Sessile oak (Quercus petraea Liebl.) site index variations in relation to climate, topography and soil in even-aged high-forest stands in northern France

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Original article

Sessile oak (*Quercus petraea* Liebl.) site index variations in relation to climate, topography and soil in even-aged high-forest stands in northern France

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Abstract – The relationships between *Q. petraea* site index and site variables were studied using data from 99 even-aged high-forest stands located in north-western and north-eastern France. Stepwise multiple regressions using climate, topography and soil factors were adjusted and explain 49 to 60% of the variance in site index. This clearly demonstrates that an autecological study can be successfully performed over a large geographical area if an appropriate sampling strategy is applied. Moreover, the autecology of sessile oak was specified: (1) the role of soil water capacity, topographic position, log(Mg), log(S), K/P_2O_5, Mg/K and humus form was emphasized; (2) no regional differences in site index were observed, which was corroborated by few climatic effects; (3) models adjusted to each region were consistent; (4) nutrient factors explained a higher portion of variance of *Q. petraea* site index compared to climate/water-related factors, however the confounding effect was significant.

site index / ecological factors / soil analyses / *Quercus petraea* (Mattus) Liebl.

Résumé – Variations de l'indice de fertilité du chêne sessile (*Quercus petraea* Liebl.) en fonction du climat, de la topographie et du sol dans des futaies régulières adultes du nord de la France. Les relations entre l'indice de fertilité de *Q. petraea* et le milieu ont été étudiées dans 99 peuplements de futaies régulières adultes du centre-ouest et nord-est de la France. Des régressions multiples pas à pas basées sur le climat, la topographie et le sol expliquent de 49 à 60 % de la variance de l'indice de fertilité. Ce résultat indique clairement qu'une étude autécologique peut être menée avec succès sur un grand secteur géographique si une stratégie d'échantillonnage adaptée est appliquée. De plus, l'autécologie du chêne sessile est précisée : (1) nous soulignons le rôle de la réserve utile en eau du sol, de la position topographique, de log(Mg), log(S), K/P_2O_5, Mg/K et du type d'humus sur l'indice de fertilité ; (2) aucune différence inter-régionale n'est observée sur l'indice de fertilité, ce qui est corroboré par le faible effet du climat sur la croissance ; (3) les modèles prédictifs ajustés au niveau de chaque région sont très proches ; (4) la part de variance de l'indice de fertilité expliquée par le niveau trophique est plus élevée que celle liée aux facteurs hydriques et climatiques, mais la part commune expliquée par ces trois facteurs est importante.

indice de fertilité / facteurs écologiques / analyses de sol / *Quercus petraea* (Mattus) Liebl.

1. INTRODUCTION

The potential productivity in various site conditions is one of the most important criteria for decision making in forest management [49]; it allows the forester to select the most suitable crop species, to precisely forecast stand production and to make species-specific and site-specific silvicultural prescriptions (rotation age, intensity and frequency of thinnings) [48]. Knowledge of the species response to site conditions could help identify particular sites on which the species is or may become unsuitable, especially in the context of climate warming and/or nitrogen deposition.

Potential productivity for a given species has been widely assessed by site index measurement, defined as the top height of dominant trees at a reference age for forest stands which are regular, even-aged, pure and closed [34].

Systems for evaluating site quality and predicting forest productivity based on site-growth relationships have received considerable attention over the past 50 years [64]. Numerous studies, known as soil-site studies, have focused on predicting site index in various ecological conditions and forest species [22, 25].

In France, most of these studies are being criticised because they have not provided enough precise results in spite of their relatively high cost. The main drawback is that a large variability can persist within forest site types in a study which relates site index to a pre-established forest site type classification

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(= synoptic approach). This variability may be related to the heterogeneity of the soil water capacity within the site types [29]. But when sampling data are stratified according to soil water capacity, the precision of the results delivered with a synoptic approach can be as good as with an analytical approach that directly links ecological descriptors to site index [29].

The quality of the results mainly depends on 4 factors: (1) the species' ecological range, which determines the magnitude of the response to site variations; (2) the sampling strategy applied (an extended range of forest site types, equal sampling in each forest site type or regular distribution along the ecological gradients is recommended), (3) the stand selection (stands must follow Eichhorn's rule) [34] and (4) the quality of the collected data.

The problem of spatial scale has also been widely discussed [21]. Most of the studies on tree species in lowland forests have been restricted to small regions where climatic variability is reduced. Only a few studies cover large regions [29, 38, 51]. More accurate results are expected if studies are restricted to small areas with little climatic and geomorphologic variability and understory vegetation is used to diagnose site quality. However, restricting the study to a small, climatically uniform region is questionable when site diagnosis is not based on understory layer [35] or when the study is located in mountainous regions where altitude, aspect and topography are the main ecological gradients [10, 29]. Indeed, most of the studies have limited success in accounting for site index variation over large areas [23, 66]. In addition, only a few test the hypothesis that enlargement of the study area could cause a decrease in site index prediction quality [23, 29].

Sessile oak (*Quercus petraea* Liebl.) is the most widespread and important deciduous timber species in France; together with pedunculate oak (*Q. robur* L.), it represents 30.5% of the forest surface and 28% of the standing volume [44]. Sessile oak has adapted to a large range of ecological conditions. It displays a different, larger ecological amplitude compared to pedunculate oak: it is less nutrient-demanding, more tolerant to drought but less tolerant to the presence of calcium carbonate in soils [8, 17, 26, 42, 65]. Young sessile oaks are less tolerant to waterlogging in the soil than pedunculate oaks; however, adult sessile oaks show a better growth in waterlogged soils that are frequently exposed to summer drought, because drought is a more limiting factor than watterlogging for pedunculate oaks [58]. Recent studies have been restricted to particular forests or small natural regions [20, 46], except for one in north-western France which focused on radial growth [56]. Most of them have been carried out by students from the French Forest Engineering School (ENITEF) but have not been published in French or international journals. An extrapolation of the results to a large area, a clarification of the role of the climate, soil water regime and nutrient richness in predicting sessile oak growth and an estimate of the magnitude of their effects [41] are necessary.

The objectives of this study are: (1) to test the feasibility of a study on the relationships between site index and ecological factors over a large territory (550 by 250 km), i.e., 9 "départements" and 12 "régions IFN" and (2) to quantify the respective effects of radiation, water and nutrient budgets on sessile oak site index.

Our hypothesis is that accurate site index predictions can be made even if the study area is large if the following rules are respected: (1) to cross soil water content and nutrient status in a balanced sampling design, (2) to sample regularly along these ecological gradients and especially in edges and (3) to collect high-quality ecological indices.

