

# Assessment of allometric algorithms for estimating leaf biomass, leaf area index and litter fall in different-aged Sitka spruce forests

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## Summary

The relationship between leaf area and diameter at breast height (d.b.h.) or sapwood area (AS) has been used to estimate stand leaf area or biomass of forest canopies. It has been suggested that intra-specific variations in the relationship between stand leaf area and d.b.h. or AS can introduce a systematic error in these estimates for younger and older stands unless additional parameters relating to canopy structure are included in allometric functions. We collected data from a Sitka spruce chronosequence to parametrize and test different algorithms for the estimation of foliar biomass (FB) and litter inputs over a range of forest ages. FB estimates were significantly improved when additional biometric information relating to crown structure (canopy openness and height of live crown) was included in the models. Although the use of the relationship between leaf area and AS for the estimation of leaf area is justified by theoretical considerations (pipe model theory), we show that d.b.h. and other canopy parameters provided the most robust estimation of leaf area across different-aged stands. Our results also suggest that the accuracy of litter input estimates depends on needle retention time and annual turnover rate, particularly immediately before and after canopy closure.

## Introduction

The leaf area index (LAI) of a stand is a key parameter in describing canopy characteristics (Law *et al.*, 2001). Defined as the projected leaf area per unit surface area of the ground, it exhibits a strong effect on net ecosystem CO<sub>2</sub> and H<sub>2</sub>O exchange (Buchmann and Schulze, 1999) and,

therefore, is used as an input for process-based forest productivity and hydrology models (Parton *et al.*, 1992; Potter *et al.*, 2001). In attempting to simulate biosphere–atmosphere interactions with atmospheric circulation models, plot-level LAI measurements are required to integrate with satellite remote sensing data obtained over large geographic areas (White *et al.*, 1997). Relating

spectral vegetation indices produced from satellite images to LAI also depends on precise measurements of LAI at a number of geo-referenced sites over the range of potential LAI values (Turner *et al.*, 2000).

Litter fall, the most important source of nutrient flux to the forest floor (Pedersen and Bille-Hansen, 1999), has long been seen as a useful index of ecosystem productivity (Olson, 1963). Needle/foilage biomass constitutes one of the most important pools of essential nutrients, which is vital for forest nutrient cycling (Waring and Schlesinger, 1985), including carbon cycling. Litter fall can be seen as an indirect expression of forest canopy status, a consequence of the genetic make-up of the trees and the influence of environmental fluctuations, and thus, litter fall has been used as an indicator of forest health (Pedersen and Bille-Hansen, 1999). Estimates of litter fall or leaf area, based on allometric functions, have to accommodate a lot of changes due to inherent dynamics. However, analysis of several years' data may be required to accommodate inter-annual variability (Trofymow *et al.*, 1991; Turner *et al.*, 2000). The change of C in litter is one of the five C-pools required by the Marrakesh Accords for reporting to the Kyoto Protocol as well as to the United Nations Framework Convention on Climate Change, thereby providing a policy-based incentive for robust and reliable estimation methods.

The leaf area of needle biomass can be estimated directly or indirectly. Direct approaches use sapwood area (AS) and litter fall, based on the pipe model theory (Waring *et al.*, 1982; Whitehead *et al.*, 1984) which describes a linear relationship between leaf area and AS. The physiological basis for this linear relationship is supported by the observations that water transport in trees occurs exclusively in sapwood and experimental manipulations of leaf area result in a concomitant reduction in AS (Margolis *et al.*, 1988). There are, however, problems with existing algorithms: (1) they are species specific, each species requiring the application of its own regionally derived equation; (2) they commonly overestimate LAI and biomass in old mature stands (Turner *et al.*, 2000) and (3) they have not been developed for an entire age sequence, particularly not in young afforested stands, which are important e.g. for Article 3.3 of the Kyoto

Protocol (Schlamadinger *et al.*, 2003). Although AS or sapwood volume has proved a good predictor of various forest parameters in the past (Whitehead *et al.*, 1984; Keane and Weetman, 1987), it has not been routinely measured in national forest inventories (NFIs). Therefore, relationships between routinely available measures of diameter at breast height (d.b.h.) and estimates of stem AS are required.

The objectives of this study were to develop algorithms, based on data from a Sitka spruce (*Picea sitchensis* Bong. (Carr.)) chronosequence; to estimate foliar biomass (FB), LAI and litter fall using basic forest inventory data and also to improve the predictability and accuracy of further algorithms using more detailed parameters such as crown diameter, taper functions and stand density.

## Materials and methods

### Site description

The research was conducted on a Sitka spruce chronosequence (Table 1) growing on wet mineral soil located in County Laois (~52° 57' N, 7° 15' W, altitude of 160–280 m) in the Irish midlands (Black *et al.*, 2004). The 30-year mean annual temperature was 9.3°C, with a mean annual rainfall of 850 mm. The general Yield Class (YC) of the chronosequence stands was 20–24 m<sup>3</sup> ha<sup>-1</sup> a<sup>-1</sup>; the national average for Sitka spruce in Ireland is 18–22 m<sup>3</sup> ha<sup>-1</sup> a<sup>-1</sup>.

Two events occurring during the time of litter collection were important to record. First, in 2002, there was an aphid infestation in the area, affecting many spruce plantations. Second, based on meteorological data (closest station is Kilkenny, ~30 km away from forest area), there was an 18 per cent reduction in annual rainfall in 2003 compared with the 30-year mean.

