

Incorporating uncertainty into the parameters of a forest process model

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Abstract

‘Process-based’ models have been advanced to incorporate current knowledge regarding forest processes explicitly into model structure, yet uncertainty regarding these processes is often omitted from parameter estimation. This problem reflects the fact that parameters have been traditionally viewed as constants. In process models this is often unrealistic, since physiological rates and morphological characteristics, which have known variation, are often parametrized. Reasonable estimates for parameters can, and should be, abstracted from the vast body of forestry literature, and formulated into probability distributions which reflect uncertainty in their potential value. Here probability distributions are estimated for 14 physiological or morphological parameters of *Pipistem*, a stand-level model of carbon allocation and growth for loblolly pine (*Pinus taeda*), based on an extensive review of published information. Investigation of parameters revealed a wide range of variation in accumulated knowledge regarding their value, and led to the development of generic parameters which may be transferrable to other similar models. Parameter uncertainty also appeared tractable in some cases and might be reduced through reformulation of the model. Some parameters investigated had known co-dependency on model variables or other parameters, and may be better expressed as dependent variables. This study was part of a larger study in which a Bayesian analysis was used to assess the uncertainty in the predictions of a forest growth model. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

Many ‘process based’ models have been advanced in recent years, which attempt to capture the underlying mechanisms of forest processes

into workable mathematical forms. Process models are often contrasted with so-called ‘empirical’ models which explain patterns in observational data without addressing the mechanisms explicitly (Parysow and Gertner, 1997). Since forest processes are complex and not fully understood, uncertainty is necessarily incorporated into any such model, but is often unaccounted for (Green et al., 1999). Part of this uncertainty is inherent in model

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structure and part of it is attributable to uncertain estimates of model parameters (Raftery et al., 1995; Poole and Raftery, 1998; Green et al., 1999). The modeler often ignores the uncertainty in the model relationships, assuming that they are a reasonable simplification of forest processes, and attempts to estimate the various parameter values.

Parameters in models are traditionally considered to have constant values, but this is problematic in process models because parameters often represent physiological rates or morphological characters, which have known variation. Thus, it is not always clear what the difference is between a variable and a parameter in a process model (Gertner et al., 1999). Although many model parameters have known variation they are ordinarily stated as point estimates, which simply ignores uncertainty in the true value of the parameter (Green et al., 1999). It also seems pointless to design a model to describe forest processes and then fail to incorporate what we know about these processes into our estimates of its parameters. Hence, it is important to recognize that many parameters are in fact variable, and incorporate what we know about their variation into the modelling process.

One way of incorporating uncertainty regarding a parameter's value is to define it as a probability distribution, which places different weight on the various potential values a parameter could assume (Gardner et al., 1990; Gertner et al., 1996; Green et al., 1999). In process models, these parameter distributions should reflect accumulated knowledge regarding plausible values for a given parameter, what have been referred to as 'pre-model distributions' in Bayesian techniques (Green et al., 1999). For example, a narrow distribution of values would reflect a general agreement in experimental measurements of a parameter's value, while a wide flat distribution reflects vague knowledge about its value. However, obtaining knowledge regarding the parameters of a process model is not necessarily a simple matter. Ideally, such parameter distributions should be based upon measurements obtained from real trees (Gertner et al., 1999). On the other hand, we must face the fact that sometimes we have no informa-

tion. Fortunately, Bayesian Synthesis techniques have been developed in recent years to allow for the use of non-informative prior probability distributions for selected model parameters (Raftery et al., 1995; Poole and Raftery, 1998; Green et al., 1999).

Here we describe the methods by which we estimated probability distributions for the values of 14 physiological and morphological parameters used in *Pipistem*, a carbon allocation and growth model (see Valentine et al., 1997), based upon an extensive review of published literature. In another study (Green et al., 1999), we describe statistical methods for using these distributions as 'pre-model' probability distributions for parameters in a Bayesian analysis of model uncertainty.

The paper is organized as follows: (1) we briefly describe *Pipistem*; (2) we describe general methodology; and (3) we describe estimation methods and results for each parameter, supported by a review of the literature.

2. The model

Pipistem, a model of carbon allocation and growth of an even-aged, mono-specific stand of trees, was originally derived by Valentine (1988) from the carbon-balance equations of Thornley (1976) and the 'pipe-model theory' of Shinozaki et al. (1964a), Shinozaki et al., 1964b). Hereafter, *Pipistem* refers to the version of the model that was calibrated for loblolly pine (Valentine et al., 1997).