2. MATERIALS AND METHODS

2.1. Sampling strategy and study area

In order to accurately analyse the relationships between ecological parameters and growth variables, we chose to use an analytical approach [40] and to precisely assess the three main budgets for wood production: radiation, water and nutrients [28]. However, this does not mean that these budgets are easy to estimate (for example, numerous input parameters – climatic, topographic and soil – are required to estimate water budget). As recommended by Franc and Houllier [34], a sampling strategy was defined to: (1) explore the largest site variations possible regarding soil water capacity and mineral nutrient conditions; (2) respect an orthogonal sampling plan, i.e., a complete, balanced two-factor plan for soil water and mineral richness which would allow a proper estimation of the main effects and their interaction and (3) limit the effects of other factors, especially those related to silvicultural practises; we only sampled adult (> 60 years), nearly pure, even-aged, closed, high-forest stands of oaks grown from seedlings. Stands were selected according to official information on the origin of the stand (seedling or sprout) in the forest management plan (if available) and/or by observing stem form (absence of twin stems within the stand). However, in order to find site conditions that were infrequent but necessary for statistical analyses, some variation in purity and even-age characteristics of the oak stands was accepted. In this case, at least 60% of the dominant trees were either sessile or pedunculate oaks (the normal criterion was 80%) and the age variation of the dominant trees was less than 10% of the mean age [31]. Height plots did not meet this last condition but were retained because of particular site conditions.

The general study area partly covers the South-east of the Paris Basin and the North-east of France. Within this area, a previous climatic analysis published by Gilbert and Franc [39] helped us to define two distinct, climatically homogeneous regions using relative annual water budgets (see Fig. 1): the eastern region where the annual water deficit was under 15% ("Lorraine" and "Alsace" administrative "Régions", "Alsace Plain" excluded), and the western region where the annual water deficit was over 15% ("Centre" and "Pays-de-Loire" Régions). Despite this climatic stratification, moderate climatic variations remained within the study area. The calculation for the annual water deficit is detailed in Gilbert and Franc [39] who used climatic means for the 1961–1990 period from the French meteorological stations network. The water balance model is based on the following algorithm where PET: potential evapotranspiration, AET: actual evapotranspiration, P: precipitation and SWC: soil water capacity. Monthly potential evapotranspiration (PETm) is calculated using Thornthwaite or Turc's formula. If Pm ≥ PETm then AETm = PETm. If Pm < PETm then soil water reserve is used and the amount of water collected is a function of the water deficit accumulated over the previous months: in this case, AETm = Pm + P_{SWC}m, where P_{SWC} is the portion of the soil water capacity that is collected. When the period of water deficit is finished, the extra-water not transpired by the plant is used first to reconstitute the soil water reserve, then is flown out of the system. Finally, the annual soil water deficit is computed as follows:

$$\sum_{m=1}^{12} \frac{(AETm - PETm)}{PETm}.$$

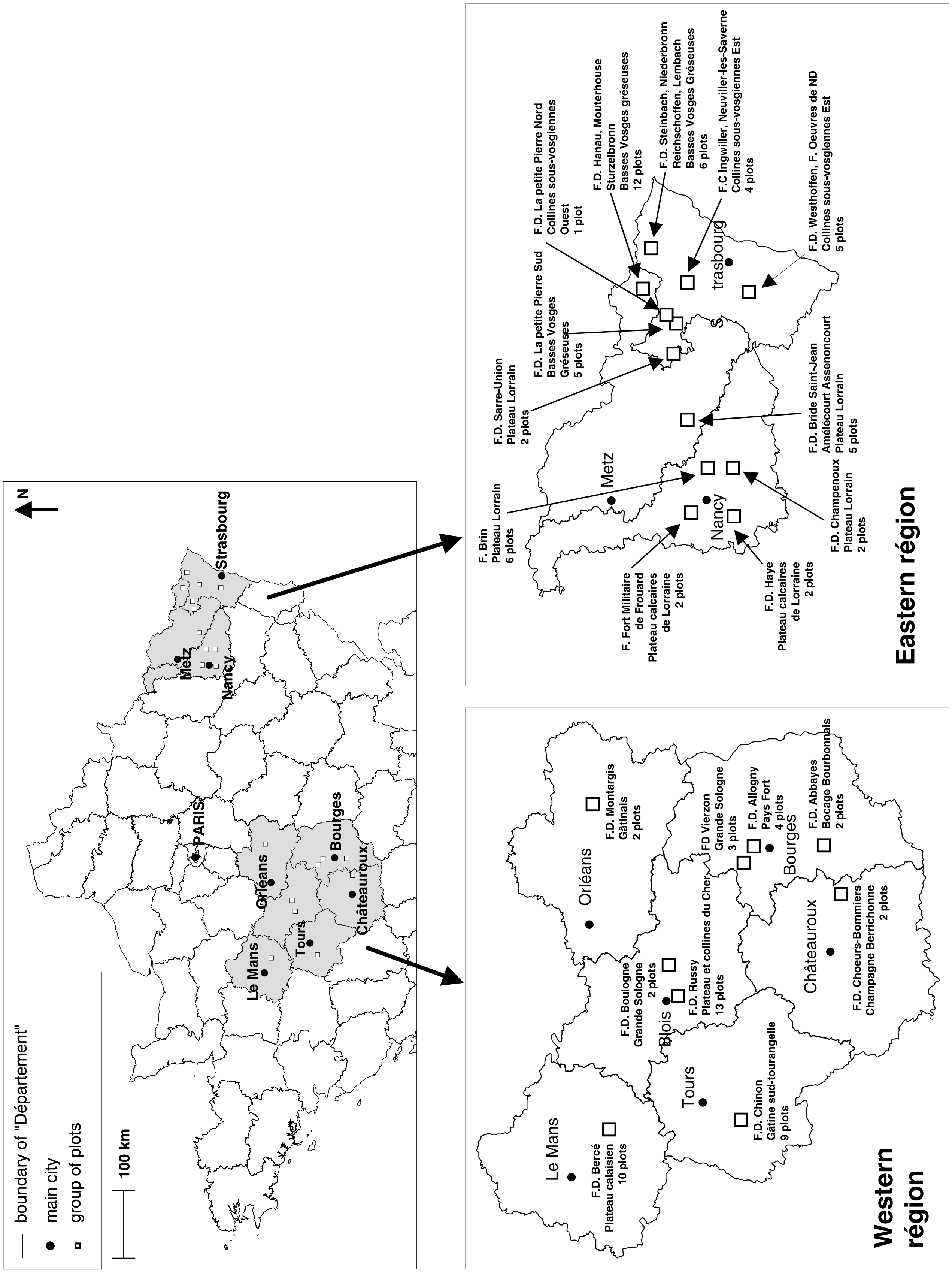

Figure 1. Geographical location of the 99 plots sampled in the two regions (East and West). The number of plots sampled by forest or group of forests is provided.