Thinning operations in this region generally occur during the summer months because of the low load-bearing capacity of the wet, gley soil. Also, because of the high moisture status of this soil type, and the implications for stability, thinnings tend to occur as early in the rotation as possible, often beginning at 17–19 years. The general pattern used in the first thinning is the

Table 1: Site and tree characteristics of the Sitka spruce chronosequence in the Coillte Portlaoise forests

Forest	Age (years)	Sample plot size (ha)	Stem ( $\text{ha}^{-1}$ )	d.b.h. (cm)	Height (m)	Crown to height ratio
Baunoge	10	0.01	2300	7.7	4.4	0.08
Clontycoe	15	0.01	2366	12.9	7.8	0.18
Dooary	15	0.01	2400	14.3	9.3	0.33
Glenbarrow	28	0.02	1049	23.4	16.9	0.49
Dooary	31	0.02	824	26.2	19.6	0.55
Cullenagh	46	0.03	733	31.4	27.0	0.67

The third forest in the chronosequence, Dooary, 15 years, was a site of higher productivity where YC was  $24 \text{ m}^3 \text{ ha}^{-1} \text{ a}^{-1}$  compared with  $18\text{--}20 \text{ m}^3 \text{ ha}^{-1} \text{ a}^{-1}$  at the other sites.

systematic removal of one row in every seven, followed by some degree of selective thinning between these rows. Subsequent thinnings are selective and conservation of stand stability is regarded as a high priority.

#### Tree and shoot dimensions

Data used in the development of leaf biomass and leaf area models were based on measurements made in 2003 on harvested trees. The height and d.b.h. of trees in three randomly located plots at each site (~100 individuals) were measured. Six trees closest to the mean of the product of d.b.h. and height were selected for harvest. These were cut at ground level and their d.b.h. and height measured and subsequently divided into their component parts (stem, dead branches and live branches). Branches were classified as dead branches based on a visual assessment, where more than 75 per cent of the attached needles were brown. The point along the stem where live branches predominated was marked (the base of the crown), and all branches originating from the stem below this point were considered dead. After trees were felled, the crowns were stratified into three parts, from 0 to 33, 33 to 66 and 66 to 100 per cent of the crown height (Snowdon, 1986). The total fresh weight of each crown section, and all tree component parts, was obtained using a portable spring balance to a precision of 0.1 kg. Sub-samples were taken from the components and dried to constant weight at  $80^\circ\text{C}$ . Fresh to dry weight ratios were used to calculate the dry weight of each tree component (Mund *et al.*, 2002). To measure sapwood diameter, disks were taken at two points along the

stem, at d.b.h. (1.3 m above soil level) and at the base of the crown. Sapwood diameter was calculated from averages of measurements made on two diameters oriented in perpendicular directions (Drexhage *et al.*, 1999; Mund *et al.*, 2002) per disk. In most cases, sapwood and heartwood were easily differentiated by eye, where the definition was obscure methyl orange stain was used (USDA-FS, 1962).

Estimates of specific leaf area (SLA) and the dry mass of shoots were made on sub-samples from different-aged locations on branches within the crown. Shoot-projected surface area was assessed using captured images from a flat bed scanner, and the area was determined using Scion Imaging Software (Beta 4.0.1, Scion Corporation, Maryland, USA). The dry mass of each shoot was determined following drying at  $65^\circ\text{C}$  for 48 h in a ventilated oven. The FB was converted to a projected stand-level leaf area (LAI,  $\text{m}^2 \text{ m}^{-2}$ ) using a mean half-surface SLA for all shoots (see equations 6 and 7).

#### Tree-level leaf mass models

FB per tree was estimated using five different regression functions, based on harvested biomass data and d.b.h. or AS. All functions were developed using individual tree- and/or stand-specific variables. The  $r^2$  and slope of the observed against model-predicted values are reported as indicators of goodness of fit for linear, non-linear and log-transformed regression models. The  $F$ -ratio was used to indicate the degree of variation in the observed data, which was explained by the model. The percentage error of estimate (per cent SEE) was used as an indicator of the accuracy of the

estimate based on the difference between the actual and predicted values, expressed as an average percentage deviation.

*The d.b.h.-based allometric estimates of FB*

This approach was based on the relationship between d.b.h. and FB as described by Turner *et al.* (2000):

$$FB_1 = \exp(a + (b \times \ln(\text{d.b.h.}))), \quad (1)$$

where FB is given in kilogram per tree and  $a$  and  $b$  are the species-specific coefficients. An alternative function for the FB ( $FB_2$ ) uses two additional variables to account for differences in canopy openness:

$$FB_2 = a \times \exp((\text{d.b.h.} \times C_o \times \text{HC}) \times b), \quad (2)$$

where  $a$  and  $b$  are specific coefficients; HC is the live crown depth or length (m), as determined from measured total tree heights and crown height ratios (Table 1), and  $C_o$  is canopy openness, based on the formula described by Leech (1984):

$$C_o = \pi \times w^2 \times n / 10000. \quad (2a)$$

This calculation of canopy openness is based on crown radius ( $w$ ) and the number of trees per hectare ( $n$ ), assuming trees are regularly spaced. The value for  $w$  was derived from the linear relationship:

$$w = a \times \text{d.b.h.} + b \quad (r^2 = 0.89), \quad (2b)$$

where the solved coefficients  $a$  and  $b$ , 0.0456 and 0.693, respectively, were derived from inventory measurements taken in 2002.

