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## Soil characteristics for *Tuber aestivum* (syn. *T. uncinatum*)

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### Abstract

*Tuber aestivum* Vittad. is characterized by a broad ecological amplitude and geographical distribution. It is the most widespread truffle species found in Europe. *Tuber aestivum* is mainly harvested in natural habitats and in previously cultivated soils recolonized by ectomycorrhizal tree species. Production in orchards is less common. In this chapter, we describe the soils in which this species fructifies. Soil descriptions and characteristics were obtained from different sources and countries. The data set presented here is the largest of its kind for such a broad geographic scale. The bedrocks are mainly of sedimentary origin. The textures vary considerably from silty clayey to loamy sandy. In most of the soils, the pH is alkaline or neutral, and less frequently, slightly acidic. The soils are mostly calcareous or rich in exchangeable alkaline cations, mainly calcium. Despite the fact that they are found mostly in natural habitats, *T. aestivum* exhibits high potential for settling in new environments.

**Key words:** Burgundy truffle, *Tuber aestivum*, soil texture, soil structure, chemical properties, physical properties

### 1. Introduction

*Tuber aestivum* Vittad. has for several years been considered to be synonymous with *Tuber uncinatum* Chatin (Ceruti et al. 2003; Paolucci et al. 2004; Wedén 2004; Wedén et al. 2004a, 2004b, 2005). A recent multigene phylogenetic study confirmed that *T. aestivum* and *T. uncinatum* are conspecific (Molinier et al. 2013b). See Chapter 3 for more details.

Among *Tuber* species of culinary interest, *T. aestivum*, the Burgundy truffle, displays the most extensive geographic range and is found in almost all European countries. Harvests of fruiting bodies have been recorded from Ireland to Azerbaijan, and from North Africa to Sweden (see Chapter3).

37 Gotland Island at a latitude of 57-58°N is considered to be the northernmost outpost of *T. aestivum*  
38 (Wedén and Danell 2001).

39 *Tuber aestivum* is a truffle with great economic value and mostly occurs in natural habitats and  
40 habitats that have been previously cultivated and recolonized. Its maturity period occurs in autumn,  
41 when soil temperatures remains above 0°C, protecting fruiting bodies from frost damage.

42 The aim of this chapter is to define the soil characteristics necessary throughout the life cycle of the  
43 Burgundy truffle, including those essential for ascomata formation. The beginning of this chapter  
44 describes bedrock characteristics, followed by the physical and chemical properties of soils suitable  
45 for the Burgundy truffle.

46

## 47 **2. Methodology**

48 Data presented in Table 1 and Figs 2 to 10 have two origins. An initial soil data set was the result of  
49 direct contact with truffle growers, technicians and scientists working on *T. aestivum*, both within  
50 and outside Europe. We requested their data from sites known to have produced *T. aestivum*  
51 ascomata at least once. A second data set was compiled from papers published in scientific journals,  
52 books or included in proceedings of international truffle conferences. We refined our search to  
53 consider only those papers which contained soil information clearly indicating that *T. aestivum*  
54 ascomata had been collected in these soils. Papers which posed any doubt were rejected.

55 We will present and discuss here the largest data set ever collected on soils favorable to *T. aestivum*  
56 in such a large geographic area; a total of 129 soils from 10 countries were included in this review  
57 (see Figure 1). This data set cannot be considered to be representative for all situations, yet it can  
58 help to form additional hypotheses which should be verified in the future.

59 Methods of soil analysis were carefully evaluated prior to integrating a dataset in the study. We only  
60 considered those analyses which used standard soil testing methods:

- 61 - soil granulometry with organic matter destruction but without carbonate dissolution prior to  
62 analysis with the following size threshold: clay between 0 and 2 µm, silt between 2 and 50  
63 µm, sand between 50 and 2000 µm;
- 64 - pH in water (1:5 in volume, ISO 10390);
- 65 - soil organic matter and total nitrogen content determined by dry combustion (ISO 10694 and  
66 ISO 13878, respectively);
- 67 - total calcium carbonate content determined by volumetric method (ISO 10693);
- 68 - available phosphorus according to Olsen (ISO 11263) or Joret-Hebert;
- 69 - exchangeable cations (Ca, Mg and K) and cationic exchange capacity (CEC) were either  
70 determined at soil pH (for example cobaltihexammine) or at pH 7 (for example Metson), both  
71 extraction types were considered separately as CEC values are highly dependent on soil pH  
72 (Ciesielski and Steckerman, 1997).

73

74 As units differed from one method to another one, we recalculated several values prior to data  
75 processing in order to homogenize the data. We discarded data when soil analysis methods or units  
76 were not recorded in the file or the paper. R software (R core team, 2013) was used to establish the

77 soil texture triangle and to transform granulometry data with silt to sand thresholds of 63  $\mu\text{m}$  to 50  
78  $\mu\text{m}$  (soil texture package: Moeys, 2014) and to draw figures (ggplot2 package: Wickham, 2009).

79  
80

### 81 **3. Nature of the bedrock and soil types**

82 *Tuber aestivum* fructifies naturally on a range of diverse geological substrates from the Paleozoic era  
83 (540 million years ago) to present day (Cenozoic), including the Mesozoic (252-66 million years ago)  
84 (Table 1). While bedrock which is sedimentary in origin is the most common trait, *T. aestivum*  
85 ascomata can occur on alkaline volcanic substrates and on quaternary formations (loess and glacial  
86 formations). Below are examples of fructification situations in countries for which information has  
87 been found.

88 **France:** in northeastern France, the parent rock dates from the Jurassic, the Cretaceous, and to a  
89 lesser extent, to the Trias periods. In central France, around Paris and Limagne (near Clermont-  
90 Ferrand), *T. aestivum* is found on limestone from the Tertiary (Eocene and Oligocene) period. In  
91 some cases, the parent material is a gravel formation dating from the glaciation period (Table 1 and  
92 Le Tacon et al. 1997). In most documented cases, *T. aestivum* has been found on Rendzic Leptosol  
93 and Calcic to Calcaric Cambisol.

94 **Czech Republic** (Gryndler et al. 2013): a productive area near Prague is Rendzic Leptosol (Skeletal)  
95 formed on Silurian limestone.

96 **Germany** (South West, Baden-Württemberg: Stobbe et al. 2012; Stobbe et al. 2013): a broad range of  
97 calcareous bedrocks have been associated with truffle sites (*T. aestivum* was recorded on 116 of 121  
98 sites where truffles have been found). The Jurassic rock formations of the Swabian Jura and the  
99 Rhine valley slopes, as well as Quaternary glacial deposits of the northern pre-Alps, are the most  
100 common bedrocks, followed by molasses, loess and volcanic tuff.

101

102 **Hungary** (Bratek and Halász 2005; Gogan et al. 2012): *T. aestivum* is uniformly spread in the  
103 Carpathian basin. The bedrock has various origins: limestone, tertiary loess, middle Miocene volcanic  
104 ashes covered with loess, etc. The most famous *T. aestivum* habitat is the located in the Jászság  
105 region. This area is situated in the middle of Hungary, between the Danube and Tisza rivers. This  
106 flatland area is basically covered by river alluviums leading to Chernozems, Fluvisols, Solonchaks and  
107 Arenosols formation.

