Modelling the Growth of Sitka Spruce (*Picea sitchensis* (BONG.) CARR.) in Wales using WENK's Model Approach

(With 7 Figures and 1 Table)

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WENK-Modell; Stammanalyse; Volumenzuwachs-Stichprobe (VIS); Parameterschätzung; Umweltfaktoren.

1. INTRODUCTION

One of the current requirements of the British forest industry is for updated yield forecasting that is flexible enough to encompass both existing and new forest management methods. In a review of modelling related research projects for the Forestry Commission MASON (1999) stated that "Great Britain has missed a whole generation of management-level growth and yield models by focussing too much on process growth models".

To fill this gap a growth modelling project was launched in 2001 at Bangor and the late Professor GÜNTER WENK indicated his interest in exploring the applicability of his growth modelling approach to data from Wales. This was followed by a series of discussions that eventually led to the development of a single tree growth model prototype (POMMERENING and WENK, 2002; POMMERENING, 2005; MURPHY, 2008) to which Professor WENK frequently contributed as external advisor and friend.

1.1 The WENK modelling approach

Between 1965 and 2008 Professor WENK worked on a unique approach to forest modelling leaving a valuable legacy for the forest science community. This approach is best documented in his text book "Waldertragslehre" (WENK et al., 1990) and in WENK (1994)[3]. WENK's approach is unique because:

1. Relative increment is modelled rather than absolute increment.
2. The primary focus is on volume growth and its allometric relation to diameter and height growth.
3. The model is generic in that it can be applied at different scales.

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[3]) The WENK modelling approach was also implemented in the Norway spruce yield table for the German Democratic Republic (WENK et. al., 1984). The construction of the volume and height development in this yield table is based on Equations 1–4.

1.1.1 Relative increment

WENK (1978) defined relative increment $py_{i,t+\Delta t}$ of a tree i as the absolute increment of a given growth variable y divided by the value of the growth variable at the end of the observation period $t+\Delta t$.

$$py_{i,t+\Delta t} = \frac{y_{i,t+\Delta t} - y_{i,t}}{y_{i,t+\Delta t}} \quad (1)$$

For growth projections, relative increment can be converted to a growth multiplier, $My_{i,t+\Delta t}$, using Equation 2. The future value of y can be estimated by multiplying the current value, $y_{i,t}$, with the growth multiplier (WENK, 1971).

$$My_{i,t+\Delta t} = \frac{y_{i,t+\Delta t}}{y_{i,t}} = \frac{1}{1 - py_{i,t+\Delta t}} \quad (2)$$

Modelling relative increment is similar to a covariance analysis where the influence of the growth variable is excluded. Studying relative increment also allows for easier comparisons between different tree species and environmental conditions. This can be motivated by the fact that small trees have usually a lower absolute increment than larger trees. When comparing relative increment the opposite relationship can be observed: Small trees tend to have a comparatively high relative increment whilst large trees show small relative increments (see also STERBA and ZINGG, 2001). In fact, the maximum value of relative increment as defined in Equation 1 is 1 and decreases gradually in the first couple of years followed by a dramatic drop towards the end of the juvenile phase. Shortly before senescence relative increment approaches 0 (WENK et al., 1990, p. 78). In order to model relative increment WENK chose to use a modified version of the Gompertz function containing three main parameters, which proved to be very reliable in long-term growth projections (GOMPERTZ, 1825; WENK, 1969).

$$py_{i,t+\Delta t} = \exp\left[-c_{1,i,t}t^*(1-\exp\left[-c_{2,i,t}t^*(1-\exp[-c_{3,i,t}t^*])\right])\right] \quad (3)$$

The variables and model parameters are single tree specific (indicated by index i) and depend on time (indicated by index t). The main parameter, $c_{1,i,t}$, also referred to as the growth parameter, accounts for the overall shape of the growth curve and has been linked to individual tree vigour and to site quality. It can be considered to be a mathematical expression of the "growth energy" of a tree and is used as a summary characteristic of this energy (see section 1.1.3). At stand level, and in the absence of systematic changes in environmental conditions, the growth parameter has proved to be constant through time for many tree species and in such situations c_1 (as a stand characteristic) equals relative volume increment at the time of culmination of the current annual increment (WENK, 1978). The growth parameter is negatively correlated with relative volume increment and for individual trees, on any given site, it has been shown that lower values of $c_{1,i,t}$ imply increased tree vigour. The smaller, more suppressed trees have lower relative increment and therefore higher $c_{1,i,t}$ values (WENK et al., 1990). The effect of the growth parameter is modified in the early years of growth by parameters $c_{2,i,t}$ and $c_{3,i,t}$. With most European tree species this effect lasts only for 40 to 60 years depending on parameter values. Parameters $c_{1,i,t}$, $c_{2,i,t}$ and $c_{3,i,t}$ are always positive and based on empirical studies the latter can, in the majority of cases, be set to a fixed value of 0.4 for a wide range of European species including spruces. In temperate zones absolute age of the tree or stand is transformed according to $t^* = (age_i - 10)/10$ (WENK et al., 1990; MURPHY, 2008). The model is extremely flexible whilst remaining relatively parsimonious.

1.1.2 Focus on volume growth and allometric relations

Models ought to be considered in the context of the period of their development and the primary focus on volume growth of the WENK model, was motivated partly by the fact that volume was a production and sustainability criterion of paramount importance in the second half of the 20th century. Another reason for this focus was that, by modelling volume as a three-dimensional growth variable and deriving height and diameter as one-dimensional characteristics from volume growth, possible error propagation was effectively reduced (WENK et al., 1990, p. 174ff.). Equation (4) illustrates how the relative growth of one growth variable, y, is related to the relative growth of another, x, by the allometric coefficient $m_{i,t}$ (WENK, 1978).

$$1 - py_{i,t} = \left(1 - px_{i,t}\right)^{m_{i,t}} \quad (4)$$

1.1.3 A generic model approach

The model principles developed by WENK and his colleagues present a generic and consistent model framework, applicable at various levels of resolution. The model parameters and variables can be applied to single trees (POMMERENING and WENK, 2002), diameter classes (GEROLD, 1990) or forest stands (WENK, 1994) and the higher level information of single trees and diameter classes can be integrated by a stand model. The model parameters were selected in such a way that they could be used as diagnostic tools, providing valuable summary characteristics about the growth performance of a tree or a forest stand. The relationship between the growth parameter $c_{1,i,t}$ and tree vigour for example has already been referred to in section 1.1.1. Considering y as diameter and x as height in Equation 4, small allometric coefficients indicate that height increment is large relative to diameter increment, resulting in slender trees with little taper. Large allometric coefficients indicate growth patterns with slower height relative to diameter growth and trees have more pronounced taper.