*AS-based models for leaf biomass*

(National) Forest inventory measurements do not usually include AS assessments. Therefore, a species-specific model for AS at breast height ( $AS_{\text{d.b.h.}}$ ) was first developed using d.b.h. and sapwood diameter measurements obtained from harvested stem discs:

$$AS_{\text{d.b.h.}} = a / (1 + \exp(-(\text{d.b.h.} - b) / c)). \quad (3a)$$

The following algorithms, based on  $AS_{\text{d.b.h.}}$ , were used to estimate FB:

$$FB_3 = a \times \exp(AS_{\text{d.b.h.}} \times b), \quad (3)$$

$$FB_4 = a \times \exp((AS_{\text{d.b.h.}} \times C_o \times \text{HC}) \times b), \quad (4)$$

where  $a$  and  $b$  are the specific coefficients,  $AS_{\text{d.b.h.}}$  is the estimated AS at breast height (equation 3a) and  $C_o$  is the canopy openness factor (equation 2a). A derivative of the ZELIG-PNW forest succession gap model (Garman *et al.*, 1992; Turner *et al.*, 2000) was used to estimate  $FB_5$ , based on AS at the base of the crown ( $AS_{\text{HZ}}$ ):

$$FB_5 = a \times \exp((AS_{\text{HZ}} \times C_o \times \text{HC}) \times b). \quad (5)$$

For this application,  $AS_{\text{HZ}}$  was estimated using a taper function from breast height to HC:

$$AS_{\text{HZ}} = AS_{\text{d.b.h.}} \times \text{TF}, \quad (5a)$$

where TF is a modelled taper factor derived from the measured taper from the diameter at the base of the stem to the base of the crown (Kozak *et al.*, 1969; Turner *et al.*, 2000). The observed  $TF_1$  values were modelled against tree and crown height:

$$TF_1 = (a - b \times (\text{HC}/\text{HT}) + c \times (\text{HC}^2/\text{HT}^2))^{1/2} \quad (r^2 = 0.91), \quad (5b)$$

where the solved coefficients  $a$ ,  $b$  and  $c$  are 0.88, 2.08 and 1.43, respectively, and HT is the total height of the tree.

An alternative to the taper factor was derived to account for smaller trees, where the crown height was lower than breast height. Therefore, in theory, the AS at crown height in small trees should be greater than the AS at breast height, which is not accounted for in equation (5b). The alternative taper factor ( $TF_2$ ) was derived from the measured taper from diameter at crown height to d.b.h. The observed  $TF_2$  values were modelled against tree and crown height:

$$TF_2 = a + b \times \exp(\text{HC}/\text{HT}) \times c \quad (r^2 = 0.87), \quad (5c)$$

where the solved coefficients  $a$ ,  $b$  and  $c$  are 0.49, 0.85 and  $-3.87$ , respectively.

*Scaling from tree- to stand-based estimates of leaf area and litter fall measurements*

Four selected sampling plots at each site within the chronosequence (Table 1) were surveyed over a period of 1 week in July 2002 to obtain inventory information including HT, HC and d.b.h. measurements. The survey was repeated in the summer of 2004 on the same plots. The plot sizes

varied from 0.01 to 0.03 ha depending on the age and management of the site (see Table 1). In 2002, trees were marked with white paint at 1.3 m high so that the survey could be repeated in 2004. Tree height was estimated to the closest centimetre using a laser hypsometer (Laser Technology Inc., Colorado, USA). Crown radius measurements were taken in 2002 using the procedure outlined by Gill *et al.* (2000).

The biomass of foliage litter was estimated using stand FB, calculated from the inventory data and the best-fit FB algorithm, based on an equation described by Law *et al.* (2001):

$$LAI = (M_{lit} \times (1 + F_{abs}) \times SLA) / F_t, \quad (6)$$

where  $M_{lit}$  is the annual foliage litter fall ( $t \text{ ha}^{-1} \text{ year}^{-1}$ ), SLA is the half-surface SLA of needles,  $F_t$  is the annual foliage turnover rate ( $F_t = 0.20$ , Norman and Jarvis, 1973) and  $F_{abs}$  is the fractional mass loss on abscission ( $F_{abs} = 0.1$ , Law *et al.*, 2001). Equation (6) was rearranged to solve for  $M_{lit}$  using FB directly (since  $LAI = FB \times SLA$ ):

$$M_{lit} = FB \times (n/10\,000) \times F_t / (1 + F_{abs}), \quad (7)$$

where  $n$  is the number of trees per hectare. The direct estimation of FB reduced the potential error in the estimate because SLA, which may vary from tree to tree, is not required.

For comparison with estimates, litter fall was collected every month from ten 25-l plastic buckets, randomly located within one  $30 \times 30$ -m plot at every site in the chronosequence. The litter was separated into green needle, dead needle, bud

scale and woody components prior to oven drying to a constant mass.

## Results

### Estimation of AS

Scatter plots of AS at breast height ( $AS_{d.b.h.}$ ) *vs* d.b.h. show a non-linear relationship (Figure 1). The best fit was obtained by applying a sigmoidal function to the  $AS_{d.b.h.}$  and d.b.h. data (Figure 1A). Analysis of residuals for predicted *vs* observed data showed a standard error of estimate of 2.1 with no bias towards either an over- or an underestimation for trees of different d.b.h. and age classes (Figure 1B). Although there was a larger residual error in older stands, this was associated with a larger variation in d.b.h. and  $AS_{d.b.h.}$  between individual trees in the older stands (Figure 1B). The coefficients of variation were, however, similar for younger and older trees.

