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Abstract

Ecological studies need environmental descriptors to establish the response of species or communities to ecological conditions. Soil water resource is an important factor but is poorly used by plant ecologists because of the lack of accessible data. We explore whether a large number of plots with basic soil information collected within the framework of forest inventories allows the soil water holding capacity (SWHC) to be mapped with enough accuracy to predict tree species growth over large areas. We first compared the performance of available pedotransfer functions (PTFs) and showed significant differences in the prediction quality of SWHC between the PTFs selected. We also showed that the most efficient class PTFs and continuous PTFs compared had similar performance, but there was a significant reduction in efficiency when they were applied to soils different from those used to calibrate them. With a root mean squared error (RMSE) of 0.046 $cm^3\ cm^{-3}$ (n = 227 horizons), we selected the Al Majou class PTFs to predict the SWHC in the soil horizons described in every plot, thus allowing 84% of SWHC variance to be explained in soils free of stone (n = 63 plots). Then, we estimated the soil water holding capacity by integrating the stone content collected at the soil pit scale (SWHC') and both the stone content at the soil pit scale and rock outcrop at the plot scale (SWHC") for the 100.307 forest plots recorded in France within the framework of forest inventories. The SWHC" values were interpolated by kriging to produce a map with 1 km^2 cell size, with a wider resolution leading to a decrease in map accuracy. The SWHC" given by the map ranged from 0 to 148 mm for a soil down to 1 m depth. The RMSE between map values and plot estimates was 33.9 mm, the best predictions being recorded for soils developed on marl, clay, and hollow silicate rocks, and in flat areas. Finally, the ability of SWHC' and SWHC" to predict height growth for *Fagus sylvatica*, *Picea abies* and *Quercus petraea* is discussed. We show a much better predictive ability for SWHC” compared to SWHC’. The values of SWHC” extracted from the map were significantly related to tree height growth. They explained 10.7% of the height growth index variance for *Fagus sylvatica* (n = 866), 14.1% for *Quercus petraea* (n = 877) and 10.3% for *Picea abies* (n = 2067). The proportions of variance accounted by SWHC” were close to those recorded with SWHC” values estimated from the plots (11.5, 11.7, and 18.6% for *Fagus sylvatica*, *Quercus petraea* and *Picea abies*, respectively). We conclude that SWHC” can be mapped using basic soil parameters collected from plots, the predictive ability of the map and of data derived from the plot being close. Thus, the map could be used just as well for small areas as for large areas, directly or indirectly through water balance indices, to predict forest growth and thus production, today or in the future, in the context of an increasing drought period linked to a global change of climatic conditions.

Keywords: Digital soil mapping, soil water holding capacity water balance, GIS, site index, vegetation modelling.

1. Introduction

Relating plant species to environmental factors is a central topic in plant ecology since pioneers recognized the importance of climate in determining global vegetation types (Von Humboldt, 1807). Currently, plant species or communities response to ecological conditions is increasingly studied and concerns many applications, such as modelling ecological niches and mapping distribution range, evaluating species abundance, diversity or productivity (Coops and Waring, 2001). For these studies, the availability of accurate environmental descriptors is of crucial importance (Dirnböck et al., 2002). Most of the time, climatic factors are considered alone because of their availability in large climatological datasets or because geographic information systems (GIS) programs allow their calculation (Piedallu and Gegout, 2008). Although soil factors have been recognized for their importance (Coudun et al., 2006), they are poorly used as input in predictive models (Guisan and Zimmermann, 2000), particularly for broad areas, due to the high cost and long duration of fieldwork required to obtain relevant data. The availability of accurate digital soil information at scales relevant for plant ecologists and forest managers is now a crucial factor in plant modelling studies (Cresswell *et al.*, 2006; Carré *et al.*, 2007b).

The soil water regime is recognized to be one of the most important soil factors for plant growth, influencing photosynthesis rate, carbon allocation, microbial activity and nutrient cycling (Lebourgeois *et al.*, 2005; Breda *et al.*, 2006). On the other hand, available water for plants remains difficult to evaluate due to the lack of accessible data, its estimation requiring expensive laboratory measurements (Wosten *et al.*, 1999).It is most of the time estimated by plant ecologists thought climatic water balance (rain – actual evapotranspiration), more easily available (Piedallu and Gegout, 2007). However, the water contained in the soil enabling to compensate the lack of rain over dry periods during the year (especially during summer), the maximum amount of water available for plants stored in a soil is particularly important to evaluate. It is characterised by the soil water holding capacity (SWHC), defined as the difference between the water content at field capacity and at wilting point (specified in cm of water for a soil of a given depth) (Bruand et al., 2003). This local characteristic is related to the vegetation production variability and, combined with climatic variables, allow the calculation of soil water balance.

Numerous studies focus on the development of pedotransfer functions (PTFs) (Bouma, 1989), allowing the prediction of complex soil hydraulic characteristics from basic soil properties which are easier to collect in the field (Wösten et al., 2001). The simplest ones are PTFs providing average values of the hydraulic properties of soil horizons grouped in classes (class PTFs). Their use requires easy-to-collect data, allowing the sampling density to be increased for the same effort, in order to better describe the soil spatial heterogeneity (Islam et al., 2006). During the last two decades, continuous PTFs which relate particle size distribution, bulk density or organic carbon content to hydraulic parameters by empirical equations have been developed. Unlike class PTFs, continuous PTFs require input variables that are costly to collect. Comparison of PTFs for water content estimation shows poor to good prediction accuracy depending on calculation method and on the location and characteristics of soil samples used for their calibration (Cornelis et al., 2001; Wagner et al., 2001; Givi et al., 2004). Comparison between continuous and class PTFs shows contrasting results, some studies highlighting lower uncertainty with continuous PTFs (Van Alphen et al., 2001), others pointing out that the choice between class and continuous PTFs can be unclear when calculating soil functional characteristics (Al Majou et al., 2007; Rubio et al., 2008). Other authors such as Nemes (2003) have discussed the geographical origin of PTFs and achieved better prediction with PTFs developed locally than with PTFs developed with soils originating from a large territory. Finally, it has been shown that PTFs developed on soils similar to those of the studied area perform well, thus avoiding the undesirable effect of regional specificity (Rawls et al., 2001; Schaap et al., 2001).

In forest areas, the relation between water content and stand productivity has been studied for several decades but the lack of available data is actually a major limit to model species productivity over large and diversified areas. The knowledge of SWHC is particularly important in the present climate change context, with an expected decrease in water availability in a large part of the world (Nemani et al., 2003). However, most studies have focused on the creation of PTFs to predict water hydraulic soil properties but only a few have evaluated the performance of such PTFs, particularly when they are used for vegetation modelling (Nemes et al., 2006). The validity of PTFs to predict the hydraulic properties of forested soils is thus poorly known, most samples used for their elaboration originating from cultivated soils, whose characteristics are different (Vincke and Delvaux, 2005). In this context, little research has focused on mapping the SWHC despite a clear interest for ecological studies and forest management (Romano and Santini, 1997; Orfanus and Mikulec, 2005). The existing SWHC maps are generally achieved at a local scale using inventories requiring information that is costly to collect and those few existing for large territories are generally derived from soil maps achieved at low resolution (McBratney et al, 2003; Al Majou et al, 2008b). The quality of these maps is difficult to estimate and their predictive ability is generally unknown.

