

Improved estimates of biomass expansion factors for Sitka spruce

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Abstract

Allometric regressions for estimating forest biomass were developed and used to predict changes in biomass expansion factors (BEF) for a Sitka spruce chronosequence. Cross validation of the biomass models obtained from a USDA inventory data base and an Irish biomass data set indicated that stand and regional-specific allometric models need to be developed due to the influence of different management practices or climatic conditions. Analyses of the algorithms suggest that DBH, tree height and stand density should be used as inputs for biomass and BEF models to reduce the error of estimate. Based on the analyses presented in this work, BEF values could vary from 1.4 to 5.0 for a selected chronosequence depending on age, yield class and total stem biomass. Our results also suggest that recent carbon sequestration predictions for Sitka spruce forests may have been underestimated by 2 to 4-fold due to an underestimation of BEF, particularly for afforested stands planted since 1990.

Key words: Biomass expansion factors, Sitka spruce, allometric regression

Introduction

Forest soils and vegetation comprise an important part of regional and global carbon (C) pools. Changes in the size of these pools due to forest succession, disturbance and management practices may result in significant changes in the sinks for C or atmospheric levels of carbon dioxide. The advent of the United Nations Framework Convention on Climate Change (UNFCCC) and its Kyoto Protocol has increased the need for accurate inventories of forest C storage and sequestration. While standardised C inventory methodologies have been developed by the Intergovernmental Panel on Climate Change (Houghton et al. 1997) there is a clear need for studies to reflect national circumstances. There are many uncertainties in estimates of forest biomass C pools, such as the amount of forest biomass (Schroeder et al. 1997, Brown et al. 1997), the appropriate biomass expansion factors (Brown 2002), and values for biomass density and carbon fraction (Lowe et al. 2000).

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Studies on the sink capacity of Irish forests are limited. It is estimated that the average rate of carbon sequestration by Irish forests is approximately $3.36 \text{ t C ha}^{-1} \text{ yr}^{-1}$ (Kilbride et al. 1999), based on the model developed by Dewar and Cannell (1992). However, this estimate of the sink capacity of Irish forests is based on a single biomass expansion factor (BEF) value of 1.3 t t^{-1} for all species, age and yield classes (Kilbride et al. 1999) and ignores the below ground component. Since the allocation of biomass between different forest components is dependent on stand density, forest species and nutritional status, current national estimates of sink capacity would be improved using classified age and species-specific BEF values that include the below ground fraction.

By definition, BEF (the ratio of above ground biomass to merchantable timber volume) may not be suitable for calculation of C storage in forest ecosystems because of the exclusion of younger, smaller trees ($\text{DBH} < 7 \text{ cm}$). To incorporate younger stands of a chronosequence into current BEF estimates, BEF has to be redefined as the ratio of above ground biomass to growing stem volume (Schroeder et al. 1997). While BEF values expressed on a mass to volume basis are useful for the conversion of growing stem volumes to forest biomass, the BEF value required to calculate C stocks in forests, as set out by the IPPC guidelines (Houghton et al. 1997), is expressed on a mass to mass basis, since biomass densities are included in the calculation. In this study, we include below ground tree biomass in the BEF calculations to enable the determination of total biomass from growing stem biomass.

In addition to their importance for compiling C inventories in forests, biomass estimations are relevant for studying biogeochemical cycles and understanding variations in structural and functional attributes of forest ecosystems across a wide range of environmental conditions and silvicultural practices. While many ecological studies have used allometric algorithms to predict forest biomass (Cannell 1984, Kauppi et al. 1992, Brown et al. 1997, Schroeder et al. 1997 and 1999, Nelson et al. 1999), the accuracy of estimating standing biomass through the development of empirical models is reduced due to many factors. First, few universal species-specific allometric equations have been developed that are applicable at different regional scales or appropriate for different environmental conditions. Second, since most models are parameterised using national inventory data, estimates are generally limited to older age classes. Consequently, the application of models to younger stands may lead to errors when predicting forest biomass. The prediction of C storage by younger forests, in particular, is important with regard to Article 3.3 of the Kyoto Protocol wherein only that carbon sequestered at sites afforested since 1990 is eligible for the issuance of RMUs (removal units).

The specific objectives of the study were:

1. to develop allometric relationships for the prediction of above ground biomass, below ground biomass and growing stem biomass using inventory data,
2. to validate the empirical models against published data and separately obtained harvest data from trees grown in Ireland,
3. to apply the validated models to Sitka spruce stands for the estimation of biomass and BEF in a 9 to 45-year-old chronosequence and
4. to provide guidelines for the establishment of an improved Irish national forest inventory.

The wider objective of the work reported in this paper is to develop empirical models and to identify the required allometric inputs that will aid in a national C sequestration inventory for reporting to the UNFCCC. We also discuss the implications of using classified BEF values, based on age and yield class for individual species, for the establishment of an Irish national C forest inventory.

Methods

The overall approach was to develop regression equations for estimating above ground, below ground and growing stem biomass. Estimated values were then validated against an independent data set and the best-fit equations were applied to an experimental data set taken from a 9 to 45-year-old Sitka spruce chronosequence. Redefined biomass estimates were then used to calculate a BEF ratio of total biomass to growing stem biomass.