Pipistem projects the growth of a model stand, which is composed of foliage, fine roots and two kinds of pipes, 'active' and 'disused'. The pipes represent sapwood and heartwood. Coarse roots are modeled as below-ground pipes. Each active pipe connects foliage to fine roots and is assumed to have a constant cross-sectional area. Five main variables characterize the state of the model stand at any given time: N , the number of trees per hectare, A , the total cross-sectional area of active pipes (m^2/ha), X , the total cross-sectional area of disused pipes (m^2/ha), L , the average length of an active pipe (m); and C , the average height to the base of a live crown (m).

Pipestem projects temporal changes in the state variables and other response variables that include stand basal area, average tree height, total woody dry matter, net primary productivity and annual estimates of gains and losses of foliage, fine roots and woody biomass. Because *Pipestem* was derived from carbon-balance equations, with pipe-model theory as a morphological framework, many of its parameters are physiological rates or morphological ratios. It is estimates of these parameters that we address in this paper.

3. Methods

Our methodology was straightforward: the literature was searched for multiple values pertaining to each parameter in order to quantify variation. If data specific to loblolly pine were unavailable, then analogous data from other pine species were used as surrogate measures, and the expected dispersion of the parameters were inflated. Some of the data were reported in units which needed to be converted to the units used in *Pipestem*, conversion factors and sample calculations are provided in Appendix A. If no empirical data were available, then theoretical values were used.

Table 1
Parameter values estimated for *Pipestem*

Parameter	Units	Value ^a	Density
c_F	kgC/kgC	0.222 (0.058)	Normal
c_R	kgC/kgC	0.290 (0.108)	Normal
c_W	kgC/kgC	0.213 (0.057)	Normal
m_F	kgC/year/kgC	0.698 (0.198)	Normal
m_R	kgC/year/kgC	1.380 (0.445)	Normal
m_W	kgC/year/kgC	0.057 (0.020)	Normal
s	kgC/year/kgC	–	Uniform
z_F	kgC/m ²	282.3 (14.5) ^b	–
z_R	kgC/m ²	180.7 (76.8)	Normal
z_W	kgC/m ³	246 (24.0)	Normal
v_F	Years	1.60 (0.04)	Normal
v_R	Years	0.478 (0.161)	Normal
ρ	m ² /ha	–	Uniform
λ	kgC/year/kgC/y ear	0.713 (0.014)	Normal

^a Mean (S.D.).

^b Estimate provided by Green et al. (1999).

Once converted into the same units, resultant values were analyzed to obtain a mean and standard deviation, that were used, in turn, to specify a probability distribution for the parameter (Table 1). We assumed that the shape of the distribution was normal, unless no information was available, then the parameter was assigned a uniform distribution (Table 1). We chose normal distributions because of the well-known robust qualities of this distribution. Published values reported without associated statements of variation were averaged together to form a mean and standard deviation. We weighted all estimates equally in analyses unless otherwise noted.

If mean values were reported with an associated statement of variance we used the following method to incorporate variation within each estimate. We generated a hypothetical data set containing common and more extreme values from each estimate. For example, suppose we had three sets of means with standard errors from the literature. Denote these by x_i and s_i , $i = 1, 2, 3$. We created a data set of size $n = 9$ containing the observations x_i , $x_i + s_i$ and $x_i - s_i$, $i = 1, 2, 3$. We then computed the mean and standard deviation of this data set and used these as our estimate for the value of the parameter in question. We used this technique to capture the uncertainty in each individual estimate, which would have been lost if we simply averaged their means. Hence, the resulting means were identical to the average of the three means, but our estimates of dispersion were quite liberal. We also used a modification of this method if we needed to weigh one estimate more than another; for example, if it was determined that among two estimates, x_1 and x_2 , that x_1 should weigh twice as much as x_2 in our analysis, our hypothetical data set would include a set of $n = 3$ values $\{x_1, x_1, x_2\}$. If statements of variance were also available then the data set would contain $n = 9$ values, as described above, except that there would be three pairs of identical values in the set.

If parameters were derived as products, we multiplied the means and employed this formula for the standard deviation:

$$s = \sqrt{x_1^2 s_2^2 + x_2^2 s_1^2} \quad (1)$$

where x_i and s_i^2 are the sample mean and variance of the estimate $i = 1, 2$. If parameters were derived as quotients, we used the formulas described by Mood et al. (1974). Both derivations assume that the estimates are independent of each other. Note that throughout this paper a standard deviation appears in parentheses immediately following its associated mean.