Rather than deriving model parameters for large geographic areas WENK treated each tree and particularly each stand as an individual case. He identified the optimal combination of model parameters for each forest stand separately and interpreted individual growth patterns in relation to the combination of parameters.

Another advantage of the WENK approach is its flexibility at stand level to allow "backcasting", i.e. simulating historical stand conditions. This is a very useful property for harmonising inventories taken at different times.

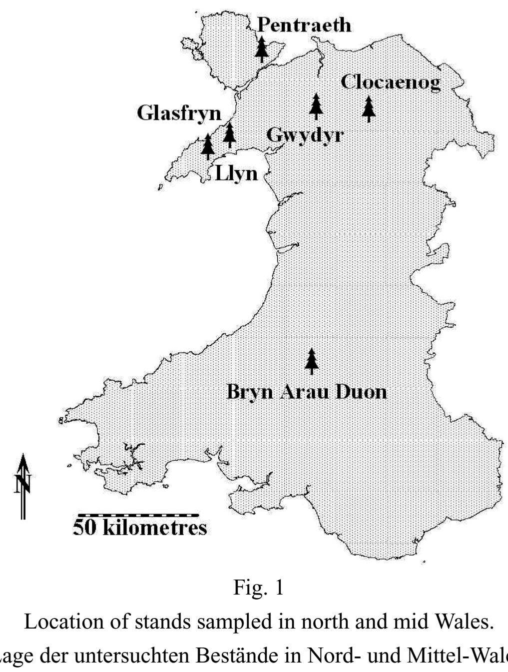

Fig. 1

Location of stands sampled in north and mid Wales.

Lage der untersuchten Bestände in Nord- und Mittel-Wales.

1.2 Objectives

In Britain the forest industry has been geared towards maximum volume production (FORESTRY COMMISSION, 2002) and traditional forest management generally favours monospecific stands grown in relatively short rotations culminating in clearfelling. The main commercial tree species are conifers, in particular Sitka spruce (*Picea sitchensis* (BONG.) CARR.) which occupies 84,000 ha in Wales, i.e. 31.5% of total woodland cover.

When this research project was first established, little was known of the likely magnitude and range of values of the WENK model parameters for Sitka spruce growing in Britain. The aim of this study was to provide values of the model parameters from different site types and to investigate the relationship between the main model parameters and environmental variables. An important aspect of this was that the data needed to estimate model parameters should be capable of being gathered relatively quickly from a greater number and wider range of site types than would be provided by long-term permanent monitoring plots.

2. MATERIALS AND METHODS

2.1 Site selection

The criteria used to guide stand selection were:

1. A wide range of yield classes and site types to capture the range of relationships between species and environmental factors.
2. Pure stands of Sitka spruce to limit the study to intraspecific interactions.
3. Stands of at least 40 years of age to sample growth patterns well beyond the juvenile phase.
4. Stands that were unthinned or not thinned in the previous 10 years to minimise the effect thinning would have on parameter values.
5. Site uniformity to maintain constancy of environmental variables.

A total of 17 stands from six forest areas were chosen, representing a wide range of productivity classes and environmental conditions. They include near coastal and more continental locations as

Tab. 1

General characteristics of the stands sampled in north and mid Wales.

Allgemeine Kenngrößen der untersuchten Bestände in Nord- und Mittel-Wales.

Location	**Gwydyr**						**Glasfryn**	**Bryn Arau Duon**	
Stand name	**GWY 3**	**GWY 4**	**GWY 5**	**GWY 6**	**GWY 7**	**GWY 8**	**GFS 1**	**BAD 1**	**BAD 2**
Longitude **Latitude**	3° 50’ W 53° 06’ N	3° 51’ W 53° 05’ N	3° 51’ W 53° 05’ N	3° 51’ W 53° 05’ N	3° 50’ W 53° 03’ N	3° 50’ W 53° 03’ N	4° 22’ W 52° 58’ N	3° 50’ W 52° 07’ N	3° 50’ W 52° 07’ N
Altitude [m.a.s.l.]	105	305	265	295	360	360	150	250	410
Accumulated temperature (day degrees above 5°C)	1619	1265	1336	1283	1170	1170	1565	1272	1129
Moisture deficit (mm)	136	84	95	87	70	70	119	81	62
Windiness (Detailed Aspect Method of Scoring; QUINE AND WHITE, 1993, 1994)	8	16	12	16	18	18	15	12	19
Soil type	(Gleyed) Brown earth	Deep peat Peaty Gley	Peaty gley	Deep peat	Peaty gley	Deep peat	Peaty gley	Upland brown earth	Unflushed Deep peat
Soil moisture regime	fresh/moist	very wet	wet	very wet	wet	very wet	very moist	fresh	very wet
Soil nutrient regime	medium	very poor	poor	very poor	poor	very poor	medium	poor	very poor
Total plot size [m²]	6000	1500	7500	7500	7500	7500	7500	3000	1500
Stand age at survey [yr]	37	40	40	40	40	40	41	39	40
Number of trees ha^{-1}	1242	2650	1673	2213	2193	3133	1405	1460	3520
Top height H_{100} [m]	25.3	18.1	26.8	15.4	22.0	10.9	23.5	24.7	13.6
Quadratic mean diameter D_g [cm]	20.13	15.6	19.8	16.0	20.5	10.6	20.3	25.6	14.8
Basal area [m²/ha]	35.42	50.72	51.49	–	72.25	27.46	45.51	-	-
Yield class [m³ ha^{-1} yr^{-1}]	22	12	23	10	17	6	18	20	6