Biomass regression equations

While the best approach for estimating forest biomass on a regional scale is to use data from national forest inventories (Schroeder et al. 1997), Irish forest inventory practice to date has not provided the data necessary to derive the allometric equations required for biomass estimation. Therefore, regression equations were initially derived based on an inventory of ~2000 individual Sitka spruce trees from the USDA Forest Service FIA unit website: <http://www.srsfia.usfs.msstate.edu/scripts/ew.htm>. The database contains information from inventories conducted over a cycle of 10 years. We acquired data from the 1990 inventory for all living Sitka spruce trees with a diameter at breast-height (DBH) of 2.54 to 40 cm growing in the states of Alaska and Washington. Allometric models were developed using data for tree height (H), DBH and total above ground biomass (ADW). The following indicators of goodness of fit for linear, non-linear and log transformed regression models are reported:

1. the coefficient of determination, r^2 of the simple regression or R^2 of the multiple regression,
2. standard error, reported for both the intercept and the partial regression coefficients of the independent variables,
3. the significance level of the t-value, for each independent variable and combination of different variables used in multiple regressions,
4. the average error of estimate, based on the difference between the actual and predicted values and expressed as the modulus of the average percentage deviation.

Regional biomass inputs

Individual components of total biomass, including roots, of a total of 60 trees obtained from published and unpublished data for Irish Sitka spruce (Table 1), were used to derive site-specific allometric equations. The biomass distribution (DBH range) and management history, such as planting densities, of these stands are representative of current national forests, except for the Glenmalure site (Table 1), where the planting density (3700 stems ha^{-1}) was higher than current practice (2500 stems ha^{-1}).

Unless otherwise stated (Carey and O'Brien 1979, Wills et al. 1999), trees were

Table 1. Forest age, yield class, soil type, stand characteristics and tree dimensions used for the modelling exercise.

Forest	Age (yr)	Yield class (m ³ ha ⁻¹ yr ⁻¹)	Soils	Stem ha ⁻¹	Mean DBH (cm)	Mean Height (m)	Source
Ballygar	5-7	20-24	Wet gley	2,500	2.6	2.7	Wills 1999; Wills et al. 1999
Lullymore	19	20-24	Industrial cutaway peatland	1300	21	15.2	K.A. Byrne unpublished data
Rossmore	20	20-24	Wet gley	2,500	18	14.3	Wills 1999; Wills et al. 1999
Derrybrien	31	20-24	Gley brown podzol overlaying a gley	2,000	36	22.8	Wills 1999; Wills et al. 1999
Glenmalure	33	14	Peaty gley	3,700	17.3	13.8	Carey and O'Brien 1979

harvested that were representative of the mean DBH of a 100 individuals within each site. Branch whorls and inter-whorls were stratified (Snowdon 1986) and sampled systematically after trees were felled. The height of each whorl was recorded and the total fresh weight of each whorl and inter-whorl was obtained using a portable spring balance to a precision of 0.1 kg. Five stem-wood discs were collected at DBH, mid-diameter, 7 cm diameter, 4 cm diameter and halfway between mid-diameter and 7 cm diameter for fresh weight, dry mass and volume determinations. The volume of the stem was calculated assuming a frustum shape (Hamilton 1975), based on the five diameters and height measurements. Roots were manually excavated from a 2 x 2 m trench surrounding the root collar to a depth of 90 cm. Fresh weight was determined for the stump, fine (< 0.3 cm diameter), small (0.3-0.5 cm), medium (0.5-5 cm) and large roots (> 5 cm) which were then sub-sampled for dry mass estimates. All biomass components were oven dried at 70 °C and weighed after three days when the dry mass was constant.

Biomass, DBH, basal area, tree height, growing stem volume and biomass were used to derive above ground (ADW), below ground (BDW), and stem biomass equations. The same accuracy of estimation and goodness of fit parameters were used as described previously.

Experimental data set

The sites representing the Sitka spruce chronosequence were located in five different Coillte forests in the Portlaoise area (~52° 57' N, 7° 15' W). Selected stands (9- to 45-year-old trees) were representative of the typical yield class (18-20 m³ ha⁻¹ yr⁻¹) for Sitka spruce growing on wet mineral soils in Ireland (Table 2). An additional 14 year-old stand, with a yield class of 24 m³ ha⁻¹ yr⁻¹, was also selected. Total height (H), height to

Table 2. Site and tree characteristics of the Sitka spruce chronosequence in the Coillte Portlaoise forests.

Forest	Age	Yield class	Sample plot size	Stem ha^{-1}	Mean DBH	Mean Height	Crown to height ratio	LAI
	yr	$m^3 ha^{-1} yr^{-1}$	ha		cm	m		$m^2 m^{-2}$
Baunogue*	9	16-20	4 x 0.01	2,300	5.4	3.8	0.08	4.5
Clontycoe*	14	16-20	4 x 0.01	2,366	10.8	5.8	0.13	7.8
Dooary	14	20-24	4 x 0.01	2,400	13.6	7.6	0.41	10.5
Glenbarrow	25	16-20	4 x 0.03	1,133	22.8	14.9	0.56	8.2
Dooary*	30	16-20	4 x 0.03	1,083	25.2	17.6	0.59	7.2
Cullenagh*	45	16-20	4 x 0.03	730	31.4	21.0	0.61	6.5

* One to three random trees were harvested from each of these sites and the biomass data were added to the Irish data set (Table 1) used to derive allometric equations (see Table 5).

crown (HC) and DBH of individual trees from four sampling plots per site was recorded over a period of one week in July 2002. The plot sizes varied from 0.01 to 0.03 ha, depending on the age and management of the site (see Table 2). Tree height was estimated to the closest cm using a laser hypsometer (Laser Technology Inc., Colorado, USA), calibrated against the actual height of selected trees (1-20 m). Height to crown (HC) was defined as the height from the ground to the lowest live branch. Leaf area index (LAI) was calculated using sapwood allometric estimates based on the pipe-model theory as described by Gill et al. (2000). Sapwood area (Asw) was estimated using a regression equation: $Asw = 2.37 \times 10^{-5} (DBH^2 HC)$. Leaf area was then estimated using the linear regression $LAI = (0.163 \times Asw - 2.594) \times \text{stand density (trees } ha^{-1})$.