When AS at crown height ( $AS_{HZ}$ ) was directly estimated as the product of  $AS_{d.b.h.}$  and the taper function, based on the predicted taper between the base of the stem and crown height ( $TF_1$ ),  $AS_{HZ}$  was significantly underestimated in young, and overestimated in older, stands (Figure 2A,B). This bias was partially removed when the improved taper function (d.b.h.: diameter at HC,  $TF_2$ ) was used to estimate  $AS_{HZ}$ , with a slope of the linear regression of the observed against predicted

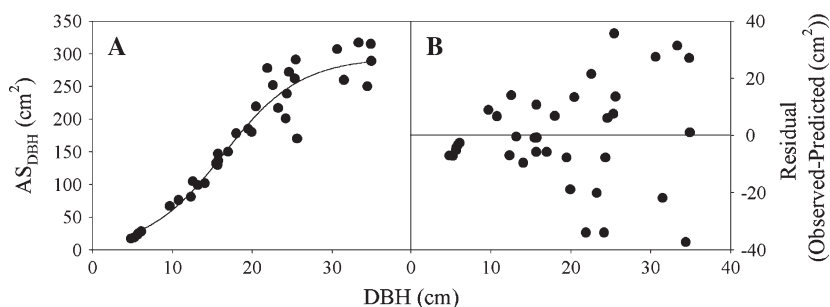


Figure 1. Non-linear relationship between d.b.h. and (A) the measured AS at breast height ( $AS_{d.b.h.}$ ) and (B) the residuals of the modelled values. The sigmoidal function used was  $AS_{DBH} = 294 / (1 + \exp(-(DBH - 4.7) / 16.4))$ , with  $r^2 = 0.95$ ,  $F$ -value = 241 ( $P < 0.0001$ ),  $SEE = 25.3$  and a slope for the observed *vs* predicted linear regression of 0.97.

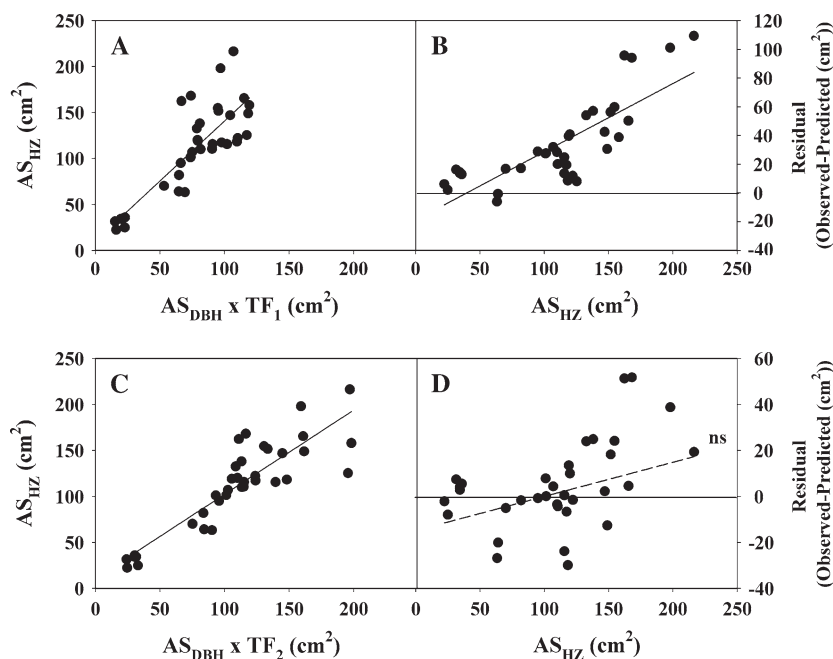


Figure 2. The linear regression between observed AS at crown height ( $AS_{HZ}$ ) and the calculated value, based on the product of AS at breast height ( $AS_{d.b.h.}$ ) and different taper factors ( $TF_1$  (A),  $TF_2$  (C)). Scatter plots of the residuals *vs* the measured  $AS_{HZ}$  (B and D) show the significant over- and underestimation of  $AS_{HZ}$  when  $TF_1$  was used (B). The linear relationships, shown by the solid lines for panel (A) ( $y = 0.65x + 1.26$ ,  $r^2 = 0.65$ ), panel (B) ( $y = 0.91x + 2.1$ ,  $r^2 = 0.79$ ) and panel (C) ( $y = 0.47x - 18.3$ ,  $r^2 = 0.43$ ), were all significant ( $P \leq 0.05$ ). The linear relationship shown by the broken line (D) was not significant ( $P > 0.05$ ).

values of 0.91. Analysis of the predicted and observed residuals demonstrated that the significant relationship of Figure 2B degenerated to non-significance in Figure 2D where the magnitude of the residuals was also reduced.

#### Tree-level FB estimates

There was a strong relationship between d.b.h. and FB ( $r^2 = 0.72$ , Table 2). However, analysis of the residuals between observed and predicted values showed that FB was underestimated in the youngest stand, prior to canopy closure (Figure 3B). When canopy openness and live crown height (HC) were included in the  $FB_2$  algorithm, the coefficient of determination ( $r^2$ ) and the  $F$ -ratio of the relationship increased, and there was a smaller standard error of estimation (Table 2) and no residual under- or overestimation of FB in different-aged stands (Figure 3C,D). The algorithm  $FB_2$  provided the best fit for FB, giving

an  $r^2$  of 0.91, the lowest error of prediction (1.9) and a slope of  $\sim 1$  for the regression of predicted *vs* measured data (Table 2).

