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**Original article**

# Can understory vegetation accurately predict site index? A comparative study using floristic and abiotic indices in sessile oak (*Quercus petraea* Liebl.) stands in northern France

Laurent BERGÈS[a]*, Jean-Claude GÉGOUT[b], Alain FRANC[c]

[a] Cemagref, Forest Ecosystems Research Unit, Domaine des Barres, 45290 Nogent-sur-Vernisson, France
[b] ENGREF, LERFOB, Équipe Écosystèmes Forestiers et Dynamique des Paysages, 14 rue Girardet, 54042 Nancy, France
[c] INRA, Département Écologie des Forêts, Prairies et Milieux Aquatiques, CDA UMR Biodiversité, Gènes et Écosystèmes, 69 route d'Arcachon, Pierroton, 33612 Cestas Cedex, France

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**Abstract –** We investigated the relevance of understory vegetation in indicating site productivity as expressed by sessile oak (*Quercus petraea* Matt. Liebl.) site index over a large territory. The relationships between site index and (1) understory vegetation or (2) soil, topography and climate were studied using data from 99 even-aged high-forest stands located in northern France. Multiple regressions using floristic indices as predictors explained the same part of variance in site index as regressions using climate, topography, and soil factors ($R^2$ = 0.49 to 0.60). However, better models were obtained by combining floristic and abiotic variables ($R^2$ = 0.57 to 0.69). We concluded that (1) site productivity can be assessed with the same precision using understory vegetation or abiotic variables separately, even over a large region, but (2) it would be more appropriate to combine soil physical and chemical properties, climate and topography with floristic indices to estimate sessile oak site index.

**site index / ecological factors / floristic indices / soil analyses / *Quercus petraea* (Matt.) Liebl.**

**Résumé – La végétation du sous-bois peut-elle prédire correctement l'indice de fertilité ? Comparaison de l'efficacité des indices floristiques et abiotiques en futaie régulière adulte de chêne sessile dans la moitié nord de la France.** L'objectif était d'étudier sur un vaste territoire la pertinence de la végétation du sous-bois pour prédire le niveau de productivité d'un peuplement, mesurée par l'indice de fertilité du chêne sessile (*Quercus petraea* Liebl.). Les relations entre cet indice et (1) la végétation du sous-bois ou (2) le climat, la topographie et le sol ont été étudiées sur 99 peuplements adultes de futaie régulière situés dans la moitié nord de la France. Les régressions multiples basées sur ces indices floristiques expliquent la même part de variance de l'indice de fertilité que les régressions basées sur le climat, la topographie et le sol ($R^2$ = 0,49 à 0,60). Cependant, de meilleurs modèles sont obtenus en combinant les variables floristiques et abiotiques ($R^2$ = 0,57 à 0,69). Nous concluons que la productivité d'une essence peut être évaluée avec le même niveau de précision en utilisant séparément la végétation du sous-bois et les descripteurs abiotiques, y compris sur un vaste territoire. Mais nous recommandons pour une meilleure estimation de combiner à la fois les propriétés physiques et chimiques du sol, le climat, la topographie et les indices floristiques.

**indice de fertilité / facteurs écologiques / indices floristiques / analyses de sol / *Quercus petraea* (Matt.) Liebl.**

## 1. INTRODUCTION

The approach of using indicator plants for site quality assessment developed early in the last century [11, 14] from a hypothesis that understory vegetation is related to tree growth [3]. The relationships between site quality, understory vegetation and tree growth have since been analysed using 3 different methods.

(1) The connection between vegetation data and site quality has been studied by examining vegetation-site relationships [4, 15, 28, 50]. Understory vegetation has become the fundamental component of many forest site classifications in several European countries [4, 12, 61].

(2) Systems for predicting forest productivity based on site-growth relationships have received considerable attention over the past 50 years [39]. Numerous studies, known as soil-site studies, have focused on predicting site index from climate, topography and soil variables [19, 58].

(3) Other studies have tested the feasibility of using understory vegetation – alone or in combination with abiotic factors – to predict site index [27, 35, 51]. The authors generally refer to previous site classifications and use indicator species groups to evaluate site index; they consider that it is more efficient to concentrate on a few understory species with high indicator values rather than on a total list of species [52, 58]. Few authors

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* Corresponding author: laurent.berges@cemagref.fr

directly correlate tree growth with continuous vegetation data as expressed by ordination axis [6, 41]. This method, which does not require prior site type classification, avoids the problems of misclassification and differences in homogeneity of site classes and should be more precise in assessing the predictive ability of understory vegetation.

Understory vegetation is considered to be an accurate diagnostic tool for site quality assessment because plant species composition indicates many growth-related factors that are difficult to measure directly [3, 30, 59, 61]. However, the environmental relationships and predictive values of individual understory species can vary geographically in response to climatic, physiographic and genetic differences [7, 30, 39, 51]. Understory vegetation can also reflect differences in canopy cover or disturbance history [50]. All these sources of variation explain why some studies across large areas fail to accurately predict site index variations using understory vegetation exclusively [51] and why understory vegetation is often only used within small areas with a homogeneous climate, especially in France [4, 12].

From a methodological point of view, the quality of the two types of ecological descriptors – abiotic and biotic – has seldom been compared. Lastly, different methods for linking site productivity to understory vegetation can be proposed but they have not yet been applied to the same data set.

This study focuses on sessile oak because it is an indigenous species that covers a large surface area in France and autecological studies on this species have hesitated to use understory vegetation as a potential predictor of site productivity [34, 36] (but see Becker [4] for an example of this approach). This article is part of a global study of the autecology of sessile oak in two large regions in northern France [9].

The aims of this study are: (1) to test if understory vegetation is a relevant indicator of site productivity over a large territory by comparing the quality of sessile oak height growth prediction by floristic indices and abiotic parameters; (2) to test the potential complementary use of floristic indices and abiotic parameters and; (3) to compare 3 different understory vegetation-based methods of site productivity assessment.

Our main hypothesis is that floristic indices can be equally good predictors of site index compared to topographic, climatic, chemical and physical soil properties, even if the study area is large. We tested and compared three types of understory vegetation-based approaches: (1) Ellenberg indicator values associated with Ellenberg's calibration method [22, 43, 45, 54]; (2) floristic indices based on the principal components of a correspondence analysis performed on the floristic matrix [41]; (3) species indicator values directly related to site index through a species response curve, an original method derived from the first one. To what extent this approach is relevant to assess site productivity has rarely been studied [43].

## 2. MATERIALS AND METHODS

### 2.1. Sampling strategy and study area

The sampling strategy was based on the following three next principles: first, to explore the largest possible range of site conditions regarding soil water capacity and mineral nutrition; secondly, to achieve an orthogonal sampling plan, i.e. a complete and balanced two-factor plan for soil water and mineral richness; and thirdly, to limit the effects of other factors, especially those related to silvicultural practises. We sampled only mature, nearly pure, even-aged, closed high-forest stands grown from seed.

The initial study area partly covered the south-eastern Paris Basin and the north-eastern France. Two climatically homogeneous regions were defined within this area. The western region had a degraded oceanic climate and the eastern region had a more continental climate (see Bergès et al. [9] for more details). Ninety-nine plots were sampled.