Results

Universal species-specific regressions

Scatter plots of data obtained from the USDA web site were used to determine if the three biometric parameters showed a strong relationship with ADW (Figure 1A-C). The plots show a clear non-linear relationship for DBH v ADW, and a similar relationship but with more scatter for H v ADW. Exponential, quadratic and power curves were fitted using the best predictor (DBH) for ADW. The best fit was obtained from a power curve ($y = a x X^{\beta}$), giving an r^2 of 0.93 and a β coefficient of 2.71 (Model 1, Table 3). Similarly, the best model for ADW based on H was a power curve (Model 2, Table 3), but with a lower r^2 of 0.89 and a larger variance in the partial coefficient predictors.

Several linear models were fitted to log-transformed data because these functions tend to stabilize the variance and linearise the relationships. However, this did not completely remove the curvature underlying the model (Figure 2) resulting in an

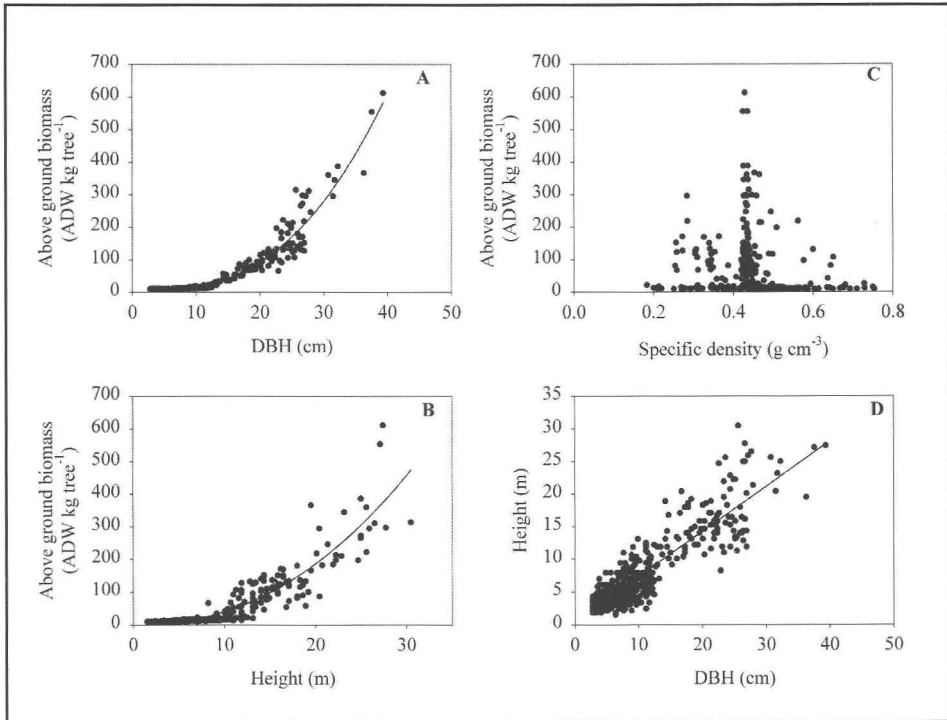


Figure 1. Relationships between DBH (A), tree height (B), specific density (C), and above ground biomass (ADW). Panel D illustrates the linear relationship between DBH and tree height. Data were obtained from the 1990 USDA inventory data base of selected trees with a DBH varying from 2-41 cm.

Table 3. Regression models for estimating above ground biomass (ADW) based on USDA inventory data. Trees range in size from 2 to 40 cm DBH.

Regression model	Coefficient symbol	Coefficient value	t-value	Standard error	r^2	Standard error of estimate (%)
1) $ADW = \alpha DBH^\beta$	α	0.028	11.8	0.002	0.93	16.1
	β	2.71	101.1	0.026		
2) $ADW = \alpha H^\beta$	α	0.23	9.5	0.026	0.85	24.1
	β	2.22	63.5	0.035		
3) $ADW = 0.5 + 15000(DBH^\beta)/(DBH^\beta) + c$	β	2.71	18.2	0.037	0.95	2.5
	c	346629	58.6	3524		
4) $ADW = \alpha (DBH \times H)^\beta$	α	20.76	70.9	0.290	0.98	8.9
	β	1.39	179.2	0.007		

underestimation of ADW for younger trees. Non-linear, half-saturation functions (Cieszewski and Bella 1989) using DBH as a predictor of ADW significantly increased the correlation coefficient to 0.95, but this also increased the standard error of estimate by 5.3% when compared to model 1 (Table 3). The coefficient β for this model (model 3) was derived from model 1. The chosen constants, 15000 and 0.5, were based on the maximum asymptotic biomass of a tree and an intercept or minimum biomass (Cieszewski and Bella 1989).