Location	**Clocaenog**					**Pentraeth**	**Llŷn**	
Stand name	**CLG8**	**CLG9**	**CLG10**	**CLG11**	**CLG12**	**PEN1**	**UPM1**	**UPM2**
Longitude **Latitude**	3° 34’ W 53° 05’ N	3° 26’ W 53° 03’ N	3° 27’ W 53° 04’ N	3° 33’ W 53° 07’ N	3° 33’ W 53° 07’ N	4° 11’ W 53° 17 N	4° 29’ W 52° 54’ N	4° 31’ W 52° 56’ N
Altitude [m.a.s.l.]	420	325	345	445	435	115	25	155
Accumulated temperature (day degrees above 5°C)	1058	1229	1192	1012	1030	1585	1789	1552
Moisture deficit (mm)	58	85	79	52	54	127	149	115
Windiness (Detailed Aspect Method of Scoring; QUINE AND WHITE, 1993, 1994)	20	16	15	20	20	13	13	12
Soil type	Peaty gley Deep peat	Brown earth	Brown earth	Peaty gley	Deep peat	Peaty gley	Deep peat	Brown earth
Soil moisture regime	very wet	fresh	moist	very moist	very wet	very moist	very wet	fresh
Soil nutrient regime	very poor	medium	medium	poor	very poor	medium	medium	poor
Total plot size [m²]	6000	7500	1500	7500	7500	7500	7500	7500
Stand age at survey [yr]	41	38	35	45	45	48	43	49
Number of trees ha^{-1}	2147	1027	1567	1227	3027	1080	1860	1527
Top height H_{100} [m]	19.3	25	31.5	24.7	14.1	30.8	22.5	22.7
Quadratic mean diameter D_g [cm]	17.8	27.6	26.0	27.2	11.7	29.8	21.5	23.5
Basal area [m²/ha]	53.38	61.45	82.98	71.45	32.69	75.32	67.42	65.27
Yield class [m³ ha^{-1} yr^{-1}]	14	21	30	17	6	24	16	14

well as lowland and upland sites. A location map is shown in *Fig. 1* and *Table 1* gives an overview of the main stand and site characteristics.

2.2 Sampling procedure

A volume increment sampling method (VIS) was used which allowed volume increment data to be gathered without recourse to either time consuming repeated measurements from sample plots or stem analysis (GEIßLER and WENK, 1988). Using this method, 10-year increment data reflecting short-term growth information for a large number of trees covering a wide range of site types can be gathered relatively quickly. Several stem analyses were carried out for each stand to check and complement the method with long-term growth information. In addition to measurements for determining volume increment, basic inventory information was also collected (e.g. stems per hectare, diameter distributions and height). The soil type was identified from field observation and additional environmental information (*Table 1*) taken, or derived, from existing databases (RAY, 2001). The yield class of the stand, defined as the maximum mean annual increment (EDWARDS and CHRISTIE, 1981), was estimated from top height (MATTHEWS and MACKIE, 2006).

Following GEIßLER and WENK (1988) between 10 and 15 temporary circular plots of 0.01 or 0.05 ha size were established at each stand. One tree from each plot was selected, for sampling, in such a way that a representative sample of the diameter range of the stand was obtained. Three of the trees were also sampled for stem analysis in order to provide additional data on tree growth and as a check for the sample tree method. Wherever possible the plots were laid out in a grid pattern to ensure even distribution across the site and to decrease variance.

Tree volume was determined from tree height, h, and mean cross sectional area, ba_q, using:

$$v = h \cdot ba_q \tag{5}$$

where

v tree volume (m^3)
h current tree height measured from cutting point
ba_q mean cross sectional area (m^2)

To determine mean cross sectional area, the corresponding mean diameter was calculated following RADONJIC (1954):

$$d_q = \sqrt{\frac{k}{3} \cdot \left(d_{1/8}^2 + d_{4/8}^2 + d_{7/8}^2\right)} \tag{6}$$

where

d_q mean diameter (cm)
$d_{n/8}$ diameter at n/8 of the height of the tree (cm)
k a tree species specific constant

The constant, k, was determined through stem analyses of over 40 trees, sampled during the Tyfiant Coed Project (POMMERENING, 2005) and a value of 1.0395 was established for Sitka spruce in Wales (MURPHY, 2008).

Current volume was estimated from field measurements of felled trees. To estimate volume from 10 years previously height from 10 years ago, h_{-10}, was determined by counting back branch whorls and mean cross sectional area from 10 years ago, ba_{q-10} from a disc sample. The height, h_{0-10}, at which the disc sample was taken, was determined using Equation 7, on the assumption that the form factor had not changed over the previous 10 years. The variables required are illustrated in *Fig. 2*.

$$h_{0-10} = \frac{h_0}{h} \cdot h_{-10} \tag{7}$$

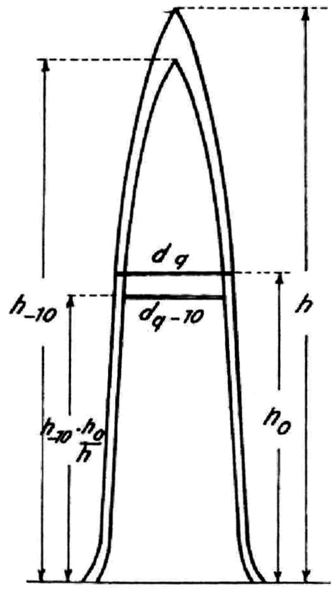

Fig. 2
The variables to be measured for the determination of the volume increment of the last ten years (GEIßLER and WENK, 1988).
h – current tree height measured from cutting point,
h_{-10} – tree height 10 years ago, d_q – diameter of mean cross sectional area, h_0 – height to current mean cross sectional area,
h_{0-10} – height of mean cross sectional area 10 years ago,
d_{q-10} – diameter of mean cross sectional area 10 years ago.