### 2.2. Site index measurement and climate and soil data collection

The dominant height of the plot ($H_0$) was measured using a variant of Duplat's protocol [20]. Site index was computed at a reference age of 100 years (called $SI_{100}$ below) using height-age curves (model B) by Duplat and Tran-Ha [21].

Monthly median precipitation and mean temperature for the 1961–1990 period were provided by Meteo France and are detailed in Bergès et al. [9]. Topographic characteristics, elevation, slope, aspect, topographic position and parent material were measured in the field or by referring to suitable maps.

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. The presence of an R-horizon (bedrock) was the only condition to stop digging. The soil profile was described using a standard protocol [2]. Samples of A-horizon were collected for soil analysis. 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 [24]: pH-$H_2O$, pH-KCl 1 N, CEC at soil pH, exchangeable Ca, Mg, K, Al and $H^+$, total organic carbon C, total organic nitrogen N and potentially available phosphorous. Soil water capacity was computed using a classical formula [2]. Humus form was described in three different locations according to the Pedological Reference frame classification [33].

### 2.3. Floristic data collection

Vegetation was measured within 20-×-20-m quadrats and separated into 3 layers: tree, shrub and herbaceous-moss. Trees with a DBH above 7.5 cm corresponded to layer 1, trees with a DBH below 7.5 cm and a height above 50 cm to layer 2, and trees with a height under 50 cm to layer 3. Species relative cover was assessed using a classical Braun-Blanquet coefficient notation [11]. Floristic data were collected between the 23rd and the 27th of July 1995 in the East, and between the 4th and the 20th of June 1996 in the West and plant nomenclature followed Rameau [46]. East and West data were then combined.

### 2.4. Data analysis methods

#### *2.4.1. Mean Ellenberg indicator values*

Vascular and non-vascular plants were assigned the 6 Ellenberg values: light L, temperature T, continentality K, soil moisture F, soil reaction R and soil nitrogen N. Each indicator value ranges from 1 to 9: L varies from closed-canopy cover to open; T from alpine to foothill thermophilous species, K from atlantic to continental climate, F from dry soils to soils with a permanent hydromorphy, R from very acidic to alkaline soils, and N from nitrogen-poor to nitrogen-rich soils. For each plot, mean indicator values were calculated using the list of species present in the plot to obtain 6 mean Ellenberg indicator values [22]. For this analysis, the different layers were grouped into a single layer.

### 2.4.2. *Floristic indices based on correspondence analysis (CA)*

A correspondence analysis (CA) was applied to a floristic matrix with 99 plots and 163 species: 141 species in the East, 123 in the West, and 101 present in both regions. The CA was applied to presence-absence data with tree species split into 3 layers. Principal coordinates were interpreted according to climate, topography, physical and chemical soil properties and mX using multiple linear regressions. The first three principal coordinates were used as floristic indices to predict $SI_{100}$.

### 2.4.3. *Method using species response curves along site index gradient*

The first step in this method consisted of computing a species response curve. Among the different methods [10, 53, 62], we chose a non-parametric kernel estimation method developed by Yee and Mitchell [63] and as used by Gégout et al. [23, 25]. The method estimates the probability of occurrence of each woodland plant species as a function of a quantitative variable, and does not require assumptions about the form of the species response curve [25]. It works by estimating the probability of a species *i* for a value *x* of the variable (e.g. sessile oak site index) by a weighted average of presence/absence data of the species, giving each plot a decreasing weight with increasing distance between *x* and the site index of the plot [10, 23, 62]. The weights are defined by a kernel function *K* and a smoothing parameter, the bandwidth *h*. The equation is as follows:

$$p_i(x) = \sum_{j=1}^{n} K\left(\frac{x-x_j}{h}\right) y_{ij} \Big/ \sum_{j=1}^{n} K\left(\frac{x-x_j}{h}\right)$$

where *n* is the total number of plots, $y_{ij} = 1$ when species is present in plot *j* and 0 otherwise; $x_j$ = site index in plot *j*. The Kernel function *K(t)* is maximum at $t = 0$ and decreases towards 0 when $|t|$ increases. It is generally accepted that its precise form is not very important. For the present study, the standard Gaussian kernel was chosen [25]:

$$K(t) = \frac{1}{0{,}37\sqrt{2\pi}} \exp-(1/2(t/0{,}37)^2).$$

Much more important is the value of the bandwidth *h*. This parameter determines how local or how smooth the response curve will be. There is a trade off between smoothness and localness: as *h* increases, the smoothness increases, but the localness decreases [25]. The smoothing parameter $h = 12$ m (half the observed range of site index) was used. A response curve was computed only when the species was present in more than 5 plots.

The second step was to compute the species indicator value for site index ($IVSI_{100}$) defined as the value of site index when the occurrence probability of the species is maximum.

The third step consisted of computing predicted site index on each site using the same method as above for mean Ellenberg indicator values (this variable was called $mIVSI_{100}$).

### 2.4.4. *Testing the link between understory vegetation and site index*

Linear or polynomial regressions were used to test the effect of the different floristic indices on $SI_{100}$. The accuracy of the predictions based on the species response curve was tested more precisely using two tests: Test 1) a *t*-paired test to compare predicted and observed mean values; Test 2) an ANOVA that compared the following two models: $y = x$ and $y = ax + b$, with $y$ = observed site index and $x$ = predicted site index, to detect if site index prediction was biased according to site index.

Then, stepwise multiple regressions were used to test the additive effects of ecological factors and to find the best predictive models. We considered 3 groups of ecological variables: (1) mean Ellenberg indicator values, (2) CA principal coordinates and (3) both these groups plus predicted site index based on species response curve ($mIVSI_{100}$) and the abiotic variables analysed in Bergès et al. [9].

The simple, multiple stepwise regressions, *t*-paired test and ANOVA were performed using S-Plus version 6.2® software. Variance homogeneity and the distribution of residuals were visually checked. CA was performed using ADE Version 4 freeware [55].

## 3. RESULTS

### 3.1. Effects of climate, topography and soil factors

Single and multiple regression models based on abiotic factors are given in Table I and Table II. They are detailed in Bergès et al. [9].

### 3.2. Effects of mean Ellenberg indicator values

Table III shows that the mean Ellenberg indicator value for soil humidity mF had the lowest standard deviation (SD = 0.22) compared to soil reaction mR and nitrogen mN (1.53 and 0.91), whereas mL, mT and mK exhibited intermediate values (0.41–0.49). $SI_{100}$ is significantly related to the 6 mX (Tab. I). The model was linear for mL, mK, mF and curvilinear for mT, mR and mN. The mean indicator value for soil reaction mR was a better predictor than log(Ca) or log(S) ($R^2 = 0.28$ versus 0.22 or 0.20). The mean indicator value for soil humidity mF only explained 20% of the variance in $SI_{100}$ *vs* 25% for SWC 0–150.

The model fitted on the 6 mX contained mK, mF and mR as significant explanatory variables and their effects on site index were logical (M4, see Tab. II): the variable mK had a negative linear effect, mF a positive linear effect and $SI_{100}$ was linked to mR by a polynomial, convex model. Mean Ellenberg indicator values were equally good predictors compared to climate, topography and soil variables (compare models M1 to M3 with M4).