An alternative improvement using non-linear functions was found by adding a second biometric predictor to the equation to account for differences in mass between trees of the same diameter. By adding H as another independent variable to a commonly used multivariable regression ($\ln(\text{ADW}) = c + \alpha(\ln(\text{DBH})) + \beta(\ln(\text{H}))$), would result in an increase in R^2 , when compared to r^2 (Neter and Wesserman 1974), but because the correlation between the two independent variables is high (Figure 1D), multicollinearity generally causes one or both of the estimated partial coefficients to become less precise (t-values get smaller). A mathematically equivalent derivation of the above equation and one which avoids using log-transformation and multiple regressions with collinear variables, is Model 4 (Table 3): $\text{ADW} = \alpha + (\text{DBH} \times \text{H})^\beta$, obtained from the simple relationship between ADW and DBH x H (Figure 2). Relative to model 1, the standard error of estimate decreased by 7.2% and the estimated coefficients were more precise (t-values larger). The best coefficient of determination ($r^2 = 0.98$) was obtained using model 4 (Table 3).

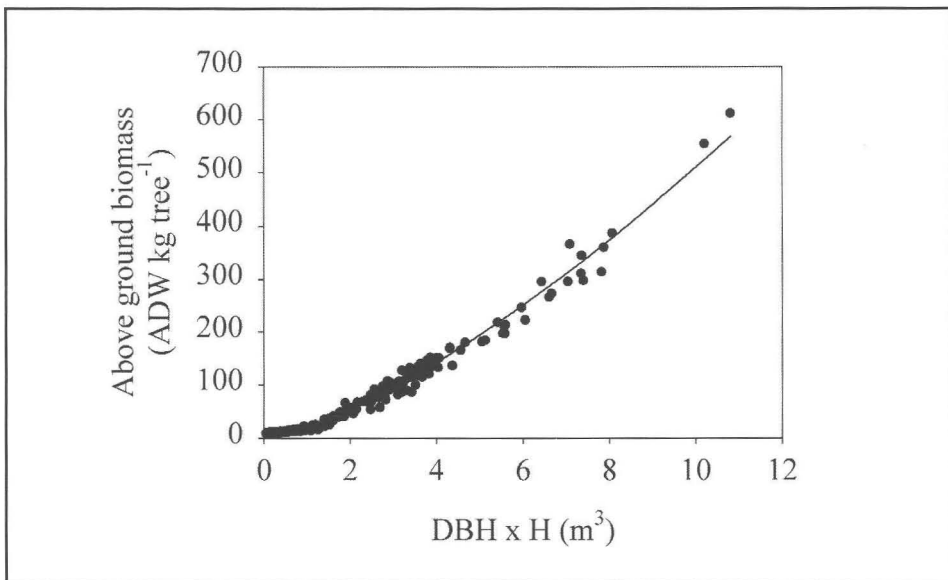


Figure 2. The non-linear relationship between, the product of DBH and H, and above ground biomass (ADW) in selected trees (DBH 2-40 cm) from the 1990 USDA data base. The exponent from the power curve function was used in Model 4 (see Tables 3 and 5).

Validation of universal models against an Irish data set

Cross-validation of the models derived from the FIA database against the Irish data suggest ADW was overestimated when DBH was used as a predictor, while H underestimated ADW (Table 4). When both variables were used to predict ADW the slope of the linear relationship (α) between predicted and observed values was close to 1 (Model 4 Table 4). Although this model also predicted ADW of an independent data set with the least variance (F-ratio) and the smallest unsigned error of estimate, the error of estimate was greater than 26% (Table 4).

Another problem associated with the use of the FIA inventory data to predict BEF over a chronosequence was the limited information on total stem biomass and below ground biomass (BDW). Biomass equations were, therefore, modified using the Irish data set.

Table 4. *Validation of models derived from the USDA data against an Irish data set. Correlation coefficients (r^2), F ratios for correlation, slope, t-value of the predicted slope and the unsigned standard error of estimate were derived from linear regressions between predicted and actual ADW for 60 harvested trees from the Irish forest sector (Tables 1 and 2).*

<i>Regression model</i>	<i>r^2</i>	<i>Slope (α)</i>	<i>t-value</i>	<i>F-ratio</i>	<i>Standard Error of Estimate (%)</i>
1) $ADW = \alpha DBH^\beta$	0.89	1.04	21.9	470	35.2
2) $ADW = \alpha H^\beta$	0.89	0.69	22.7	517	43.7
3) $ADW = 0.5 + 15000(DBH^\beta)/(DBH^\beta) + c$	0.81	1.55	22.6	509	64.2
4) $ADW = \alpha (DBH \times H)^\beta$	0.91	0.98	26.4	606	26.1

Region-specific equations

Scatter plots and allometric relationships for DBH, H and ADW for the Irish data set were derived using the same procedures as described for the universal data set (Table 5). Best fits for ADW based on DBH were also found to be power functions, although the coefficient of β for Sitka spruce in this case was 1.63, compared to 2.71 for the USDA data (Tables 3 and 5). The best coefficient of determination (0.97), the smallest standard error of estimate (18.6%) and the most precise estimated coefficients were obtained using model 4 (Table 5).