The coefficient of determination ( $r^2$ ) and the  $F$ -ratio for the prediction of FB, based on  $AS_{d.b.h.}$  ( $FB_3$ ), decreased from 0.91 to 0.76 and 347 to 107, respectively, when compared with  $FB_2$  estimates (Table 2 and Figure 4A). An improvement to the non-linear  $FB_3$  function was found by including the same extra biometric predictors ( $C_o$  and HC) as used for the  $FB_2$  model, to account for differences in FB between trees of the same  $AS_{d.b.h.}$  (see algorithm  $FB_4$ , Table 2 and Figure 4C). When AS at crown height ( $AS_{HZ}$ ) was used as a predictor ( $FB_5$ , Figure 4E) instead of  $AS_{d.b.h.}$  ( $FB_4$ ),  $r^2$  did not increase significantly (0.85 to 0.87), but predicted ( $FB_5$ ) values were generally underestimated when compared with the predicted  $FB_4$  values (i.e. slope reduced from 0.94 to 0.81, Table 2).

Table 2: Coefficients for various FB algorithms derived from harvested data

Algorithm	Coefficient symbol	Coefficient value	Slope ( $\alpha$ )	$r^2$	F-ratio	% SEE
$FB_1 = \exp(a + (b \times \ln(\text{d.b.h.})))$	$a$	-3.07	0.94	0.72	91	3.11
	$b$	1.73				
$FB_2 = a \times \exp((\text{d.b.h.} \times C_o \times \text{HC})b)$	$a$	3.36	1.02	0.91	347	1.90
	$b$	$4.3 \times 10^{-3}$				
$FB_3 = a \times \exp(\text{AS}_{\text{d.b.h.}} \times b)^*$	$a$	2.22	0.78	0.76	107	2.84
	$b$	$7.1 \times 10^{-2}$				
$FB_4 = a \times \exp((\text{AS}_{\text{d.b.h.}} \times C_o \times \text{HC}) \times b)^*$	$a$	3.43	0.94	0.85	175	2.77
	$b$	$4.6 \times 10^{-4}$				
$FB_5 = a \times \exp((\text{AS}_{\text{HZ}} \times C_o \times \text{HC})b)^*$	$a$	2.29	0.81	0.87	142	2.79
	$b$	$9.6 \times 10^{-4}$				

Correlation coefficients ( $r^2$ ), F-ratio, slope ( $\alpha$ ) of linear relationship and the unsigned standard error of estimate (% SEE) were derived from linear regressions between predicted and measured FB data.

\* $\text{AS}_{\text{d.b.h.}}$  and  $\text{AS}_{\text{HZ}}$  values were measured values.

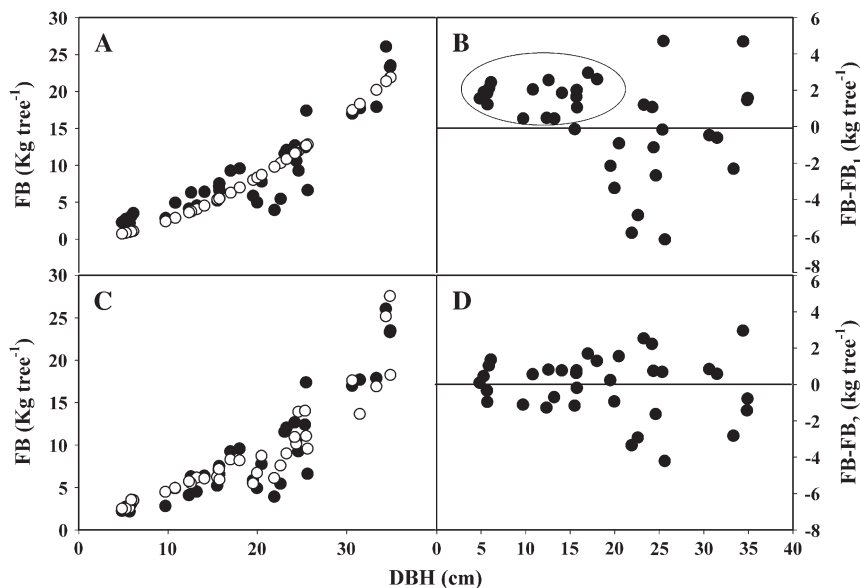


Figure 3. Scatter plots of the measured (filled symbols) FB (panels A and C) or residuals (panels B and D) vs d.b.h. The open symbols represent the relationship between the predicted FB and d.b.h., using different algorithms:  $FB_1 = \exp(a + (b \times \ln(\text{d.b.h.})))$  (panel A) and  $FB_2 = a \times \exp(\text{d.b.h.} \times C_o \times \text{HC}) \times b$  (panel C). Symbols highlighted by the circle in panel (B) show that the FB of smaller trees was underestimated, when the  $FB_1$  model was used.

Coefficients of determination for the algorithms  $FB_3$ ,  $FB_4$  and  $FB_5$  were calculated using the modelled  $\text{AS}_{\text{d.b.h.}}$  (Figure 1A) and  $\text{AS}_{\text{HZ}}$  (Figure 2C) because AS is not normally a measured parameter in NFIs. When the estimated

$\text{AS}_{\text{d.b.h.}}$  values were used as predictors of FB, the values for  $r^2$ , slope, F-ratio and per cent SEE (Table 3) were similar when compared with values obtained using the measured  $\text{AS}_{\text{d.b.h.}}$  (Table 2). FB was, however, underestimated when