The aim of this study is thus to discuss if easy-to-collect soil information observed on numerous forest plots during broad scale inventories can be used to achieve a fine resolution SWHC map over large areas. Firstly, we studied the performance of six class PTFs available for French soils to convert the textural classes of horizons recorded by the National forest inventory into SWHC values. Their prediction quality was compared with values recorded with three more sophisticated continuous PTFs, using a dataset of 227 horizons for which particle size distribution, organic carbon content, bulk density and SWHC values were known. The class PTFs giving the best performance were selected to estimate soil water holding capacity at the pit scale by taking into account the stone content of the soil (SWHC') and at the plot scale by taking into account both the stone content of the soil and the proportion of rock outcrop (SWHC'') for 120,902 plots scattered over the whole of France. In a second step, we used 100,307 of these plots to map the SWHC” using geostatistical methods. The map resolution was chosen according to the cell size after comparison of the prediction accuracy recorded with a validation dataset containing 20,595 independent plots. The quality of the final map was evaluated according to the type of bedrock and at different scales using the same validation dataset. Finally, on the basis of previous studies showing an effect of SWHC on forest productivity (Bravo-Oviedo and Montero, 2005; Mitsuda et al., 2007), we compared the ability of SWHC’ and SWHC” to predict potential growth for three common tree species of European forests. The suitability of using basic soil information available in forested areas to map SWHC” and to improve potential production modelling is then discussed.

2. Material and methods

2.1. PTFs selected to identify the class PTFs used for study

We selected 6 class PTFs established on soil datasets collected in France or including soils located in France:

- The class PTFs established by Jamagne et al. (1977) using soils originating from the North of the Paris basin (Jamagne class PTFs) and which provide SWHC values according to 16 texture classes;
- The class PTFs developed by Bruand et al. (2002) and Bruand et al. (2004) using 219 and 302 horizons (85 horizons A and 217 horizons E, B, C), respectively, originating from soils located in different French regions (Bruand-2002 and Bruand-2004 class PTFs). The Bruand-2002 class PTFs are volumetric water contents at different matrix potentials according to classes combining 8 textures and bulk density values. The

Bruand-2004 class PTFs are also volumetric water contents at different matrix potentials but according to 13 texture classes without any reference to bulk density;

- The class PTFs established by Al Majou et al. (2008) using 320 horizons (90 topsoil and 230 subsoil horizons) corresponding to a large range of French soil characteristics (Al Majou class PTFs). The Al Majou class PTFs are volumetric water contents at different matrix potentials but according to the 5 texture classes of the CEC texture triangle (Commission of the European Communities, 1985) and location of the horizon in the profile (topsoil or subsoil);

- The class PTFs developed by Schapp et al. (2001) and which correspond to the H1 first level of prediction of the Rosetta software which was developed using 2134 soil samples originating from North American and European soils (Shaap class PTFs). The Shaap class PTFs were sets of parameter values according to the 12 texture classes of the USDA triangle (SSSA, 1997) for the water retention curve established by Van Genuchten (1980):

$$\theta(h) = \theta_r + \frac{\theta_s - \theta_r}{[1 + (\alpha|h|)^n]^{1-1/n}} \quad (1)$$

with θ(h), the volumetric water content ($cm^3\ cm^{-3}$) at the matrix potential h (cm), θs and θr the saturated and residual water contents ($cm^3\ cm^{-3}$), respectively, α (cm^{-1}) a parameter related to the reciprocal of the air entry matrix potential, and n another parameter related to the pore-size distribution;

- And finally the class PTFs developed by (Wosten *et al.*, 2001) using the European Hypres soil database (Wösten class PTFs). Among the 5521 horizons making up Hypres, 171 originate from French soils. The Wösten class PTFs were also sets of parameter values for the water retention curve established by Van Genuchten (1980) according to the 5 texture classes of the CEC triangle (Commission of the European Communities, 1985).

The prediction quality of the 6 above class PTFs was compared with the prediction quality of 3 continuous PTFs requiring particle size distribution, organic carbon content and bulk density information:

- The continuous PTFs developed by Vereecken et al. (1989) using soils from Belgium (Vereecken continuous PTFs) and recognized as leading to the best prediction when used for soils with similar characteristics in Belgium (Cornelis et al., 2005), Switzerland (Mermoud and Xu, 2006) and Germany (Tietje and Tapkenhinrichs, 1993);
- The continuous PTFs developed by Teepe (Teepe et al., 2003) with German soils located exclusively under forest (Teepe continuous PTFs);
- And the continuous PTFs developed by Al Majou et al. (2007) using soils originating from different regions of France (Al Majou continuous PTFs).

2.2. Evaluation of efficiency of the selected PTFs

The ability of the selected class PTFs to predict water content at different matrix potentials was discussed and compared to continuous PTFs, by using a database containing water content measurements. We brought together 227 horizons corresponding to 63 entire soil profiles, independent of the plots used to map SWHC and not used to develop the selected PTFs. A set of 140 horizons originating from the SOLHYDRO database (Bruand et al., 2003), the other 87 horizons originating mainly from the work published by Bigorre (2000). The 227 horizons were collected in different soil types distributed mainly in lowlands throughout the whole of France and cover various texture conditions (35 sandy, 128 loamy and 73 clayey horizons). Since most of available PTFs are derived from measurements on cultivated soils, we evaluated their performance to predict water content for soils under forest using a subset of 95 horizons. The horizons were sampled during winter when the soil was near to field capacity. The bulk density was measured using cylinders of 1236 cm^3 in volume. The mean gravimetric water content was determined at different matrix potentials with pressure membrane or pressure plate apparatus by using twelve to fifteen undisturbed clods 5-10 cm3 in volume per sample (Bruand and Tessier, 2000). The volumetric water content (θ, in $cm^3\ cm^{-3}$) was calculated by multiplying the mean gravimetric water content by the bulk density. The database also contained for each horizon the particle size distribution and the organic carbon content. The SWHC was computed by the difference between the volumetric water content at -100 hPa ($\theta_{2,0}$) and -15,000 hPa ($\theta_{4,2}$) matrix potential for each horizon, for a soil depth to a maximum of 1 m. The water content at field capacity corresponded to its value at -100 hPa according to the results recorded by Al Majou et al. (2008). The efficiency of the PTFs was discussed by comparing the SWHC predicted using the 6 class PTFs and 3 continuous PTFs selected with the SWHC measured for the 227 horizons. It was also assessed by comparing the predicted SWHC to its calculated value using the measured SWHC and the soil characteristics collected in every plot (horizon thickness, soil depth) for all 63 soils studied.

2.3. Estimation of soil water holding capacity on plots

The most efficient class PTF allowing the prediction of water content was selected for SWHC estimation on plots. A set of 120,902 soil descriptions surveyed in forest within the framework of the National Forest Inventory (NFI, IFN in French) and scattered over the whole territory of France (550,000 km²) was used to realize and to validate the map (Figs. 1a and b). From 1989 to 2004, 100,307 of these plots were collected over the whole of France by quasi-systematic sampling with a mean density of 1 plot per 1.1 km^2 (Drapier and Cluzeau, 2001). Then, from 2005 to 2007, 20,595 other plots located on a regular mesh on the whole French territory with a density of 1 plot per 25 km² were surveyed, the mesh being moved each year. The part of the protocol concerning information required for SWHC estimation remains unchanged between the two methods. The 100,307 plots originating from the 1989 to 2004 protocol were used to establish the map, and the 20,595 plots from the 2005 to 2007 protocol were used for validation.

On each 400 m² surveyed plot, the proportion of surface area occupied by rock outcrop (RO) was visually estimated and a soil pit was dug down to 1m depth when possible thus allowing to assess the stone content (i.e. volumetric proportion of visible mineral fragment > 2mm in size) in every horizon of the vertical faces of the pit (Baize and Jabiol, 1995). At most two horizons were distinguished in every soil pit. For every horizon the upper and lower limits were noted with a precision of 10 cm and the texture was manually estimated according to 9 classes (1, sand; 2, loamy sand; 3, sandy clay loam; 4, silt loam; 5, silty clay loam; 6, silt; 7, silty clay; 8, clay loam; and 9, clay). For a limited area in southern France (i.e. in the four French administrative departments Pyrénées Orientales, Aude, Ariege and Tarn), the survey performed between 1989 and 1992 distinguished only one soil horizon and the depth of the pit was limited to 70 cm.