108

109 **Italy:** the most represented situations in Tuscany are the marly limestones (Alberese and Macigno di  
110 Londa formations), stratified limestones (Cretaceous and Jurassic), the coarse sediments (sands  
111 mixed pebbles in sandy matrix) (Gardin 2005). Around Parma, burgundy truffle grows on land derived  
112 from sedimentary rock (limestone marl) Mesozoic (Cretaceous) and Cenozoic (Paleocene, Eocene,  
113 Oligocene), called Flysch (Belloli et al. 1999; Gregori 2010).

114

115 **Poland:** parent soil material suitable for *T. aestivum* in Poland is from Cretaceous marlstone, marly  
116 limestone and gypsum (Hilszczanska et al. 2008) and of Miocene clays and sand. Soil cover consists  
117 primarily of Cambisols and Chernozems (Hilszczanska et al. 2013).

118

119 **Slovakia** (Miko et al. 2008): ascomata are harvested in clayey soils rich in organic matter. Soils are  
120 Rendzic Leptosols, Cambisols or Luvisols.

121

122 **Spain** (García-Montero et al. 2014; Menta et al. 2014): *T. aestivum* is mainly present in central Spain  
123 (province of Guadalajara) on Jurassic and Cretaceous limestones and dolomites. Soils are Lithic and  
124 Rendzic Leptosols.

125

126 **Sweden** (Wedén et al. 2004a): the bedrock belongs to five different groups (from the youngest to the  
127 oldest): 1) bedrock belonging to the Hemse group, partly fine oolitic limestone, reef shaped  
128 limestone, reef limestone, marly limestone and marlstone (nine sites); 2) Mulde marlstone –  
129 marlstone and marly limestone (one site); 3) Halla limestone – stratified, more or less marly  
130 limestone and reef limestone (one site); 4) Slite group – stratified, crystalline limestone and reef  
131 limestone, marlstone and marly limestone, sand limestone and lime sandstone (six sites); 5) Höglint  
132 limestone – stratified, more or less marly limestone and marlstone, and reef limestone (one site)  
133 (Wedén et al. 2004a).

134

135 **United Kingdom** (Hall et al. 2007): though rarely found, *T. aestivum* is mainly present in southern  
136 England, Scotland and Wales, in shallow, lime-rich soils over Secondary and Tertiary limestones.

137

138 **Israel:** *T. aestivum* does not appear to occur naturally in this country. Ascomata have been found in  
139 planted areas in Upper Galilee on bedrock from Cretaceous with dolomitic soils (Turgeman et al.  
140 2012).

141

142 **Canada** (Berch pers. comm.): *T. aestivum* does not occur naturally in Canada and has only been found  
143 in one orchard planted following liming treatment on Vancouver Island on Mesozoic-upper  
144 Cretaceous undivided sedimentary rocks. According to Canadian System of Soil Classification, the  
145 soils are orthic dystric brunisol, shallow lithic, glaciomarine deposits (Berch and Bonito 2014).

146

147

#### 148 **4. Physical properties**

149

##### 150 **4.1 Soil texture.**

151

152 *Tuber aestivum* can be found in soils with a large variety of textures as shown in the soil textural  
153 triangle (Figure 2) established from 86 soils analyses of productive sites: clay, silty clay, silty clay  
154 loam, clay loam, loam, sandy loam, sandy clay loam, silt loam. The broad range in soil particle size  
155 distribution demonstrates that *T. aestivum* has a wider soil texture tolerance than the Périgord black  
156 truffle (see Chapter 11). Clearly, fruiting bodies can be harvested in soils that contain low to high  
157 sand percentages (2.8 to 79.8%), low to high silt percentages (9.8 to 67.4%) and low to medium clay  
158 percentages (5 to 55%). Only soils with extreme textures have been excluded (sand, silt and clay  
159 contents superior to 80, 70 and 60%, respectively) (Figure 2).

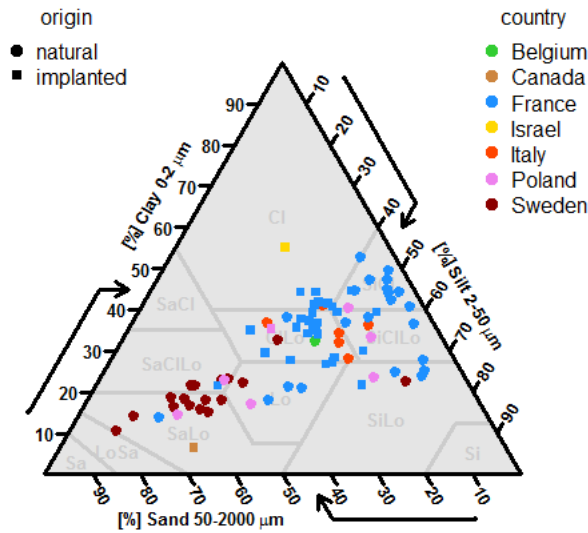
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162

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165  
 166  
 167 **Figure 2:** soil texture (USDA texture triangle) of sites where *T. aestivum* ascomata have been  
 168 harvested (83 soils in 7 countries). Natural forest sites are represented by a square and implanted  
 169 sites by a round point. Each site is represented by a colored point specific to each country.

170  
 171 **4.2 Soil water holding capacity and drainage**

172 Many soils of *T. aestivum* truffle orchards are characterized by a high water holding capacity due to  
 173 their silty clayey texture and/or their high organic matter content. High soil water availability is  
 174 favorable to fruiting body production by lowering water stresses during drought periods. The  
 175 topographic position at the base of slopes is particularly favorable, as observed in temperate  
 176 climates. Under Mediterranean climate, ascomata production in summer months is often cancelled  
 177 due to insufficient water availability.

178  
 179 The bedrock is often cracked and the presence of stones, associated with the granular and stable  
 180 structure, ensures good drainage. Proper water infiltration prevents erosion (on sloped terrain) or  
 181 waterlogging (on flat terrain), the latter being deleterious for mycorrhiza physiology. In Italy, the  
 182 production sites are generally located on shallow soils, with depths of roughly 50-60 cm and  
 183 consistently well-drained (Gardin 2005).

184  
 185 **4.3 Soil structure**

186 In sites where *T. aestivum* is harvested, the soil structure is generally good to excellent, being highly  
 187 loose and stable (with a granular structure). Organic matter content together with the presence of  
 188 CaCO<sub>3</sub> provide the soils with good structure, which can compensate for the clayey texture often  
 189 found in eastern France. A loose and stable structure ensures high porosity throughout the year,  
 190 which in turns increases soil water infiltration and aeration. Yet, soil structure and porosity also  
 191 depend on cultivation practices. Soil compaction due to heavy traffic and/or intensive grazing in wet  
 192 soils should be avoided.