### 3.3. Effects of correspondence analysis axes

The correspondence analysis showed that vegetation is influenced by a limited number of ecological gradients that were very similar in both regions [8]. Species displayed a U-shape on the factorial plan (1, 3) (Fig. 1), which indicates a Guttman effect: hyper-acidophilous and acidophilous species were on the top left, neutrophilous or calcicolous species on the top right and meso-acidiphilous or neutrophilous species in the middle. Indeed, CA Axes 1 and 3 were linked by the polynomial model: Axis 3 = Axis $1^2$ + Axis 1 ($R^2 = 0.61$). The factorial plan (2, 3) clearly discriminated the two regions (Fig. 2).

The first axis (9.3%) was a nutrient axis because it was linked to humus form ($R^2 = 0.82$); it was also positively correlated to S/T ($R = 0.81$), log(Ca) (0.79), log($P_2O_5$) (0.57), mN (0.91), mR (0.87) and negatively to $H^+$ (–0.73). Plots with negative values were very acidic soils and plots with positive ones were calcareous.

The second axis (6.0%) was a regional axis because it separated species present in one region and not in the other. It was positively correlated to altitude (0.65), mF (0.47) and soil water

**Table I.** Results of the simple or polynomial regressions between $SI_{100}$ and selected abiotic variables [9] (soil water capacity computed to a depth of 150 cm (SWC 0-150), log(S), $K/P_2O_5$ and humus form), the 6 mean Ellenberg indicator values and the first three principal coordinates of the correspondence analysis.

| Variable | Equation | $R^2$ | $p > F$ | SE (m) |
|---|---|---|---|---|
| Topography, soil and climate variables | | | | |
| SWC 0-150 | $SI_{100} = 20.3 + 0.032$ (SWC 0-150) | 0.247 | < 0.0001 | 3.98 |
| log(Ca) | $SI_{100} = 27.3 + 1.37 (\log(Ca)) - 3.99 (\log(Ca))^2$ | 0.220 | < 0.0001 | 4.07 |
| log(S) | $SI_{100} = 26.4 + 4.14 (\log(S)) - 5.34 (\log(S))^2$ | 0.201 | < 0.0001 | 4.10 |
| $K/P_2O_5$ | $SI_{100} = 29.9 - 1.52 (K/P_2O_5)$ | 0.160 | < 0.0001 | 4.21 |
| 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 |
| Mean Ellenberg indicator values (mX) | | | | |
| mL | $SI_{100} = 50.1 - 5.09$ (mL) | 0.206 | < 0.0001 | 4.09 |
| mT | $SI_{100} = -161.9 + 75.35 (mT) - 7.50 (mT)^2$ | 0.275 | < 0.0001 | 3.93 |
| mK | $SI_{100} = 44.0 - 5.71$ (mK) | 0.281 | < 0.0001 | 3.89 |
| mF | $SI_{100} = - 16.4 + 8.14$ (mF) | 0.158 | < 0.0001 | 4.21 |
| mR | $SI_{100} = -0.04 + 12.16 (mR) - 1.30 (mR)^2$ | 0.283 | 0.0003 | 3.91 |
| mN | $SI_{100} = -20.2 + 21.63 (mN) - 2.46 (mN)^2$ | 0.291 | 0.0001 | 3.89 |
| Floristic variables based on CA | | | | |
| Axis 1 | $SI_{100} = 28.6 - 2.52 (\text{Axis 1}) - 6.04 (\text{Axis 1})^2$ | 0.438 | < 0.0001 | 3.46 |
| Axis 2 | $SI_{100} = 25.2 + 1.60$ (Axis 2) | 0.051 | 0.024 | 4.47 |
| Axis 3 | $SI_{100} = 24.9 - 5.29$ (Axis 3) | 0.455 | < 0.0001 | 3.39 |

**Table II.** Results of the stepwise multiple regressions of $SI_{100}$ according to site variables. Models were successively adjusted for 4 groups of variables: topography, soil and climate, mean Ellenberg indicator values, CA Axes and finally the different variables combined. The table gives model number, equation, $R^2$ and standard error. G: lateral water gain; L: lateral water loss (topographic position).

| Name | Model equation | $R^2$ | SE (m) |
|---|---|---|---|
| Topography, soil and climate variables | | | |
| M1 | $SI_{100} = 23.0 + 0.022 (\text{SWC 0-150}) + 0 (G < L) + 1.8 (G = L) + 3.9 (G > L) - 5.76 (\log(Mg)) - 6.59 (\log(Mg))^2 - 0.764 (K/P_2O_5)$ | 0.491 | 3.36 |
| M2 | $SI_{100} = 19.2 + 0.026 (\text{SWC 0-150}) - 5.39 (\log(Mg)) - 6.13 (\log(Mg))^2 + 0$ (Dysmoder-Mor) + 3.82 (Eumoder) + 4.82 (Hemimoder to Oligomull) + 4.86 (Mesomull) + 1.40 (Eumull) | 0.600 | 3.00 |
| M3 | $SI_{100} = 21.7 + 0.019 (\text{SWC 0-150}) + 3.70 (\log(S)) - 3.96 (\log(S))^2 - 0.70 (Mg/K) + 0$ (Dysmoder-Mor) + 4.16 (Eumoder) + 5.31 (Hemimoder to Oligomull) + 5.45 (Mesomull) + 1.72 (Eumull) | 0.596 | 3.03 |
| Mean Ellenberg indicator values | | | |
| M4 | $SI_{100} = -5.56 + 5.50 (mF) - 4.54 (mK) + 8.51 (mR) - 0.92 (mR)^2$ | 0.530 | 3.19 |
| Floristic variables based on CA | | | |
| M5 | $SI_{100} = 26.3 - 0.46 (\text{Axis 1}) - 2.34 (\text{Axis 1})^2 + 1.47 (\text{Axis 2}) - 3.66 (\text{Axis 3})$ | 0.553 | 3.12 |
| All variables | | | |
| M6 | $SI_{100} = 24.3 + 0.011 (\text{SWC 0-150}) - 1.61 (\text{Axis 1})^2 + 1.25 (\text{Axis 2}) - 3.54 (\text{Axis 3})$ | 0.571 | 3.06 |
| M7 | $SI_{100} = 26.5 + 0.015 (\text{SWC 0-150}) - 0.94 (Mg/K) - 2.32 (\text{Axis 1})^2 - 2.92 (\text{Axis 3})$ | 0.625 | 2.86 |
| M8 | $SI_{100} = 24.5 + 0.017 (\text{SWC 0-150}) - 0.80 (Mg/K) + 0$ (Dysmoder-Mor) + 2.74 (Eumoder) + 1.85 (Hemimoder to Oligomull) + 2.75 (Mesomull) + 0.03 (Eumull) $- 1.87 (\text{Axis 1})^2 - 2.53 (\text{Axis 3})$ | 0.686 | 2.67 |
| M9 | $SI_{100} = 9.4 + 0.014 (\text{SWC 0-150}) + 0 (G < L) + 0.5 (G = L) + 3.2 (G > L) - 3.37 \log(Mg) - 3.12 \log(Mg)^2 + 0.54 (mIVSI_{100})$ | 0.660 | 2.75 |