We first calculated the soil water holding capacity at the soil pit scale (SWHC' in mm of water) by taking into account the stone content recorded in the soil in every pit as follows:

$$\mathrm{SWHC}' = \sum_{i=1}^{n} \left[(1 - \sqrt[3]{\mathrm{SC}^i})(\theta^i_{2,0} - \theta^i_{4,2})\mathrm{T}^i \right] \quad (2)$$

with n the number of horizons in the soil profile, SC^i the stone proportional content in horizon i, θ_2^i the water content at -100 hPa matrix potential of horizon i, $\theta_{4.2}^i$ the water content at -15,000 hPa matric potential of horizon i and T^i the thickness of horizon i in mm.

We also calculated the soil water holding capacity at the plot scale (SWHC”) by taking into account both the stone content recorded in the soil studied and the proportion of rock outcrop recorded on each plot. We considered that RO corresponded to the proportion of soil volume which was actually occupied by rock. Thus, SHWC” was calculated as follows:

$$\mathrm{SWHC}'' = (1-\mathrm{RO})\left\{\sum_{i=1}^{n}\left[(1-\sqrt[3]{\mathrm{SC}^i})(\theta_{2,0}^i-\theta_{4,2}^i)\mathrm{T}^i\right]\right\} \quad (3)$$

The SWHC” was assumed to be more closely related to the actual soil water holding capacity of every plot and particularly smaller than SWHC’ in mountain areas or on calcareous plateaus where rock outcrops are frequent.

2.4 Mapping of soil water holding capacity

Ordinary kriging available on the ARCGIS 9.2 geostatistical module was used to predict SWHC” values at unsampled locations using estimates on NFI plots (Matheron, 1963). It is one of the most used interpolation methods, providing the best linear unbiased estimates (Brus *et al.*, 1996; Mueller T.G. *et al.*, 2004). Effectiveness of kriging is known to depend on the representativeness of the observations (Rosenbaum and Söderström, 2003). The calculation is based on spatial dependence, proximal observations being supposed to be more similar than distant ones. The modelling of spatial autocorrelation is summarized by an experimental semivariogram, which represents the dissimilarity of values as a function of their distance. In order to perform the calculation, sample points are grouped in pairs, separated by a distance called the lag. In our analysis, a semivariogram was visually fitted with an exponential model and no anisotropy was considered. We used the SWHC” predicted for the 100,307 plots of the NFI database. Lag spacing was chosen at 2000 m and experimental variograms were calculated up to distances of 120 km. A limit search radius of 60 km, the distance beyond semivariogram showed lower spatial autocorrelation, and the values of 40 neighbour plots were the parameters chosen to calculate values in the grid according to the kriging procedure. These parameters ensure that the root mean square prediction errors calculated by cross validation with Arcgis software are minimised.

The kriging procedure enables the generation of output surfaces for different cell size or resolution. The resolution can affect the map quality. A large resolution is quicker to build and easier to handle, because the file size is smaller, but local information can be averaged and the map can be less efficient at predicting local heterogeneity. At the opposite extreme, a small resolution can contain no more information than a higher one, due to the input plot density and errors in measurements. We built different grids according to the kriging procedure with a resolution varying from 100 m to 50 km grid spacing. We thus considered 0.1, 0.25, 0.5, 1, 2.5, 5, 10, 15, 25 and 50 km mesh sizes. We estimated the quality of map predictions for these various resolutions by comparison with the SWHC” calculated on 20,595 independent NFI plots. The largest cell size showing no degradation of prediction was selected to produce the final map.

2.5. Validity of the map according to its scale

The elaborated map was validated for the whole of France using an independent dataset of 20,595 validation plots. The difference between SWHC" estimated on these plots and values extracted from the map has been calculated and interpolated using ordinary kriging to produce a bias map over the whole country. We evaluated map validity when considering reduced surfaces, a local use representing an evident interest. We divided France in decreasing areas ranging from 200 km to 5 km side length (with intermediate analysis at 10, 25, 50 and 100 km), corresponding to 6 levels of analysis. For all the squares of each level of analysis, we compared predicted values extracted from the map with SWHC" calculated on the independent NFI plots included in the area. The calculation was not carried out for areas with less than 10 plots. The quality of map predictions was then averaged for each level of analysis.

2.6. Ability of soil water holding capacity to predict species production

We examined the ability of SWHC' and SHWC", calculated on plots by using the different class PTFs or extracted from the map, to predict potential productivity of three frequent tree species in Europe: one coniferous (*Picea abies*) and two broadleaf species (*Fagus sylvatica* and *Quercus petraea*). *Picea abies* and *Fagus sylvatica* are mainly located in mountain areas or in elevated atmospheric moisture areas. *Quercus petraea* is at present mainly established in the lowlands of France and is a species more tolerant to drought than *Fagus sylvatica*. We used 3762 NFI plots with site information about productivity and independent from the soil dataset used to establish the SWHC" map (Fig. 1c). Site index values were calculated on even age and pure stands on 2068 plots for *Picea abies*, 816 plots for *Fagus sylvatica*, and 878 plots for *Quercus petraea* (Seynave *et al.*, 2004; Seynave *et al.*, 2008). In order to eliminate an age effect, the site productivity index was defined as the height of the dominant trees at a reference age. The height at 70 years was chosen for *Picea abies* and at 100 years for *Quercus petraea* and *Fagus sylvatica*. This index has been commonly used for decades by forest managers to estimate the production of pure and even aged stands (Zeide, 1993). The height of dominant trees was supposed to be independent of competition and to vary only with site conditions and resources. Following previous studies studying site index variations in relation to ecological factors, an effect of water content was expected for each of the 3 studied species (Seynave *et al.*, 2004; Seynave *et al.*, 2008). We examined the performances of SWHC' and SWHC" calculated with the different class PTFs at predicting spatial variations of site indices for *Picea abies*, *Fagus sylvatica* and *Quercus petraea* and we compared SWHC" predictive ability estimated on plots or extracted from the map.

2.7. Statistical analysis

The coefficient of determination (R^2), mean error (ME), root mean square error (RMSE) and the relative RMSE (RMSEr) were used to compare PTF efficiency, to validate the map, or to estimate SWHC ability to predict potential production of forest stands. They were computed as follows:

$$\mathrm{ME} = \frac{1}{m}\sum_{j=1}^{m}\left[(y_j - \bar{y}_j)\right] \qquad (4)$$

$$\mathrm{RMSE} = \sqrt{\frac{1}{m}\sum_{j=1}^{m}\left[(y_j - \hat{y}_j)\right]^2} \qquad (5)$$

$$\text{RMSEr} = \frac{\sqrt{\frac{1}{m}\sum_{j=1}^{m}\left[(y_j - \hat{y}_j)\right]^2}}{\bar{y}} \times 100 \qquad (6)$$

where m is the number of recordings, y_j the observed value, $\hat{y}_j$ the predicted value, and $\bar{y}_j$ the average of the observed values. R^2 was used to assess the proportion of variance explained, ME to estimate the bias in prediction, RMSE to determine the standard deviation of error and RMSEr to know the variation of standard deviation of error around the mean expressed in %.

3. Results

3.1. PTF selection

Water content between the wilting point and field capacity was predicted by using the 6 class PTFs selected (Table 1). The predicted and measured differences of water content between the wilting point and field capacity were compared for the 227 horizons of the database, for the 6 class PTFs and for the 3 continuous PTFs selected (Fig. 2). The quality of the prediction was quantified for the 63 plots for every PTF using ME, RMSE and R^2 (Table 2). The Al Majou and Vereecken continuous PTFs explained the highest proportion of variance (R^2 = 0.40 for both sets of PFTs) but they showed a bias and RMSE higher than for the best class PTFs. The lowest RMSE was obtained with the Al Majou class PTFs (RMSE = 0.046 $cm^3\ cm^{-3}$), with the Bruand-2002 and Bruand-2004 class PTFs showing similar performances (RMSE = 0.047 $cm^3\ cm^{-3}$). These RMSEs represent 20% of the water content range recorded for the 227 horizons of the validation dataset, ranging from 0.039 to 0.25 $cm^3\ cm^{-3}$ for a mean value of 0.114 $cm^3\ cm^{-3}$. The Jamagne, Schaap and Wösten class PTFs, and the Verrecken and Teepe continuous PTFs showed poor performance with RMSE ranging from 0.053 to 0.070 $cm^3\ cm^{-3}$.