In addition to ADW, algorithms were also derived for below ground biomass (BDW) based on DBH. Whilst DBH was a good predictor of BDW (Model 5, Table 5), giving an r^2 of 0.94, the error of estimate was large (27%) due to variations in root biomass with trees of a similar DBH. This was particularly true for larger trees, as they are probably

older and have had more time to exploit the available resources (Figure 3A). Theoretically, an allometric relationship between a measured ADW and BDW should be, and was (data not shown), significant due to a linear increase in shoot to root ratio over time, but this was not a feasible input parameter to use, as inventories do not report on shoot to root ratios. An alternative model tested was the linear relationship between predicted ADW, based on the best fit from Model 4, and BDW (Model 6). However, a large standard error of the intercept (c) and a low probability (60% confidence level) of the t-value for c resulted in an increase in the error of estimate by 13% (Table 5). The same linear model was then fitted to log-transformed data to stabilize the variance (Figure 3B and C). In contrast to ADW linearised models, any curvature underlying the model was not evident after log transformation of the predicted ADW and BDW data (Figure 3C). In addition, the best fit was obtained using Model 7, giving an r^2 of 0.98 and the lowest error of prediction of 20.1%.

Based on the data presented in Table 5, the best predictors for ADW and BDW were models 4 and 7, respectively. These models were combined to give an estimate of total biomass (TBIOM):

$$TBIOM = [53.96 (DBH \times H)^{0.93}] + [0.9 \ln\{53.96 (DBH \times H)^{0.93}\} - 1.29]$$

Table 5. Regression models for above ground (ADW), below ground (BDW) and stand growing stem biomass (SSDW) based on the Irish data. Tree DBH varied from 2 to 37 cm.

Regression model	Coefficient symbol	Coefficient value	t-value	Standard error	r^2	Standard Error of Estimate (%)
1) $ADW = \alpha DBH^\beta$	α	1.48	4.88	0.23	0.97	20.4
		1.63	26.99	0.06		
2) $ADW = \alpha H^\beta$	α	1.06	3.08	0.35	0.92	33.7
		2.22	63.5	0.03		
3) $ADW =$	β	1.63	18.2	0.03	0.95	23.5
	c	214568	58.6	3524		
4) $ADW = \alpha (DBH \cdot H)^\beta$	α	53.69	17.69	3.03	0.97	18.6
		0.93	29.99	0.03		
5) $BDW = \alpha DBH^\beta$	α	0.39	4.10	0.09	0.94	27.1
		1.37	18.61	0.07		
6) $BDW = \alpha (ADW \text{ model 4}) + c$	c	0.55	0.83*	0.66	0.93	39.0
		0.14		0.04		
7) $\ln BDW = \alpha \ln (ADW \text{ model 4}) + c$	c	-1.29	-29.95	0.04	0.98	20.1
		0.90	72.51	0.01		
8) $\ln SSDW = \alpha \ln (H \cdot G) + c$ (DBH < 7cm)	c	-0.39	-5.11	0.07	0.87	26.4
		0.87	11.03	0.04		
9) $\ln SSDW = \alpha \ln (H \cdot G) + c$ (DBH > 7cm)	c	-1.65	-3.52	0.28	0.84	27.2
		0.99	9.45	0.11		

* indicates the t-value is not significant ($p \leq 0.05$)