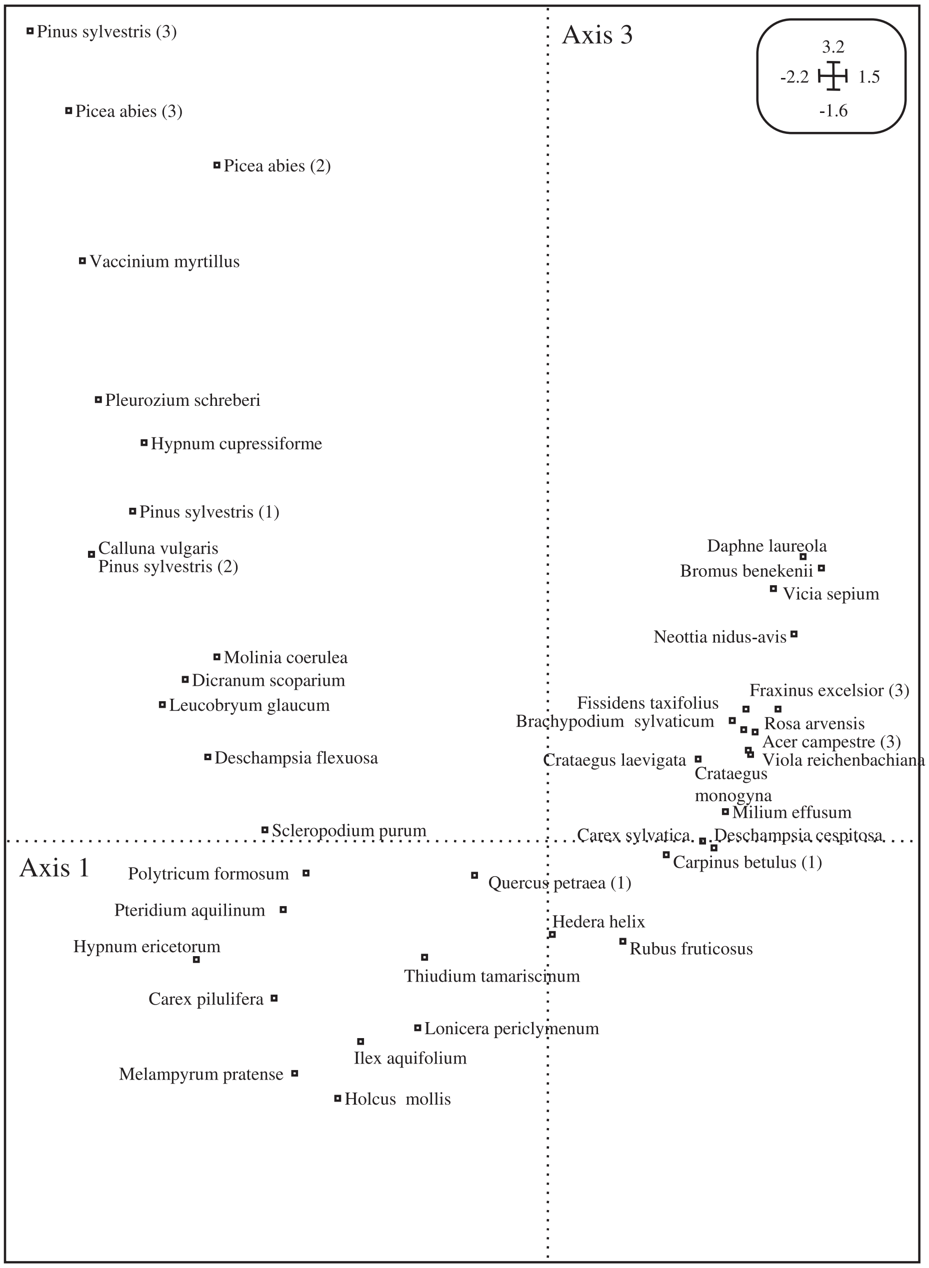

**Figure 1.** Representation of the species in the factorial plan (1, 3) of the correspondence analysis. Only the 42 species that are correlated to the plan with $\cos^2 > 0.2$ are indicated. Tree species are split into 3 layers (see text for their definition).

**Table III.** Elementary statistics for site index and mean Ellenberg indicator values.

| Variable name | Code | Min | Mean ± SD | Max |
|---|---|---|---|---|
| Site index at 100 years (m) | $SI_{100}$ | 12.1 | 25.3 ± 4.60 | 34.8 |
| Mean Ellenberg coefficient for light | mL | 3.70 | 4.87 ± 0.41 | 5.93 |
| Mean Ellenberg coefficient for temperature | mT | 3.67 | 4.95 ± 0.49 | 6.00 |
| Mean Ellenberg coefficient for continentality | mK | 2.00 | 3.27 ± 0.42 | 4.35 |
| Mean Ellenberg coefficient for soil humidity | mF | 4.70 | 5.13 ± 0.22 | 5.71 |
| Mean Ellenberg coefficient for soil reaction | mR | 2.00 | 4.41 ± 1.53 | 7.25 |
| Mean Ellenberg coefficient for soil nitrogen | mN | 2.33 | 4.18 ± 0.91 | 6.09 |

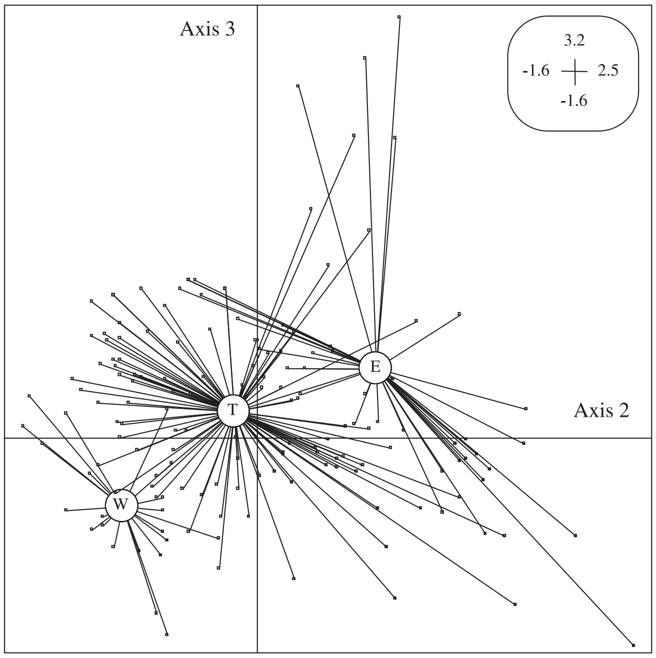

**Figure 2.** Representation of the species in the factorial plan (2, 3) of the correspondence analysis. Species are clustered in 3 groups: species present in the Eastern region only (E) or in the Western region only (W) or in both regions (T). The group centre is the barycentre of the coordinates of the species that belong to this group.

capacity (0.23) and negatively correlated to PET-P (–0.68), $K/P_2O_5$ (–0.53) and mL (–0.36). Plots with negative values were western plots with dry soils and low $K/P_2O_5$; plots with positive values were eastern plots with moist soils and high $K/P_2O_5$.