The following site factors were fixed or controlled during field operations: the upper altitudinal limit was fixed at 500 m (the northern "Vosges" mountains were the highest points); waterlogged conditions were controlled and we only selected stands where (1) temporary waterlogging below 50 cm was present whatever the intensity of the gleyed layer discoloration or (2) temporary waterlogging above 50 cm was present but with very moderate gleyed layer discoloration. Other ecological factors (topographic position, aspect, parent material, soil texture and type) were not stratified but only measured; this allowed us to test their effect on tree growth.

Though the final sampling design was composed of 99 plots, it was incomplete and unbalanced. More precise measurements were done on these 99 plots.

2.2. Site index measurement

Twenty-meter-radius circular plots (0.126 ha) were set up within homogeneous site conditions following Brêthes' recommendations [21]. When site conditions were not sufficiently homogeneous, the sample plot area was reduced to 0.07 ha (a 15-m-radius circular plot or rectangle).

Dominant height (H_0) was measured using a variant of Duplat's protocol [31] that is normally based on the measurement of the 1st, 3rd and 5th biggest trees on a 0.06-ha plot to estimate the mean height of the 100 biggest trees per ha. We identified the 6 biggest trees in the circular plot and randomly chose 3 oaks among the following 3 couples: 1st and 2nd, 3rd and 4th and 5th and 6th. This provided an estimate of the mean height of the population which approached the 50 biggest trees per ha. We chose one tree in each couple as a compromise between systematic selection and to avoid coring very high-quality trees. The total height of each tree was estimated from two opposite sides at a variable distance from the tree by measuring angular characteristics with a clinometer. Tree height measurement error was less than 0.7 m. Each tree was cored twice to the pith with a 5-mm Pressler corer at a height of 1 and 1.10 m. Cores were made in the same direction to ensure a very short distance from the pith. Following Duplat and Tran-Ha's recommendations [30], 4 years were added to the age counted on the best increment core to obtain a tree age at 0.30 m height. The height and age of the 3 measured trees were averaged to assess plot dominant height (H_0) and mean age. Site index was computed with a reference age of 100 years (called SI_{100} below) using height-age curves (model B) from Duplat and Tran-Ha [30] (Fig. 2).

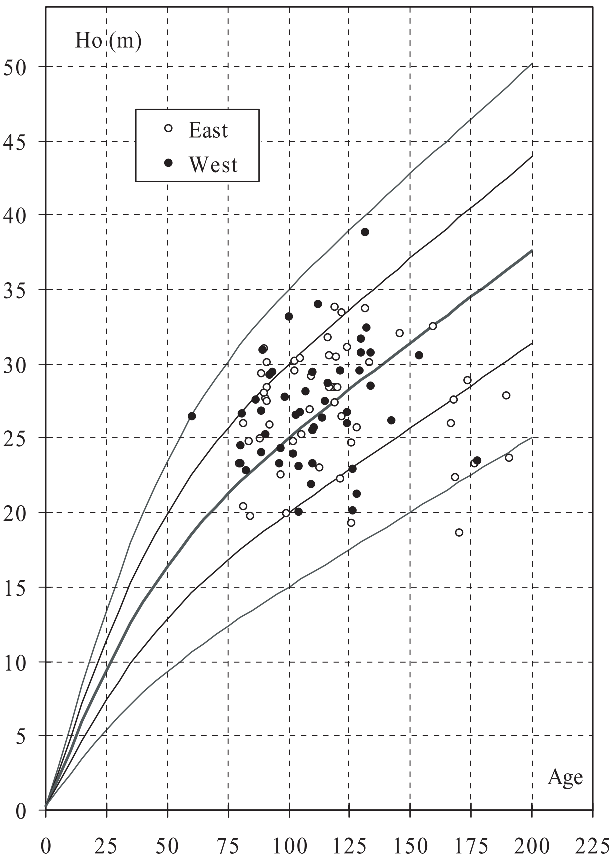

Figure 2. Modelisation of sessile oak dominant height as a function of stand age according to model B of Duplat and Tran-Ha [30]. Simulation of H_0 as a function of age for 5 site indices at the reference age of 100 years (15, 20, 25, 30 and 35 m) and data observed (East and West samples).

2.3. Climate and soil data collection

Monthly median precipitation and mean temperature for the 1961–1990 period were provided by Meteo France and came from two databases: (1) for 36 eastern plots, digitised data from thematic maps (AURELHY method) with a resolution of 1 km^2; (2) for the remaining 16 eastern plots, data came from 5 stations for precipitation and 2 stations for temperature and for the 47 western plots, data came from 5 stations for temperature and from 13 stations for precipitation. Several climatic indices were computed (see Tab. I).

Topographic characteristics, elevation, slope, aspect, topographic position and parent material were measured in the field or collected on suitable maps. Humus form was described in three different locations according to the Pedological Reference frame classification [45]. According to Llyod et Lemmon [60] aspect was transformed into a continuous variable for plots where aspect was over 4% using the following formula: Aspect = cos(RA–A), where A is the plot azimuth and RA is a given reference azimuth (in grades); Aspect = 1 if A = RA and –1 if A = RA ± 200; a value of 0 for Aspect was assigned to plots where slope was less than 4%. The RA is known to be between north and east [6, 60] and was optimised for our data by calculating the maximum correlation between SI_{100} and Aspect: it was 75 gr.

A soil pit, 2 m in depth, was excavated with a mechanical shovel at a distance of 3 m from one of the cored trees. Digging was continued until an R-horizon (bedrock) was reached. Two plots were dug manually because access for the shovel was impossible: these two plots had very shallow soil. Soil profile was described using a standard protocol, which included observations on the intensity and location of an HCl effervescence (localised or generalised effervescence of the fine soil fraction), size and percentage of coarse elements, soil drainage assessed by hydromorphic mottling using Baize and Jabiol's classification [2].

In order to carry out complementary physical and chemical analyses, A-horizon soil samples were collected in 5 locations within the plot. Soil samples were air-dried, then sieved at 2 mm. Soil particle size distribution was determined on mineral horizons using the hydrometer method. The following chemical analyses were performed according to recommendations from Gégout and Jabiol [37]: pH-H_2O, pH-KCl 1 N, cationic exchangeable capacity at soil pH, exchangeable Ca, Mg, K, Al and H^+, total organic carbon C, total organic nitrogen N and potentially available phosphorous. Analytical results were expressed as concentrations over dry-mass (cmol$^+$/kg for cations and g/kg for C, N and P_2O_5). Saturation rate of the absorbing complex, C/N ratio and several mineral element content ratios identified as important for tree nutrition were also calculated [15].