Die Variablen zur Bestimmung des Volumenzuwachses der letzten zehn Jahre (GEIßLER and WENK, 1988).
h – gegenwärtige Baumhöhe vom Fällschnitt gemessen,
h_{-10} – Baumhöhe vor 10 Jahren, d_q – Durchmesser der mittleren Querschnittsfläche, h_0 – Höhe zur mittleren Querschnittsfläche,
h_{0-10} – Höhe zur mittleren Querschnittsfläche vor 10 Jahren,
d_{q-10} – Durchmesser der mittleren Querschnittsfläche vor 10 Jahren.

2.3 Estimation of model parameters

In the past model parameters were commonly established through trial and error guided by modelling experience, largely because of the complexity of Equation (3). In this study, parameter estimation techniques new to the WENK modelling approach were tested and applied to both the VIS and the stem analyses. These techniques include:

1. simulated annealing (SA) (CHEN and GADOW, 2002; POMMERENING and STOYAN, 2008) and
2. LEVENBERG-MARQUARDT algorithm of nonlinear regression (NLR) (BUYS and GADOW, 1987).

With both techniques, the model parameter c_3 was kept constant with a value of 0.4 for all trees analysed. Model parameters c_1 and c_2 were assumed to be tree-specific but constant through time to facilitate the correlation with environmental factors. Initial values were established through a grid search in which combinations of c_1 and c_2 were tested using incremental steps of 0.001. Inspired by discussions with GÜNTER WENK, optimal c_2 was defined as that value, which produced the lowest coefficient of variation in c_1 of the VIS trees from a given stand or throughout the annual time steps of the stem analysis of a single tree.

With stem analysis trees the parameter estimation is complicated because Equation 3 is designed to use 10-year increment data (WENK et al., 1990, p. 79). If used for time intervals other than 10 years a marked estimation bias is incurred (POMMERENING, 2005).

GEROLD and RÖMISCH (1977) developed a method for interpolating annual volume increment which is based on 10-year growth multipliers (Equation 8).

$$mv_{i,t+1} = \frac{\prod_{j=1}^{n} mv_{i,t+j\cdot 10}}{\prod_{j=1}^{n} mv_{i,t+j\cdot 11}} \qquad (8)$$

where

$mv_{i,t+1}$ annual volume growth multiplier

$j, \ldots, n$ iterations

With increasing n the ratio $mv_{i,t+n\cdot 10}/mv_{i,t+n\cdot 11}$ approaches 1 and n can conveniently be defined by the point when $mv_{i,t+n\cdot 10}/mv_{i,t+n\cdot 11}$ falls below a certain threshold value, e.g. 1.0001. As a pre-requisite, this algorithm requires the function of the relative increment to approach zero with increasing age which Equation 3 fulfils. The algorithm by GEROLD and RÖMISCH (1977) allows the estimation of model parameters for Equation 3 for any time period other than 10 years and was integrated into both the NLR and the SA routines.

2.3.1 Simulated Annealing (SA)

At a predetermined starting temperature of T = 1,000 an objective or energy function, E, was calculated for the initial parameter combination defined as the sum of squared differences between observed and predicted relative volume increment observations. In every simulated annealing iteration a model parameter (c_1 or c_2) was then randomly selected and assigned to a new candidate value within a predefined parameter space which was derived from the literature and defined as $0.1 \leq c_1 \leq 1.0$ and $0.5 \leq c_2 < 5.0$. Afterwards the energy was recalculated. If the new energy value was lower, the candidate parameter value was accepted and preferred to the earlier one. To avoid getting caught in a local energy minimum a higher new energy value may still have been chosen depending on the so-called METROPOLIS probability P(E) (Equation 9) and on the temperature T.

$$P(E) = e^{\frac{-\Delta E}{T}} \qquad (9)$$

where

$$\Delta E = E_{new} - E_{old} > 0$$

A higher energy value is accepted when a uniform random number in the interval [0, 1] was less than the METROPOLIS probability. As temperature falls the likelihood of higher energy values being chosen diminishes. At the end of each iteration the temperature T was reduced by a cooling factor which was selected as 0.99 in this study. The iterations continued until a maximum of 10,000 steps was exceeded.

2.3.2 LEVENBERG-MARQUARDT algorithm/Nonlinear regression (NLR)

Model parameters were also estimated using the LEVENBERG-MARQUARDT algorithm to minimize the sum of squared errors and programmed in JAVA after an implementation by BUYS and GADOW (1987). This algorithm is commonly available in software used to fit nonlinear models.

2.3.3 Aggregation of tree model parameters

As a result of SA and NLR, model parameters were established for all sample trees. Since an objective of the study was to identify relationships between stand growth at the 17 sites in Wales and their environmental factors the sample tree model parameters were aggregated at stand level. Rather than averaging the single tree results this was achieved through a variant of both SA and NLR methods. Instead of limiting the parameter estimation to the observed data of just one single tree all observed data relating to any one site, VIS and stem analysis data, were included in the analysis. This allowed a simultaneous estimation of the model parameters. By combining VIS and stem analysis data in the simultaneous estimation short-term and long-term growth information was integrated.

3. RESULTS

3.1 Estimation of model parameters

Estimating the model parameters for single trees achieved generally good results with the exception of marginal sites, such as waterlogged and very acidic soils, where Sitka spruce had suboptimal growing conditions. In such conditions, the species tends to suffer from growth stagnation during its juvenile phase. Often Sitka spruce recovers in later years, but the first years of stagnant growth have an effect on the estimation of parameters which has been difficult to interpret.