193  
 194

195 **5 Chemical properties**

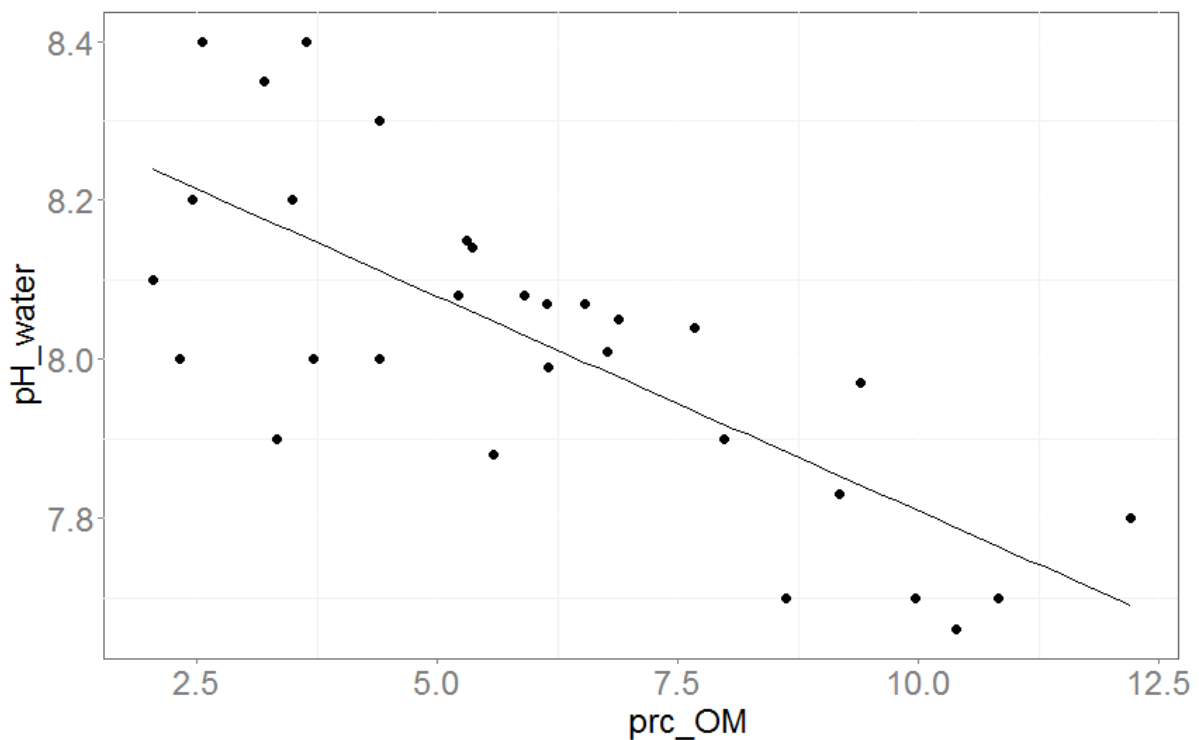
196

197 5.1 pH

198 The meta-analysis indicates a relatively large range of soil pH variation (from slightly acidic, neutral to  
199 basic). Thus, the range of soil pH in water where *T. aestivum* fructifies (5.9 to 8.4) is quite similar to  
200 the pH of soils where *Tuber melanosporum* Vittad. is harvested (5.5 to 8.4) (Jaillard et al. 2014; see  
201 Chapter 11).

202 Soil pH is more often basic, due to the presence of limestone in all soil horizons. On limestone  
203 derived soils, one of the factors explaining variations in pH levels is the content and composition of  
204 the soil organic matter. For example, a negative correlation between soil organic matter content and  
205 water pH (Spearman's rho = -0.72) can be observed in the implanted truffle grounds of France (solely  
206 limestone derived soils) (Figure 3).

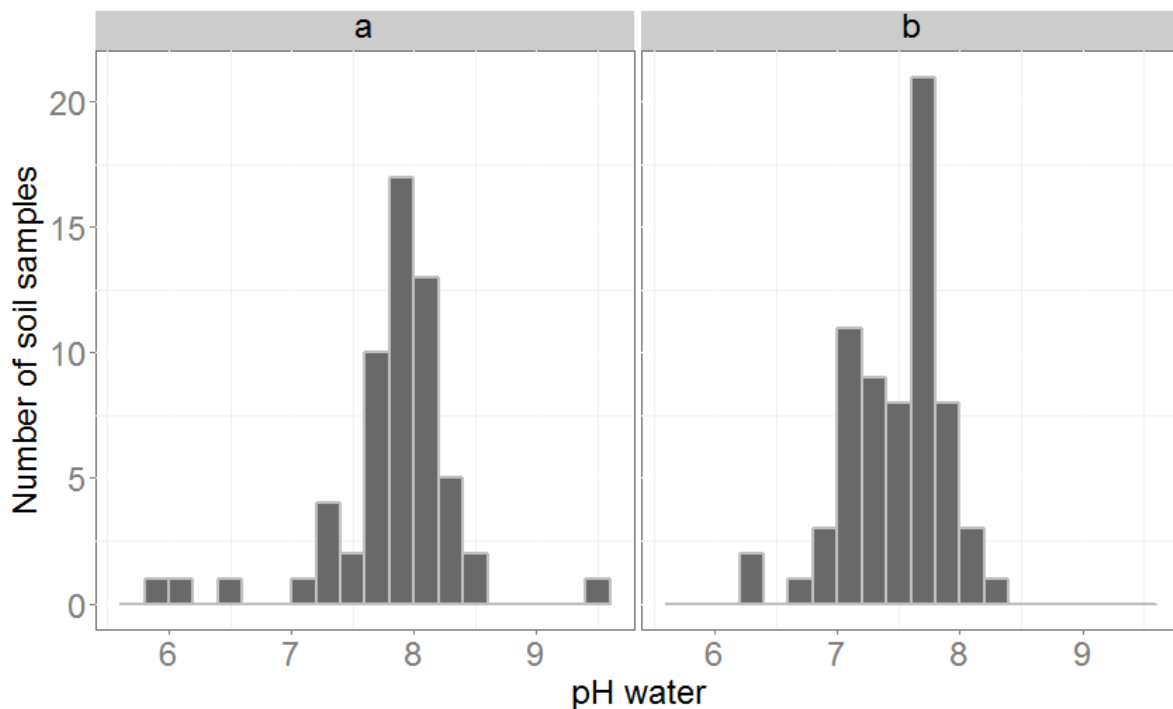
207



208

209 **Figure 3:** The relationship between soil pH in water (pH\_water) and organic matter content (in %, organic matter: prc\_OM) for the French truffle orchard considered in this study (among 129 soils  
210 from 10 countries, we considered only limestone derived soils that had been subject to the same  
211 historical uses prior to implanting *T. aestivum* and which provided a sufficient number of samples to  
212 assess the relationship between soil pH in water and organic matter content).  
213

214



215

216 **Figure 4:** Distribution of soil pH (in water) in sites where *T. aestivum* ascomata were harvested:  
 217 orchards (a), natural forest sites (b).