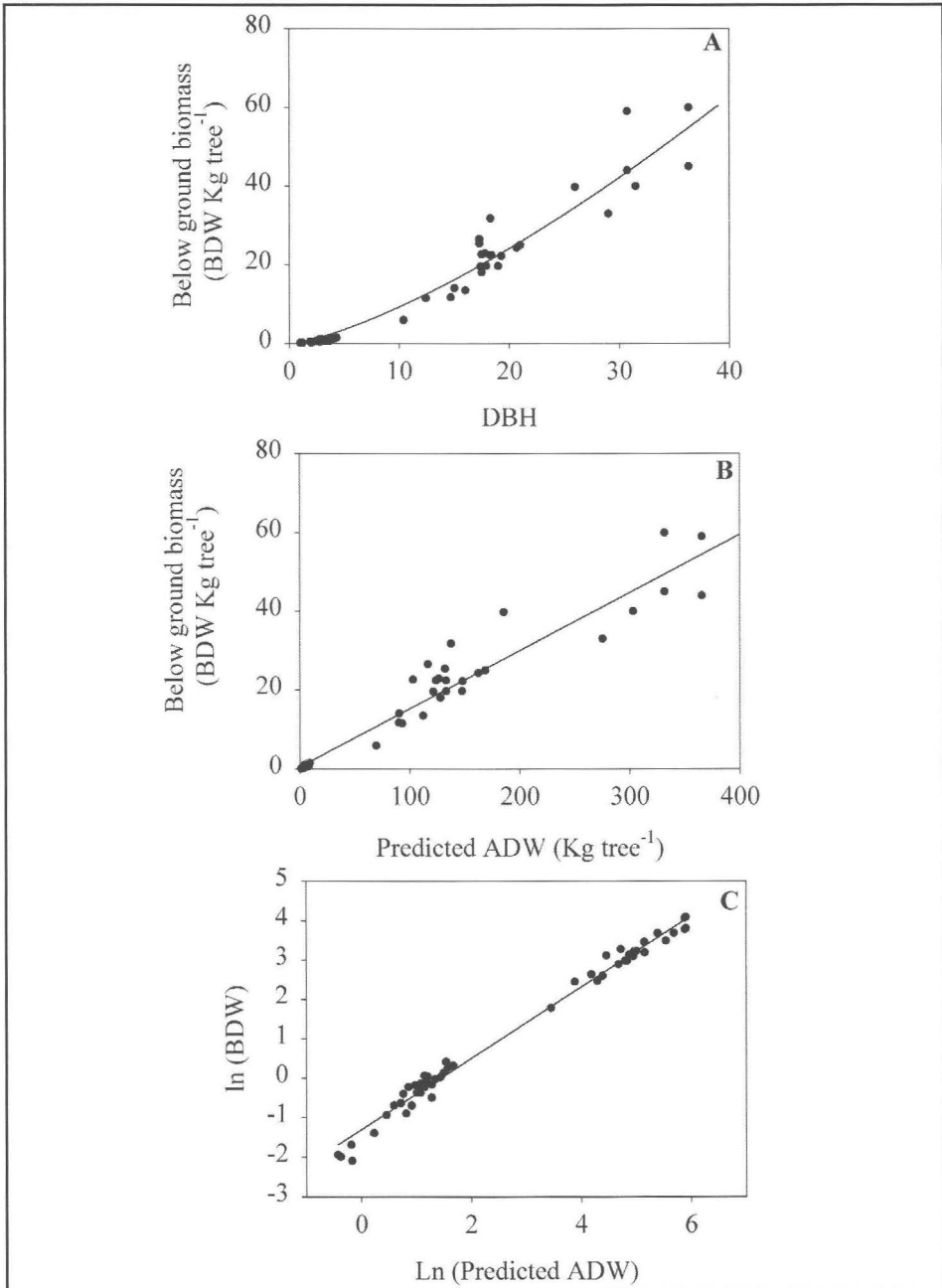


Figure 3. The relationships between DBH (A), predicted ADW (B, C) and below ground biomass (BDW). The log-log transformation of predicted ADW and BDW (C) illustrated that there was no curvature underlying the relationship. Data were obtained from trees harvested from Irish forests (see Tables 1 and 2).

Analysis of the residuals of predicted versus observed TBIOM values (Figure 4A) showed an overall error of estimate of 21%. Although there were larger errors associated with predictions for older trees (DBH > 10 cm), compared to young trees, there was no bias towards over or under estimation of TBIOM for the whole data range (Figure 4A).

The estimation of total stem biomass per ha (SSDW) was based on an allometric regression of the form $SSDW = F(HG)D$ (Cannell 1984); where F is a stand form factor, H is tree height, G is over bark basal area and D is specific wood density. The algorithm was simplified to the form $\ln(SSDW) = \ln(HG)$, since most inventory data would not report on stand specific F or D values. Analysis of the Irish data set revealed that F (0.4-0.8) and D (0.2-0.6 g cm⁻³) values varied depending on stand age and the ratio of merchantable stem to total stem biomass. Therefore, separate regression equations for SSDW were developed for young and old stands (Table 5). The standard error of estimate (~27%) was higher and the coefficient of determination (~0.86) was lower for SSDW, for young and older stands compared to those for ADW and BDW. This was caused by the smaller data sets associated with the separate analysis of young and older stands. However, analysis of residuals showed that there was no bias towards young or older stands (Figure 4B).

Calculation of BEF

The residuals for the predicted and observed BEF values from the Irish data set showed a standard error of estimate of 21% with no bias toward either an over or an under estimation for younger or older stands (Figure 4C). Best-fit models for TBIOM and SSDW were applied to the inventory data from the experimental chronosequence to derive BEF values using models 4, 7, 8 or 9, depending on individual DBH values (see Table 5). The estimated BEF for stands of different age classes showed that it varied from 1.4 to 5.01 t t⁻¹ (Figure 5). There was a non-linear decrease in BEF as SSDW increased from 6 to 225 t ha⁻¹, that was best described by the function $BEF = \alpha SSDW^\beta$ ($r^2=0.92$), where α and β are 10.11 and -0.31, respectively (Figure 5). It was also evident that BEF was higher for stands of a higher yield-class, within the same age-class (age-class 14, Figure 5).

Discussion

While there have been attempts to produce general models for the estimation of forest biomass over a wide range of conifer and hardwood forest types (Schroeder et al. 1997, Brown 2002), the application of these models to a stand and region specific scale can lead to large errors in the prediction of forest biomass. For example, the application of a widely used model (Model 3, Table 3) to the Irish data set resulted in an error of estimate of 64% and over estimation of above ground biomass, particularly in older stands of Sitka spruce (Table 4). This may be due, in part, to different management and climatic conditions. Although data from the USDA forest inventory was selected to represent the types of Sitka spruce grown in Ireland, these data are essentially from semi-natural forests where stand densities are seldom higher than 300 trees ha⁻¹ (Schroeder et al. 1997, Brown et al. 1999). Clearly, inherent differences in forest stand form, degree of self-thinning, crown characteristics and management practices, necessitate the