Table I. Elementary statistics of forest mensuration and ecological data (see text for further explanation for variable description and computation). Ecological data are separated into climatic and soil data. Chemical data were measured in the A-horizon. The different classes used are provided and the number of plots per class are mentioned between brackets.

Variable name and unit	Code	Min	Total Mean ± SD	Max	Eastern region Mean ± SD	Western region Mean (± SD)
Number of plots			*n* = 99		*n* = 52	*n* = 47
Stand characteristics						
Age (at 0.30 m)	Age	56	110.7 ± 26.6	187	114.8 ± 30.0	106.2 ± 21.8
Site index at 100 years (m)	SI_{100}	12.1	25.3 ± 4.6	34.8	24.9 ± 4.9	25.8 ± 4.2
Basal area at 1.30 m (m^2/ha)	G	13.1	27.2 ± 6.3	53.3	27.4 ± 6.8	27.1 ± 5.8
Climatic data						
Mean annual temperature (°C)	MAT	8.4	10.0 ± 1.0	11.1	9.1 ± 0.4	11.1 ± 0.1
Median annual precipitation (mm)	MAP	644	793 ± 114	1008	881 ± 80	695 ± 40
PET-P from April to October (mm)	PET-P	53.0	115.0 ± 42.1	199.0	81.7 ± 25.8	152 ± 20
Soil water deficit (mm)	SWD	11.4	68.3 ± 45.8	181.5	30.8 ± 17.4	109.7 ± 28.2
Altitude (m)	Altitude	85	224 ± 109	476	314 ± 68	124 ± 32
Aspect (after cos transformation)	Aspect	–1.00	–0.02 ± 0.53	1.00	–0.02 ± 0.59	–0.02 ± 0.46
Topographic position (3 classes with L: lateral loss; G: lateral gain)	Topo	L > G (*n* = 13); G = L (*n* = 75); G > L (*n* = 11)			L > G (*n* = 10); G = L (*n* = 34); G > L (*n* = 8)	L > G (*n* = 3); G = L (*n* = 41); G > L (*n* = 3)
Physical and chemical soil properties						
Soil depth (cm)	SD	35	159 ± 38	200	156 ± 48	162 ± 25
Stone content (%)	SC 0-150	0	28.6 ± 24.5	91.0	21.3 ± 24.3	36.7 ± 22.3
Soil water capacity on 150 cm (mm)	SWC 0-150	5	153 ± 69.7	275	156 ± 81	149 ± 56
pH-H_2O	pH-H_2O	3.94	4.69 ± 0.66	7.13	4.76 ± 0.58	4.60 ± 0.74
pH-KCl 1N	pH-KCl	2.80	3.72 ± 0.75	6.28	3.77 ± 0.68	3.66 ± 0.82
Exchangeable calcium ($cmol^+$/kg)	Ca	0.07	4.86 ± 8.36	47.00	4.95 ± 8.12	4.76 ± 8.71
Exchangeable magnesium ($cmol^+$/kg)	Mg	0.05	0.92 ± 0.91	5.44	0.85 ± 1.04	1.00 ± 0.75
Exchangeable potassium ($cmol^+$/kg)	K	0.07	0.35 ± 0.23	1.08	0.37 ± 0.27	0.32 ± 0.16
Exchangeable base sum ($cmol^+$/kg)	S	0.20	6.13 ± 9.08	49.83	6.17 ± 9.00	6.08 ± 9.27
Exchangeable proton ($cmol^+$/kg)	H^+	0.05	1.08 ± 1.01	5.28	0.74 ± 0.50	1.47 ± 1.28
Exchangeable aluminium ($cmol^+$/kg)	Al	0.05	1.54 ± 1.37	7.68	1.58 ± 1.29	1.50 ± 1.47
Cationic exchange capacity ($cmol^+$/kg)	CEC	2.22	10.20 ± 9.71	57.62	9.99 ± 9.60	10.43 ± 9.93
Saturation rate (%)	S/T	4.7	50.4 ± 32.8	100	47.7 ± 34.6	53.5 ± 31.1
Organic carbon (g/kg)	C	17.1	58.4 ± 37.5	236.9	42.6 ± 14.8	75.8 ± 46.6
Nitrogen (g/kg)	N	0.91	3.30 ± 1.67	10.25	2.78 ± 1.09	3.88 ± 2.00
C/N	C/N	8.52	17.47 ± 4.61	37.55	16.05 ± 3.96	19.06 ± 4.80
Phosphorous (g/kg)	P_2O_5	0.02	0.13 ± 0.11	0.82	0.16 ± 0.15	0.10 ± 0.04
Humus form (5 classes)	Humus	1- Dysmoder-Mor (*n* = 25); 2- Eumoder (*n* = 16); 3- Oligomull to Hemimoder (*n* = 22); 4- Mesomull (*n* = 13); 5- Eumull (*n* = 23)			1 (*n* = 7); 2 (*n* = 6); 3 (*n* = 15); 4 (*n* = 4); 5 (*n* = 20)	1 (*n* = 18); 2 (*n* = 10); 3 (*n* = 7); 4 (*n* = 9); 5 (*n* = 3)

Soil water capacity, i.e., plant-available water between field capacity and the permanent wilting point, was calculated using Jamagne's coefficients [47] and the classic formula given by Lévy [59]. C, M, R and D-horizons also contain a small quantity of water that was taken into account only if fine roots were observed in the horizons. We used specific, arbitrary coefficients for the C-horizon of granite arenas (0.6 mm/cm), Mn-horizons of marl (0.5 mm/cm) and R-horizon of soft sandstone (0.2 mm/cm).

2.4. Data analysis methods

The effect of SWC, climate and soil nutrients on site index were first analysed using ANOVA, linear or polynomial regressions. This allowed us to detect the nature of the relationship between site index and explanatory variables. Then, stepwise multiple regressions were used to test the additive effects of these factors. Models were adjusted to each regional sample then to the whole sample. Specific two-way

ANOVA were also adjusted to test the interaction between soil water and nutrient-related factors. Variance homogeneity and distribution of residuals were visually checked.

Multiple regression fitting was followed by variance partition using Type I sum of squares, which allows the respective parts of the 3 basic budgets (climate, water and nutrients) and the confounding part of these factors to be quantified. The variables were clustered into 2 groups: climate/water-related and nutrient-related factors. The models were successively fitted (1) with first the climate/water group and second the nutrients group entered into the model (2) then the contrary.

ANOVA, simple and multiple stepwise regressions were performed using S-plus version 6.2®.