Values of c_1 and c_2 estimated using simulated annealing and the LEVENBERG-MARQUARDT algorithm are compared in *Fig. 3*. Both methods used the same criterion to optimise parameter estimation, i.e. the least sum of squared errors. Three NLR results, where c_1 was greater than 1, were excluded and, apart from a few instances where c_1 (NLR) had a value greater than 0.6, there was little difference in the results from the two methods. This confirms the value

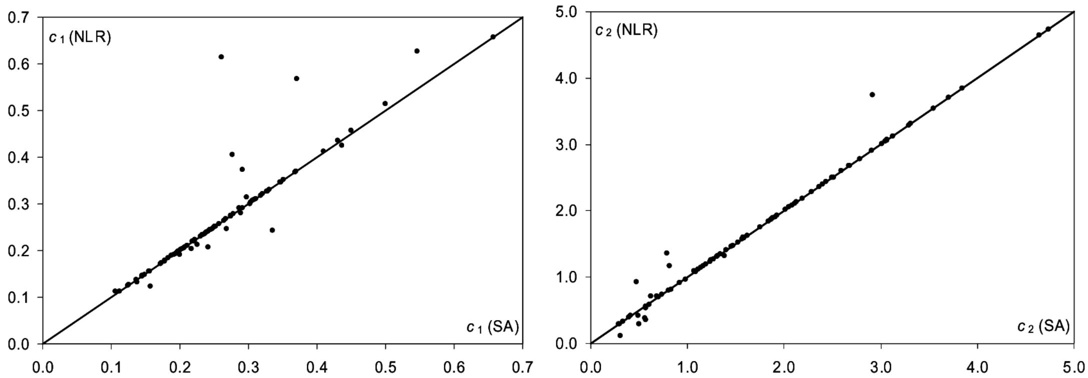

Fig. 3

Comparison of values of model parameters c_1 (left) and c_2 (right) estimated with simulated annealing (SA) and the LEVENBERG-MARQUARDT algorithm (NLR).

Vergleich der Werte der Modellparameter c_1 (links) und c_2 (rechts), die mit Hilfe des Simulierten Abkühlens (SA) und des LEVENBERG-MARQUARDT-Algorithmus (NLR) geschätzt wurden.

of simulated annealing as an alternative for the LEVENBERG-MARQUARDT algorithm. However, SA produced c_2 values beyond the acceptable range, in some cases, and NLR was preferred in the subsequent analysis.

Fig. 4 illustrates the range of values for stand c_1 obtained from analysis using volume increment samples and stem analysis trees, separately and then aggregated, for a total of three sets of parameter estimates. In most cases there was wide variation between VIS and stem analysis values. This is not completely unexpected, since VIS data represent short-term growth information whilst stem analysis data reflect long-term patterns. If, for example, a tree suffered from stagnation in early stages of growth, parameter estimates based on short-term data from those early years will be different from those of later years. Only CLG10 shows any similarity in value between the three methods. In most cases the VIS value is greater than that from stem analysis trees, CLG9, GFS1, BAD1 and BAD2 being the exceptions. For some sites both methods would not give a parameter value which may have been due to extreme variation in growth conditions e.g. a tree recovering quickly from stagnation. VIS values tended to be quite high, ranging from 0.15 to 0.37. Except for CLG10, values for stem analysis trees are markedly lower, ranging in value from 0.13 to 0.33.

The range of values of c_2 is illustrated in *Fig. 5.* The VIS trees generally had lower values than stem analysis trees with the exception of CLG9, GWY4 and BAD1. As with the c_1 value, only CLG10 showed a similarity in values between the three methods. For four of the sites, the aggregated value was higher than either of the others. For one stand, it was lower. The maximum value was 6.90 and the minimum value was 0.29. Such figures represent the extreme limit of plausible values. If c_2 is much above 5.0, the curve of relative volume increment is very similar to a one parameter model. If values are below 0.5, then early growth would be very rapid.

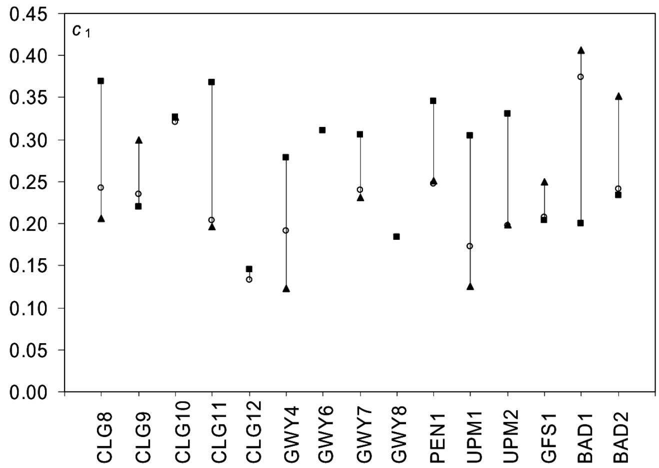

Fig. 4

Stand values of c_1 estimated with the LEVENBERG-MARQUARDT algorithm (NLR) from VIS and stem analysis for 15 sites. Solid squares are VIS trees, solid triangles are stem analysis trees and open circles are aggregated results. Results for GWY6 and GWY8 could not be computed.

c_1-Bestandeswerte geschätzt mit Hilfe des LEVENBERG-MARQUARDT-Algorithmus (NLR) aus Daten der Volumenzuwachs-Stichprobe (VIS) und der Stammanalyse für 15 Versuchsflächen. Ausgefüllte Rechtecke symbolisieren die VIS-Probebäume, ausgefüllte Dreiecke die Stammanalyse-Bäume und unausgefüllte Kreise geben die Ergebnisse für die aggregierten Werte wieder. Ergebnisse für GWY6 and GWY8 konnten nicht ermittelt werden.