218 The distribution of soil pH in water is similar for both natural sites and orchards (Figure 4).

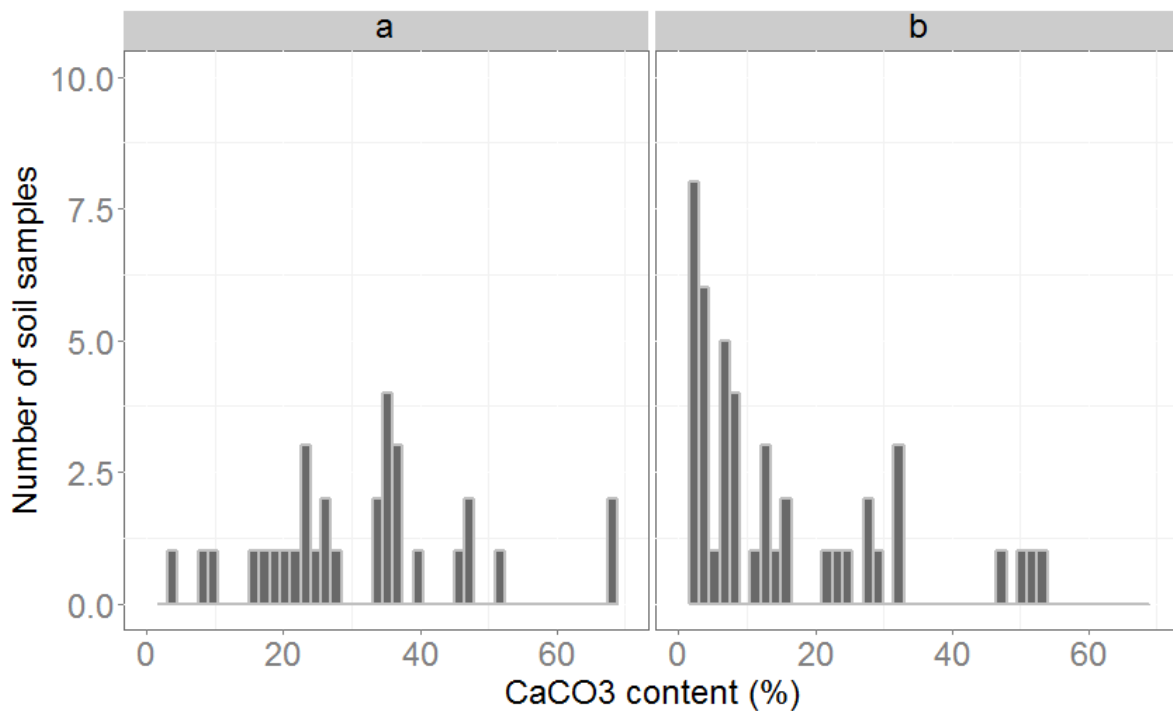
219 5.2 Carbonates

220 Soil carbonate content is highly variable, with values ranging between 0 and 69%. Our data set shows  
 221 differences of soil carbonate distribution between natural and implanted truffle orchards (Figure 5).  
 222 No direct correlation between Figure 4 and Figure 5 can be made as several soils were analyzed only  
 223 for pH in water and not for carbonate content. *T. aestivum* orchards are implanted in soils that tend  
 224 to be more carbonated than soils in which *T. aestivum* occurs naturally. The soil calcium carbonate  
 225 content ranges from 0 to 55% in natural forest soils where *T. aestivum* is harvested, but it is mainly  
 226 harvested in soils with limited amounts of calcium carbonate (0.1 to 1.5%) and most of the natural  
 227 sites with a CaCO<sub>3</sub> content lower than 20%. These results reinforce findings that unlike truffles with  
 228 high commercial value such as *T. magnatum* Pico and *T. melanosporum*, *T. aestivum* is able to live  
 229 and form fruiting bodies in soils poor in carbonates. In productive orchards, the soil calcium  
 230 carbonate content ranges from 3% to 80%.

231 The contents of total or active carbonate are not reliable descriptors of truffle habitats as numerous  
 232 authors have proposed (Callot, 1999; García-Montero et al. 2007; Jaillard et al. 2008). *T. aestivum*  
 233 orchards are more often than not implanted on carbonated soils with a water pH higher than 7. But  
 234 in natural habitats, *T. aestivum* fructification can occur in non-carbonated soils provided that, in the  
 235 upper horizons, the pH in water does fall below 5.9 (according to this data set which may be not  
 236 representative of all situations).

237





238

239 **Figure 5:** Distribution of soil carbonate content in soils of orchards (a) and in soils of natural or  
 240 secondary forest sites (b).

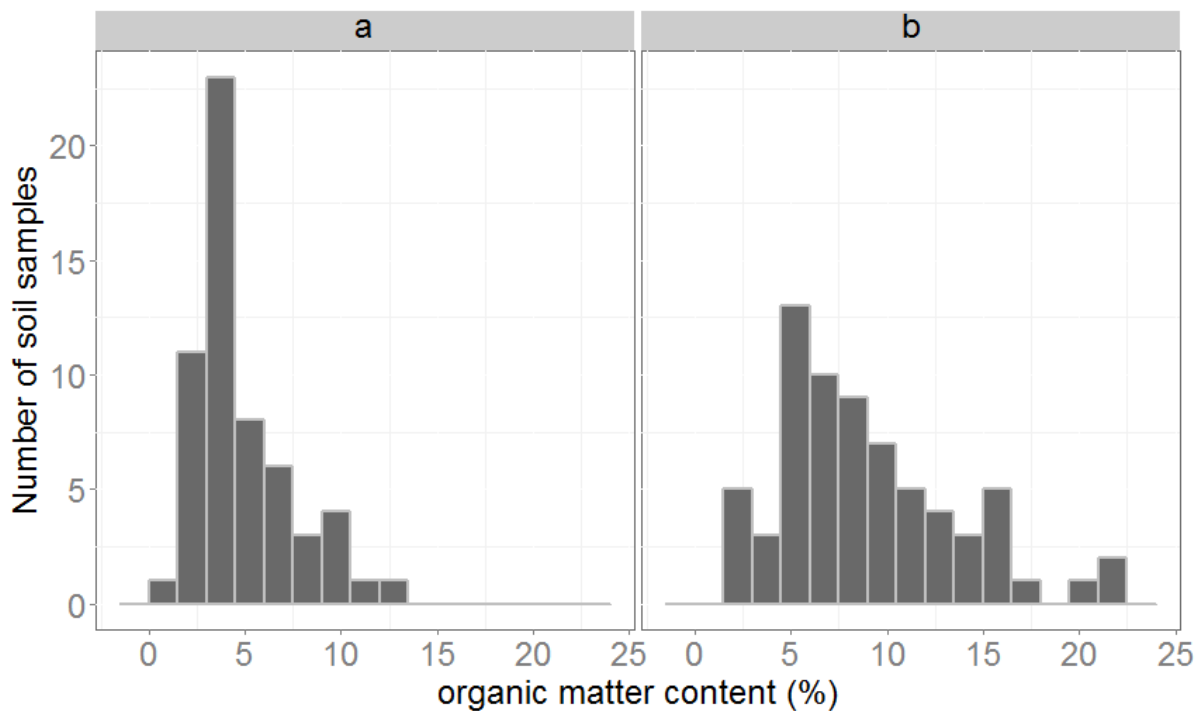
241

242

### 5.3 Organic matter

243 The range of organic matter is considerable (0.7 to 21.2%). In non-cultivated carbonated soils, CaCO<sub>3</sub>  
 244 coats the organic matter and prevents mineralization despite the high levels of biological activity. The  
 245 organic matter combined with CaCO<sub>3</sub> is partly responsible for the exemplary structure of Burgundy  
 246 truffle soils found in eastern France (Le Tacon et al. 1997). The data collected show that most of the  
 247 truffle orchards display relatively low organic matter content, which is most likely related to the  
 248 land's agricultural history (i.e. it is difficult to implant truffles in soils of a former forest), whereas  
 249 natural truffle grounds display the highest organic matter content (Figure 6).