3. RESULTS

3.1. Sampling characteristics

Elementary statistics for forest mensuration, climate and soil variables are presented in Table I. The 8 basic humus forms were grouped into 5 simplified classes for analysis purposes. Plot age distribution was dispersed but 84% of the plots were 80 to 130 years old (Fig. 2). Site index was more variable compared to Duplat and Tran-Ha's observations [30]: these authors indicated that site index at 100 years varied between 15.1 and 30.7 m and plot age varied between 102 and 216 years. The comparison of the two samples was not rigorous because age ranges were not similar in both data sets. However, minimum SI_{100} corresponded to the same ages. After eliminating the youngest plots (the maximum SI_{100} was 34.8 m for a 56-year-old plot), maximum site index was higher compared to Duplat and Tran-Ha's sample [30] because a 135-year-old plot with SI_{100} = 33.9 m was included. The lowest SI_{100} in our sample corresponded to extremely poor site conditions not sampled by Duplat et Tran-Ha [30].

3.2. Relationships between site index and ecological variables

3.2.1. Role of soil water capacity and topographic position

SI_{100} was correlated with SWC (Tab. II). Complementary analyses not presented here allowed us to keep the SWC computed to a depth of 150 cm (called below SWC 0-150) as the SWC reference value in the next analyses. SI_{100} increased by 3.2 m when SWC 0-150 increased by 100 mm.

SI_{100} was correlated with topography (Tab. II): compared to neutral positions (gain = loss), site index was reduced (–3.8 m) in deficit positions (loss > gain) whereas it increased (+2.7 m) in favourable positions (gain > loss).

3.2.2. Role of climatic factors, water balance and soil water deficit

Aspect had an effect on site index, but the effect is more significant if only plots where slope was over or equal to 4% were kept (Tab. II): site index was reduced (–2.9 m) when aspect was 275 gr and it increased (+2.9 m) when aspect was 75 gr, compared to neutral aspects (175 or 375 gr). However, precipitation, temperature, altitude, PET-P or SWD had no significant effect on SI_{100}.

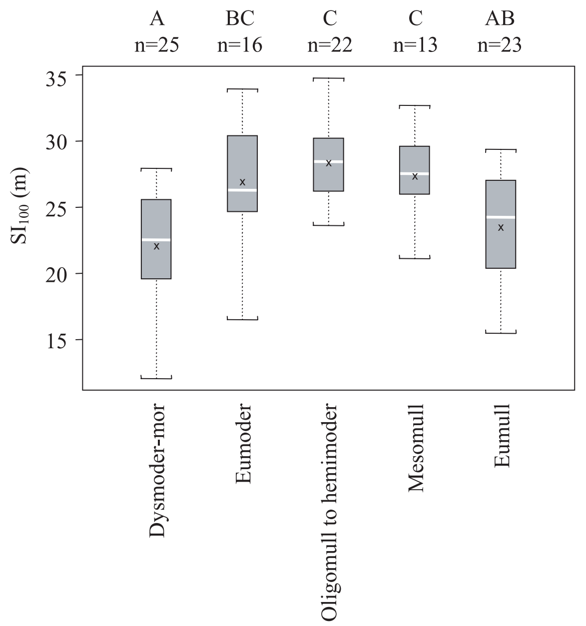

Figure 3. Boxplot of site index (SI_{100}) according to humus form: the thick horizontal line within the box corresponds to the median and the cross corresponds to the mean; the letter above each class indicates the result of pairwise multiple comparisons (Tukey method).

3.2.3. Role of nutrient richness

Humus form had a strong effect on SI_{100} (31% of the variance explained): growth was low on extreme humus forms (eumull and dysmoder-mor) and high on oligomull-to-hemimoder, but no significant differences were found between mesomull, eumoder and oligomull-to-hemimoder (Fig. 3).

Simple or polynomial regressions were fitted after graphical observation of SI_{100} = f(X) and after log transformation for exchangeable cations (Tab. II). The relationship between SI_{100} and S/T, pH-KCl or pH-H_2O was parabolic, with an optimum value around 50% for S/T.

According to the threshold values provided by Bonneau [15], the proportion of plots low in K and Ca was large but this was less important for Mg. More than 50% of the eastern plots and about 75% of the western plots were K-deficient. But the percentage of plots where Ca and Mg were deficient or in excess was similar in both regions. The comparison to threshold values that correspond to analysis at pH = 7 was correct because soil measurement at pH = 7 does not overestimate real exchangeable Mg and Ca contents for acidic soils. However, this is not the case for CEC [24]. The relationships between exchangeable cation contents and site index were more often significant compared to the synoptic variables mentioned above (Tab. II). The variables log(Ca), log(Mg) and log(S) were the best predictors of SI_{100}, providing parabolic models with flat convexity. Growth reduction was more pronounced for high values than for low ones because residuals were less spread for high values.

Table II. Results of the simple or polynomial regressions between SI_{100} and different soil, climate and topography variables for the whole sample and for soils with or without a carbonated horizon. Chemical soil variables were measured on A-horizon. The variables for the whole sample are given in ascending order of R^2.