Comparison of the PTFs performance with the 95 horizons originating from soils under forest showed similar results although PTF performances were slightly lower: the RMSE was 6% higher using the Al Majou class PTFs, 15% and 21% higher using the Bruand-2002 and Bruand-2004 class PTFs, respectively.

The comparison of the 9 PTFs selected to predict SWHC for the entire soil showed that RMSE ranged from 18.5 mm with the Al Majou class PTFs to 50.1 mm with the Jamagne class PTFs (Table 2). Using the Al Majou class PTFs, we predicted 84% of SWHC variance for the soil profile and the bias was small (ME = 3.8 mm.).

3.2. Mapping of soil water holding capacity

The SWHC" calculated for the 100,307 NFI plots using the Al Majou class PTFs was interpolated at different resolutions over the whole of France. The performance of the interpolation procedure was evaluated by comparing the SHWC" of the 20,595 independent NFI plots with its value resulting from interpolation of the 100,307 plots. The performance decreased when the cell size increased: R^2 varied from 0.35 to 0.15 and RMSE from 33.9 to 39.9 mm for resolutions ranging from 100 to 50,000 m. (Fig. 3a). The accuracy loss started beyond 1 km^2 cell size and increased greatly beyond 5 km^2 resolution. With R^2 = 0.35 and RMSE = 33.8 mm, we selected a 1 km^2 resolution to map SWHC" (Fig. 3b).

The map shows a large range of values over the country. The SWHC" estimated for a maximum soil depth of 100 cm ranged from 0 to 148 mm, with an average of 78 mm (Fig. 4b) and with important variations on a local scale (Fig. 4c). A spatial structure in SWHC" distribution is visible on the map, the semivariogram realized to interpolate the 100,307 plots showing a spatial autocorrelation up to 60 km (Fig. 5). The predicted SWHC" was the highest on flat areas compared to steeply inclined areas, except for massive calcareous rocks (Table 3). The highest SWHC" were found in regions H1, H2, H3 and H4 which correspond to sedimentary plains with alluvium, marl, clay or hollow silicate rocks (Fig. 4a and 4b). The predicted SWHC" was low in areas located over igneous, metamorphic or calcareous rocks (Table 3). This concerns regions L5 and L6 mainly in the South East of France (Fig. 4a) and the four regions L1, L2, L3 and L4 dispatched in the rest of France (Fig. 4a and Fig 4b). These regions with a low SWHC" can show an important variability with a range of SWHC" which can reach 100 mm such as on calcareous plateaux in region L2 or L5.

The comparison of SWHC" between map and field values showed a difference < 20 mm for 46% of the 20,595 validation plots and a difference > 40 mm for 23% of the same set of plots. The map of prediction errors shows SWHC" underestimations by the map particularly in two regions, the South of Bretagne (Fig. 4d, region A) and the South-East of the Massif Central (Fig. 4d, region B). Areas where mapped SWHC" was overestimated are mainly located on the Garonne plain and Perigord (Fig. 4d, region C). The lowest map accuracy found in the South of region A can be attributed to the small number of plots in this area, due to the limited presence of forest areas. Uncertainties located in regions B and C concern heterogeneous landscapes with important soil depth variations due to bedrocks outcropping. In these areas we expected more survey errors and lower performance of kriging due to the heterogeneity of landscape. In general, the

RMSE was higher when the area was steeply inclined and for igneous, metamorphic, massive or hollow silicate rocks (Table 3). In order to compare the quality of predictions for different rock types, we calculated the RMSEr, allowing the variations of predictions around the mean unit value to be estimated. The RMSEr highlighted an important dispersion of predictions for calcareous rocks, probably due to local heterogeneity of those units which have a globally low SWHC”: the standard deviation of errors varied from 75% around the mean in flat areas to 88% in the steep ones (Table 3). At the opposite end, marls and clays, mainly located in sedimentary plains, are geological units having a good quality of prediction, in spite of their high SWHC”.

Map prediction accuracy varied little depending on the size of the study site, for areas ranging from 10×10 km^2 squares to the whole of France (table 4). On a local scale, using 94 10×10 km^2 squares containing more than 10 plots, the mean RMSE between the SWHC” extracted from the map and the estimated values on independent plots was 32.1 mm, close to those recorded when considering the whole of France (33.9 mm.).

3.3 Ability of soil water holding capacity to predict potential production of forest stands.

SWHC’ and SHWC” estimated on the plots with the different class PTFs selected led to important differences in prediction quality of the site indices of the 3 species studied. SWHC’ showed globally a lower predictive ability than soil depth alone for *Picea abies* and *Fagus sylvatica*, but higher prediction for *Quercus petraea* (Table 5). On the other hand, SWHC” showed a much better ability than SWHC’ to predict site indices, on average 65% for *Fagus sylvatica*, 58% for *Picea abies*, and 27% for

Quercus petraea. SWHC" was more efficient than soil depth alone at predicting the potential growth of the 3 studied species for all the class PTFs studied except for the Schaap class PTFs. Compared to soil depth, SWHC" calculated from the Al Majou class PTF explained 30% more site index variance for *Picea abies*, 60% more for *Fagus sylvatica*, and 56% more for *Quercus petraea*. The variance of site indices accounted for by SWHC" varied from 7.2% to 20.4% for *Picea abies*, from 4.3% to 11.5% for *Fagus sylvatica*, and from 7.7% to 12.1% for *Quercus petraea*, depending on the class PTF used. The best results have been recorded using the Al Majou, Bruand-2002 and Bruand-2004 class PTFs, their performance being statistically different from the Jamagne and the Schaap class PTFs ($p < 0.05$), Wösten class PTFs showing intermediate performance. The SWHC" computed with the Al Majou class PTFs and extracted from the 1 km cell size map was less efficient than estimations based on plots at predicting the site index for *Picea abies* (R^2 = 10.7 vs. 18.6), more efficient for *Quercus petraea* (R^2 = 14.1 using the map vs. 11.7), the results being close for *Fagus sylvatica* (R^2 = 10.3 using the map vs. 11.5) (Fig. 6).

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4. Discussion

Among the data required to perform a water balance, the SWHC is one of the most difficult to obtain, its estimation requiring complex and costly measurements and analysis. A method for its evaluation may involve digging a soil pit at each required location, determining manually the textural class, noting the depth and proportion of stone and using a class PTF to convert soil texture into water content value. We have combined such basic soil information collected from numerous plots by forest inventories and have established a map over a large area. The accuracy of our map depends on the original soil information (sample locations, positions, attributes), the soil water estimation based on PTFs and the mapping procedure (Carré *et al.*, 2007a).

4.1 Uncertainties linked to the initial soil information

The original soil information collected to elaborate the map and to validate the results can be affected by different kind of uncertainties. Errors are expected to be found in the NFI database due to the fact that texture class, soil depth and stone content are difficult to evaluate in the field, and because numerous operators are concerned by the data survey. Errors are particularly expected for the textural classes that are manually determined and the stone content that is visually quantified, involving a part of subjectivity in their estimation. Moreover, soil depth can be under-evaluated due to the aleatory presence of stones preventing to dug the pit, particularly in calcareous and mountainous areas, explaining probably a part of the highest uncertainties founded in these areas. Despite the limitation to one meter of the maximum prospectable depth in the NFI protocol is in agreement with recommendations made in previous studies (Berges and Balandier, 2010) , it can can also lead to SWHC under-estimations, the part of the soil prospectable by roots can be more important (Breda *et al.*, 1995). An important source of errors can be due to the influence of local soil conditions, particularly on soil depth or stone content, that can make information collected on the pit not representative of the plot area (Smithwick *et al.*, 2005). These different errors concerning the raw data are difficult to evaluate but are expected to be one of the most important source of uncertainties at the plot scale, probably explaining a part of the important nugget effect found in the semivariogram elaborated for the kriging procedure.