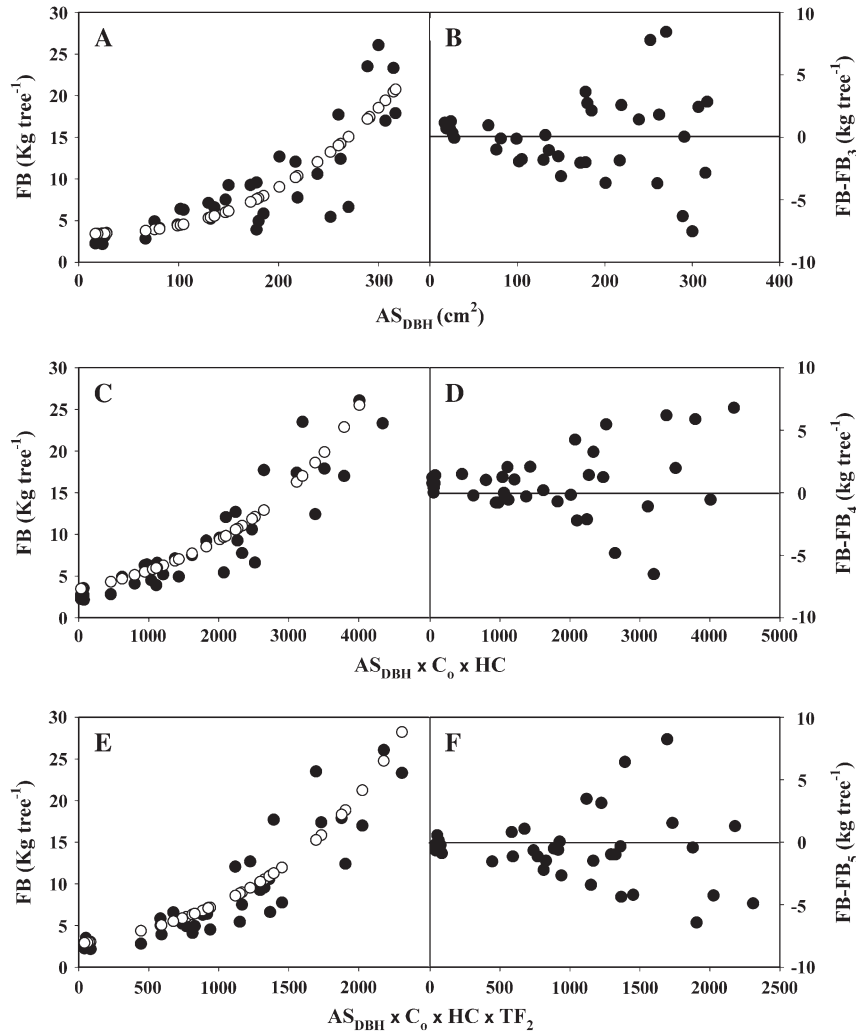


Figure 4. Scatter plots of the measured (filled symbols) FB (panels A, C and E) and residuals of the observed *vs* predicted values (B, D and F) in relation to the various sapwood predictors: AS at breast height ( $AS_{d.b.h.}$ , panels A and B); the product of  $AS_{d.b.h.}$ , canopy openness ( $C_0$ ) and height of the crown (HC, panels C and D) and the product of sapwood area at crown height ( $AS_{HZ}$ ),  $C_0$  and HC (panels E and F). The open symbols show the relationship between the predicted FB and the following AS algorithms:  $FB_3 = a \times \exp(AS_{d.b.h.} \times b)$  (panel A),  $FB_4 = a \times \exp((AS_{d.b.h.} \times C_0 \times HC) \times b)$  (panel C) and  $FB_5 = a \times \exp((AS_{HZ} \times C_0 \times HC) \times b)$  (panel E).

derived  $AS_{HZ}$  values were used, instead of measured values, because of underlying errors in the estimation of  $AS_{HZ}$  (Figure 2D).

#### Canopy characteristics of different-aged stands

The algorithm  $FB_2$ , based on d.b.h.,  $C_0$  and HC, was used to calculate stand FB and tree

leaf area to AS ratios ( $AL : AS_{d.b.h.}$  or  $AL : AS_{HZ}$ ) shown in Table 4. The tree leaf area to AS ratios varied significantly, depending on age and YC. The structural characteristics of the canopy in different-aged stands also varied considerably (Table 4). Canopy openness ( $C_0$ ), which is a function of crown radius and stem density



Table 3: Coefficients for FB derived from estimated AS values (see Figures 1 and 2)

Algorithm	Coefficient symbol	Coefficient value	Slope ( $\alpha$ )	$r^2$	F-ratio	% SEE
$FB_3 = a \times \exp(AS_{d.b.h.} \times b)$	$a$	1.33	0.80	0.76	109	3.01
	$b$	$9.3 \times 10^{-2}$				
$FB_4 = a \times \exp((AS_{d.b.h.} \times C_o \times HC) \times b)$	$a$	2.95	0.82	0.83	170	2.44
	$b$	$5.3 \times 10^{-4}$				
$FB_5 = a \times \exp((AS_{HZ} \times C_o \times HC) \times b)$	$a$	2.29	0.71	0.73	81	2.90
	$b$	$1.5 \times 10^{-3}$				

Correlation coefficients ( $r^2$ ), F-ratio, slope ( $\alpha$ ) of the linear relationship and the unsigned standard error of estimate (% SEE) were derived from linear regressions between predicted and measured FB data.  $AS_{d.b.h.}$  and  $AS_{HZ}$  values were estimated from sapwood algorithms.

varied from 0.88, in the youngest stand, to 1.24  $m\ m^{-2}$  in the 15-year-old Dooary stand.  $C_o$  could reach values of  $>1$  because the branches of the crown overlapped, particularly after canopy closure and prior to the first thinning cycle (at  $\sim 20$  years).