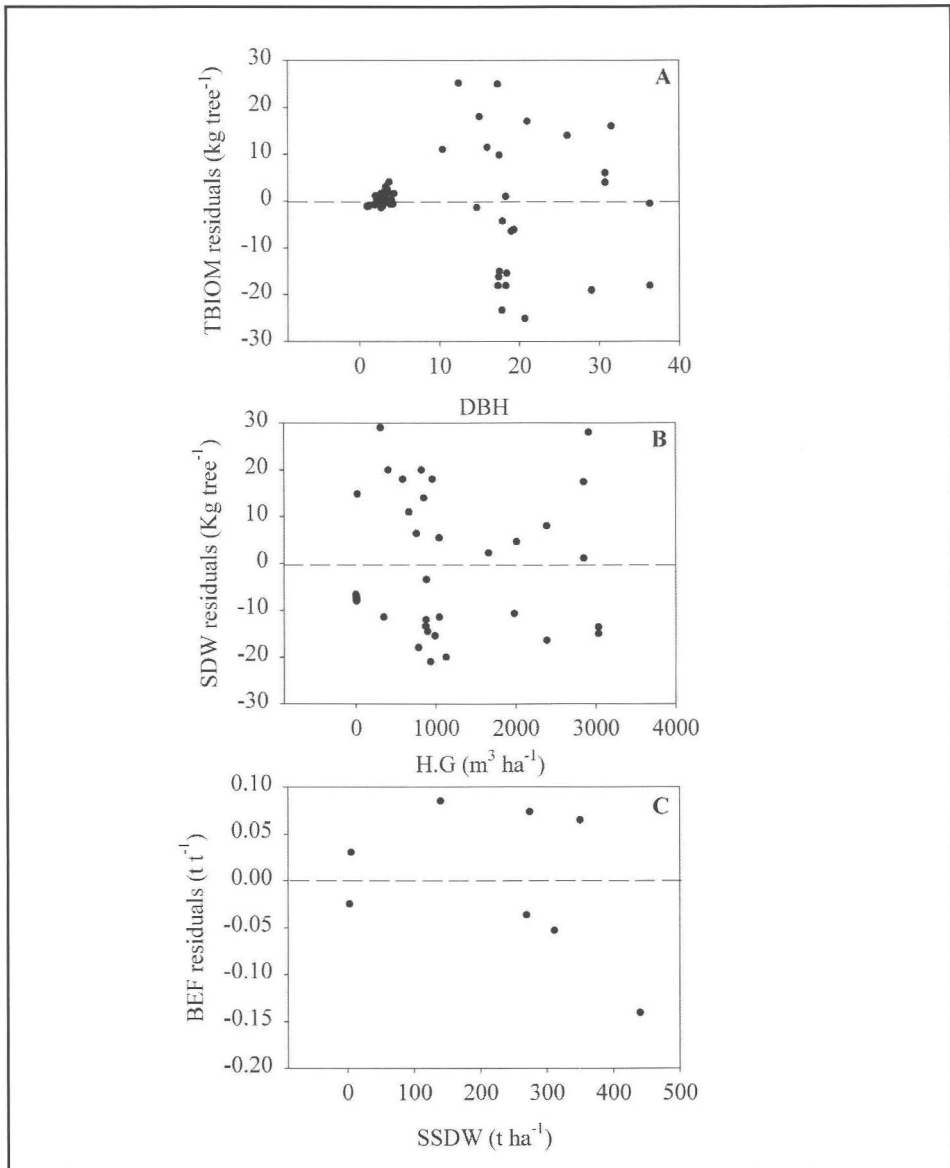


Figure 4. Residuals associated with the regression equations used to predict total biomass (TBIOM, A), growing stem biomass (SDW, B) and BEF (C). Errors are expressed as signed residuals obtained from predicted and observed values. The tendency of a model to over or underestimate biomass or BEF is indicated by the distance of a point from zero (dashed line). Regression analysis of the residuals and the predictors revealed that no trend was observed, suggesting that the models were not biased toward an over or under estimation of biomass or BEF for either small or larger trees.

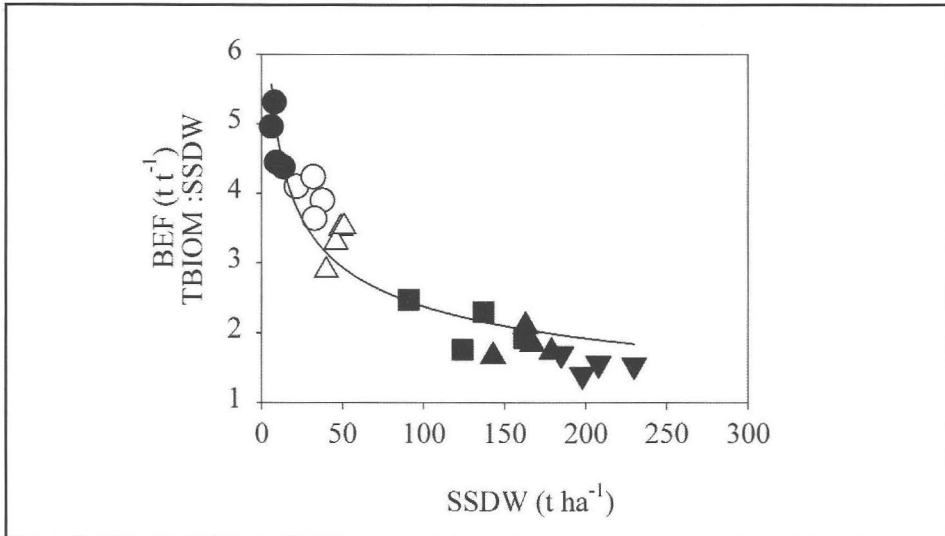


Figure 5. The non-linear relationship between stand growing stem biomass (SSDW) and BEF, expressed as the ratio between total biomass and growing stem biomass, using data from the Sitka spruce chronosequence. Symbols indicate the age class of stands ● 9 yr-old, ○ 14 yr-old, △ 14 yr-old yield class 20-24, ■ 25 yr-old, ▲ 30 yr-old and ▼ 45 yr-old stand. All stands were yield class 16-20 unless otherwise stated.

development of region-specific allometric relationships. This was evident from the differences in the partial coefficients (β) for the power functions obtained from the USDA and Irish data sets (see Tables 3 and 5). The lower value of β for Irish grown Sitka spruce suggests that trees with the same DBH would produce a lower above ground biomass, compared to US grown trees, probably due to higher plant densities and, consequently, a smaller crown area.