4. Parameter estimation

Each parameter is discussed individually along with any relevant background information. Detailed references to *Pipistem* are worked into the discussion to illustrate how the assumptions of the model constrain parameter estimation. The results of this study are summarized in Table 1. Definitions of parameters and variables are provided in Appendix B.

4.1. Biomass

Standing carbon biomass at any given point in time is represented in the model by the variables F , R , and W , the carbon biomass of foliage, fine roots and wood, respectively. Three parameters are used to establish the amount carbon biomass associated with an area of active pipes (sapwood). z_F and z_R specify kilograms of carbon in foliage and fine roots per m^2 of cross sectional area of active pipes, respectively, so that $F = z_F A$ and $R = z_R A$. The parameter z_W specifies kilograms of carbon biomass associated with a cubic meter of wet wood, so that $W^* = z_W A L$, where W^* is the living portion of W .

4.1.1. z_R -Fine root biomass

No direct estimates of fine root biomass (< 2 mm in diameter) per unit of cross-sectional area of sapwood were found, so we proceeded to approximate z_R from the $z_R:z_F$ ratio, where z_F was estimated from data (see Green et al., 1999). Pipe-model theory suggests a strong relationship between root mass and foliage (Shinozaki et al. 1964a) and empirical studies by Pearson et al. (1984), Johnson et al. (1985) show strong correlations between root volume, foliage area and sap-

wood area in pines. There is substantial evidence that the $z_R:z_F$ ratios vary as a function of site quality and annual variations in rainfall amounts (Albaugh et al., 1998; Comeau and Kimmins, 1989; Harris et al., 1977). Trees tend to produce lower root:shoot ratios on well watered and fertilized sites and higher ones on dry or nutrient poor sites (Comeau and Kimmins 1989). Hence our estimate of $z_R:z_F$ needed to be site-specific.

We used data presented in Albaugh et al. (1998), who compared fertilized, unfertilized and irrigated loblolly pine plantation plots on sandy, dry, and infertile soils in Scotland County, North Carolina, to estimate $z_R:z_F$ for our model stand. We estimated fine root (< 2 mm) to foliage ratios from their (Albaugh et al., 1998) data to be 0.73 (0.36) on the control site, 0.64 (0.27) on irrigated only, 0.51 (0.30) on the fertilized plots, and 0.219 (0.07) on irrigated plus fertilized plots. We estimated the site conditions of our model stand from the site conditions of a real stand growing in Roanoke Rapids, North Carolina, assuming they were planted on Lynchburg sandy loam and Rains fine sandy loam soils (Amateis, personal communication). These soils are somewhat poorly drained or poorly drained and naturally low in fertility (N.C. Soil Conservation Service, personal communication). We chose estimates from Albaugh's irrigated, unfertilized plots (Albaugh et al., 1998) (0.64 (0.27)) since the fertility between the two sites is roughly equal, but our site should have a higher available water capacity because of the slightly finer textures and somewhat impeded drainage. Thus, we estimated a $z_R:z_F$ ratio of 0.64 (0.27), and multiplied by our estimate of $z_F = 282.3$ (14.5) kgC/m^2 to obtain $z_R = 180.7$ (76.8) kgC/m^2 .

4.1.2. z_W -Live wood biomass

The bulk density of woody tissue, z_W was calculated from estimates of the specific gravity (g/cm^3) of loblolly pine wood, denoted here as (g_s). Koch (1977) reported specific gravity of *P. taeda* wood to be $g_s = 0.510(0.042)$ estimated from older stands and Tasissa and Burkhart (1998) reported $g_s = 0.455(0.076)$ estimated from younger stands. Many factors, however, influence specific gravity in wood, including the percentage of late wood,

physiological age and geographic variation. An estimated 80% of the variation in the specific gravity of loblolly pine wood is attributable to differences in late wood measurements (Tasissa and Burkhart, 1998). We estimated that late wood is 2.4(0.29) times more dense than early wood from Koch (1977). Tasissa and Burkhart (1998) reported values of $g_S = 0.339(0.041)\text{g/cm}^3$ for early wood and $g_S = 0.637(0.142)\text{g/cm}^3$ for late wood. The proportion of late wood increases as the tree ages and is lower higher up in the tree, when calculated from radial increment (Tasissa and Burkhart, 1998). Geographic variation also has an effect on variation in specific gravity, with higher values for trees growing on the coastal plain and lower values for those growing inland (Koch, 1977; Zobel and Talbert, 1984). Regional means for the coastal plain of N. Carolina were estimated to be $g_S = 0.475(0.007)\text{g/cm}^3$ (Koch, 1977) and $g_S = 0.525(0.021)\text{g/cm}^3$ (Zobel and Talbert, 1984). Geographic variation, however, varies considerably with the physiological age of the tree measured (Tasissa and Burkhart, 1998). Thus, we expect that variation of z_W in *Pipestem* should be large since it makes predictions for stands of many different ages.

