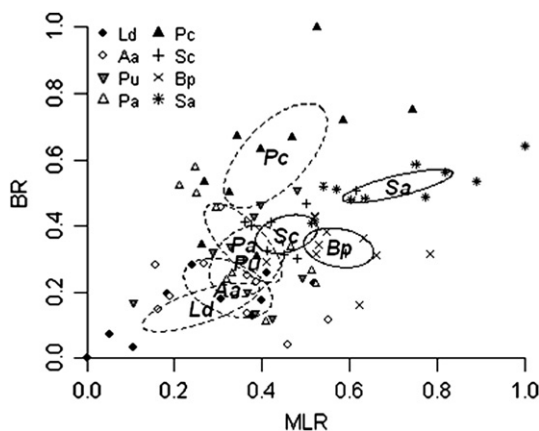


Fig. 2. Burning efficiency of trunks of tree species expressed by both mass loss rate (MLR) and burning rate (BR), rescaled on 0–1 axes (Eq. (3)). 95% confidence intervals for average coordinates of species (means \pm SE) are depicted by ellipses (dashed for needleleaf species). The species are labeled as follows: “Ld”, *Larix decidua* (larch), “Aa”, *Abies alba* (fir), “Pu”, *Pinus uncinata* (mountain pine), “Pa”, *Picea abies* (spruce), “Pc”, *Pinus cembra* (arolla pine), “Sc”, *Salix caprea* (goat willow), “Bp”, *Betula pendula* (silver birch), “Sa”, *Sorbus aucuparia* (rowan).

Table 2

Multiple regression analysis between combustibility variables and plant traits representing simple effects of WD and BT on combustibility (top); and interaction effect between WD and ID (MLR: mass loss rate; BR: dynamic burning rate; ID: ignition delay; WD: wood density; BT: bark thickness). *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; n.s. $p > 0.05$.

MLR		BR	
<i>t</i> -value		<i>t</i> -value	
WD	3.79***	WD	−4.79***
BT	−5.54***	BT	−5.79***
df = 77	$F = 21.37$		$F = 29.92$
	$R^2 = 0.34***$		$R^2 = 0.42***$
WD	5.39***	WD	−1.48 n.s.
BT	−6.19***	BT	−6.48***
WD: ID	3.54***	WD: ID	−3.63***
df = 76	$F = 20.57$		$F = 27.49$
	$R^2 = 0.43***$		$R^2 = 0.50***$

during flaming combustion. Furthermore, WD increases significantly the MLR during flaming combustion (Fig. 3a), whereas BR decreases significantly ($p < 0.001$, Table 2) during the same period (Fig. 3b). WD was negatively correlated with MLR and BR during the ignition period (Fig. 3), dense woods retarding ignition ($r = 0.29$, $p < 0.01$). Moreover, this inhibiting effect of WD remained during flaming combustion for BR, contrary to MLR. Removing the interaction effect between WD and ignition delay, WD loses its significant effect on BR ($p > 0.05$, Table 2) contrary to MLR ($p < 0.001$, Table 2).

The relationships between these functional traits and burning efficiency metrics are illustrated in Fig. 4. Linear regressions indicate that the ratio WD on BT explain 40% of MLR variance (df = 78, $F = 53.03$, $p < 0.001$) whereas 42% of BR variance is explained by the inverse of the product between WD and BT (df = 78, $F = 57.8$, $p < 0.001$). Species ranking of burning efficiency (Fig. 2) fits well with bark thickness (Fig. 5a) and more coarsely with wood density (Fig. 5b). *Larix* has the highest BT and the lowest MLR and BR means (Figs. 4 and 5). *Sorbus* and *P. cembra* have the lowest BT and the highest BR (Figs. 4 and 5). Broadleaf trees, having relatively thinner bark and denser wood (Fig. 5), have higher MLR than needleleaves (Fig. 4a).