250

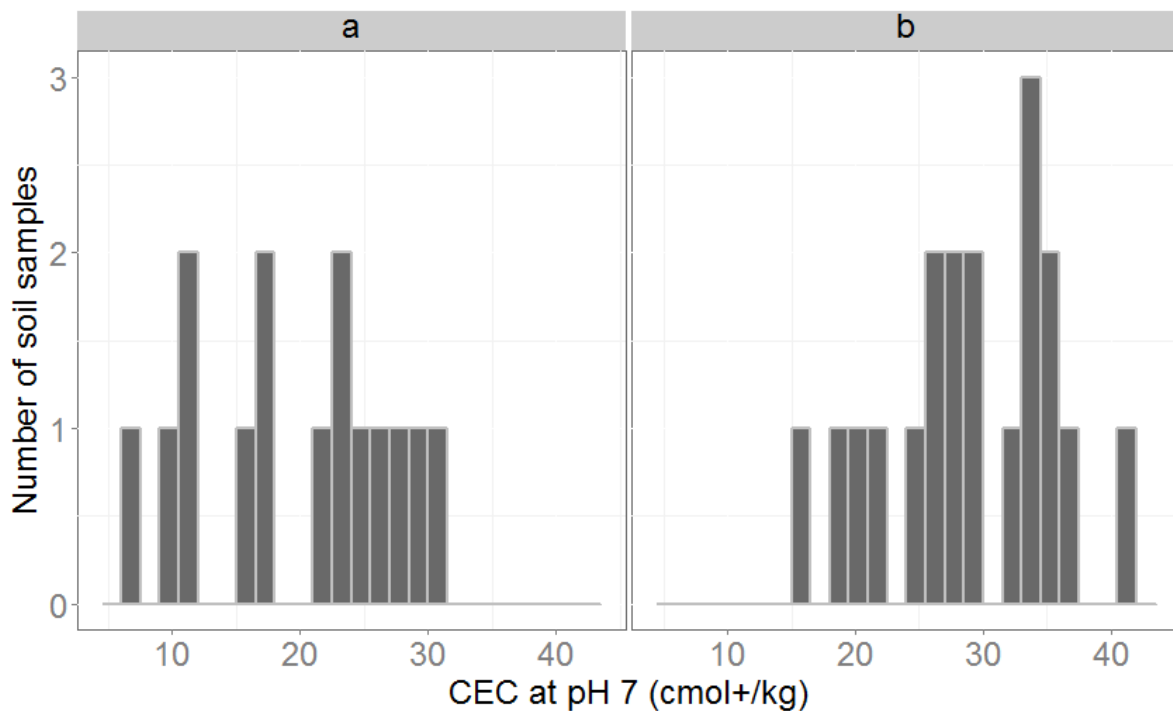


251

252 **Figure 6:** Distribution of soils according to their organic matter content. Orchards (a) and natural  
 253 forest sites (b).

254

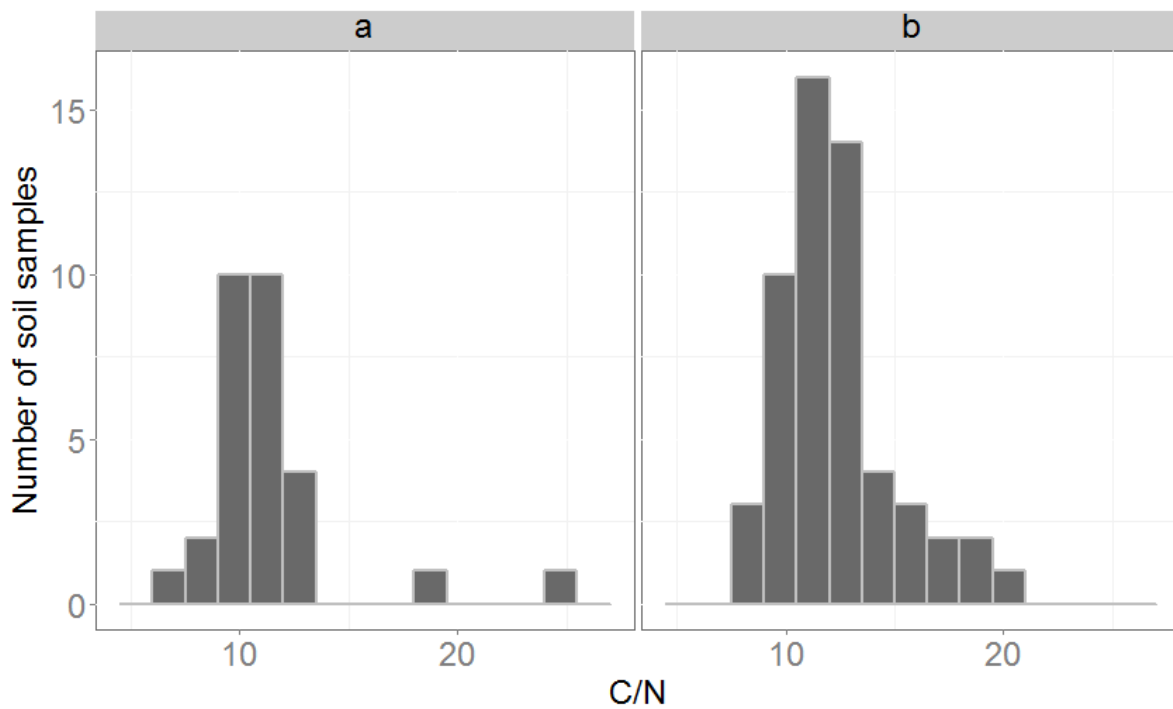
255 The Cationic Exchange Capacity (CEC) ranges from 5 to 30 cmol+/kg in orchards, and from 15 to  
 256 45cmol+/kg in natural or secondary forest sites where the content of organic matter is often higher  
 257 than in truffle orchards. CEC of calcic and calcaric soils [(Rendzic Leptosols, Epileptic Cambisols  
 258 (Calcaric), Cambisols (Calcaric), Cambisols (Hypereutric)] are higher than CEC of acidic soils although  
 259 values vary considerably (Badeau et al. 1999). At neutral or basic pH levels, the CEC increases in  
 260 proportion to the organic matter content (Badeau et al. 1999). The data collected show that, despite  
 261 higher pH in soils with implanted truffles (mostly former agricultural soils), the proportion of high  
 262 CEC soils is relatively low due to their lower organic matter content (Figure 7).



263

264 **Figure 7:** Distribution of soils according to their CEC at pH 7. Orchards (a) and natural or secondary  
 265 forest sites (b).

266 Most of the time, the C:N ratio of the *T. aestivum* soils is quite low, at around 10-12, which is  
 267 characteristic of fertile soils rich in stabilized organic matter. Only a few soils showed a C:N ratio  
 268 higher than 20 (Figure 8). A low C:N ratio confers to the micro-organisms in soils the capacity to  
 269 decompose the organic matter and thus, to supply mineral nitrogen to the ecosystem. It is  
 270 interesting to note that 90% of agricultural soils have a C:N ratio less than 11 when compared to 8%  
 271 of forest soils. Nearly 50% of agricultural soils have a C:N ratio ranging between 9 and 10 (Badeau et  
 272 al. 1999). Thus, for this parameter, the collected data once again underlines that the main  
 273 differences in soil properties between implanted and natural *T. aestivum* production sites relate  
 274 directly to their original use (agricultural or forest land).