We used the estimates mentioned above (0.525(0.021), 0.475(0.007), 0.51(0.042) and 0.455(0.076)) to obtain an estimate of specific gravity $g_S = 0.492(0.048)\text{g/cm}^3$, which we converted (see Appendix A) to obtain our estimate of $z_W = 246(24)\text{ kgC/m}^3$. However the variation in this estimate may be too low because *Pipestem* makes predictions across 50 years of stand development and Tasissa and Burkhart (1998) show changes in specific gravity ranging from 0.37 to 0.51 g/cm^3 from age 1 to 25. In this case, the parameter z_W , in *Pipestem*, might be better expressed as a time-dependent variable. On the other hand, changes in g_S with age, as reported by Tasissa and Burkhart (1998), may be due to the use of radial increment rather than cross-sectional area increment as a basis for calculations. Thus, as Koch (1977) noted, the continuously changing nature of trees may make it difficult, if not impossible, to establish meaningful tree-average values for specific gravity.

4.2. Production

Pipestem relates net primary production to the total dry matter in the model stand with the following equation:

$$(1 + c_F) \frac{\delta F^+}{\delta t} + (1 + c_R) \frac{\delta R^+}{\delta t} + (1 + c_W) \frac{\delta W^+}{\delta t} = sI F - (m_F + m_R R + m_W W^*) \quad (2)$$

The left side of Eq. (2) is the total annual production of carbon biomass, including constructive respiration costs; $\delta F^+/\delta t$, $\delta R^+/\delta t$, and $\delta W^+/\delta t$, respectively are the rates of production of foliar, fine-root and woody dry matter. The right side is the difference between gross photosynthetic carbon gain and maintenance respiration of total biomass. c_i and m_i ($i = F, R, W$) are for the overhead costs of construction and specific rates of maintenance respiration costs of foliage, fine root and live woody dry matter. sI is the average specific rate of production of carbon substrate, where the parameter s is the units of carbon substrate produced per unit of unshaded foliar dry matter per year, and $I = \rho/(\rho + A)$ adjusts the unshaded rate to an average rate for all foliage. ρ is a scaling parameter for carbon substrate which reduces the average specific production rate of unshaded foliage (sI) as self-shading (foliar density) increases across the stand.

4.2.1. s and ρ -Photosynthetic production parameters

Gross primary production varies from leaf to leaf, tree to tree, species to species, day to day and year to year, which makes it difficult to estimate total photosynthesis on an annual basis (Jarvis et al., 1990; Thornley and Johnson, 1990). Published estimates of s are usually obtained from short-term measurements that do not extrapolate well to a yearly time scale (Valentine et al., 1997), and so we assigned s a uniform probability distributions with liberal guesses for the upper and lower bounds. ρ , was also assigned a uniform distribution, although it may be estimated as a function of total foliar biomass (F), because we were unaware of any studies which estimated total stand photosynthesis between different levels of self-shading or foliar densities.

4.3. Respiration

We found wide variation in published estimates of respiration within plant communities. Lambers (1985), for example, estimated that respiration consumes between 30 and 60% of the carbon fixed in photosynthesis per day. Forested ecosystems have been estimated to consume between 50 and 70% of annual production through respiration (Ryan, 1991). These wide intervals reflect the difficulty in isolating and measuring respiration rates. Ryan et al. (1994) noted that respiration is a large, environmentally sensitive component of the carbon balance for pine ecosystems, and unfortunately, most estimates of respiration are taken at very small time intervals, which reflect only a moment in a time-series of environmental variability. If we consider fluctuations in respiration rates, between or within environments, it may not even be possible to establish meaningful average values (Lavigne, 1996).