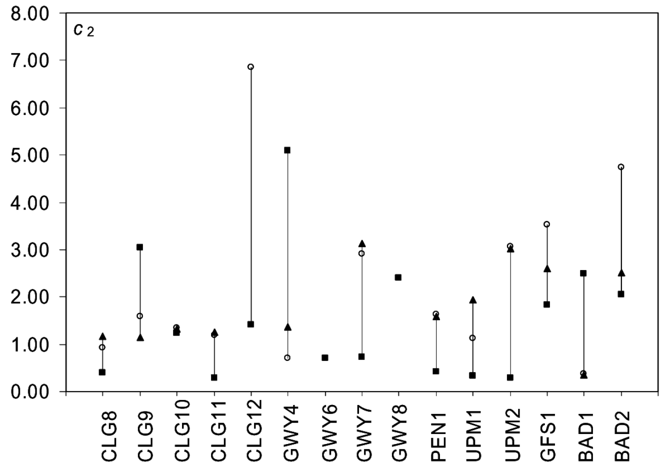

Fig. 5

Stand values of c_2 estimated with the LEVENBERG-MARQUARDT algorithm (NLR) from VIS and stem analysis for 15 sites. Solid squares are VIS trees, solid triangles are stem analysis trees and open circles are aggregated results. Results for GWY6 and GWY8 could not be computed.

c_2-Bestandeswerte geschätzt mit Hilfe des LEVENBERG-MARQUARDT-Algorithmus aus Daten der Volumenzuwachs-Stichprobe (VIS) und der Stammanalyse für 15 Versuchsflächen. Ausgefüllte Rechtecke symbolisieren die VIS-Probebäume, ausgefüllte Dreiecke die Stammanalyse-Bäume und unausgefüllte Kreise geben die Ergebnisse für die aggregierten Werte wieder. Ergebnisse für GWY6 and GWY8 konnten nicht ermittelt werden.

3.2 Relationship of model parameters with environmental variables

ZIMMERMANN (1974) detected a strong correlation between the growth parameter c_1 and yield class. Therefore, as a first step in the investigation of the relationship between model parameters and environmental variables, yield class was interpreted as a variable of aggregated environmental information.

Aggregated values of c_1 were regressed against yield class for each site and the results are illustrated in *Fig. 6*. It is possible to improve this positive correlation by removal of extreme values. For example the removal of BAD1 and BAD2, two stands which showed growth patterns largely deviating from those of the other sites, from the analysis gives a coefficient of determination of $R^2 = 0.78$. However, such manipulation naturally has to be treated with great care and a larger data set may indicate that these extreme values are part of natural variation.

In a second step values of c_1 were regressed against a number of individual environmental variables. Because soil moisture regime and soil nutrient regime are class variables, a set of dummy variables were substituted for them in the linear regression (WORRELL and MALCOLM 1990; FIELD, 2005). Only 13 data points were available for the analysis and the individual correlations were relatively poor. The strongest relationships were with soil moisture regime (SMR), an expression of windiness measured using the detailed aspect method of scoring (DAMS, QUINE and WHITE, 1993, 1994) and soil nutrient regime (SNR).

The relationships are shown in *Fig. 7* and, despite the lack of significance in the R^2 values, indicate the importance of soil moisture and nutrients for the growth of Sitka spruce. The influence of increasing exposure as a limiting factor to growth is also suggested. *Fig. 7* implies that the value of the growth parameter c_1 increases as the soil becomes drier and more nutrient rich but decreases on

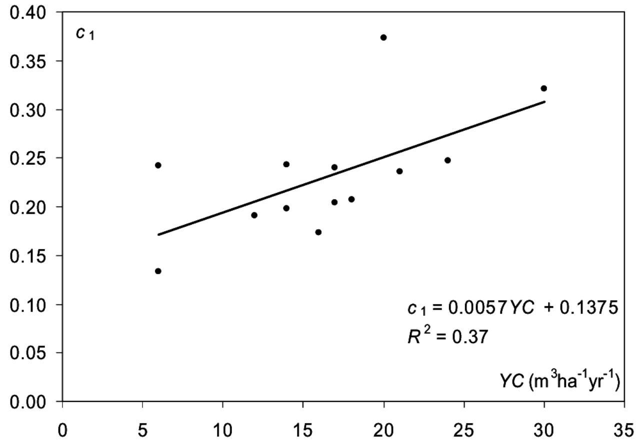

Fig. 6

Aggregated VIS and stem analysis values of c_1 compared to estimated yield class (*YC*).

Aggregierte c_1-Werte aus Volumenzuwachs-Stichprobe und Stammanalyse aufgetragen über der Ertragsklasse (*YC*).

more exposed sites. The relationship between individual environmental variables and c_2 was weaker and similar analysis of c_2 values gave R^2 values of less than 0.1 for nearly all variables.

Based on these encouraging findings, a multiple regression model was developed for estimating c_1 parameter values from environmental factors. Accumulated temperature was excluded during the regression process because it was so strongly correlated with elevation. A model which included only moisture deficit, exposure, soil moisture regime and soil nutrient regime gave an R^2 value of 0.74 and is shown in Equation 10. Analysis of c_2 failed to produce such a strong relationship with environmental factors and age of the stand had a major influence in the model (Equation 11).

$$c_1 = 1.3767 - 0.0045MD - 0.0413DAMS - 0.0803SMR2 - 0.1015SMR3 - 0.1570SMR4 - 0.1627SMR5 - 0.1115SNR1 + 0.0746SNR3 + \varepsilon \quad (10)$$

$R^2 = 0.74$

$$c_2 = 4.0770 - 0.0930AGE + 0.0008EAST + 0.2217SMR2 + 0.4819SMR3 + 0.6026SMR5 - 0.2819SNR1 + 0.8944SNR3 + \varepsilon \quad (11)$$

$R^2 = 0.65$

where

MD	moisture deficit
DAMS	detailed aspect method of scoring
*SMR*2, …, *SMR*5	dummy variables for soil moisture regime
*SNR*1, …, *SNR*3	dummy variables for soil nutrient regime
AGE	age of tree in years
EAST	longitude based on British Ordnance Survey co-ordinate system
ε	error term

Previous modelling work has emphasised the strong relationship between elevation and growth of Sitka spruce in Britain (PROE et al., 1996; BATEMAN and LOVETT, 1998). This is also reflected in the decrease in potential yield class with decreasing accumulated temperature (PYATT et al., 2001). In Equation 10, moisture deficit seems to replace elevation and accumulated temperature with which it is highly correlated.