4.2 Uncertainties linked to the soil water estimation

The transformation of soil information collected on the plots to water content values can be another source of uncertainties, due to the choice of PTF, the method defined to estimate the storage volume free of stones, or the simplifications done to characterise the soil hydraulic properties. Indeed, we considered the soil just as a reservoir for water although it is constituted of hydraulically different soil layers whose sequence can influence soil-water storage. If the determination of the wilting point from the water retention curve at a matric suction of 15,000 hPa ($\theta_{4,2}$) is commonly accepted (Becker, 1974), the characterisation of field capacity is more ambiguous. It should be viewed as a process-based parameter of soil, determined using specifically-designed field experiments, for example as described by (Romano and Santini, 2002). However, for practical reasons, field capacity is most of the time associated with a specific point of the soil water retention curve, various potentials being suggested by different authors (Minasny and McBratney, 2003). We estimated SWHC using the available PTF based on this classical method and choose the matric suction of 100 hPa ($\theta_{2,0}$), for field capacity, in relation with previous studies carried in the same soil conditions, showing this value was the closest to in situ volumetric water content whatever the texture (Al Majou *et al.*, 2008). A comparison with SWHC determined using matric suction of 330 hPa for field capacity showed similar results, ensuring our analysis is not linked to the choice of a specific threshold. However, this classical static approach based on benchmark pressure-can be criticized, field capacity being attached to water retention values rather than hydraulic conductivity characteristics of soils. The evaluation of SWHC using field capacity values defined as the soil water content when the drainage flux become negligeable could be a solution to overcome these limits (Twarakavi *et al.*, 2009). Improvements could also be made by using the integral energy principle, a method based on the entire soil water retention curve to evaluate the energy required by plants to remove soil water, avoiding to consider water between the two potentials is equally available(Minasny and McBratney, 2003).

The comparison of available PTFs showed an RMSE recorded between estimated and measured SWHC ranged from 0.046 to 0.070 cm^3 cm^{-3} depending on the set of PTFs used and are consistent with those gathered together by Wosten et al. (2001) or Schhap (2004) in their review of PTF performance. The relatively low efficiency of the PTFs allow nevertheless to explain an important part of SWHC variance for soils free of stone (between 72 and 85 % depending of the PTF used), showing the importance of soil depth in the SWHC calculation. Prediction of stand productivity for the three studied species showed a similar hierarchy between PTFs as in a comparison of their performance with measured SWHC: the Al Majou, Bruand-2002 and Bruand-2004 class PTFs gave the best results. The important variations in tree growth prediction illustrate the need to compare the efficiency of the available PTFs (the worse being less efficient than soil depth alone). On the other hand, our results showed also that using class PTFs does not involve a reduction in the prediction quality when compared to more sophisticated PTFs such as continuous PTFs. Indeed both types of PTF led to similar prediction performance which is in agreement with the results recorded by Wösten et al. (1995) and Al Majou et al. (2007). This study complements those showing a lower performance for PTFs developed with large scale databases or using soils different from those of the studied area (Nemes et al., 2003). This probably explains the lowest performance recorded with the Vereecken and Teepe continuous PTFs, and the Wösten and Schaap class PTFs. We noted that the reduction in prediction accuracy for SWHC estimates based on PTF is relatively low when validating with forested soils, particularly when using Al Majou class PTFs, despite the fact that most of the soil samples used for the development of PTFs originated from agricultural soils.

Our results have also shown that the proportion of surface area occupied by rock outcrops on the scale of every elementary plot was required to estimate the amount of water available for that plot. Indeed, we showed a much better prediction of the stand productivity by using SWHC” than SWHC’. In addition, its prediction performance with SWHC’ was similar when using soil depth alone. When the plot was rocky, the pit was usually dug were the rock outcrops were fewer thus leading to an underestimation of the stone content at the plot scale. Our results also highlight the significance of appropriate estimates of both stone content and proportion of surface area occupied by rock outcrop in SWHC” estimations.

4.2 Uncertainties linked to mapping procedure

The uncertainties linked to mapping procedure can be evaluated by comparison of SWHC’’ values extracted from the map and estimated on the plot, and by determining their respective predictive ability in regard of tree growth. With a R^2 of 0.35 and an RMSE of 33.9mm, the prediction errors between the map and the independent validation dataset can appear relatively important. However, this comparison is arduous because it concern information at different scales, map prediction representing a mean SWHC’’ value over a cell, and the validation plot a local measurement. SWHC’’ is know to be very heterogeneous due to variations in soil type, topography or presence of rocks for example, and the plot estimation can be not representative of the mean conditions of the area (Mummery *et al.*, 1999). Moreover, the validation has been realised using NFI plots collected with the same protocol as plots used for mapping, probably affected by measurement errors as described above. If this comparison allow to describe the spatial distribution of uncertainties linked to mapping procedure, the averaging of a large number of measurements recorded at different locations for a same cell of the map could provide a more realistic idea of the quality of the predictions.

Despite variations with the species being considered, the map shows a global performance close to estimates based on plots for predicting tree species productivity. This surprising result can be explained by the combination of two opposing effects. A negative effect is linked to the interpolation procedure, which used an average of neighbouring values to predict SWHC" for a specified location, thereby smoothing local features of the plot. On the other hand, this smoothing can have a positive effect, by limiting the impact of field survey errors. By predicting SWHC" at un-sampled locations while considering the effect of many neighbourhood plots, the impact of survey errors is limited. These two opposing effects can be more or less important depending on location: in steeply undulating areas, map interpolation can be less efficient than estimation on plots, probably due to the high spatial variability induced by topography and geology changes. This likely explains why the productivity *of Picea abies*, a mountain species, is better explained by the SWHC" estimated from plots than the SWHC" extracted from the map. In contrast, *Quercus petraea* is principally located in sedimentary plains, where units are more homogeneous over large areas. Due to this relative homogeneity, an average of soil water content over various neighbouring plots provides a better estimate for a site than a single estimate carried out locally. This likely explains the observed higher predictive ability of SWHC" extracted from the map compared to that calculated from plots for this species. *Fagus sylvatica* being a species located both in sedimentary plains and in mountainous areas, the two effects probably compensate for each other, and close predictive ability is found using SWHC" estimated from plots or extracted from the map. These results suggest uncertainties involved by the mapping procedure could be relatively low comparing to those associated to SWHC estimate, and locally the mapping procedure could compensate a part of survey errors.

Uncertainties associated with mapping procedure are dependent on output resolution and interpolation method. The choice of output resolution is in general rarely discussed in studies leading to map production, despite its importance. We have shown that a maladapted resolution can lead to a significant increase in map uncertainty. The 1 km^2 resolution selected to elaborate this map is logically close to the distance between NFI plots on the mesh (0.9 plots km^{-2}). Uncertainties generated by kriging are more important for extreme values which are smoothed. We had greater difficulty in predicting SWHC" in areas with abrupt changes in conditions and achieved better prediction in homogeneous geomorphological or topographical conditions. The evaluation of other mapping methods could be a way to reduce interpolation uncertainties, although little is known about their validity in large area studies. For example, cokriging or regression-kriging using ancillary variables such as geology and terrain attributes have given good results in local studies in previous research, (Bourennane et al., 2000; Minasny and McBratney, 2007). Instead of interpolate the SWHC'' value estimated on plot, an other possibility could be to interpolate first the raw properties required and after to use PTF to calculate SWHC'' with GIS. Both procedures has already been compared at local scale (Voltz and Goulard, 1994; Sinowski *et al.*, 1997), and they showed very small differences in comparison with the large uncertainties associated with PTF estimates (Vanderlinden *et al.*, 2005).

