1 Supplementary information

1.1 Height growth and site index

Height was measured as stand top height, commonly defined in UK forestry as the average height of the 100 largest trees by diameter at breast-height (dbh) per hectare. Top height was used as it is relatively invariant to different stand densities compared to mean height. Height growth was thus parameterised as an independent sub-model which also classified the site general productivity: a site index (SI) model.

The SI model relating top height to stand age was estimated using the *EasySDE* package (`http://forestgrowth.unbc.ca/sde`). This models height growth with a differential form of the von Bertalanffy model, whereby the change in height at any point in time was a function of the current height:

$$\frac{dH^{b_3}}{dt} = b_2(b_1^{b_3} - H^{b_3}) \tag{S.1}$$

The parameters $b_1 - b_3$ may either be local (and thus site quality dependent) or global parameters. Two ways of including site quality were tested:

1. b_1 as local parameter q
2. b_2 as local parameter q

Each model was fitted using all 51 Permanent Sample Plot (PSP) sites. The two models were compared by the log-likelihood of each formulation, in addition to Akaike information criterion (AIC) which attributes a cost to the addition of extra parameters.

Integration of equation (S.1) allowed height to be predicted at a point forward in time:

$$H_2 = b_1 \left(1 - \left[1 - \left(\frac{H_1}{b_1}\right)^{b_3}\right] e^{-b_2(t_2 - t_1)}\right)^{1/b_3} \tag{S.2}$$

Here H_1 was the initial height, H_2 predicted height and $t_2 - t_1$ the time change between heights. Site index (H_s) may be determined from this given a fixed origin $[t_1, H_1] = [0, 0]$, and a reference age for site index t_s:

$$H_s = b_1(1 - e^{-b_2 t_s})^{1/b_3} \tag{S.3}$$

The log-likelihoods provided by *EasySDE* for each of the two alternative ways of including site quality in the SI model are given in Table S1 along with calculated AIC values. The best parameterisation for the SI model was selected by both log-likelihood and AIC as model 1.

Table S1: Log-likelihood and Akaike information criterion (AIC) values of the four alternative parameterisations for including site quality (a local parameter) in the height growth model

Model number	1	2
Log-likelihood	726.1	701.7
AIC	-1444.2	-1395.4

1.2 Mortality

Mortality was modelled as a function of the stand height and current number of stems as in (García, 2009). Basal area is excluded as an explanatory variable, as previous accumulation of woody tissue should not cause mortality in itself. As height is determined by site quality in the model, mortality is thus linked with site quality. The model is given here as:

$$\frac{dN}{dH} = -b_4 H^{b_5} N^{b_6} \tag{S.4}$$

The equation may be expressed in terms of dN/dt by multiplying by dH/dt: equation (S.1). The 3 parameters (b_4, b_5, b_6) were estimated using least-squares method using consecutive pairs of PSP measures from unthinned plots representing natural mortality. Thinned plots were excluded due to lack of information concerning the timing of thinnings. A log transformation of the integral of equation (S.4) allowed the parameters to be estimated more efficiently:

$$\log(N_2) = \log\left(N_1^{1-b_6} + \left[b_4 \frac{b_6 - 1}{b_5 + 1}({H_2}^{b_5+1} - {H_1}^{b_5+1})\right]\right)/1 - b_6 \tag{S.5}$$

1.3 Basal area and Occupancy

Basal area is modelled indirectly, by predicting the increase in the product of B and H: W. W is linearly related to both biomass and volume, and additionally W behaves more simply than B alone.

Change in W is given by the balance of the gross increment (W^+) increase and stem wood loss (W^-) decrease for a given change in H:

$$\frac{dW}{dH} = W^+ - W^-$$

The gross increment is modelled by simple function of H and N. The function is:

$$W^+ = b_7 H^{b_8} N^{b_9} \tag{S.6}$$

Loss of stem wood (W^-) is a function of the relative size of of trees lost due to mortality defined in the previous section:

$$W^- = -k \frac{W}{N} \frac{dN}{dH} \tag{S.7}$$

Where k represents the relative size of dead trees. Here it is assumed a constant and equal to b_9.