275

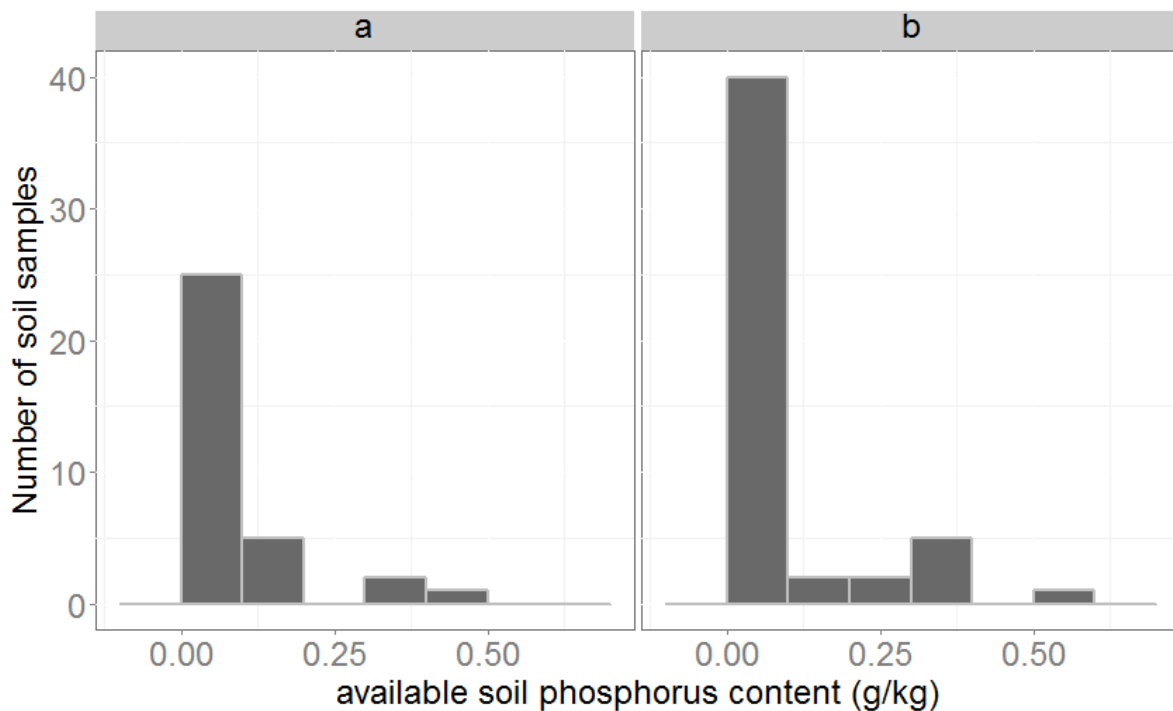
276 **Figure 8:** Distribution of soils according to their C:N ratio. Orchards (a) and natural sites (b). *T.*  
 277 *aestivum* ascomata have been harvested on each of the sites included in the graph.

278

279

#### 5.4 Nutrients

280 The available phosphorus content in soils (Joret-Hebert or Olsen methods) is comprised between  
 281 0.0035 and 0.51 gP kg<sup>-1</sup>. Most of the soils show low concentrations of available P (between 0.0035  
 282 and 0.1gP kg<sup>-1</sup>) (Figure 9) which is characteristic of the majority of limestone soils. Le Tacon et al.  
 283 (1997) analyzed 25 sites in France which indicated a general range of available P values from 0.009 to  
 284 0.044gP kg<sup>-1</sup>.

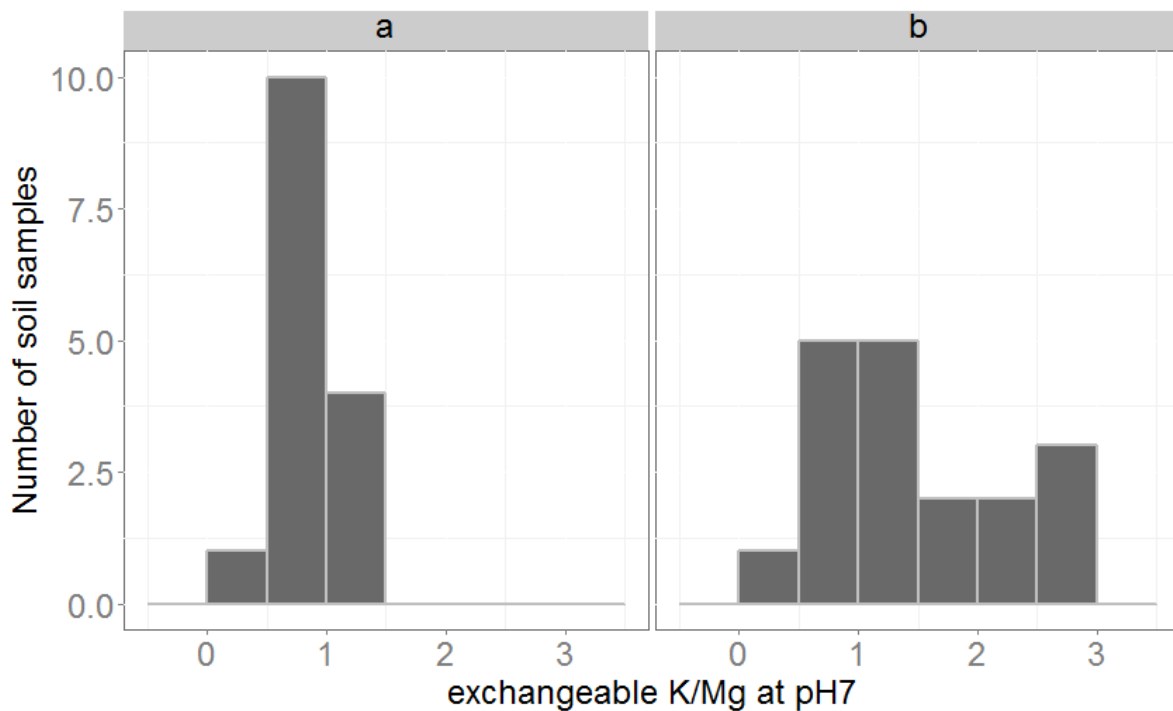


285

286 **Figure 9:** Distribution of soils according to their phosphorus content. Orchards (a) and natural or  
 287 secondary forest sites (b).

288

289 Soils suitable for *T. aestivum* are saturated in exchangeable Ca (66 to 97%), and the ratio of  
 290 exchangeable K and Mg over the CEC is relatively low (1.3 to 15% and 1.4 to 19%, respectively). A  
 291 K:Mg ratio over 2 has a negative effect on plants' uptake of Mg (Eriksson et al. 1997); Mg availability  
 292 problems may occur more often or may be more pronounced when soil available K content is twice  
 293 as high as the Mg content. The exchangeable K to Mg ratio is never > 2 in implanted *T. aestivum*  
 294 orchards, whereas it is higher than 2 in a few naturally productive areas (Figure 10). It should be  
 295 noted that Mg deficiencies due to excess K content have to date not been documented for truffle  
 296 production, and it remains difficult to draw conclusions for cases of higher than 2 K:Mg ratios in  
 297 natural truffle orchards.



298

299 **Figure 10:** Distribution of soils according to their K:Mg ratio measured at pH 7. Orchards (a) and  
 300 natural sites (b). *T. aestivum* ascomata have been harvested on each of the sites included in the  
 301 graph.