4. Discussion

4.1. Burning properties of subalpine wood

Burning properties of barked-wood of eight European subalpine species was experimentally quantified by two combustibility variables. Both species ranking and relationships with functional traits change with the process taken into account. The burning efficiency rating of species is better established based on bark thickness compared to wood density (Fig. 5; Table 2). Potential wood conversion into charcoal decreases with increasing bark thickness. The latter inhibits wood combustibility whatever the process considered, i.e., proportion or amount of charred biomass (described by BR or MLR, respectively). MLR was higher for angiosperms (*S. aucuparia*, *B. pendula* and *S. caprea*) than gymnosperms (*P. cembra*, *P. uncinata*, *P. abies*, *A. alba* and *L. decidua*) indicating that amount of charred biomass is higher for species with dense wood (angiosperms) (ratio WD/BT, Fig. 4a), wood density enhancing combustibility (Table 2). This phylogenetic distinction disappears when considering the burning rate of a fuel particle (BR, Fig. 4b), because the speed with which a bark-wood volume burns is not affected by wood density after accounting for ignition ability (Table 2). Therefore, high ranks of BR are given for species with both light wood and thin bark (*P. cembra*) or for species such as *Sorbus* that exhibited both dense wood and thin bark. These two rankings

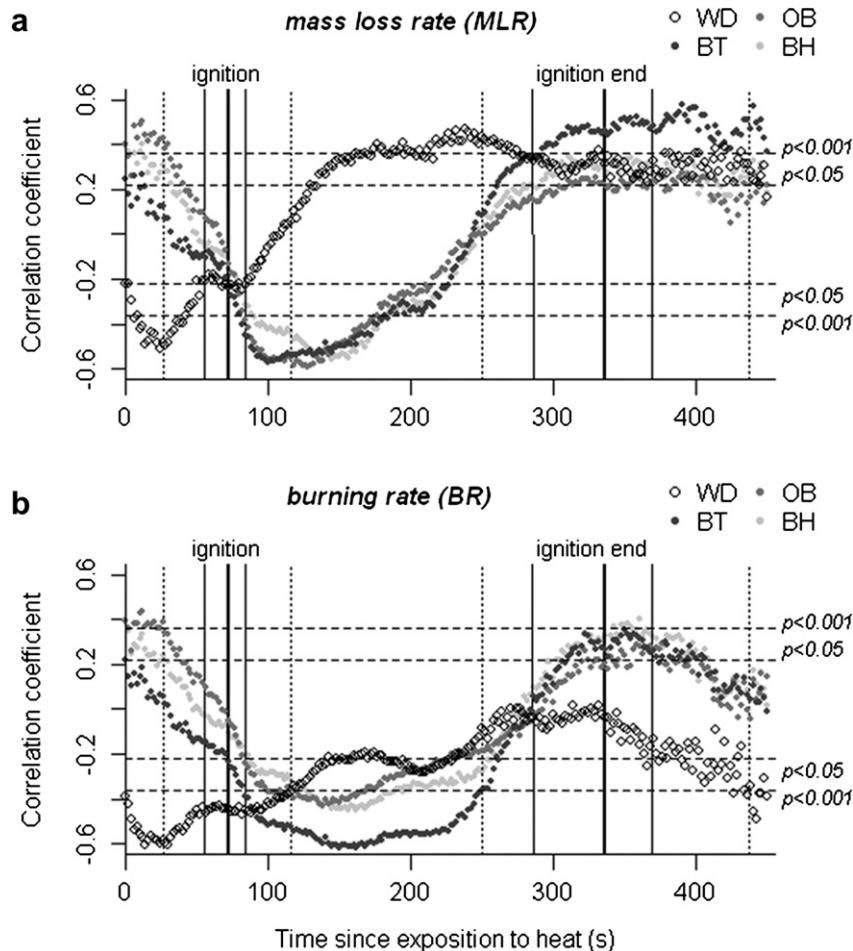


Fig. 3. Temporal pattern of correlations between combustibility variables and functional traits during burning tests. Spearman coefficients were computed between individual trait values (BT = bark thickness; BH = bark heterogeneity or bark roughness; OB = outer bark or rhytidome; WD = wood density) and running means of combustibility variables calculated from all individuals taken all together ($n = 80$) [MLR (a), BR (b)] per time windows of 20 s. Vertical dotted lines delimit from left to right 5th, 25th, 50th, 75th and 95th percentiles of overall ignition times (left) and overall times of flame extinction (right). Levels of significance are represented by horizontal dashed lines.

clearly support the fact that biomass conversion into charcoal is more controlled by functional traits of species than by phylogenetic traits.