4.3 Interest of the SWHC''map and its use for tree growth modelling

The established maps allow to provide for the first time in the French forests relatively fine spatial information about SWHC’’ and associated prediction errors, for an area corresponding to 150,000 km². Uncertainties seems to be mainly influenced by the estimate of the soil volume prospectable by plants (linked to soil depth and stone volume estimation) and the method allowing to convert these volume in potential water content. Simple methods based on class PTFs showed near performances compared to continuous ones, demonstrating the interest of using only textural classes for large scale SWHC’’ predictions. The mapping procedure seems to have contrasted effects, increasing prediction errors in heterogeneous areas but improving the map predictive ability in homogeneous ones.

The obtained digital map can be used for a large range of scales, making it an useful tool for policy makers and land managers. However, due to the forest origin of the samples used, the validity of the map has to be considered for forest areas alone. Its ability to predict SWHC” in unforested areas remains to be determined but can be assumed to be lower, the distance to sample plots being longer and the soil concerned being different. Most existing large SWHC maps are based on the use of numerical maps of soils, thus providing averaged soil property values per soil mapping unit (Batjes, 1997; Wosten *et al.*, 1999). This approach is criticized because it does not account for variations of soil properties within soil units, and soil classification criteria cannot correspond to the soil property being mapped (Leenhardt et al., 1994; Voltz et al., 1997; Utset et al., 2000). We have shown here that the use of easy-to-collect information surveyed on numerous plots located at regular spatial intervals allow to overcome these limits, offering new perspectives for large scale digital mapping of soil parameters.

This study also highlight the potential of SWHC'' maps for modelling tree growth, which can provide values with a comparable efficiency as data recorded on the plot, without a ground survey for each location in the space. SWHC'' extracted from the map allow to predict between 10.3% and 14.1% of the site index variance for the three studied species, in agreement with previous results obtained for the same species by Seynave et al (2005; 2008) . She showed that climatic factors were the main drivers of growth, soil richness and soil moisture acting as complementary variables, as already shown in previous studies (Curt *et al.*, 2001; Chen *et al.*, 2002). Due to the lack of data, the soil moisture effect appeared in these models thought different proxies as soil depth, stone content or topographic position, or thought SWHC estimated using Jamagne PTFs. The availability of SWHC'' values calculated using efficient methods allow to improve existing models and to progress in the understanding of three growth. By combination with climatic factors, it also offer the possibility to improve the characterisation of the soil moisture available for plants through the soil water balance estimation, thus providing indices having a direct effect on plant physiology and taking into account water fluxes determined by precipitation, actual evapotranspiration or runoff (Zierl, 2001).

5. Conclusion

A SWHC" map showing local variations over a large area is a useful tool as much for decision maker who generally need information over vast areas as for land managers who need descriptors for more local studies. We have demonstrated the potential of using basic information that already exists or can be collected through national or international networks, for characterizing water content properties on numerous plots with appropriate PTFs, thus allowing the derivation of maps by interpolation procedures. In this study the site indices selected appeared to be appropriate biological indicators to compare soil water holding capacity estimation methods or to evaluate map predictive ability, showing concordant results with those obtained with water content measurements for comparison of PTFs. The SWHC" values extracted from the map can be used alone or can be combined with climatic factors to estimate spatially-distributed soil water balance. Those indices which have a physiological significance can be used to characterize the relation between water available for plants and to improve plant productivity or distribution models. This knowledge is particularly important in the current climate change context to determine and to monitor the potential impacts of global warming on vegetation.

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Figures

Figure 1 : Location of the 100,307 plots used to establish the map (a), the 20,595 plots used to its validation (b), and the 3,762 plots with site information about productivity for *Picea abies* (n = 2,068), *Fagus sylvatica* (n = 816), and *Quercus petraea* (n = 878) (c).

Figure 2 : RMSE (cm^3 cm^{-3}) and coefficient of determination (R^2) between soil water holding capacity (θ_2 - $\theta_{4.2}$) predicted using 6 class-PTF and 3 continuous-PTF, and measured values for all horizons (n = 227) and only for forested ones (n = 95, in bracket).

Figure 3 : Relation between SWHC" estimated on plots and obtained from the map (in mm), for different resolutions (a), and for1 km² cell size (b) (n = 20,595).

Figure 4 : Schematic view of France indicating natural regions with extreme values of SWHC" (a), SWHC" map (b), with an insert showing local variations (c), and (d) spatial distribution of prediction errors interpolated from validation dataset (n = 20,595).

Figure 5 : semi-variogram computed with the ordinary kriging technique, using 100,307 plots with SWHC” values. Each dot represent a pair of points that have a common distance (lag size) between each other, 60 lags of 2,000 m are represented, showing relationships between plots for a distance up to 120 km.

Figure 6 : *Picea abies* (n = 2,068), *Fagus sylvatica* (n= 816), and *Quercus petraea* (n = 878) site indices variance explained by logarithm of SWHC” estimated on NFI plots and extracted from the map (in %).

Tables

Table 1 : Soil water holding capacity (SWHC, θ_2 - $\theta_{4.2}$, in cm^3 cm^{-3}), given by different class-PFTs for the 9 NFI textural classes (STD = standard deviation).

Table 2 : RMSE (mm.), mean error (ME, in mm.), and coefficient of determination (R^2) between predicted SWHC using 6 class-PTF and 3 continuous-PTF, and measured SWHC, for a soil free of stone. Measured mean SWHC is 87 mm, ranging between 32 and 215 mm. R^2 between soil depth and measured SWHC 0,73 (n = 63).

Table 3 : SWHC” map mean values, RMSE (in mm.) and relative RMSE (RMSEr, in %) between map and plot estimations (n = 20,551), by bedrock units and according to topography types. Flat and steep areas are determined using the NFI topography code determined by field observation. n = number of plots.

Table 4 : Average SWHC” map prediction accuracy for different study site sizes, ranging from the entire France to a mesh of 10*10 kms square. For each of the 6 level

of analysis considered, number of squares used (repeats), mean number of plots per square (mean n, at least 10 records per square being required), RMSE and standard deviation between SWHC” predicted by the map and estimations on validation plots are summarized (n = 20595). ND : not calculated.

Table 5 : *Picea abies* (n = 2,068), *Fagus sylvatica* (n= 816), and *Quercus petraea* (n = 878) site indices variance (in %) explained by soil depth and logarithm of SWHC estimated on NFI plots using 6 class-PFTs at pit scale (SWHC’) or at plot scale (SWHC”).