Variable	Model equation	R^2	$p > F$	SE (m)
Whole sample (n = 99)				
Aspect	SI_{100} = 25.4 + 2.65 (Aspect)	0.056	0.018	4.46
	Plots where slope ≥ 4% (n = 47): SI_{100} = 26.6 + 2.88 (Aspect)	0.157	0.0059	4.04
pH-H_2O	SI_{100} = –8.5 + 14.49 (pH-H_2O) – 1.52 (pH-H_2O)^2	0.068	0.034	4.45
log(K)	SI_{100} = 20.9 – 19.93 (log(K)) – 16.82 (log(K))^2	0.110	0.0034	4.35
Mg/K	SI_{100} = 23.1 + 2.30 (Mg/K) – 0.415 (Mg/K)^2	0.126	0.0015	4.31
Topo	SI_{100} = 21.7 + 0 (G < L) + 3.81 (G = L) + 6.51 (G > L)	0.129	0.0013	4.30
S/T	SI_{100} = 20.9 + 25.25 (S/T) – 23.0 (S/T)^2	0.134	0.001	4.30
pH-KCl	SI_{100} = –13.8 + 19.90 (pH-KCl) – 2.42 (pH-KCl)^2	0.150	0.0003	4.25
K/P_2O_5	SI_{100} = 29.9 – 1.52 (K/P_2O_5)	0.160	< 0.0001	4.21
log(S)	SI_{100} = 26.4 + 4.14 (log(S)) – 5.34 (log(S))^2	0.210	< 0.0001	4.10
log(Mg)	SI_{100} = 26.3 – 6.42 (log(Mg)) – 8.32 (log(Mg))^2	0.213	< 0.0001	4.09
log(Ca)	SI_{100} = 27.3 + 1.37 (log(Ca)) – 3.99 (log(Ca))^2	0.220	< 0.0001	4.07
SWC 0-150	SI_{100} = 20.3 + 0.032 (SWC 0-150)	0.247	< 0.0001	3.98
Humus form	SI_{100} = 22.1 + 0 (Dysmoder-Mor) + 4.86 (Eumoder) + 6.29 (Oligomull to hemimoder) + 5.29 (Mesomull) + 1.44 (Eumull)	0.312	< 0.0001	3.87
Soils with a carbonated horizon (n = 30)				
log(Ca)	SI_{100} = 28.5 – 4.86 (log(Ca))	0.260	0.004	3.35
K/P_2O_5	–	–	–	–
Ca/Mg	SI_{100} = 26.1 – 0.27 (Ca/Mg)	0.157	0.029	3.58
Mg/K	SI_{100} = 29.9 – 0.85 (Mg/K)	0.143	0.039	3.61
	SI_{100} = 30.4 – 0.34 (Ca/Mg) – 1.09 (Mg/K)	0.381	0.0015	3.12
Soils without any carbonated horizon (n = 69)				
log(Ca)	SI_{100} = 27.6 – 3.88 (log(Ca)) + 1.99 (log(Ca))^2	0.186	0.0011	4.46
K/P_2O_5	SI_{100} = 31.8 – 2.15 (K/P_2O_5)	0.225	< 0.0001	4.22
Ca/Mg	–	–	–	–
Mg/K	–	–	–	–

Lastly, SI_{100} was not correlated with C/N ratio, decreased with increasing K/P_2O_5 and displayed a parabolic, convex response to Mg/K.

Regressions for each soil type (with and without a carbonated horizon) between SI_{100} and several nutrient descriptors (Tab. II and Fig. 4) showed that soil types could be distinguished on the graph representing SI_{100} as a function of log(Ca). SI_{100} decreased with increasing log(Ca) on soils with a carbonated horizon. However, the other soil types still showed a curvilinear relationship between SI_{100} and log(Ca). SI_{100} decreased with increasing Ca/Mg and Mg/K only on soils with a carbonated horizon (Tab. II). In contrast, SI_{100} decreased with increasing K/P_2O_5 only on soils without any carbonated horizon.

3.3. Additive effects of ecological variables on site index

3.3.1. East region (E1 à E4)

The models contained either 2 or 3 predictors (Tab. III). Climatic water balance (PET-P) had a negative effect and SWC 0-150 had a positive effect on SI_{100} (E1). Topographic position had an additive effect on SI_{100} which increased by 5.2 m from a deficit position to a neutral position and increases further by 1.1 m in a favourable position. SI_{100} was optimum when S was between 1.08 and 1.35 cmol$^+$/kg (E2-E3) or when Mg was 0.41 cmol$^+$/kg (E4). SI_{100} was optimum when humus form was mesomull (E3-E4) and higher on eumull compared to eumoder. The best models in this region explained 74% of site index variance (E3 and E4).

Table III. Results of the stepwise multiple regressions of SI_{100} according to site variables. Models are adjusted for Eastern (n = 52), Western (n = 47) and both regions (n = 99). The table gives model number, equation, R^2 and standard error (SE).

Code	Model equation	R^2	SE (m)
E1	SI_{100} = 27.0 + 0.037 (SWC 0-150) – 0.059 (PET-P) – 1.10 (K/P_2O_5)	0.457	3.71
E2	SI_{100} = 23.1 + 0 (G < L) + 5.2 (G = L) + 6.3 (G > L) + 4.03 (log(S)) – 6.65 $(\log(S))^2$	0.542	3.43
E3	SI_{100} = 18.9 + 0.71 (log(S)) – 4.48 $(\log(S))^2$ + 0 (Dysmoder-Mor) + 5.95 (Eumoder) + 10.84 (Oligomull to Hemimoder) + 11.18 (Mesomull) + 9.61 (Eumull)	0.744	2.63
E4	SI_{100} = 13.61 + 0.022 (SWC 0-150) – 7.15 (log(Mg)) – 4.00 $(\log(Mg))^2$ + 0 (Dysmoder-Mor) + 4.12 (Eumoder) + 9.10 (Oligomull to Hemimoder) + 10.31 (Mesomull) + 7.92 (Eumull)	0.744	2.66
W1	SI_{100} = 25.0 + 0.025 (SWC 0-150) –1.62 (K/P_2O_5) + 0 (Dysmoder-Mor) + 3.31 (Eumoder) + 3.37 (Oligomull to Hemimoder) + 3.54 (Mesomull) – 1.62 (Eumull)	0.506	3.17
W2	SI_{100} = 24.4 + 0.031 (SWC 0-150) – 3.06 (log(Mg)) – 10.10 $(\log(Mg))^2$ – 1.65 (Mg/K) + 0 (Dysmoder-Mor) + 3.39 (Eumoder) + 3.87 (Oligomull to Hemimoder) + 4.95 (Mesomull) + 5.81 (Eumull)	0.625	2.83
T1	SI_{100} = 23.0 + 0.022 (SWC 0-150) + 0 (G < L) + 1.8 (G = L) + 3.9 (G > L) – 5.76 (log(Mg)) – 6.59 $(\log(Mg))^2$ – 0.764 (K/P_2O_5)	0.491	3.36
T2	SI_{100} = 19.2 + 0.026 (SWC 0-150) – 5.39 (log(Mg)) – 6.13 $(\log(Mg))^2$ + 0 (Dysmoder-Mor) + 3.82 (Eumoder) + 4.82 (Oligomull to Hemimoder) + 4.86 (Mésomull) + 1.40 (Eumull)	0.600	3.00
T3	SI_{100} = 21.7 + 0.019 (SWC 0-150) + 3.70 (log(S)) – 3.96 $(\log(S))^2$ – 0.70 (Mg/K) + 0 (Dysmoder-Mor) + 4.16 (Eumoder) + 5.31 (Oligomull to Hemimoder) + 5.45 (Mésomull) + 1.72 (Eumull)	0.596	3.03

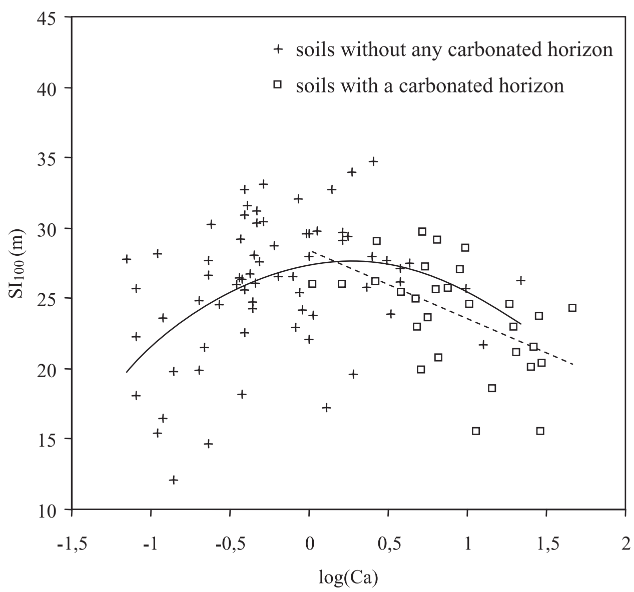

Figure 4. Relationships between SI_{100} and exchangeable Ca in the A-horizon according to soil type (with and without a carbonated horizon) and corresponding regression lines.