Although fuel density controls the thermal conductivity of fuel (Anderson, 1970; Nagaoka et al., 1998) and therefore the propagation and intensity of combustion on a given surface or volume, bark thickness appears to be the main trait controlling the potential of charcoal production during fires. Consequently, hardwood species with thin bark, such as the selected broadleaf trees, tend to burn more efficiently and would thus produce more charcoal relative to their biomass than species with thick bark and or light wood such as *L. decidua* (Fig. 4). These results imply that charcoal load is mainly produced by stems with thin or no bark, i.e. by woody debris on soils (twigs, stems, trunks) and small trees, especially in subalpine ecosystems where fires are of low to medium intensity and rarely affect tree crowns, leaving trees with fire-scars (Genries et al., 2009b), in contrast to forest-fires in the hill and mountain belts where the high intensity results in high tree mortality and all trees are scorched (Moser et al., 2010). However, fire intensity linked to weather, fuel type, and vegetation structure is rarely reported information in the data base from the Alps (Zumbrunnen et al., 2009). For comparison, it was reported in the northern boreal forest, which is analogous to the subalpine, that most charcoal produced in crown fires was related to woody debris on the ground

and to the understory vegetation, i.e. saplings and shrubs (Bégin and Marguerie, 2002).

4.2. Potential of charcoal production

The relative coefficients of burning efficiency assigned to the MLR means (see Table 1) can be used to rank species in ascending order of charcoal production potential during surface fires of low to medium intensity whatever the cause of the fire, natural or human. MLR can be used for calibrating the species charmass from soil assemblages because char load in soils can be treated in quantity (charmass) but not in proportion of wood biomass. Nevertheless, BR scores could be used to calibrate the inverse process, which is the proportion of living tissue burned during fires, involving functional processes including carbon fluxes. The MLR ranking clearly show that *L. decidua* has a lower potential for charcoal production compared to *P. cembra*, among needleleaf species, with intermediate representation for *A. alba*, *P. uncinata* and *P. abies* (Fig. 4). Broadleaf-hardwood trees have a better conversion rate compared to needleleaf-softwood, with *S. aucuparia* having the highest score. Based on the huge similarities of wood structure between woody *Rosaceae* species (Schweingruber, 1990), the high rate of charcoal conversion calculated by the MLR for *S. aucuparia* (0.75) should apply to this taxonomic group. In the western

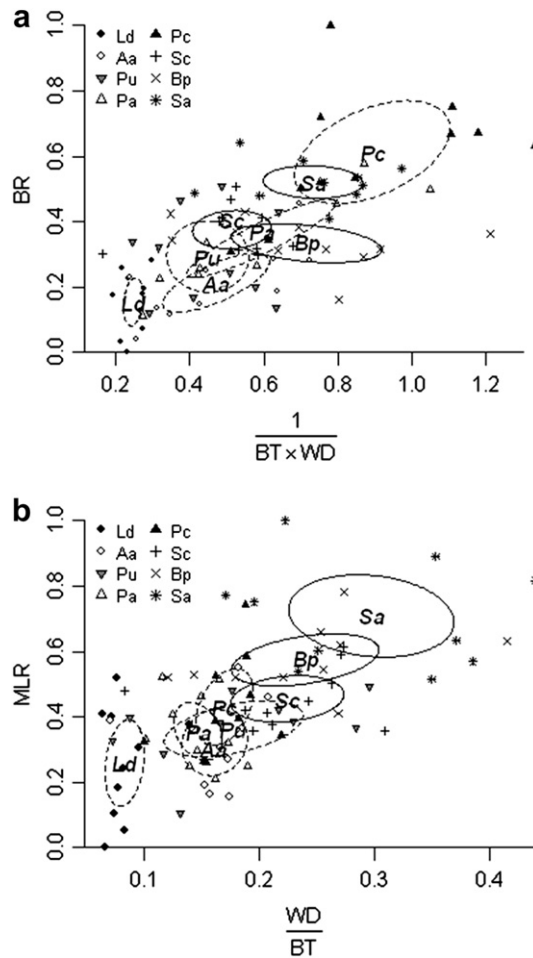


Fig. 4. Relationship between tree combustibility (MLR and BR) and functional traits (a: ratio of BT and WD or, b: the inverse of product of BT and WD, respectively) carried out by linear regressions on all observations (see Table 2). 95% confidence intervals for average coordinates of species (means \pm SE) are depicted by ellipses (dashed for needleleaf species). The species are labeled as follows: "Ld", *Larix decidua* (larch), "Aa", *Abies alba* (fir), "Pu", *Pinus uncinata* (mountain pine), "Pa", *Picea abies* (spruce), "Pc", *Pinus cembra* (arolla pine), "Sc", *Salix caprea* (goat willow), "Bp", *Betula pendula* (silver birch), "Sa", *Sorbus aucuparia* (rowan).