302

303

304 **6 Conclusions**

305 In natural or semi-natural conditions, *T. aestivum* ascomata are found in soils exhibiting a wide range  
 306 of pH levels, from slightly acidic, to neutral and basic, when limestone is present. In plantations, the  
 307 soil pH is more often basic. Many soils in which *T. aestivum* are found are characterized by a high  
 308 water holding capacity due to their silty clayey texture and/or their high organic matter content.  
 309 Moreover, these sites are often well supplied with water due to their topographic positioning at the  
 310 base of slopes. This high soil water availability is favorable to fruiting body production by decreasing  
 311 water stress during drought periods. *Tuber aestivum* can be cultivated in almost all neutral to alkaline  
 312 soils showing small to medium compactness (Bragato et al. 2009). The ecological and pedo-climatic  
 313 requirements of the Burgundy truffle confer to this species an increased capacity to adapt to many  
 314 environments. Anthropogenic areas (roads and rail embankments, etc.) are also favorable to the  
 315 development of this truffle (Gardin 2005). The large diversity of host trees should also be emphasized  
 316 (Table 1). This high flexibility explains why *T. aestivum* can be found spread across Europe. In many  
 317 cases, in natural habitats or planted areas, *T. aestivum* is found together with other truffles species,  
 318 including *T. melanosporum*.

319 The main challenges for future research related to *T. aestivum* soils will be to precisely identify  
 320 optimal soil conditions for the initiation and growth of ascomata, and to characterize conditions  
 321 which facilitate the colonization and persistence of *T. aestivum* mycorrhiza in root systems. This

322 knowledge should help to establish future best management practices for ascomata production and  
323 to optimize the current ones (irrigation, soil tillage, mulching, supplies of organic matter,  
324 micronutrients, etc).

325 In order to extend the study to more sites, we invite the readers to send additional soil data sets of  
326 sites known to produce *T. aestivum*; please contact the corresponding author for guidelines  
327 (Christophe.Robin@nancy.inra.fr).

328

329

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334 Yverneau (Humbauville), Bernard Vonflie (Munchhouse), Hubert Meyer (Otterswiller), Jean-Luc  
335 Dubois (Beine), Jean-Jacques Sauvaget (La Foye Montjault), Régis Mesnier (Saint Cybardeaux), Alain  
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337 Vado).Hungary: Andrea Gógán Csorbai (Szent István University, Gödöllő), Zoltán Bratek (Eötvös  
338 Loránd University, Budapest). Poland: Dorota Hilszczanska (Forest Research Institute, Raszyn).  
339 Slovakia: Juraj Chlpik (Slovak University of Agriculture, Nitra). Spain: Daniel Oliach (Centre Tecnologic  
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Version finale

**Figure caption**

435 **Fig. 1:** distribution of soil data set represented over the spatial predictions of soil pH in water at 5 cm  
436 depth according to ISRIC – World Soil Information ([www.soilgrids.org](http://www.soilgrids.org)). Each soil data set used in this  
437 study is represented by a cross. SoilGrids1km is a first approximation of soil properties predictions of  
438 at 1km resolution, using automated global soil mapping. The absolute values of predictions available  
439 for download at [www.soilgrids.org](http://www.soilgrids.org) are presently of limited thematic and spatial accuracy and contain  
440 artifacts and missing pixels. Yet the relative values of soil pH in water can be useful to compare  
441 distribution of soils favorable to *T. aestivum* between regions.

442 **Fig. 2:** soil texture (USDA texture triangle) of the sites in which *T. aestivum* ascomata have been  
443 harvested (83 soils of 7 countries). Natural forest sites are represented by a square and implanted  
444 sites by a round point. Each site is represented by a colored point specific for each country.

445 **Fig. 3:** The relationship between soil pH in water (pH<sub>water</sub>) and organic matter content (in %, organic matter: prc\_OM) for the French truffle orchard considered in this study (among 129 soils from 10 countries, we considered only limestone derived soils that had been subject to the same historical uses prior to implanting *T. aestivum* and which provided a sufficient number of samples to assess the relationship between soil pH in water and organic matter content).

450 **Fig. 4:** Distribution of soil pH (in water) in sites where *T. aestivum* ascomata were harvested: orchards  
451 (a), natural forest sites (b).

452 **Fig. 5:** Distribution of soil carbonates content in soils of orchards (a) and in soils of natural or  
453 secondary forest sites (b).

454 **Fig. 6:** Distribution of soils according to their organic matter content. Orchards (a) and natural forest  
455 sites (b).

456 **Fig. 7:** Distribution of soils according to their CEC at pH 7. Orchards (a) and natural or secondary  
457 forest sites (b).

458 **Fig. 8:** Distribution of soils according to their C:N ratio. Orchards (a) and natural sites (b). *T. aestivum*  
459 ascomata have been harvested on each of the sites included in the graph.

460 **Fig. 9:** Distribution of soils according to their phosphorus content. Orchards (a) and natural or  
461 secondary forest sites (b).

462 **Fig. 10:** Distribution of soils according to their K:Mg ratio measured at pH 7. Orchards (a) and natural  
463 sites (b). *T. aestivum* ascomata have been harvested on each of the sites included in the graph.

464 **Table 1** List of the sites investigated and their characteristics, when available: mean annual rainfall, elevation, nature of the bedrock(s) and of soil(s), most  
 465 putative host trees, natural site vs orchard, source of information.

Site	Country	Region	Mean annual precipitations (mm)	Elevation (m a.s.l.)	Bedrock characteristics	Soil type(s)	Natural truffiere (Yes/No)	Host trees	Source of information
Daix	France	Bourgogne	732	330-340	Upper Jurassic, Mid Oxfordian	Anthrosol (calcaric)	No	<i>Corylus avellana</i>	H Frochot (pers. comm.); Molinier et al (2013)a
Boncourt sur Meuse	France	Lorraine	1056	250-300	Upper Jurassic, Oxfordian	Epileptic Cambisols (calcaric, novic), Rendzic Leptosol and Cambisol (hypereutric) / colluvial rendzine, rendzine & brown calcisoic	No	<i>Corylus avellana</i>	Communauté de Communes du Pays de Commercy (pers. comm.). 12 soil analyses
Rollainville	France	Lorraine	940	360	Jurassic, limestone plateau	Cambisol (calcic) / brown calcisol	No	<i>Corylus avellana</i>	C Robin (pers. comm.)
Multi-sites (25).	France	Lorraine, Bourgogne, Franche-Comté, Auvergne	700-1060	700-1060	Cretaceous, upper & mid Jurassic, Trias - Paleogene (Eocene & Oligocene)	Rendzic Leptosol and Cambisol (calcic) / rendzine, brown rendzine, brown calcisol	Yes	<i>Quercus</i> sp., <i>Corylus</i> sp., <i>Carpinus</i> sp., <i>Pinus</i> sp., <i>Tilia</i> sp., ...	Le Tacon et al (1997)
Otterswiller	France	Alsace	-	185-243	-	-	No	<i>Corylus avellana</i>	H Meyer (pers. comm.)
Munchhouse 1	France	Alsace	-	220	-	-	No	<i>Corylus avellana</i> , <i>chêne</i> , <i>pin noir</i>	B Vonflie (pers. comm.)
Munchhouse 2	France	Alsace	-	220	-	-	Yes	<i>Corylus avellana</i>	B Vonflie (pers. comm.)
Lavoie	France	Lorraine	-	200-270	-	-	No	-	the owner (pers. comm.)
Harmonville 1	France	Lorraine	940	313	-	-	No	<i>Corylus av.</i> , <i>Oak</i> sp., <i>Pinus nigra</i> , <i>Carpinus</i> , <i>Betula</i> , <i>Tilia</i>	S Philippe (pers. comm.)
Harmonville 2	France	Lorraine	940	313	-	-	No	-	S Philippe (pers. comm.)
Harmonville 3	France	Lorraine	940	313	-	-	No	-	S Philippe (pers. comm.)
Beine 1 (La Noue d'Aubigny)	France	Champagne-Ardennes	-	140-290	-	-	No	<i>Corylus avellana</i> , <i>Pinus nigra</i> , <i>Carpinus betulus</i>	JL Dubois (pers. comm.)