The third axis (4.6%) was positively correlated to mK (0.79), altitude (0.44), mL (0.38), and $K/P_2O_5$ (0.36) and negatively correlated to layer-3 canopy cover (–0.47), SWC 0-150 (–0.44), ETP-P (–0.35), and mF (–0.29). The variables correlated to Axis 2 and 3 were almost the same. Plots with negative values corresponded to low altitude, closed stands with moist soils while plots with positive values corresponded to high altitude, open stands with dry soils.

The next CA axes (Axis 4…) were not explained by any site parameters.

CA Axis 1 was a better predictor of $SI_{100}$ than any of the other chemical variables and humus form (see Fig. 3 and Tab. I). Axis 3 was a better predictor than SWC, but Axis 3 was not a pure soil moisture gradient. No strong effect of Axis 2 on $SI_{100}$ was detected. The high correlation between Axis 3 and Axis 1 could partly explain the high correlation between $SI_{100}$ and Axis 3 ($R^2 = 0.45$).

CA Axes 1, 2 and 3 had additive effects on $SI_{100}$ (model M5, see Tab. II). Model M5 was similar to models M1 to M3 in terms of predictive power.

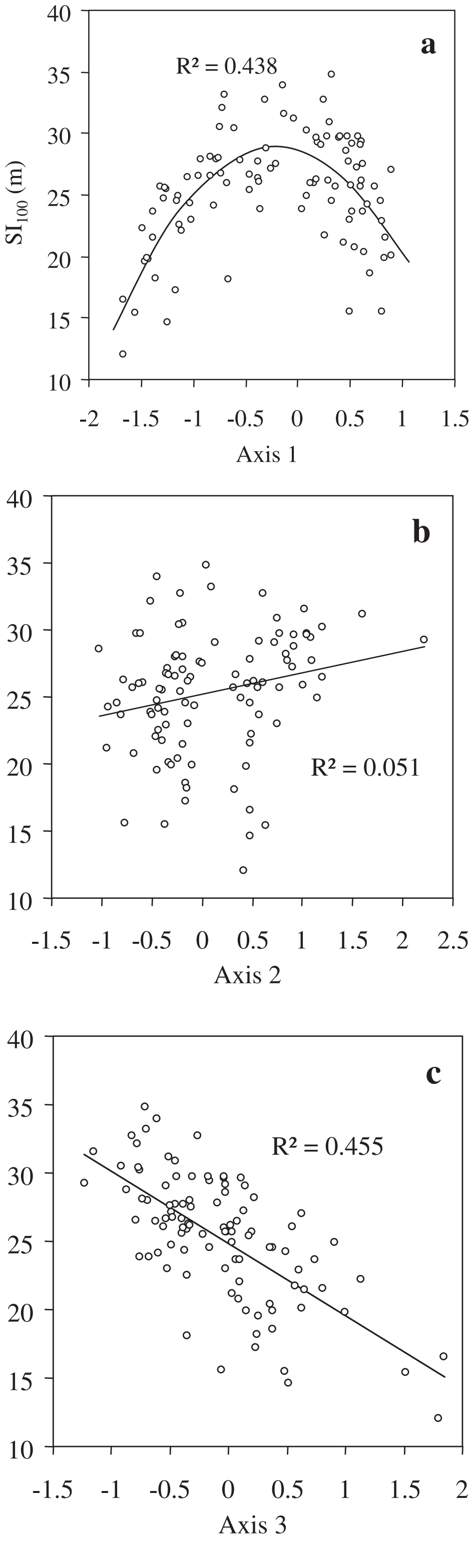

**Figure 3.** Relationships between $SI_{100}$ and the first three principal components of the CA: Axis 1 is related to soil nutrient richness (poor soils are on the left and rich ones on the right); Axis 2 is a regional gradient that is related to $K/P_2O_5$, precipitation, altitude and soil moisture; Axis 3 is a multiple gradient that is related to $K/P_2O_5$, light and soil moisture (moist, closed plots are on the left and dry, open plots on the right).

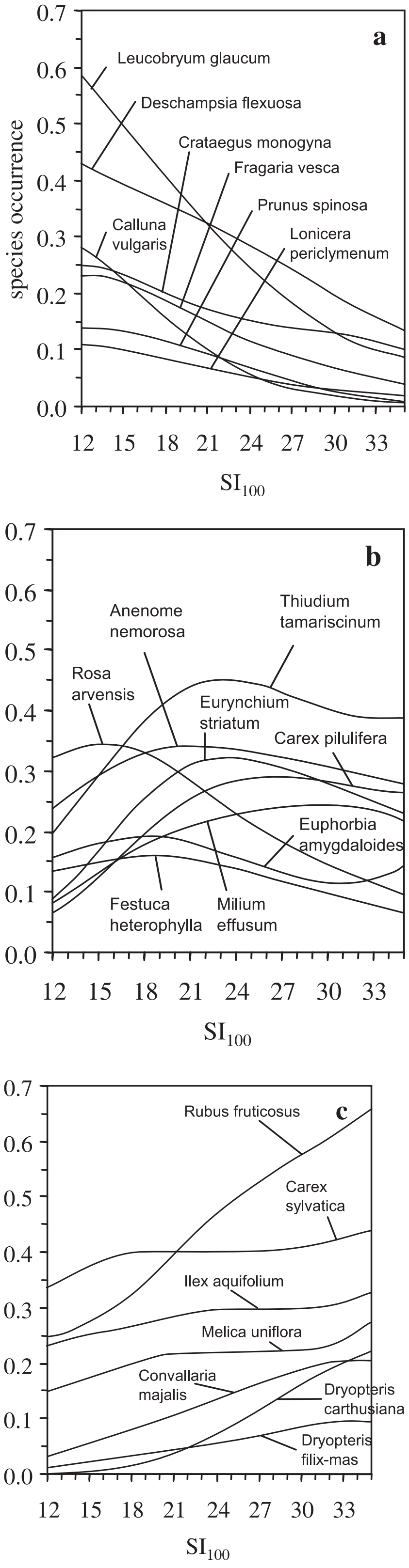

**Figure 4.** Examples of different species response curves obtained with the non parametric kernel estimation method. Species occurrence along the site index gradient for some frequent species with (a) low, (b) intermediate and (c) high optimum values.

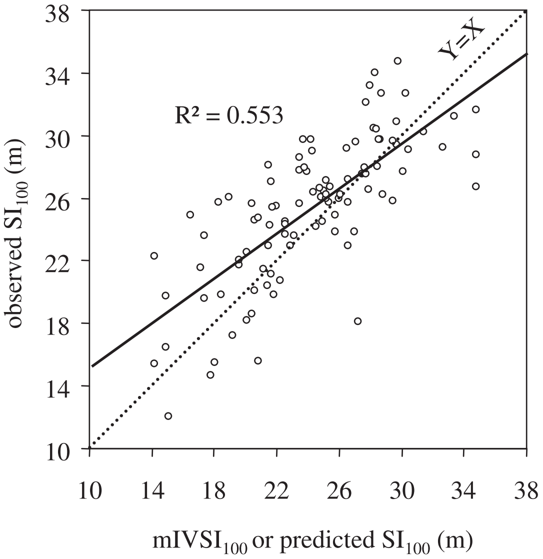

**Figure 5.** Relationships between observed and predicted site index ($SI_{100}$ and $mIVSI_{100}$).

### 3.4. Effects of floristic indices based on species response curve to site index

Figure 4 illustrates the response curve to site index for some selected species and Table IV provides the list of indicator values for site index ($IVSI_{100}$) resulting from the fitted curve. Twenty species had an indicator value for $SI_{100}$ corresponding to the minimum value (12.1 m) and 22 species to the maximum value (34.8 m). Fifty-eight species had an optimum site index value between the two extremes.