The mean half-surface SLA was found to be 4.48  $kg\ m^{-2}$ . The LAI estimates varied from 4.3 to 7.4  $m^2\ m^{-2}$  (Table 4) and were highest after canopy closure and before the first thinning cycle (at the 15-year-old stands). After the first thinning, LAI decreased markedly, but showed only small reductions following subsequent thinnings.

#### Litter fall estimation from FB

Needle litter accounted for 86–100 per cent of the total annual litter fall (August 2003–July 2004), for all of the sites investigated ( $M_{lit}$  Obs *vs* Total, Table 4). The total litter fall in the younger Dooary site was 6.71  $t\ ha^{-1}\ year^{-1}$  in 2002/2003, compared with 7.27  $t\ ha^{-1}\ year^{-1}$  in 2003/2004 (Black *et al.*, 2005). There was no general agreement between measured annual needle litter fall ( $M_{lit}$  Obs) and predicted needle litter fall ( $M_{lit}$  Pre), when FB estimates and a needle turnover rates of 20 per cent were used, based on the data from Norman and Jarvis (1973) (see Table 4). However, when the needle retention time (NRT) was reduced from 5 to 2.5 years, and the corresponding annual turnover rate increased from 20 to 40 per cent, the predicted needle litter fall ( $M_{lit}$  Pre<sub>(a)</sub>) agreed very closely with  $M_{lit}$  Obs.

## Discussion

The fact that algorithms based on single predictors, such as d.b.h. or  $AS_{d.b.h.}$ , systematically underestimate FB in younger (our data) or older stands (Turner *et al.*, 2000) suggests that the departure of the relationship between d.b.h. or AS and FB is due to variations in canopy characteristics, such as crown condition, crown depth and degree of self-shading. As expected, the inclusion of canopy openness and crown depth improved estimates of FB (Nowak, 1996) and overcame the bias for underestimating this value in younger (this study) and older stands (Turner *et al.*, 2000), most likely by accounting for differences associated with management practices (timing of thinning cycles, etc.).

As trees develop within the forest and compete for light, above-ground growth is directed largely towards crown production (and the bulk of stem necessary to support it). However, immediately prior to and after canopy closure, there is a change in allocation to tree height, induced by competition for light, resulting in a deeper rather than an expansive crown. The use of canopy openness and crown depth as parameters in the FB algorithms appears to have been successful in accounting for such changes. Based on our analysis, we suggest that FB and LAI can be estimated using standard inventory measurements such as d.b.h., HC and crown width, all of which are currently measured in the Irish NFI. It is evident from our results that the  $FB_2$  algorithm is more appropriate than  $FB_4$ , particularly as AS is not always readily available.

Table 4: Canopy characteristics and litter fall in the Sitka spruce stands across the selected chronosequence

Forest	Age (year)	Area : sapwood ratios (cm <sup>2</sup> cm <sup>-2</sup> )			C <sub>o</sub> (m <sup>2</sup> m <sup>-2</sup> )	FB <sub>2</sub> (t ha <sup>-1</sup> )	LAI (m <sup>2</sup> m <sup>-2</sup> )	Annual litter fall (2003/2004) (t ha <sup>-1</sup> year <sup>-1</sup> )		
		AL : AS <sub>d.b.h.</sub>	AL : AS <sub>HZ</sub>	AL : AS <sub>HZ</sub>				Total	M <sub>lit</sub> Obs	M <sub>lit</sub> Pre
Baunoge	10	0.54 <sup>a</sup>	0.26 <sup>cd</sup>	0.88 <sup>a</sup>	8.65 <sup>d</sup>	4.33 <sup>d</sup>	3.02 <sup>e</sup>	3.02 <sup>e</sup>	1.57 <sup>h</sup>	3.14
Clontycoe	15	0.23 <sup>c</sup>	0.19 <sup>e</sup>	0.98 <sup>b</sup>	16.11 <sup>a</sup>	7.22 <sup>a</sup>	n.d.	n.d.	n.d.	n.d.
Dooyary	15	0.22 <sup>c</sup>	0.32 <sup>bc</sup>	1.24 <sup>a</sup>	16.43 <sup>a</sup>	7.41 <sup>a</sup>	7.27 <sup>a</sup>	7.10 <sup>a</sup>	2.89 <sup>e</sup>	5.97
Glenbarrow	26	0.19 <sup>c</sup>	0.20 <sup>de</sup>	1.11 <sup>b</sup>	12.95 <sup>b</sup>	5.74 <sup>b</sup>	n.d.	n.d.	n.d.	n.d.
Dooyary	31	0.23 <sup>c</sup>	0.39 <sup>ab</sup>	0.98 <sup>b</sup>	12.60 <sup>b</sup>	5.64 <sup>b</sup>	6.24 <sup>b</sup>	5.62 <sup>c</sup>	2.29 <sup>f</sup>	4.58
Cullenagh	46	0.32 <sup>b</sup>	0.49 <sup>a</sup>	1.16 <sup>b</sup>	10.69 <sup>c</sup>	4.79 <sup>c</sup>	4.71 <sup>cd</sup>	4.23 <sup>d</sup>	1.94 <sup>g</sup>	3.89

Mean values for each parameter with different letters are significantly different at  $P \leq 0.05$ . Data were analysed by one-way analysis of variance and the means for different stands were compared using Fisher's least significant difference test. AL : AS<sub>d.b.h.</sub> is the one-sided foliage area (per tree) to AS (at d.b.h.) ratio; AL : AS<sub>HZ</sub> is the one-sided foliage area (per tree) to AS (at crown height) ratio; C<sub>o</sub> is canopy openness calculated using equation (2a); FB<sub>2</sub> is the FB per hectare, calculated using survey data and equation (2); LAI is based on FB<sub>2</sub> and an SLA of 4.48 kg m<sup>-2</sup> (from equation 6); total annual litter fall includes needles, twigs and bud scales; M<sub>lit</sub> Obs is the measured annual needle litter fall; M<sub>lit</sub> Pre is the estimated needle litter fall based on FB<sub>2</sub> (see equation 7) and M<sub>lit</sub> Pre<sup>(a)</sup> is estimated needle litter fall using an annual foliage turnover rate of 40%. n.d. = not determined.