4. DISCUSSION AND CONCLUSIONS

The results of this study clearly indicate that the WENK modelling approach is transferable to Sitka spruce in Wales. The majority of trees had c_1 values between 0.15 and 0.35 and c_2 values between 0.50 and 3.5. These values show correspondence with the work of WENK and his colleagues with higher values of c_1 reflecting the higher yield classes of Sitka spruce. The range of c_2 values is of particular interest and seems to be close to the theoretically plausible limits for the model. MURPHY (2008) showed that with just two parameters a wide range of growth trends of individual trees could be adequately modelled. These ranges could also be used as initial estimates for lower and upper potential values for given stands. Establishing parameters for potential growth is an important step in modelling single tree growth using the potential-modifier approach (VANCLAY, 1994; GADOW and HUI, 1999). For example, POMMERENING (2005) modelled an upper and a lower potential because of the specific distribution of the growth parameter.

The volume increment sampling method (VIS) proved to be a useful and quick method for establishing model parameter values. However, as this method provides only short-term growth information for the previous decade, it failed to produce reliable data where there were marked differences between juvenile and adult growth on suboptimal sites. The same problem arose with trees that had lost their dominant status in the main stand canopy. In such cases,

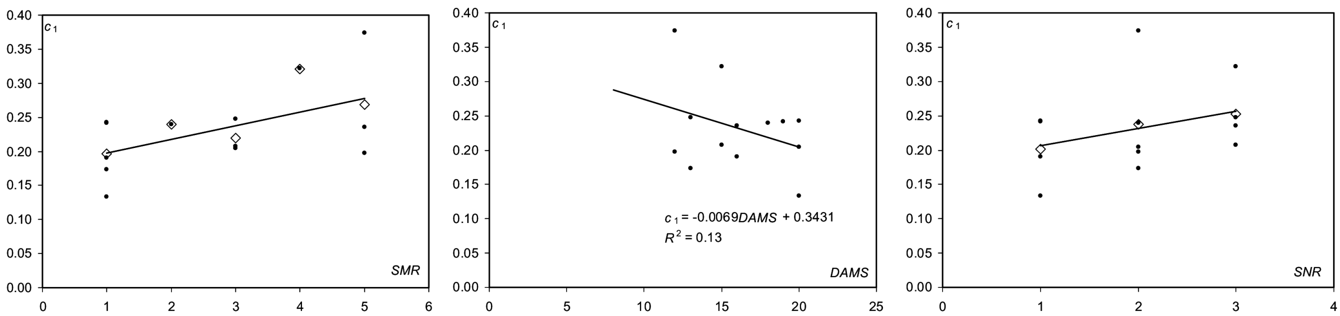

Fig. 7

Relationships between aggregated VIS and stem analysis values of c_1 and environmental factors soil moisture regime (SMR), detailed aspect method of scoring (DAMS) – an expression of windiness – and soil nutrient regime (SNR). Solid points represent original data, open diamonds are the results from linear regression using dummy variables. Trendlines for SMR and SNR are indicative only.

Beziehungen zwischen den aggregierten c_1-Werte aus Volumenzuwachs-Stichprobe und Stammanalyse und der Bodenfeuchtigkeitskennziffer (SMR), einem Maß für Windstärke (DAMS) und der Bodennährstoffkennziffer (SNR). Aufgefüllte Kreise repräsentieren die Originaldaten, die Ergebnisse der linaren Regression mit Dummy-Variablen ist mit weißen Rauten dargestellt. Die Trendlinien für SMR und SNR haben nur eine illustrierende Funktion.

stem analyses complemented the data with valuable long-term information.

The study has also shown that using two model parameters and fixing c_3 to 0.4 provided enough model flexibility to reproduce the diverse growth patterns of single Sitka spruce trees in Wales. The model parameters can be estimated in an objective way with modern estimation methods. Nonlinear regression (NLR) using the LEVENBERG-MARQUARDT algorithm proved to be slightly more reliable than simulated annealing (SA), although the results of both were generally very close.

A new method of aggregating population parameters was developed in this study and proved to be useful. Through simultaneous regression of all VIS and stem analysis trees of any one stand, parameters could be identified that reflect the growth pattern at stand level.

We also showed that both main model parameters, c_1 and c_2, are related to environmental factors and as expected the link is stronger with c_1 (ZIMMERMANN, 1974; WENK et al., 1990). Perhaps not surprisingly, the strongest links (*Fig. 7*) are those with soil moisture regime (SMR), windiness (DAMS) and soil nutrient regime (SNR). However, simple linear regressions are unlikely to be able to explain the full variation between model parameters and environmental variables and a parabolic response curve (PRETZSCH and KAHN, 1995; PYATT et al. 2001) between c_1 and SMR and SNR is more likely. There is a lack of data for sites at both the drier and richer end of the environmental spectrum where growth rates of Sitka spruce would be expected to decrease (PYATT et al., 2001). An expected correlation between parameters and elevation or accumulated temperature is evident only in a multiple regression and even then this is indirectly through the link to moisture deficit.

As mentioned in the previous section, the relationships between yield class (*Fig. 6*) and the growth parameter c_1 appears to contradict the fact that small values of c_1 indicate vigorous tree growth whilst large values of c_1 are associated with reduced single tree growth for the same values of c_2. To understand these trends it is important to distinguish between population parameters and individual tree parameters. This seemingly "inverse" behaviour is related to the fact that volume increment of forest stands with high yield classes culminates earlier than that of lower yield classes. High yield classes in plantations mean rapid growth followed by an early growth culmination and decreasing increment after culmination. This corresponds to large growth parameter values for higher yield classes and low c_1 values for lower yield classes. These growth patterns have been confirmed by many growth and yield experiments (WENK et al., 1990, p. 97).

The study confirms the special nature of the growth parameter c_1, which provides a valuable summary characteristic of the growth performance of forest sites. Extending this analysis to more sites with a wider and more even distribution of yield classes would be beneficial to further modelling work, in particular to understanding the relationship between parameters and environmental conditions. Complementary studies on within site variation and competition will provide valuable additional information. The flexibility of the model and the relationship between model parameters and environmental variables also offers the opportunity to simulate the growth of Sitka spruce under a wide range of climate change scenarios.