The model only based on $mIVSI_{100}$ ($R^2 = 0.55$) was equal to the models based on mX or CA Axes (compare Fig. 5 and models M4 and M5 in Tab. II). The two tests for fitting accuracy are significant: mean site index was underestimated (Test 1: observed – predicted values = 1.09 m, $t = 3.25$, $p = 0.0016$) and the prediction was biased (Test 2: $F = 179.91$, $p < 0.0001$) and characterised by a marked underestimate of low site index values and a slight overestimate of high values (Fig. 5).

### 3.5. Combined effects of ecological variables on site index

Four models were proposed when combining climate-topography-soil and floristic indices (Tab. II). M6 combined the CA Axes and soil water capacity and was slightly better than models M4 and M1. Model M7 combined abiotic indices (SWC 0-150 and Mg/K) and floristic indices (CA Axis 1 and Axis 3) and was better than corresponding models with only abiotic or floristic indices (M5 and M3). Model M8 including SWC, Mg/K, humus form and CA Axes 1 and 3 was a better model than M3 and M5. Model M9 with SWC, topography, log(Mg), $\log(\mathrm{Mg})^2$ and $mIVSI_{100}$ as predictors was also better than the model $SI_{100} = f(mIVSI_{100})$ ($R^2 = 0.66$ vs. 0.55).

**Table IV.** Species indicator values (except for tree species) for site productivity in site index units (IVSI$_{100}$). Rare herbaceous or moss species were excluded from the computation. Species are given in ascending order of IVSI$_{100}$ with their frequency in the data set.

| Understory species | IVSI$_{100}$ | Freq. | Understory species | IVSI$_{100}$ | Freq. |
|---|---|---|---|---|---|
| *Ajuga reptans* L. | 12.1 | 0.05 | *Carex montana* L. | 20.8 | 0.05 |
| *Calluna vulgaris* (L.) Hull | 12.1 | 0.07 | *Anemone nemorosa* L. | 21.3 | 0.31 |
| *Carex digitata* L. | 12.1 | 0.03 | *Galium odoratum* (L.) Scop. | 21.3 | 0.04 |
| *Cornus mas* L. | 12.1 | 0.06 | *Pulmonaria obscura* Dumort. | 21.3 | 0.04 |
| *Crataegus monogyna* Jacq | 12.1 | 0.15 | *Dactylis glomerata* L. | 21.5 | 0.03 |
| *Deschampsia flexuosa* (L.) Trin. | 12.1 | 0.26 | *Stachys sylvatica* L. | 21.7 | 0.04 |
| *Dicranella heteromalla* (Hedw.) Schimp. | 12.1 | 0.13 | *Eurhynchium striatum* (Hedw.) B., S., G. | 23.3 | 0.27 |
| *Dicranum scoparium* Hedw. | 12.1 | 0.26 | *Thuidium tamariscinum* (Hedw.) B., S., G. | 23.3 | 0.40 |
| *Fragaria vesca* L. | 12.1 | 0.11 | *Luzula forsteri* (Sm.) DC. | 24.0 | 0.03 |
| *Geum urbanum* L. | 12.1 | 0.03 | *Malus sylvestris* Miller | 24.0 | 0.04 |
| *Hypnum cupressiforme* Hedw. | 12.1 | 0.11 | *Ruscus aculeatus* L. | 24.0 | 0.17 |
| *Leucobryum glaucum* (Hedw.) Angstr. | 12.1 | 0.24 | *Brachypodium pinnatum* (L.) P. Beauv. | 24.9 | 0.03 |
| *Lonicera xylosteum* L. | 12.1 | 0.05 | *Carex pilulifera* L. | 26.3 | 0.25 |
| *Neottia nidus-avis* (L.) L.C.M. Richard | 12.1 | 0.07 | *Mespilus germanica* L. | 27.7 | 0.03 |
| *Pleurozium schreberi* (Brid.) Mitt. | 12.1 | 0.08 | *Viburnum lantana* L. | 27.7 | 0.03 |
| *Polytrichum formosum* Hedw. | 12.1 | 0.53 | *Carex remota* L. | 28.4 | 0.05 |
| *Prunus spinosa* L. | 12.1 | 0.06 | *Milium effusum* L. | 29.5 | 0.21 |
| *Pteridium aquilinum* (L.) Kuhn in Kersten | 12.1 | 0.37 | *Scrophularia nodosa* L. | 29.8 | 0.05 |
| *Vaccinium myrtillus* L. | 12.1 | 0.07 | *Lamium galeobdolon* (L.) L. | 30.2 | 0.13 |
| *Veronica officinalis* L. | 12.1 | 0.06 | *Poa chaixii* Vill. in Gilib. | 30.4 | 0.12 |
| *Ligustrum vulgare* L. | 12.6 | 0.16 | *Moehringia trinervia* (L.) Clairv. | 30.7 | 0.03 |
| *Viola reichenbachiana* Jordan ex Boreau | 13.2 | 0.18 | *Deschampsia cespitosa* (L.) P. Beauv. | 31.8 | 0.27 |
| *Carex flacca* Schreber | 13.5 | 0.20 | *Luzula luzuloides* (Lam.) Dandy & Wilmott | 32.5 | 0.18 |
| *Arum maculatum* L. | 14.2 | 0.07 | *Geranium robertianum* L. | 32.7 | 0.03 |
| Molinia caerulea (L.) Moench | 14.2 | 0.10 | *Galeopsis tetrahit* L. | 33.0 | 0.07 |
| *Poa nemoralis* L. | 14.4 | 0.10 | *Luzula pilosa* (L.) Willd. | 33.2 | 0.14 |
| *Hylocomium brevirostre* (Brid.) B., S., G. | 15.1 | 0.05 | *Atrichum undulatum* (Hedw.) P. Beauv. | 33.7 | 0.18 |
| *Rosa arvensis* Hudson | 15.3 | 0.21 | *Dryopteris filix-mas* (L.) Schott | 34.1 | 0.06 |
| *Brachypodium sylvaticum* (Hudson) P. Beauv. | 15.5 | 0.19 | *Athyrium filix-femina* (L.) Roth | 34.8 | 0.13 |
| *Frangula alnus* Miller | 15.5 | 0.07 | *Carex sylvatica* Hudson | 34.8 | 0.40 |
| *Hylocomium splendens* (Hedw.) B., S., G. | 15.5 | 0.04 | *Carex umbrosa* Host | 34.8 | 0.11 |
| *Scleropodium purum* (Hedw.) Limpr. | 15.5 | 0.18 | *Circaea lutetiana* L. | 34.8 | 0.08 |
| *Erica cinerea* L. | 15.8 | 0.05 | *Convallaria majalis* L. | 34.8 | 0.14 |
| *Hypnum ericetorum* (B., S., G.) Loeske | 17.1 | 0.12 | *Corylus avellana* L. | 34.8 | 0.17 |
| *Helleborus foetidus* L. | 17.6 | 0.03 | *Dryopteris carthusiana* (Vill.) H. P. Fuchs | 34.8 | 0.10 |
| *Potentilla sterilis* (L.) Garcke | 17.8 | 0.12 | *Eurhynchium stokesii* (Hedw.) B., S., G. | 34.8 | 0.07 |
| *Euphorbia amygdaloides* L. | 18.1 | 0.15 | *Hedera helix* L. | 34.8 | 0.62 |
| *Rhytidiadelphus triquetrus* (Hedw.) Warnst. | 18.1 | 0.08 | *Holcus mollis* L. | 34.8 | 0.15 |
| *Vicia sepium* L. | 18.1 | 0.06 | *Ilex aquifolium* L. | 34.8 | 0.29 |
| *Daphne laureola* L. | 18.5 | 0.04 | *Juncus effusus* L. | 34.8 | 0.06 |
| *Bromus benekenii* (Lange) Trimen | 18.7 | 0.04 | *Lonicera periclymenum* L. | 34.8 | 0.34 |
| *Festuca heterophylla* Lam. | 18.7 | 0.12 | *Melampyrum pratense* L. | 34.8 | 0.16 |
| *Polygonatum multiflorum* (L.) All | 18.7 | 0.05 | *Melica uniflora* Retz | 34.8 | 0.22 |
| *Sorbus domestica* L. | 18.7 | 0.03 | *Mnium hornum* Hedw. | 34.8 | 0.04 |
| *Crataegus laevigata* (Poiret) DC. | 19.0 | 0.28 | *Oxalis acetosella* L. | 34.8 | 0.04 |
| *Ornithogalum pyrenaicum* L. | 19.0 | 0.04 | *Rosa canina* L. | 34.8 | 0.06 |
| *Fissidens taxifolius* Hedw. | 19.2 | 0.14 | *Rubus fruticosus* L. | 34.8 | 0.48 |
| *Epilobium montanum* L. | 19.7 | 0.03 | *Stellaria holostea* L. | 34.8 | 0.05 |
| *Cornus sanguinea* L. | 19.9 | 0.03 | *Teucrium scorodonia* L. | 34.8 | 0.03 |
| *Plagiomnium undulatum* (Hedw.) T.Kop. | 20.1 | 0.03 | *Veronica montana* L. | 34.8 | 0.04 |