It is evident from this study, that at least three essential biometric inputs are required to predict stand BEF, namely DBH, height and stand volume. The inclusion of height as a second independent variable increased the biomass coefficients of determination, whilst significantly reducing the error of estimation by 8 to 3% (Tables 3 and 5), because differences in biomass between trees of the same DBH could be accounted for. This may be important for the prediction of biomass from stands where the relationship between DBH and height may vary due to climatic factors or planting densities. Based on the solutions from model 4, where height was included as a second independent variable in the single regression, the suggestion is that predictions of biomass can be improved when two independent variables are collinear, without decreasing the sensitivity of the partial coefficient predictors (Tables 3 and 5). Other studies (Brown et al. 1989, Overman et al. 1994) have also addressed this problem by using an algorithm of the form $\ln(\text{ADW}) = c + \beta \ln(\text{DBH} \times H)$, where the exponent (x) is fixed at 2. However, by arbitrarily fixing the exponent at 2, the partial regression coefficient for $\ln(H)$ could be forced away from its ideal value (Nelson et al. 1999) because DBH is a stronger

predictor of ADW than height (Tables 3 and 5). Furthermore, two forms of bias exist when using logarithmic transformations. Small variations in the biometric input from small trees can influence the slope and intercept of the linear regression coefficients more than large trees. Secondly, as evident in this study, an inherent curvature tends to underlie the model, even after log transformation. While the estimated error of model 4 for biomass is still high (~20%), when these predictors are used, the magnitude of this error is similar to those reported for other models (Brown et al. 1989, Schroeder et al. 1997, Nelson et al. 1999). Further refinement of the models developed in this study would require larger data sets from individually harvested Sitka spruce trees from stands of different age-classes, as was evident with the larger USDA data set. The requirement for more data from different yield classes may not improve the current biomass models, because allometry does, theoretically, account for differences in tree development (Cromer and Jarvis 1990, Ingestad and Ågren 1991). For example, the 14-year-old stand for the yield class 20-24 m³ ha⁻¹ yr⁻¹, would have a similar biomass and allocation pattern (e.g. BEF value) as a 19-year-old stand for yield class 18-20 m³ ha⁻¹ yr⁻¹ (see Figure 5). Therefore, if the allometric relationship covers the biomass range for all stands in a chronosequence, the prediction of biomass or BEF would not be influenced by the yield class, but by the characteristics that underlie tree allometry. Although the above ground to below ground allocation may vary with soil type, the significant relationship between ADW and BDW (Table 5) suggests that the model can be applied to soil types included in our modelling data set (see Table 1). However, more detailed analysis is required to assess the potential variation in BEFs associated with other soil types.

In this study, we have demonstrated an inverse non-linear relationship between BEF and stand stem biomass (Figure 5). These findings are consistent with other studies on a variety of tropical and temperate hardwoods, pines and spruces (Brown et al. 1989, Brown and Lugo 1992, Schroeder et al. 1997, Brown 2002). Generally, BEF values are high at low stand growing stem volumes, or biomass, and decrease to a constant BEF at a high stand growing stem biomass. Whilst the exponential decline in BEF may be associated with changes in biomass allocation in younger stands, such as a greater increment in stem wood, relative to non-woody biomass, the constant BEF in older stands may be due to the interaction between thinning practices and changes in biomass allocation after canopy closure. Alternatively, at high values for stem volumes or biomass most of the total biomass is allocated to the stem resulting in a constant BEF ratio in older stands. It is evident from the changes in leaf area index in the chronosequence examined in this study that there is a more gradual decline in BEF with an increase in stemwood biomass after canopy closure (~14 years, see Table 2 and Figure 5). The implication of these findings may be of importance when devising thinning strategies for adaptive management policies, where the carbon sequestration potential may be maximized without influencing timber production.

Our results suggest that the recent BEF value used to calculate carbon stocks for Irish forests is underestimated (Kilbride et al. 1999), particularly for younger Sitka spruce stands. The use of a single BEF value of 1.3 may result in an ~2 to 4-fold underestimation of current carbon stocks for afforested sites since 1990. However, the BEF values for stands older than 30 years are similar to the current value of 1.3, based

on an average BEF of 1.5 and an error of estimate of 21% reported for an age class of 30 years or older. The slightly higher BEF value for older stands found in this study may be due, in part, to the inclusion of all biomass components for the calculation of BEF.

Whilst BEFs are an important component of the current inventory-based methods used to estimate biomass carbon increment, it is evident from this study and others (Lowe et al. 2000) that this may require the development of stand and species-specific BEF values. A possible alternative would be to develop species-specific biomass functions based on allometric algorithms derived from forest inventories over a rotation cycle to estimate total forest biomass increment. The calculation of biomass carbon stock based on biomass functions and carbon content would eliminate the errors associated with the estimation, of stem wood growth rate, BEF and specific wood densities when calculating forest carbon stocks.

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