3.3.2. West region (W1 to W3)

The models had less predictive power than in the East region and contained 3 or 4 predictors. The predictors were almost the same: SWC 0-150, K/P_2O_5, log(Mg), humus form. Log(S) had no significant effect in this region. No climatic or topographic parameters were better predictors than SWC 0-150 and none could be significantly added to SWC 0-150. SI_{100} was optimum when Mg was 0.86 $cmol^+/kg$ (W2). The effect of humus form varied according to the model: eumull was the worst class in model W1 whereas it was one of the best in model W2; the order was the same in the two models for the other humus classes.

3.3.3. Global models (T1 to T3)

Models had 3 or 4 predictors and R^2 values were intermediate compared to regional models. Models based on (PET-P) + (SWC 0-150) were no better than models based on SWC 0-150 only and SWD gave no better models than the ones based on SWC 0-150. Topographic position was the only parameter that explained a significant part of variance in addition to SWC 0-150. SI_{100} was optimum when S was 1.60 $cmol^+/kg$ (T3) or when Mg was about 0.64 $cmol^+/kg$ (T1 or T2). The most favourable humus forms for SI_{100} were mesomull and oligomull-to-hemimoder and the most unfavourable humus forms were dysmoder-mor and eumull. Moreover, no significant regional effect was detected in these three models.

We also tested for an interaction between SWC and nutrient factors. A two-way ANOVA of SI_{100} according to SWC class (3 balanced classes) and the presence or absence of a carbonated horizon in the soil profile (whatever the depth of the reaction to HCl) indicated that only the SWC class was significant. A two-way ANOVA testing the additive effect of the SWC class (3 classes) and humus form showed that only the main factors were significant.

3.4. Respective part of water and nutrient budgets in predicting site index variations

The climate/water-related factors and nutrient-related factors explained 0 to 25% and 9 to 74% of the variance in site index, respectively (Tab. IV). For global models (T1 to T3), the climate/water-related factors and nutrient-related factors explained 6 to 16% and 20 to 35% of the variance in site index, respectively. The confounding effect accounted for 13% to 19% of the variance.

Table IV. Partition of total variance of models E1 to T3 according to: (1) sums of squares (SS) of climate/water-related factors; (2) SS (nutrient-related factors); (3) SS (confounding effect of (1) and (2)); (4) residual variance.

Sums of squares	E1	E2	E3	E4	W1	W2	T1	T2	T3
Climate/water-related factors	25%	18%	0%	7%	19%	13%	16%	12%	6%
Nutrient-related factors	9%	31%	74%	45%	19%	43%	20%	35%	35%
Confounding effect of factors	12%	5%	0%	23%	0.2%	7%	13%	13%	19%
Residual variance	54%	46%	26%	26%	61%	37%	51%	40%	40%

4. DISCUSSION

4.1. Feasibility of a large-scale autecological study: the role of the sampling strategy

The different multiple regression models explained between 49 and 60% of site index variance in the global models (Tab. III). Predictions were better in the Eastern region but predictors in regional models remained largely consistent with global models and only differed for climatic and topographic variables and quantitative response to nutrient gradient. These values were consistent with R^2 obtained for sessile oak in the Tronçais National Forest (50–61% of variance in site index, see [46]), even if our spatial scale was larger. Consequently, our results do not support the hypothesis that increasing spatial scale will decrease site index prediction quality [23, 29]. Our conclusion is that autecological studies on broadleaved species in lowland forests could be viable on an inter-regional scale, which would considerably reduce the costs. However, we emphasize the need for well-designed sampling: it is necessary to achieve a complete, balanced sampling design stratified according to the main ecological gradients (or to sample regularly along these gradients), and to select pure, even-aged and closed high-forest stands as far as possible. Common as well as marginal site conditions must be sampled with the same intensity and, since marginal site conditions are sparse, sampling efforts must be largely devoted to finding those sites.

4.2. Autecology of sessile oak

4.2.1. Role of soil water capacity and topographic position

Maximum soil water capacity played an important role; it was necessary to apply a costly, original protocol to test its effect. The influence of soil water capacity on sessile oak height and radial growth had already been frequently demonstrated but more often for radial growth [19, 32, 54, 57]. Nieminen [61] mentioned a correlation of 0.40 between sessile oak height growth and soil water capacity on silt and marl soils. Jacquemin et al. [46] indicated that site index at 100 years increases by 2 m with a 100 mm increase in soil water capacity. This is close to our estimate, even if their result was obtained with a more simple sampling protocol than the one in our study.

The effect of topography on site index was consistent with the effect of soil water capacity: the difference between favourable and unfavourable positions (3.9 m, model T1) corresponded to a difference of 175 mm in SWC 0-150, which is very important. Our results were consistent with Jacquemin et al. [46] who mentioned a 2-m decrease in site index for unfavourable topography compared to other positions, but samples for opposite positions are missing in their data.

4.2.2. Role of climatic factors and soil water deficit

Site index was influenced by aspect but only in simple models (Tab. II). This result was surprising for such a moderate relief; however, it confirms the role of aspect on sessile oak height growth [46].