## 4. DISCUSSION

### 4.1. Understory vegetation as a relevant indicator of site productivity in sessile oak stands

Our results showed that the different understory floristic indices predicted site index as well as climate, topography and soil physical and chemical data. This suggests that site productivity can be assessed using understory vegetation over a large territory and corroborates other studies that relate understory composition to site index for different tree species [27, 51, 58]. This method is quicker and cheaper than a soil-based approach that requires expensive chemical soil analyses [59]. Consequently, the capacity of plant species to be relevant bio-indicators over large regions confirm the work of Rameau et al. [46, 47] who provide species behaviour for soil moisture and nutrient status applicable across France except for the Mediterranean region.

An argument often used to justify limiting the use of vegetation to small regions is that individual species indicator values can vary geographically. This is not consistent with our results because a comparison of two distinct correspondence analyses performed on regional data sets revealed a very high correlation between the first principal coordinates for the 101 species common to the two regions ($R = 0.93$, data not shown). The nutrient gradient expressed by the first axis was practically identical in both regional samples despite the change in floristic composition. Moreover, Coudun and Gégout [18] recently showed that the pH behaviour of plant species is close in the north-eastern and north-western part of France: the correlation between regional pH indicator values is 0.78 and 75% of the species have regional pH indicator values differences lower than 0.5.

The second justification used to limit the relevance of understory vegetation is its response to canopy cover and disturbance history. These factors did not vary in our study, because we chose to only sample mature, even-aged, closed-canopy and nearly pure stands. This method could be generalised but young and/or very open stands where understory composition displays a dramatic change should be carefully avoided [42, 64]. However, we do not know to what extent the forest understory community can be affected by a large disturbance nor how long it may take to recover [13, 29, 38].

All the floristic indices were computed without using species cover as a weighting parameter. However, some authors have demonstrated that species cover can be a relevant site productivity index [52, 58] but comparison with a coarser index has rarely been tested [49]. Nieppola [43] observed that species cover was only weakly correlated to site index except for a few species. Moreover, several studies have shown that understory species cover (rather than presence or absence of species) is more responsive to a change in canopy cover [16, 40] or to forest succession [63]. Taking species cover into account as a weighting parameter to compute floristic indices did not improve the site index prediction; this was also mentioned by Schaffers et al. [49] for prediction of moisture, nitrogen and soil reaction with Ellenberg indicator values. Consequently, the predictive method based on understory vegetation needs to be tested by simultaneously studying the ecology of understory species according to canopy cover and site quality gradients as proposed by Tyler [57] or, possibly, by selecting species that are not sensitive to management practises but respond dramatically to changes in site quality.

### 4.2. Alternative methods to analyse the link between site productivity and understory vegetation

#### *4.2.1. Mean Ellenberg indicator values*

We observed that mR and mF had a logical effect on $SI_{100}$ compared to soil water regime and nutrient availability influence. On the other hand, mL, mK, mN and mT exhibited unexpected effects. For example: (1) the effect of mL reflected a positive link between canopy cover and site fertility (heliophilous species-rich plots would be on less fertile soils) and this more or less corresponds to our field observations; (2) the curvilinear effect of mN on $SI_{100}$ was surprising and did not corroborate the conclusions of Hill and Carey [31] and Schaffers and Sykora [49] who both stressed that Ellenberg N-values are strongly correlated with biomass production, suggesting that N-values could be replaced by “productivity values”. But the information revealed by mN and mR was largely redundant in our data ($R^2 = 0.68$ with a quadratic model mN = f(mR), mN increases then flattens when mR > 5.5); (3) mK did not reflect a continental gradient because it was not very closely correlated to mean annual range of temperature, latitude or longitude ($R^2 < 0.16$); (4) mT could not be interpreted as an altitudinal gradient because it was not correlated to altitude.

Despite the difficulty in interpreting the effect of mK values, our results showed that mF, mK and mN were equally predictors of site index compared to the other models (Tab. II). The consistency of Ellenberg values outside their original geographic area (Central Europe) has already been supported by numerous studies, especially for R, N and F [30, 31, 56, 60, 61]. The lack of correlation between mK or mT and the gradients they are expected to characterize was already mentioned by Badeau [1]. Likewise, Hill et al. [32] using a reprediction algorithm, also concluded that the continentality index is unusable in Britain. The use of mK as $SI_{100}$ predictor is therefore questionable.