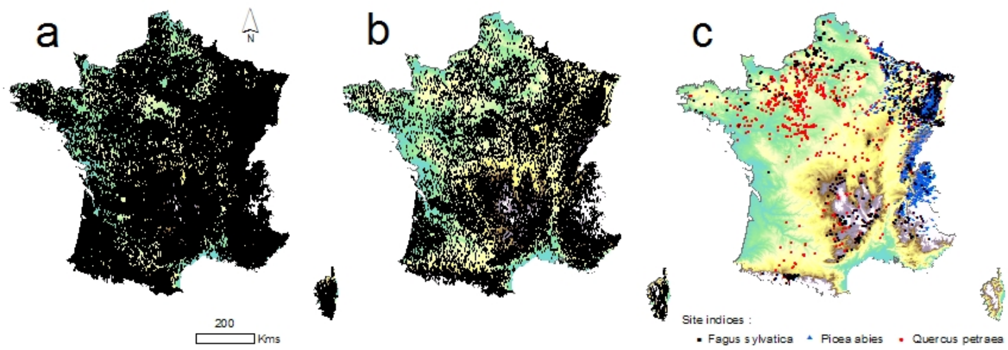

a
N
200
Kms
b
c
Site indices :
Fagus sylvatica
Picea abies
Quercus petraea

Figure 1

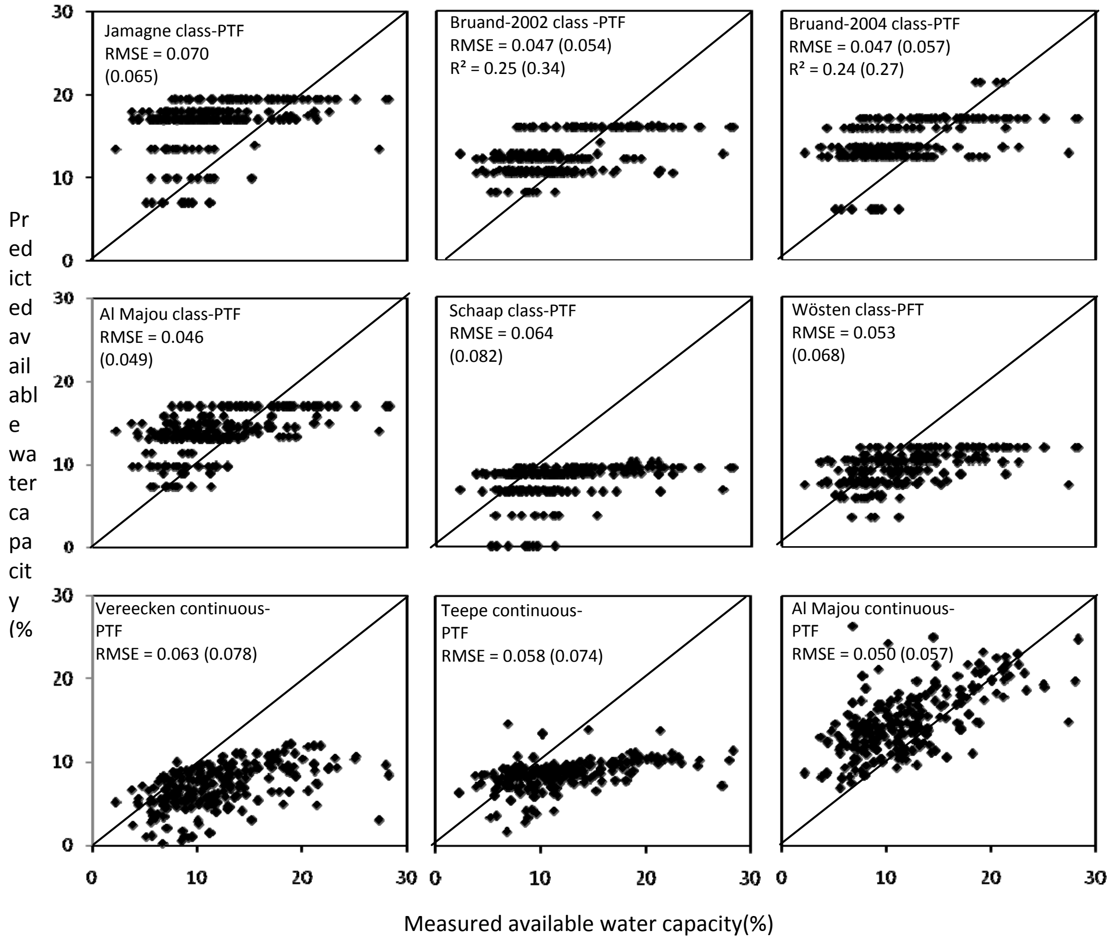
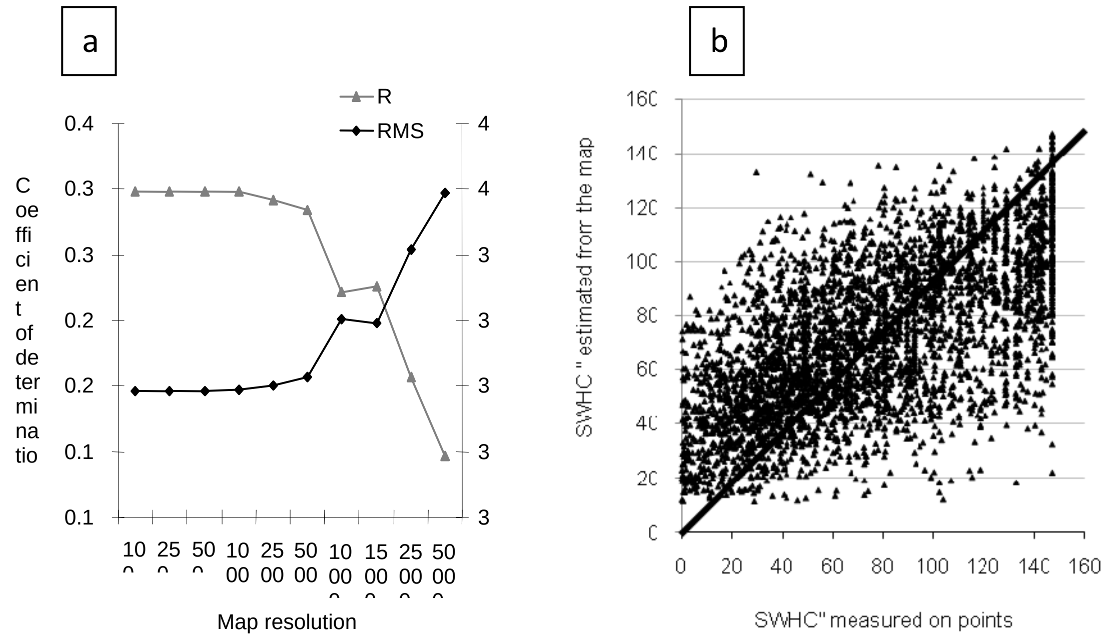
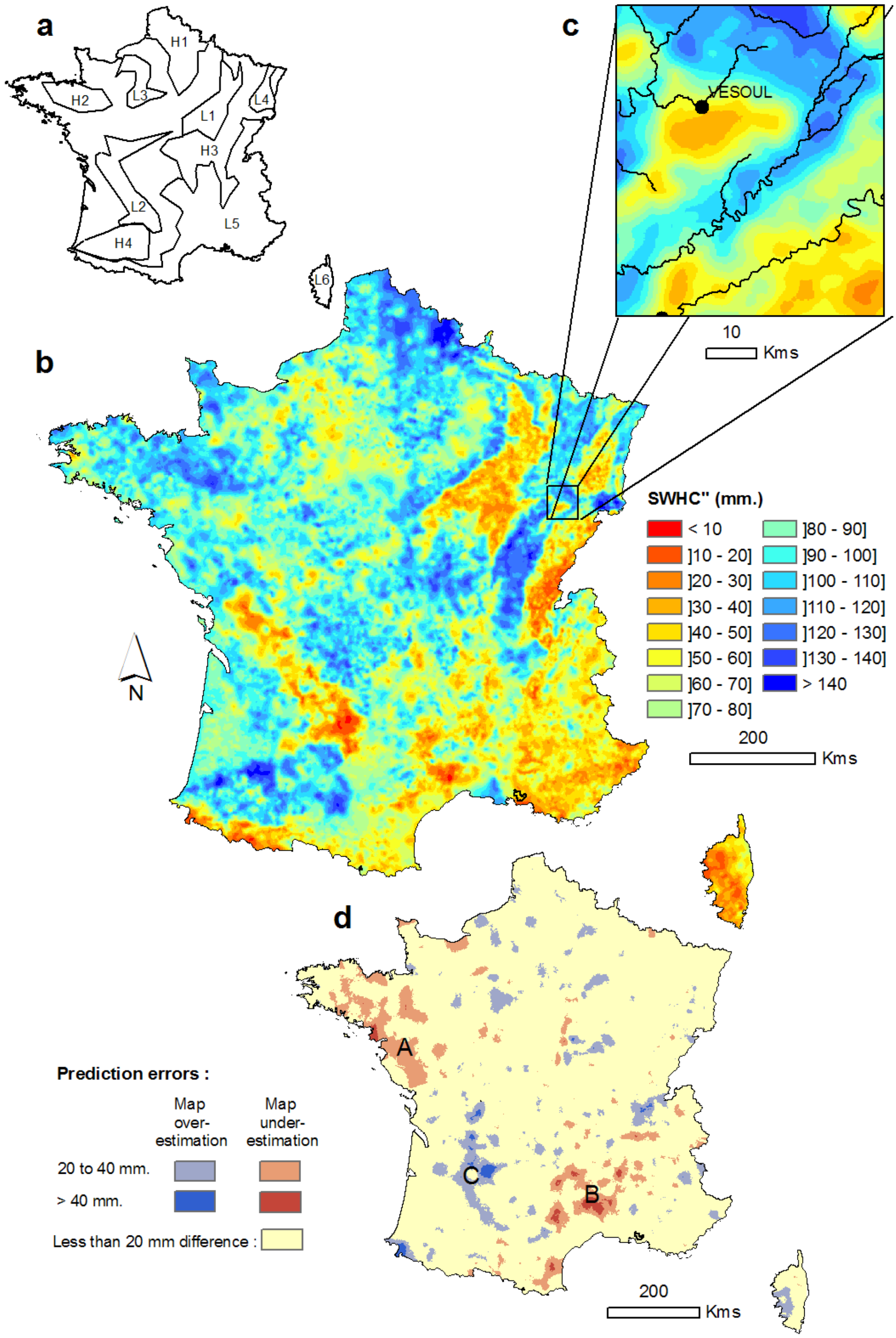