Pipestem separates components of respiration into component organs (roots, leaves and wood). Ryan et al. (1994) conducted an extensive review of experiments on respiration in the various organs of pine trees. We compared respiration rates reported by Ryan et al. (1994) and estimated that fine root respiration rates ($\text{nmol C mol C}^{-1} \text{ s}^{-1}$, at 15°C) were $\sim 1.8(0.8)$ times higher than foliage respiration and 15.5 (3.3) times higher than stem wood respiration, although collectively stemwood accounts for a large portion of the annual budget. Coarse roots were comparable to stem wood. Note that constructive and maintenance respiration rates were not separated in these experiments.

4.3.1. Constructive respiration $\{c_F, c_R, c_W\}$

A number of investigators have attempted to quantify the carbon cost for the construction of plant tissues (Penning de Vries, 1974; Chung and Barnes, 1977; McDermitt and Loomis, 1981; Williams et al., 1987) using chemical composition analyses. These analyses produce estimates of the grams of photosynthetic substrate needed to construct a gram of biomass, which includes the both the energetic cost of production (c_i , $(i = F, R, W)$ in *Pipestem*), and the carbon present in the resultant product. Chung and Barnes (1977) estimated

the cost (gram glucose per gram of biomass) of compounds produced in shoot tissues of loblolly pine, with values of 1.182 for carbohydrates, 1.484 for organic acids, 1.579 for nitrogenous compounds, 1.897 for lignin, 1.919 for phenolics, and 3.019 for lipids. They reported values for the needles and shoots of loblolly pine of 1.588 and 1.574, respectively. They also reported values based on chemical composition data from other authors. Stem wood construction costs ranged from 1.214 for the cambium of *Pinus sylvestris*, to 1.603 for *Pinus elliottii* bark. Root-wood in *P. elliottii*, was reported at 1.466. This suggests that root-wood and sapwood are less expensive than leaf tissues to construct.

Chemical composition analyses provided direct empirical data for our estimates of c_F , c_R , and c_W , (see Appendix A) but were insufficient to describe the full range of variation in constructive respiration costs. Chemical analyses ignore physiological factors which differ in different portions of the plant body. Thornley and Johnson (1990) noted that the conversion efficiency of roots, measured in grams of biomass produced per gram of substrate consumed, is considerably lower than that of shoots and leaves. The conversion efficiency of Scots pine shoots, denoted here as $Yg = 1/(1 + c_R)$, were found to be $Yg = 0.86$, compared to $Yg = 0.66$ for shoots (Lambers, 1985). Perhaps this occurs because photosynthesis may also directly supply adenosine tri-phosphate (ATP) for growth in autotrophic organs (Lambers, 1985).

We combined chemical composition analysis data with conversion efficiency data (see Appendix A) to derive mean values and standard deviations for c_F and c_R (all values were weighed equally). We had no estimates for growth efficiency specific to stemwood, so our estimate for c_W was based on chemical composition analysis alone. All values were converted into units appropriate for *Pipestem* and averaged to obtain the final values reported in Table 1.

4.3.2. Maintenance respiration $\{m_F, m_R, m_W\}$

Maintenance respiration is the energy consumed to maintain existing cellular structures. It can be broken down into two principal components; protein turnover and gradient maintenance

(Lambers, 1987). m_F , m_R , and m_W , in *Pipistem*, denote the kilograms of carbon consumed annually by the stand to maintain a kilogram of leaf biomass, fine root biomass and active pipes, respectively. Many studies suggest that maintenance respiration, on the whole, consumes a considerable portion of total fixed carbon in trees (Boyer, 1971; Ledin et al., 1976; Ryan et al., 1994; Lavigne, 1996). Maintenance respiration varies with age, temperature, and other factors, which make both investigation and modeling difficult (Ryan and Waring, 1992).

Both leaf respiration and fine root respiration vary widely over the lifetime of the tree because they are highly sensitive to changes in the environment (Hagihara and Hozumi, 1991; Ryan et al., 1994). Fine root respiration is particularly difficult to isolate and quantify (Cox, 1975; Helal and Sauerbeck, 1991). Cox (1975) showed that roots of differing diameters differed as much as 20-fold in their measured respiration rates and smaller roots respiration more than larger roots. It is important to note that cost of a symbiote is an often unacknowledged component of the cost of root maintenance. Fogel (1991), for example, found that ectomycorrhizal fungi on beech tree roots consumed 40–50% of total root respiration.