#### *4.2.2. Floristic indices resulting from the correspondence analysis*

The first three CA Axes together explained 55% of the variance of $SI_{100}$ (Tab. II). Our results for oak in France are consistent with those of Nieppola and Carleton [41] who also found a high value, supporting a dominant relationship between understory vegetation and site productivity in mature stands of *Pinus sylvestris* in southern Finland. Using a comparable method, the first ordination axis of a detrended correspondence analysis explained 69% of the variance in site index. Becker [6] also mentioned the use of the plot coordinate along the first axis of a CA as a potential predictor of the site index variation of *Abies alba* in the Vosges mountains.

#### *4.2.3. Site index indicator values*

The non-parametric kernel estimation method is interesting because it does not require assumptions about the form of the species response curve [25]. We found that 42% of the species had maximum or minimum indicator values for $SI_{100}$ ($IVSI_{100}$) and consequently, $IVSI_{100}$ values displayed a U-shape distribution. Among the species indicative of a low $SI_{100}$, some were hyper-acidophilous and xeric (*Calluna vulgaris, Dicranum scoparium, Leucobryum glaucum, Pleurozium schreberi, Vaccinium myrtillus*) or acidophilous (*Polytrichum formosum, Pteridium aquilinum, Deschampsia flexuosa, Hypnum cupressiforme*) whereas others were neutrophilous or calcicolous species (*Cornus mas, Lonicera xylosteum, Prunus spinosa, Ajuga reptans, Fragaria vesca, Crataegus monogyna, Neottia nidus-avis*). Among the species indicative of a high $SI_{100}$, most were meso-acidiphilous or neutrophilous species and typical of moist sites (*Lonicera periclymenum, Holcus mollis, Hedera helix, Rubus fruticosus, Carex sylvatica, Ilex aquifolium, Melica uniflora, Corylus avellana, Convallaria majalis, Athyrium filix-femina, Carex umbrosa, Dryopteris carthusiana*). These results were consistent with the expected effects of soil water capacity and nutrient status on site index [9]. Otoul [44] suggested that the best sites for sessile oak is associated with *Anemone nemorosa* and *Festuca heterophylla* (dominant height of 25 m). This is not consistent with our results: *F. heterophylla* and *A. nemorosa* had only medium indicator values (18.7 and 21.3 m, respectively), however, the low site index indicator value for *Vaccinium myrtillus* (12.1 m) corroborates the fact that the 19 m class is associated with this species for Otoul [44].

The indicator value method has a few limitations: first, the calibration of the indicator values for site index must be done on an independent data set [43] and secondly, even if the method of site index indicator values provides accurate results in terms of prediction, the prediction is biased.

### *4.2.4. Comparison between the three understory vegetation-based methods of site index prediction*

Our results showed that site index prediction quality did not depend on the type of floristic indices. So, prediction methods have to be compared from a practical point of view. Using Ellenberg mean indicator values is the only method that provides direct information about what type of site component is assessed but the indicator values are not calibrated for France. The mF, mK and mR values must be calculated first, using the floristic composition of a new plot before computing the predicted site index using model M4. CA principal components are more complicated to use in the field because weighted means have to be computed. The first three principal components of a new plot must be calculated using the weighted coordinates of the species in the correspondence analysis, then the predicted site index of this new plot can be computed using model M5. We also used a classic approach that consists of grouping plots according to their floristic composition using hierarchical cluster analysis (data not shown). This approach displayed worse results compared to a direct gradient analysis, probably because the floristic gradient was transformed into discrete values.

The new method proposed in this paper based on species response curve and site index indicator values requires a validation step on an independent data set, but the potential for a practical diagnostic tool to predict sessile oak site index is promising. The method would be based on the computation of predicted site index using a list of robust species indicator values. Alternatively, we could develop a classification tool, but this would require that the species be classified into ecological groups which would necessarily be somewhat arbitrary [32]. We would prefer a prediction tool that treats species individually and not as members of ecological groups.

### **4.3. Are abiotic and floristic indices complementary in predicting site index over a large territory?**

We observed that understory vegetation explained the same portion of variance in sessile oak site index as soil, climate and topography. However, this does not necessarily mean that floristic and abiotic indices were redundant. Because our results provided information about site conditions estimated by a given variable (water or nutrient), the quality of the type of predictors for water and nutrient budgets can be compared.

Nutrient-related factors were ranked in terms of site index prediction: (1) the first principal component of the correspondence analysis, (2) humus form, mN or mR, and (3) chemical data ($K/P_2O_5$, log(Ca), log(S)). This hierarchy provided good evidence for the superiority of floristic indices and humus form over soil mineral element contents from chemical analysis, which can be explained in three ways. Firstly, CA Axis 1, humus form, mN and mR are synoptic variables whereas chemical analyses are more analytical. However, the disadvantage of using analytical variables can be lessened by applying multiple regression models. Secondly, floristic indices are closer to the actual plant nutrition status compared to soil analyses that only provide element content that can – or cannot – be used by the plant. Our results showed the deficiency of soil chemical analyses in properly estimating mineral element content available for the plant and more generally, in estimating soil nutrient status. However, only a comparison between foliar analysis and the floristic or mineral indices could validate this statement. Thirdly, the measurement of any of these synoptic variables can attenuate spatial and temporal nutrient variations that are known to be important, especially soil acidity [11, 26, 48]. Humus form was measured in several locations within the sample plot and the floristic inventory covered 400 $m^2$, whereas soil analyses are less representative because they only concern the A-horizon (even if samples were collected in different locations within the sample plot).

A comparison of the accuracy of soil water-related factors to predict site index is more difficult. First, the presumably most synoptic variable – soil water deficit – was not as good a predictor of $SI_{100}$ as soil water capacity. But even with SWC, the difficulty lies in comparing SWC and CA Axis 2 or Axis 3, because these variables were not pure soil moisture gradients; they included nutrient descriptors ($K/P_2O_5$) and Axis 3 was also related to Axis 1. However, mF was a poorer predictor of site index compared to SWC. This is consistent with the hypothesis that soil water capacity is better assessed by soil parameters than floristic indices, especially because tree productivity can be affected by deeper soil horizons whereas the shallow-rooted herb-layer vegetation is not [37, 50].

The combination of floristic indices and abiotic variables into regression models improved the precision of the site index estimate (Tab. II). Our results initially supported the hypothesis that understory vegetation was a good indicator of site index variations, but a more detailed analysis actually demonstrated that a better site diagnostic was a combination of the two types of indices: physical soil properties and topography to estimate water balance and floristic indices to predict soil nutrient status. For example, model M4 was improved by including SWC 0-150 as a predictor (M6) and site index prediction by $\text{mIVSI}_{100}$ was improved by the introduction of SWC 0-150, topography and log(Mg) as supplementary predictors (M9).

The best site index predictive models were based on a combination of chemical and physical soil parameters, floristic indices (M9) and humus form (M8). This is consistent with the hypothesis that neither vegetation nor physiography alone are sufficient to classify ecosystems or to reliably predict site index [17, 27, 50, 58]. Nieppola [43] showed that the inclusion of soil type in the prediction model increases the accuracy of site index estimation by about 15%.

However, no clear information is provided in these publications concerning the following two hypotheses: (1) understory vegetation is a better predictor of nutrient-related factors compared to soil variables; (2) soil variables are a better predictor of water-related factors compared to understory vegetation. The validity of our conclusions is probably limited to lowland ecosystems where climatic variation is moderate and where soil differences are the main source of site variability [5].

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