Beine 2 (Les Commelles)	France	Champagne-Ardennes	-	140-290	-	-	No	<i>Corylus avellana, Pinus nigra, Carpinus betulus</i>	JL Dubois (pers. comm.)
Humbauville 1	France	Champagne-Ardennes	-	130	-	-	No	<i>Corylus avellana, Pinus nigra, oak</i>	M Yverneau (pers. comm.)
Humbauville 2	France	Champagne-Ardennes	-	130	-	-	No	<i>Corylus avellana, Pinus nigra, Carpinus betulus</i>	M Yverneau (pers. comm.)
Blanzac les Matha	France	Poitou-Charentes	843	23-76	Jurassic	Calcaric Leptosol (clayic)	Yes	<i>Tilia, Corylus avellana</i>	A Tribot (pers. comm.)
La Foye Monjault	France	Poitou-Charentes	814	59	-	Calcaric Leptosol (clayic)	No	<i>Corylus avellana</i>	JJ Sauvaget (pers. comm.)
Saint Cybardeau	France	Poitou-Charentes	750	24-114	-	Cambisol (calcaric, clayic)	Yes	natural ( <i>Tilia</i> )/implanted (fence <i>Corylus, Carpinus betulus</i> )	R Mesnier (pers. comm.)
Multi-sites (18)	Sweden	Gotland	528	40	belonging to the Hemse group - stratified, predominantly crystalline, partly fine oolitic limestone, reef shaped limestone, reef limestone, marly limestone and marlstone, sand limestone and lime sandstone and on Högklint limestone - stratified, more or less marly limestone and marlstone, and reef limestone		Yes	<i>Quercus robur, Corylus avellana</i>	Weden et al (2004)
Zapadné Slovensko	Slovakia	Zapadné Slovensko	-	-	-	Rendzic Leptosol, Epileptic Cambisols (calcaric), Luvisol / rendzines, rendzines cambisols, Luvisols	Yes	-	Miko et al (2008). 35 soil analyses
Malé Karpaty	Slovakia	Malé Karpaty	-	-	-	Rendzic Leptosol, Cambisols, Luvisols	Yes	-	Miko et al (2008)
Tribeč	Slovakia	Tribec	-	-	-	Rendzic Leptosol, Cambisols, Luvisols	Yes	-	Miko et al. (2008)

Vancouver Island. Nanaimo	Canada	British Columbia	967	32	upper Cretaceous undivided sedimentary rocks	Canadian System of Soil Classification: orthic dystric brunisol, shallow lithic	No	-	S Berch (pers. comm.)
Pinczow M	Poland	Nida Basin	600	250	Mesosoik, marlstone	-	Yes	-	D Hilszczanska (pers. Comm.) & Hilszczanska et al (2008 & 2013)
Pinczow SA	Poland	Nida Basin	600	312	Mesosoik, marlstone	-	Yes	-	D Hilszczanska (pers. comm.) & Hilszczanska et al (2008 & 2013)
Pinczow WR	Poland	Nida Basin	600	295	Mesosoik, marlstone	-	Yes	-	D Hilszczanska (pers. comm.) & Hilszczanska et al (2008 & 2013)
Pinczow GR	Poland	Nida Basin	600	260	Mesosoik, gypsum	-	Yes	-	D Hilszczanska (pers. comm.) & Hilszczanska et al (2008 & 2013)
Przedborz Upland	Poland	-	600	320	Jurassic limestone	-	Yes	-	D Hilszczanska (pers. comm.) & Hilszczanska et al (2008 & 2013)
Chmielnik NW	Poland	Nida Basin	600	228	marly limestone	-	Yes	-	D Hilszczanska (pers. comm.) & Hilszczanska et al (2008 & 2013)
Wolynska Upland	Poland	-	550	200	limestone	-	Yes	-	D Hilszczanska (pers. comm.) & Hilszczanska et al (2008 & 2013)
Spoletto	Italy	Umbria	869	310	Fluvial deposits with coarse fragments from Cretaceous limestones	Eutric Cambisol (Aric)	Yes/No	-	
6 sites	Italy	Provincia di Parma		800-1200	Mesozoic (cretaceous) and Cenozoic (Paleocene, Eocene, Oligocene), marly		Yes	Dominted by Carpinus	Gregori (2010)

					limestone				
2 sites	Italy	Provincia di Parma	-	-	-	-	-	-	Gregori (2010)
provincia de Teramo	Italy	provincia de Teramo	-	937	cover detritus-eluvial of the Holocene origin	Mollic Cryosol	Not indicated	<i>Quercus pubescens</i>	Menta et al (2014)
provincia de Piacenza	Italy	provincia de Piacenza	-	810	Lutetian limestones and marly limestones alternating marls and calcareous marls	Cambisol (calcaric)	Not indicated	<i>Quercus pubescens</i>	Menta et al (2014)
South Liege	Belgium	South Liège	-	240	-	-	Yes	-	the owner (pers. comm.)
Guadalajara	Spain	Guadalajara	797	1000	jurassic and cretaceous limestone and dolomites	Rendzic Leptosol	-	<i>Quercus faginea</i>	Menta et al (2014)
Velká Chuchle	Czech Republic	Velká Chuchle	-	-	Silurian limes (Paleozoic)	Rendzic Skeletic Leptosol	Yes	<i>Corylus, Tilia, Fraxinus...</i>	Gryndler et al (2013)
Kibutz Bar'am	Israel	Upper Galilee	800	736	Cretaceous (Mesozoic)	Cambisols (Dolomitic)	No	-	Y Sitrit (pers. comm.) & Kagan-Zur et al (2001)
Eger, Heves county	Hungary	Eger, Heves county	600	298	limestone	Calcic Luvisol	No	-	Z Bratek, Acs Gogan. Gogan et al (2012)
Hőgyész, Tolna county	Hungary	Hőgyész, Tolna county	630	210	tertiary loess	Chernozem and Luvisol	No	-	Z Bratek, Acs Gogan. Gogan et al (2012)
Jászság, 20 sampling places	Hungary	Jászság, 20 sampling places	515	< 150	middle Myocene volcanic ash covered with loess	Gleysol (63%), Chernozem (stagnic) (23%), Solonchak (4.5%), Solonetz (9%)	Yes	-	Z Bratek, Acs Gogan. Gogan et al (2012)
South West Germany 1	Germany	south West Germany	890	659	Jurassic	Rendzic Leptosol	Yes	-	Stobbe et al (2013)
South West Germany 2	Germany	south West Germany	857	772	Jurassic	Rendzic Leptosol	Yes	-	Stobbe et al (2013)