Other climatic factors (PET-P, SWD) had a very limited influence on sessile oak height growth that was restricted to eastern models (E1) and was not significant in global models (T1 to T3). We found that soil water deficit was a worse predictor compared to soil water capacity. Our results were not consistent with other findings that are generally established on radial growth using a dendroclimatic analysis [19, 53]. Indeed, different studies have shown that sessile oak annual radial increment is positively influenced by warm temperatures during the growing season or at the beginning of the summer [11, 56, 63] and also by precipitation accumulated over the growing season [9, 11, 52, 63]. Water balance has been found to be a limiting factor for radial growth in sessile oak [19, 53]. However, these studies have concerned radial growth and not height growth and do not analyse the role of climate at the same level: dendroclimatic studies test the effect of climate on year-to-year growth variations (using growth data averaged over 100 to 200 trees) whereas autecological studies test the influence of regional climate on plot-to-plot growth variations (using climatic data averaged over 30 years). Bréda and Pieffer [19] have provided an example of the decrease in the correlation between growth and soil water deficit from temporal to spatial scale for the same sample: the plot-to-plot correlation between soil water deficit and radial growth averaged over the 1964–1994 period is lower than year-to-year correlation between soil water deficit and radial growth averaged over all plots. A significant annual climatic effect on ring width is also observed on the data used in the present article by Bergès [14]. The difference between temporal and spatial growth responses to climate could be explained by the lower local climate variability compared to the annual climatic variability, but this was not the case in our data: the between-years standard deviation of mean annual temperature was 0.6 °C over the 1961–1990 period for Nancy, but the between-plots standard deviation was higher (1.0 °C, see Tab. I); the between-years standard deviation of annual precipitation was 136 mm over the 1961–1990 period for Nancy and the between-plots standard deviation was slightly lower (114 mm). The difference between temporal and spatial growth responses to climate should be clarified because no difference between the range of two ecological gradients was detected.

4.2.3. Role of nutrient richness

The flat, parabolic response of sessile oak height growth to soil acidity was consistent with the results of Jacquemin et al. [46] but we explored a larger nutrient gradient. These authors only considered mor to oligomull humus forms and observed that sessile oak site index is much lower on mor and dysmoder compared to eumoder, hemimoder and oligomull humus forms (–9 and –6 m respectively). Different authors have also observed a lower site index on very acidic sites and near-surface calcareous soils compared to intermediate conditions [32, 43, 62]. We found, as did Jacquemin et al. [46], that site index can be high on acidic-to-neutral soils (eumoder to mesomull), whereas the studies cited above observed an optimum restricted to slightly acidic sites with dysmull humus [27, 32] or more neutral sites with mesomull humus [1]. Regional differences might explain this variation since both Dupouey and Cuiller and Mériaux [27, 32] worked in Alsace (north-eastern France) and Abt [1] in the Orléans National Forest (western France). However, we observed a different trend with an optimum site index close to acidic sites in the West and close to neutral sites in the East.

In our study, site index response to specific chemical soil variables was consistent with previous results, and the role of potassium and phosphorous nutrition in tree growth was highlighted. Indeed, K/P_2O_5 for soils without any carbonated horizon had already been cited as a good indicator of soil mineral fertility for sessile oak stands in 3 forests in the "ligérien" geographic sector (Allogny, Blois, Bercé) [55]. An immediate increase in the radial growth of sessile oak of 40% (one year after CaO fertilisation by gypsum or lime) in a 40- to 50-year-old sessile oak coppice on poor acidic soil is mentioned by Bakker et al. [4]. Liming in moderate doses on sites showing nutrient deficiencies can stimulate the absorption capacity of the sessile oak root system by enlarging fine roots and thereby improving uptake of mineral nutrients and stand growth [4].

No effect of C/N ratio on site index was detected, despite its classical use as an indicator of nitrogen availability for plants [3]. This ratio is probably not an accurate variable for nitrogen supply because it is not very well correlated to humus form ($R^2 = 0.35$). Fertilisation experiments on adult and young trees have also stressed the importance of soil nitrogen, phosphorous and calcium supplies for sessile oak radial and height growth and foliar nutrient composition [4, 9, 16, 36]. However, most of the experiments are carried out on nutrient-deficient soils where soil acidification is known to be detrimental to root growth and nutrient uptake [5]. It has also been shown that the application of liming on oak stands has an indirect, positive influence on nitrogen and carbon dynamics [12].

Nutritional problems on calcareous soils are not very well-documented for sessile oak [13]. Oak seedling response to nitrogen fertilisation is positive for acidic soils and calcareous soils but more pronounced on a substrate with low nutrient supply. Moreover, N input can cause N-induced nutritional imbalance for base cations on substrates with high nutrient supply [13]. The presence of calcium carbonate in the soil is known to negatively affect tree growth because it can reduce nitrogen and phosphorous nutrition quality [3]; it can also lead to impaired nutrient uptake for Mg and K as the adsorption complex is saturated by Ca in calcareous soils [15]. The last effect may be more important for sessile oak growth because Mg/K and Ca/Mg had an additive, negative effect on soils with a carbonated horizon: the balance between Ca and Mg is critical but so is the balance between Mg and K.

4.2.4. Interaction between climate, soil water and nutrient factors and respective portion of variance in site index explained by the different ecological factors

We tested the hypothesis that deeper soil horizons with calcium carbonate could not be prospected by the root system and so the water they contain could not be used by the tree. To do this, we explored site index response to soil water capacity on soils with a carbonated horizon. Our result did not confirm the hypothesis that calcium carbonate was more limiting for a large SWC than for a small SWC.

Most site index variance was related to local soil factors and corroborated the hypothesis that sessile oak growth was regulated by the combined influence of soil water and nutrient budgets. Most of the autecological studies already mentioned adopt a synoptic approach based on a pre-established forest site classification, and the effects of SWC and nutrient status on site index are difficult to separate (the most acidic or calcareous sites tend to have the shallowest soils). The additive effect of soil water capacity and nutrient status is observed when the authors compare dry with fresh sites for a given nutrient supply [32, 33, 50]. For example, Lainez [50] mentioned that the mean height of dominant trees in coppice-with-standards stands is lower on meso-acidic sites where mean soil water capacity is 108 mm compared to sites where soil water capacity is 158 mm (21.2 m versus 25.8 m). Our results clearly indicated that nutrient-related factors accounted for a higher portion of variance than climate/water-related ones. However, the relatively high proportion of variance that corresponded to the confounding climate/water/nutrient-related factors effects highlights the difficulty we had in completely separating the two main gradients, in spite of the sampling effort.

4.2.5. Management implications

These results can be translated into practical recommendations to forest managers for selecting suitable site conditions for sessile oak and forecasting accurate timber yield. This species should not be planted or naturally regenerated on sites with a very low mineral supply and/or a low soil water capacity, especially when these conditions are exacerbated by a deficit topographic position (water lateral loss > gain). Although a dry climate and a south-western aspect are likely to limit site index, these two factors have a limited effect. This is consistent with the results of Lévy et al. on radial growth [56]. However, regular thinning can help to minimize water competition between trees and reduce the duration and intensity of droughts [18]. Additional work should investigate the effect of regional climate and waterlogging on sessile oak growth and validate the results obtained in previous studies [7, 56, 58].

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