A complication to the previous approach (Equation S.6.) of estimation of gross increment is that it applies only to stands with maximum canopy closure. Recently established or thinned stands have not yet occupied all available space both above ground with foliage, and below ground in root systems. The maximum resource utilisation potential is thus not being reached. This is represented in the model by occupancy (Ω): a proportion of maximum productivity achieved at stand closure. This is analogous to an interception efficiency: an index of the rate of gross photosynthesis versus a maximum potential rate, where a stand has enough leaves to intercept all photosynthetically available radiation (PAR).

Occupancy is an unobserved variable, but the relative closure (R) represents the physical extent of foliage and roots compared to a closed stand. It is similar to a leaf area index (LAI), but avoids issues with LAI measurement common in forests. R and Ω are non-linearly related: close to stand closure, additional leaves at the base of the canopy will not greatly increase productivity, but in open stands it is expected that resource capture and productivity is more closely linked to the amounts of root and foliage. The relationship suggested is:

$$\Omega = 1 - (1 - R)^{b_{10}} \tag{S.8}$$

The exponent in this function (b_{10}) is dependent on shade tolerance. The initial value of R at stand establishment is determined by a parameter b_{12} representing a planting density at which the stand would be considered fully closed. The initial value of R is the percentage that the initial planting density (N_b) makes up of b_{12}, unless N_b is greater than b_{12} in which case $R = 1$. Occupancy at planting (Ω_b) is thus derived from (S.8) as:

$$\Omega_b = 1 - (1 - \min\{N_b/b_{12}, 1\})^{b_{10}} \tag{S.9}$$

The value of R changes following a stand thinning. It is assumed proportional to basal area loss such that: $R_{\text{after}} = (B_{\text{after}}/B_{\text{before}})R_{\text{before}}$.

The rate of change of occupancy with top height is a function of height raised to the same exponent employed in equation (S.6) for W^+:

$$\frac{d\Omega}{dH} = b_{11} H^{b_8} (1 - \Omega) \tag{S.10}$$

When occupancy reaches a value of 1 (representing optimum resource use) it no longer increases, and productivity is at its maximum value. The equation for W^+ (S.6) is multiplied by Ω to account for these changes in occupancy:

$$W^+ = b_7 \Omega H^{b_8} W^{b_9} \tag{S.11}$$

Parameters b_7 - b_{12} from Equations (S.9), (S.10), and (S.11) were estimated simultaneously using the `optim` function in the R statistical system, version 2.15 (R Development Core Team, 2012) to minimise root mean standard error (RMSE) in estimates of B. Simultaneous estimation helps reduce model error. Preliminary investigations fixed values for b_9, b_{10}, and b_{12} equal to those estimated for loblolly pine (García *et al.*, 2011), and then freed to see if any model improvement resulted. Non-overlapping intervals were utilised in the parameterisation to reduce temporal autocorrelation.

1.4 Volume and Biomass

The merchantable volume (V) is linearly related to W and is thus estimated as:

$$V = \beta_v W + c_v \tag{S.12}$$

β_v and c_v are the slope and intercept of the relationship respectively. An intercept is included as a stand's top height may be shorter than 1.3m, with B and W equal to zero, yet there may still be a merchantable volume.

Whole tree biomass is is estimated using the biomass expansion factors (BEF) and root:shoot ratios of Levy *et al.* (2004). Merchantable volume is multiplied by the biomass expansion factors (BEF) and wood density to give the above ground biomass. Whole tree biomass is then given by multiplying by root:shoot ratio (1.301 for Scots pine). The biomass expansion factors (BEF) is determined by tree height for Scots pine according to the equation:

$$\text{BEF} = 1.392 - 0.4812 \log(H) \tag{S.13}$$

References

García, O. 2009. A simple and effective forest stand mortality model. *Mathematical and computational forestry & natural-resource sciences (mcfns)*, **1**(1), pp–1.

García, O., Burkhart, H. E., & Amateis, R. L. 2011. A biologically-consistent stand growth model for loblolly pine in the Piedmont physiographic region, USA. *Forest ecology and management*, **262**(11), 2035–2041.

Levy, P. E., Hale, S. E., & Nicoll, B. C. 2004. Biomass expansion factors and root : shoot ratios for coniferous tree species in Great Britain. *Forestry*, **77**(5), 421–430.

R Development Core Team. 2012. *R: A Language and Environment for Statistical Computing.* R Foundation for Statistical Computing, Vienna, Austria.