Most available information on algorithms, based on pipe theory (Kozak *et al.*, 1969; Shidei and Kira, 1977; Waring *et al.*, 1982), only consider older forests in a relatively steady state (Turner *et al.*, 2000; Law *et al.*, 2001) and do not account for alterations in the relationship between d.b.h. and AS or AS and FB over an entire growth cycle. This study suggests that this changing interaction arises from a sigmoidal relationship between d.b.h. and AS, compared with a hyperbolic relationship for older trees (Turner *et al.*, 2000). This is consistent with a larger proportional increase in heartwood to stem basal area in older compared with younger trees.

The assumption that the relationship between leaf area and AS is linear (Margolis *et al.*, 1988; Turner *et al.*, 2000) is not applicable to our data. This is likely due to variations in AL : AS<sub>d.b.h.</sub> that are related to crown conditions (Dean *et al.*, 1988), crown base height (Bartelink, 1996), tree age (our study), management and other modifications associated with differing physiological responses to altered environmental conditions (Mencuccini and Grace, 1995). While the influence of crown depth on altering AL : AS<sub>d.b.h.</sub> can be overcome by assessing FB as a function of AS at crown height (AS<sub>HZ</sub>), these measurements are not always readily available and, therefore, cannot be used to estimate FB from standard inventory data. AS<sub>HZ</sub> can be estimated using a TF, but the TF should be modified to account for small trees where the crown height is below 1.3 m (AS<sub>HZ</sub> > AS<sub>d.b.h.</sub>, Waring *et al.*, 1982). Also, there was still considerable variation in AL : AS<sub>HZ</sub> across sites of different ages, suggesting that interspecific variation should not be ignored for modelling purposes. Bartelink (1996) also warned that ignoring similar within-stand variation would substantially bias leaf area and LAI estimates. Speculation as to the causes for variations in AL : AS<sub>HZ</sub> includes climate- and site-related factors (Mencuccini and Grace, 1995), tree vigour, alterations in stem hydraulic conductance (Turner *et al.*, 2000), the extent of AS taper and variations in crown-free stem length (Bartelink, 1996).

The indirect assessment of LAI using portable scanners, such as the LAI-2000 (LI-COR Instruments, Lincoln, Nebraska, USA), has been shown to pose problems in mature spruce forests where stand-specific effects required the generation of

locally specific correction factors (Kußner and Mosandl, 2000). An underestimation of the actual LAI has been commonly reported (Smith *et al.*, 1993; Stenberg *et al.*, 1994). The need to account for clumping effects is stressed by many authors when an optical estimation of LAI is required (Chen, 1996; Law *et al.*, 2001), particularly in forests of low LAI. Because of this, the litter fall method could provide useful estimates of LAI, were it not for the climatic influences on foliage retention times, as well as considerable genetic and environmental variation in SLA. In addition, SLA should be determined using fresh foliage biomass to reduce errors associated with shrinkage (up to 25 per cent during drying, Waring *et al.*, 1982). Needle age and spatial location within the crown can also be associated with variations in SLA (Bartelink, 1996).

Theoretically, litter fall can be estimated indirectly from FB under steady state, if the NRT or needle turnover rate is known (Turner *et al.*, 2000; Law *et al.*, 2001). It is evident from our analysis that NRT is not constant and may change during canopy development and after thinning events. This suggests that an additional senescence factor that is a function, for instance, of variables that influence NRT, such as self-shading and thinning activity, which need to be incorporated into any algorithm. Our analysis also suggests that NRT is shorter on the sites studied than previously reported (Norman and Jarvis, 1973; Law *et al.*, 2001). A further complication is that annual litter fall can vary in Sitka spruce stands, even when they are of a similar age, due to insect infestation, drought, management and other factors (Pedersen and Bille-Hansen, 1999; Turner *et al.*, 2000). This is consistent with our observation that the annual litter fall in the 15-year-old Dooyary stand was higher in 2002/2003 compared with 2003/2004. This may be due, in part, to a high infestation of green spruce aphid (*Elatobium abietinum*) in 2002 (J. O'Brien, personal communication). Also, it is possible that our underestimation of litter fall in 2003/2004 may be due to the drought experienced across Europe. An 18 per cent reduction in annual rainfall was recorded during this year, when compared with the 30-year mean.

In conclusion, estimates of foliage biomass using algorithms based on d.b.h. were most

reliable, particularly after the inclusion of crown parameters. The inclusion of these parameters, such as canopy openness and crown height, can account for differences in the relationship between d.b.h. and FB in younger and older forest stands. This is particularly important with regard to reporting forest activities under Article 3.3 of the Kyoto Protocol to the intergovernmental panel on climate change (IPCC). We show that algorithms developed for older forests cannot necessarily be applied to younger forests. The algorithms produced here will contribute to a better prediction of Sitka spruce forest canopy characteristics and, most importantly, to the change associated with forest age. However, due to uncertainties involved in the measurement or estimation of LAI, further comparisons between allometric and optical methods are still required.

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