Predicted available water capacity (%
Jamagne class-PTF
RMSE = 0.070
(0.065)
Bruand-2002 class -PTF
RMSE = 0.047 (0.054)
R² = 0.25 (0.34)
Bruand-2004 class-PTF
RMSE = 0.047 (0.057)
R² = 0.24 (0.27)
Al Majou class-PTF
RMSE = 0.046
(0.049)
Schaap class-PTF
RMSE = 0.064
(0.082)
Wösten class-PFT
RMSE = 0.053
(0.068)
Vereecken continuous-PTF
RMSE = 0.063 (0.078)
Teepe continuous-PTF
RMSE = 0.058 (0.074)
Al Majou continuous-PTF
RMSE = 0.050 (0.057)
0
10
20
30
Measured available water capacity(%)

Figure 2


a
R
RMS
Coefficient of determinatio
Map resolution
b
SWHC" estimated from the map
SWHC" measured on points

Figure


a
H1
H2
L3
L4
L1
H3
L2
L5
H4
L6
b
c
VESOUL
10
Kms
N
SWHC" (mm.)
< 10
]10 - 20]
]20 - 30]
]30 - 40]
]40 - 50]
]50 - 60]
]60 - 70]
]70 - 80]
]80 - 90]
]90 - 100]
]100 - 110]
]110 - 120]
]120 - 130]
]130 - 140]
> 140
200
Kms
d
Prediction errors :
Map over-estimation
Map under-estimation
20 to 40 mm.
> 40 mm.
Less than 20 mm difference :
A
B
C
200
Kms

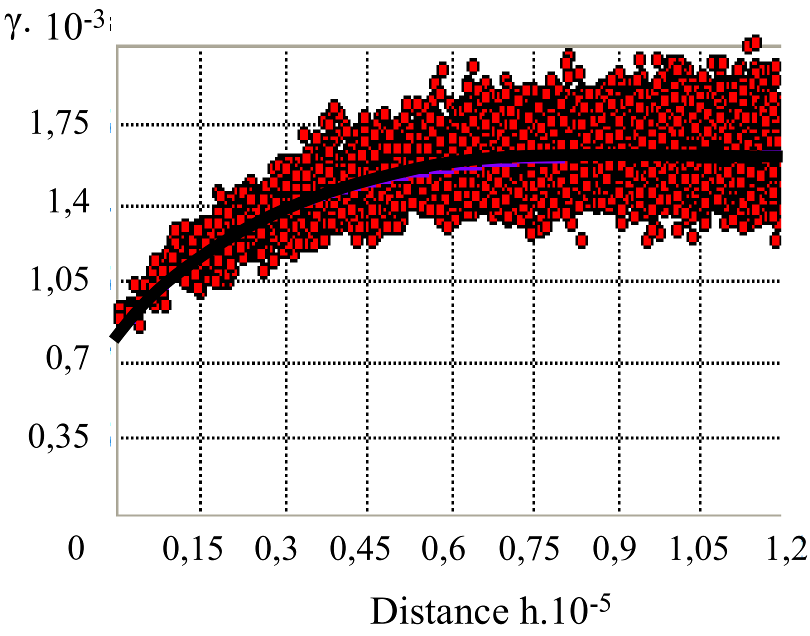

γ. 10-3
1,75
1,4
1,05
0,7
0,35
0
0,15
0,3
0,45
0,6
0,75
0,9
1,05
1,2
Distance h.10-5

Figure 5

	NFI textural class	Jamagne	Bruand -2002	Bruand -2004	Al Majou topsoil	Al Majou subsoil	Schaap topsoil	Schaap subsoil	Wösten	MEAN	STD
1	sand	0,07	0,08	0,06	0,11	0,09	0,06	0,04	0,0001	0,06	0,035
2	loamy sands	0,10	0,13	0,13	0,14	0,07	0,07	0,06	0,04	0,09	0,038
3	sandy clay loam	0,14	0,13	0,13	0,14	0,07	0,07	0,06	0,07	0,10	0,035
4	silt loam	0,14	0,14	0,17	0,17	0,14	0,09	0,08	0,09	0,13	0,036
5	silty clay loam	0,20	0,16	0,17	0,17	0,15	0,12	0,11	0,10	0,15	0,034
6	silt	0,18	0,16	0,21	0,17	0,15	0,12	0,11	0,10	0,15	0,038
7	silty clay	0,18	0,10	0,14	0,15	0,13	0,10	0,09	0,09	0,12	0,032
8	clay loam	0,17	0,11	0,16	0,16	0,14	0,09	0,08	0,07	0,12	0,041
9	clay	0,17	0,12	0,12	0,13	0,10	0,10	0,08	0,09	0,11	0,029

Table 1

	class-PFT						continuous-PFT		
	Jamagne	Bruand-2002	Bruand-2004	AlMajou	Schaap	Wösten	Vereecken	Teepe	AlMajou
RMSE	50,1	21,8	30,4	18,5	35,0	29,3	30,8	38,4	30,8
ME	41,5	8,3	20,6	3,8	-26,2	-15,3	-33,6	-22,9	23,6
R^2	0,79	0,79	0,82	0,84	0,72	0,82	0,83	0,82	0,85

Table 2

	Flat areas				Steep area			
Rock type	n	Mean	RMSE	RMSEr	n	Mean	RMSE	RMSEr
Igneous/metamorphic rocks	56	73	38	51	1783	60	35	73
Massive silicate rocks	18	86	34	43	238	65	37	74
Hollow silicate rocks	4906	93	32	32	6345	83	37	43
Massive calcareous rocks	360	46	26	75	2522	46	30	88
Hollow calcareous rocks	746	66	32	47	2919	57	34	58
Marl, clay	295	101	23	21	363	81	34	37

Table 3

	repeats	mean n	RMSE	STD
France	1	20955	33,9	ND
200 km	26	853	33,8	9,1
100 km	77	267	33,6	6,4
50 km	243	84	33,6	7,6
25 km	706	27	33,0	8,9
10 km	94	11	32,1	11,7

Table 4

	n	Depth	Formula	Jamagne	Bruand-2002	Bruand-2004	Schaap	Wösten	Al Majou
Picea abies	2068	14,4	SWHC '	9,4	14,0	12,2	4,5	10,7	11,8
			SWHC"	16,1	20,4	19,0	7,2	17,5	18,6
Fagus sylvatica	816	7,2	SWHC '	6,3	7,0	5,6	2,2	6,4	7,3
			SWHC"	10,4	11,1	9,5	4,3	10,6	11,5
Quercus petraea	878	7,5	SWHC '	6,7	9,7	9,9	6,5	8,7	9,4
			SWHC"	10,5	11,9	12,1	7,7	10,9	11,7

Table 5