European subalpine ecosystems the treed *Rosaceae* encompass, *sensu lato*, the genus *Amelanchier* (1 sp.), *Cotoneaster* (2 sp.), *Prunus* (2 sp.), and *Sorbus* (4 sp.). Among the *Rosaceae*, the sub-family of *Rosoideae* presents a clear distinct wood anatomy and can not be merged with the other *Rosaceae*. The same consideration can be adopted for the two other groups of trees that contribute to the

subalpine and mountain ecosystems. The score calculated for *S. caprea* should also apply to the very numerous *Salix* species and to *P. tremula*. *B. pendula* (MLR = 0.59) presents a very similar wood structure to the other *Betulaceae* species (i.e., *Betula pubescens* and the 2 sp. of *Alnus*). However, because the bark properties of *Betula* and *Alnus* differ greatly, controlling burning efficiency, this extrapolation from birch to alder must be taken with caution.

Because the bark thickness co-varies with the age and the shape of individuals by increasing its thickness and roughness, the poorly charred biomass of species such as *L. decidua*, *A. alba*, and *P. uncinata* are much more likely to be converted into charcoal when they are small, at the sapling stage. Furthermore, the results predict that twigs should be more transformed into charcoal than trunks that are well protected by their bark. This hypothesis matches the result of observations in the northern boreal forest reporting that living trunk is a poor charcoal producer compared to woody debris and to shrubs (Bégin and Marguerie, 2002). The amount of charcoal is a proxy of both (i) the abundance of understory-tree (sapling) due to the high combustion susceptibility of small diameter stems (thin and smooth bark), and (ii) the abundance of barkless-decayed woody debris on the ground produced by the canopy trees.

4.3. Application to Quaternary charcoal assemblages

Based on these results, an index is proposed for the estimation of the relative abundance of biomass ($RA_{biomass}$) inferred from soil charcoal concentration (Carcaillet and Talon, 2001) corrected by the species-specific mass loss rate, MLR_i , scaled between 0 and 1:

$$RA_{biomass_i} = (1 - MLR_i) \frac{m_{char_i}}{M_{soil}} \quad (4)$$

where m_{char_i} is the dried charcoal mass of the species i , and M_{soil} the dried mass of soil particles less than 2 cm in diameter.

Fig. 6 displays three theoretical charcoal assemblages composed of only two species, *P. cembra* (Pc) and *L. decidua* (Ld), expressed in percentage of charmass. Although these assemblages appear caricatural due to the low number of species, they resemble many assemblages observed in the subalpine Alps, with few charmass percentages of other taxa e.g. *Betula*, *Alnus*, *Salix/Populus*, *Ericaceae*, *Juniperus* (e.g. Talon et al., 1998; Carcaillet and Brun, 2000; Carnelli et al., 2004; Talon, 2010). These assemblages were transformed in $RA_{biomass}$ based on Eq. (4) and the MLR values of Table 1 in order to estimate the relative abundance of initial charred biomass (Fig. 6). The "black" assemblage contains 63 and 37% of charmass of Pc and Ld, respectively, resulting in an equal biomass abundance of both species (50%). The second assemblage, "grey", contains 55 and 45% of Pc and Ld, respectively, although the proportions of burned biomass reconstructed with MLR show less Pc (42%) than Ld (58%).