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6. ABSTRACT

The WENK modelling approach was applied to volume growth of Sitka spruce (*Picea sitchensis* (BONG.) CARR.) in Wales. Seventeen very different sites of low intensity management Sitka spruce plantations were sampled using volume increment sampling (VIS) and stem analysis. The two main model parameters, c_1 and c_2, which are often interpreted as summary characteristics, were estimated for single trees using two different methods, the LEVENBERG-MARQUARDT algorithm, frequently used for nonlinear regression (NLR), and simulated annealing (SA). Individual tree values were aggregated to obtain stand-level population parameters through simultaneous estimations. The authors then correlated the model parameters of the 17 stands with seven environmental factors. The results showed that the WENK modelling approach is indeed transferable to volume growth of Sitka spruce in Wales. VIS proved to be a useful method of quickly gathering current volume increment data but needs to be complemented by long-term growth information from stem analyses. The model parameters can be estimated in an objective and reliable way with both estimation methods, but NLR performed slightly better. The method of aggregating population parameters by simultaneous estimations provided good results. Finally, we could demonstrate that both model parameters are related to environmental factors. The most significant environmental variables were soil moisture regime, windiness and soil nutrient regime. The study confirmed the value of the WENK approach and particularly the value of the model parameters c_1 and c_2 as summary characteristics.

7. Zusammenfassung

Titel des Beitrages: *Modellierung des Wachstums der Sitkafichte (Picea sitchensis (BONG.) CARR.) in Wales mit Hilfe des WENK'schen Modellierungsansatzes.*

Der WENK'sche Modellierungsansatz wurde auf das Volumenwachstum der Sitkafichte (*Picea sitchensis* (BONG.) CARR.) in Wales angewendet. Siebzehn weitgehend undurchforstete Sitkafichten-Reinbestände wurden mit Hilfe der Volumenzuwachs-Stichprobe (VIS) und mit Stammanalysen beprobt. Die zwei wichtigsten Modellparameter c_1 und c_2, die häufig auch als statistische Kenngrößen interpretiert werden, wurden mit zwei verschiedenen Methoden für Einzelbäume geschätzt, dem LEVENBERG-MARQUARDT-Algorithmus, der häufig zur nicht-linearen Regression (NLR) verwendet wird, und dem Simuliertem Abkühlen (SA), und mit simultanen Schätzmethoden zu Populationsparametern aggregiert. Die Autoren haben anschließend die Modellparameter der 17 Bestände mit sieben Umweltfaktoren korreliert. Die Ergebnisse haben gezeigt, dass der WENK'sche Ansatz tatsächlich auf das Wachstum der Sitkafichte in Wales übertragbar ist. VIS hat sich als eine Methode bewährt, mit der man schnell Daten über den aktuellen Volumenzuwachs erheben kann, die aber mit langfristigen Wachstumsinformationen aus Stammanalysen ergänzt werden müssen. Die Modellparameter können mit beiden Verfahren objektiv und zuverlässig geschätzt werden, NLR erwies sich aber als etwas besser. Das Aggregieren von Einzelbaum-Modellparametern zu Populations-Parametern mit Hilfe simultaner Methoden erzielte gute Ergebnisse. Wir konnten schließlich zeigen, dass beide Modellparameter mit Umweltfaktoren korreliert sind. Die signifikantesten Umweltfaktoren waren Bodenfeuchte, Windstärke und Bodennährstoffgehalt. Die Untersuchung hat den Wert des WENK'schen Ansatzes und besonders der Modellparameter c_1 und c_2 als statistische Kenngrößen bestätigt.

8. Résumé

Titre de l'article: *Modélisation de la croissance de l'Epicéa de Sitka (Picea sitchensis (BONG.) CARR.) au Pays de Galles, à l'aide de l'approche modélisatrice de WENK.*

L'approche modélisatrice de WENK a été appliquée à la croissance en volume de l'Epicéa de Sitka (*Picea sitchensis* (BONG.) CARR.) au Pays de Galles. 17 peuplements monospécifiques d'Epicéa de Sitka, la plupart non éclaircis, ont été mesurés par la méthode d'échantillons de mesure de l'accroissement (VIS en anglais) et par analyses de tiges. Les deux paramètres modélisateurs les plus importants c_1 et c_2, qui sont également souvent interprétés comme grandeurs statistiques d'identification, ont été estimés avec deux méthodes différentes pour arbres pris isolément – l'algorithme de LEVENBERG-MARQUARDT qui est souvent utilisé dans la régression non linéaire (NLR) et l'algorithme du recuit simulé (Simulated Annealing, SA en anglais) – et agrégés en paramètres de population à l'aide des méthodes simultanées d'estimation. Les auteurs ont ensuite corrélé les paramètres modélisateurs se rapportant aux 17 stations écologiques, avec sept facteurs environnementaux. Les résultats ont mis en évidence que l'approche de WENK est réellement transposable à la croissance de l'Epicéa de Sitka au Pays de Galles. VIS s'est avérée être une méthode avec laquelle on peut rassembler rapidement des données sur l'accroissement en volume actuel, ces données devant cependant être complétées par des informations sur le long terme concernant la croissance à partir d'analyses de tiges. Les paramètres du modèle peuvent être estimés par les deux procédés de manière objective et fiable, mais NLR s'avère être un peu meilleure. L'agrégation des paramètres du modèle pour arbre pris isolément, en paramètres de population, à l'aide des méthodes simultanées, a donné de bons résultats. Nous pouvions montrer finalement que les deux paramètres modélisateurs sont corrélés aux facteurs environnementaux. Les facteurs environnementaux les plus significatifs étaient l'humidité du sol, la force du vent et la teneur du sol en matières nutritives. L'expérimentation a confirmé la valeur de l'approche de WENK et particulièrement des paramètres modélisateurs c_1 et c_2 en tant que grandeurs statistiques d'identification.

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