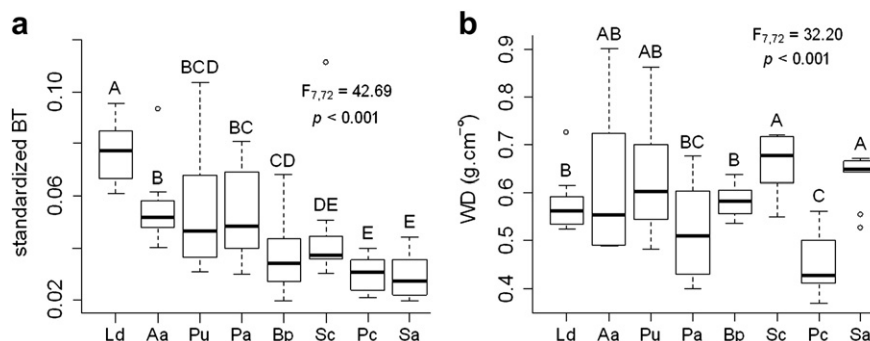


Fig. 5. Interspecific comparisons of the functional traits standardized bark thickness (a, i.e. BT standardized by the stem diameter) and wood density (b). Species are ordered by increasing burning efficiency given by biplot distribution (see Fig. 2). Interspecific comparisons of medians were performed with Kruskal–Wallis test followed by Mann–Whitney pairwise tests (W) at significance level $p = 0.05$. Different letters indicate medians significantly different.

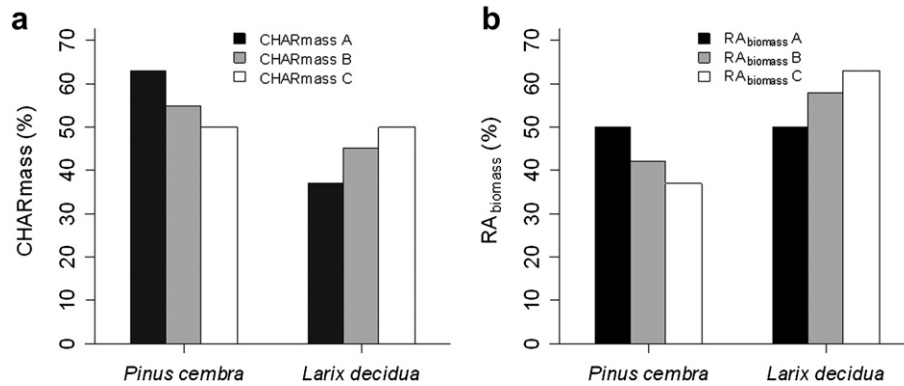


Fig. 6. (a) three theoretical assemblages (black, grey, white), each based on the ratio between two species (*Pinus cembra*, *Larix decidua*) characterized by their relative (%) charmass. (b) The reconstructed biomass based on the same assemblages corrected using the MLR scores of the Table 1 and the fourth equation.

The “white” assemblage initially shows 50% of each species, although it contains much more Ld (63%) after transformation. An overview of the three assemblages shows that the correction is important, changing the general trend. Here, the correction indicates that these assemblages are dominated (or equal, at least) by *P. cembra*, as would be normally concluded by pediaanthracological studies, but conversely the assemblages correspond to burned communities where the main charred biomass was from *L. decidua*.

This simple simulation based on a MLR ratio of ~ 2 between *Larix* (0.28) and *P. cembra* (0.47) demonstrates that such correction or calibration can be crucial especially if the assemblages are composed of both broadleaf-hardwood species with very high MLR values (>0.6) and needleleaf-softwood with low MLR values (<0.4). This type of assemblages with extremely different burning properties of wood should be common in middle mountain altitudes or in Mediterranean areas where mixed forests contain both needleleaf-softwood (e.g., *Pinus*, *Abies*, *Picea*) and broadleaf-hardwood trees (e.g., *Acer*, *Fagus*, *Quercus*).

5. Conclusion

The present experimentation demonstrates the importance of the calibration of charcoal on wood combustibility for correct interpretation of Quaternary assemblages. As the first soil charcoal studies were innovative by taking into account the botanical identification of charred fragments (Jacquot et al., 1973; Albert and Minc, 1987), it appears crucial to secure the quantitative reconstruction of burned woody paleo-communities. The use of charmass is recent (e.g. Carcaillet and Talon, 2001; Carnelli et al., 2004), but it needs correction or calibration of the charcoal to secure interpretation. Functional traits of wood density and bark structure partly explain the conversion of wood into charcoal, with hardwood species with thin and smooth bark showing a higher rate of charcoal conversion (e.g. *S. aucuparia*), compared to trees with softwood and thick-rough bark (e.g. *L. decidua*). Finally, more similar studies are needed in order to provide a solid methodological basis for burned biomass reconstruction of past woody communities. As for other bioproxies used in functional paleoecology (Philibert and Prairie, 2002; Seppa et al., 2009; Blarquez et al., 2012), the use of charcoal will gain in power only if such calibration studies are carried out.

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