We estimated values for m_F and m_R from estimates of total annual respiration for the needles and fine roots of slash pine (*P. elliottii*) presented by Cropper and Gholz (1991), using a derived relationship for the ratio of maintenance respiration to total respiration (see Appendix A). Our results are recorded in Table 1. We recognize that there are subtle species-level differences between *P. taeda* and *P. elliottii*, but chose to use the estimates of Cropper and Gholz (1991) because they were recorded directly at hourly time intervals and extrapolated well to an annual time scale. We assumed that the main difference between respiration rates for these similar species is due to temperature, which we corrected for (see Appendix A).

We used two methods for approximating the percentage of total respiration accounted for by maintenance respiration both of which yielded high values. We estimated the proportion of total respiration accounted for by maintenance respiration at the whole stand level from estimates of net primary productivity (NPP) and total respiration presented in Kinerson et al. (1977), assuming that constructive respiration was about equal to 25% of NPP (see Appendix A, also Ryan et al., 1994). Our results suggest that maintenance respiration for *P. taeda* was about 75% of total respiration. We also estimated the ratio of maintenance respiration to total respiration for loblolly pine roots from data presented by Boyer (1971), setting maintenance respiration equal to dormant season respiration rates (Appendix A, see also Cox, 1975; Ryan et al., 1994). Our results suggest that maintenance respiration accounts for 86.8% (11.7) of total annual root respiration. Lavigne (1996) reported similar values (maintenance respiration accounting for 86–88% of total annual rates) in the stems of trees in boreal forests. Maintenance respiration may be higher in roots than other tissues because the roots are responsible for ion uptake and must meet their own demand as well as the ion demands of the shoots (Lambers, 1985; Santi et al., 1995).

4.3.3. m_W -Maintenance respiration for wood

We estimated m_W directly from conifer stemwood estimates by Penning de Vries (1974). Values ranged from 0.02 to 0.13 for a core of stemwood and 1.3 for bark (mg glucose per gram of dry matter, at 15°C). These estimates were converted to $\text{kg C kg C}^{-1} \text{year}^{-1}$ (Appendix A), and averaged, to obtain $m_W = 0.057$ (0.02). We assumed that 10% of the cross-sectional area of a southern pine is bark (Koch, 1977) and our estimate was weighted accordingly (see Methods). Note the large variation in our estimate ($CV = 35\%$) reflects an attempt to obtain a generic value for stem wood respiration. Lavigne and Ryan (1997) found that much of the variation in stemwood variation occurs between stands and suggested that stand-specific parameters, rather than generic ones, may be necessary to improve model predictions.

4.4. Turnover

The carbon biomass in leaves and roots is lost and regenerated in a continuous cycle of shedding

and replacement. Wood is cycled similarly, but at a considerably slower rate. *Pipestem* accounts for the turnover of live wood by keeping track of the total cross-sectional area of active and deactivated pipes. This is calculated explicitly by the model's equations and is not parametrized. Turnover in foliage and fine roots is parameterized by v_F and v_R , the longevity (years) of foliage and fine roots, respectively.

4.4.1. v_F -Leaf longevity

The length and ecology of leaf life spans has been extensively reviewed (Chabot and Hicks, 1982; Reich et al., 1991). Pines, as a genera, with their evergreen habit and diverse geographic distribution have a wide variation in the life span of their leaves. Even within the canopy of a single tree there is considerable variation in leaf morphology and life span (Shoettle and Smith, 1991). Upper canopy leaves have faster developmental rates and shorter life spans than lower canopy leaves (Lichtenthaler, 1985).

We used the work of Horne (1993), who reviewed the typical growth cycle of loblolly pine shoots and needles in the Georgia Piedmont, to estimate variation in the value of v_F . In late winter or early spring, a new shoot elongates from the overwintering terminal bud and soon after sets out the first flush of needles. A second and sometimes a third flush may occur depending largely upon the current years' rainfall. Most of the carbon energy for growth of new shoots and needles is drawn directly from the previous years' needles, which are eventually drained completely and shed. After the last flush matures in the fall, a new, overwintering bud is set and the previous years needles begin to fall. This usually lasts for a period of 4–6 weeks (0.08–0.12 years). First flushed needles tend to last 1.5 years on the tree, although this depends on geographic location and weather. We assumed a difference of ~5% between the growing season of the Georgia Piedmont and the North Carolina Coastal Plain to account for climatic differences (McNab and Avers, 1994), and estimated the mean lifespan of loblolly pine needles to be $v_F = 1.6$ (0.04) years.

4.4.2. v_R -Fine root longevity

The lifespan of tree roots is difficult to assess because of technical problems involved in estimation (Persson, 1983; Nadelhoffer et al., 1985, Vogt et al., 1989). Few experimenters directly observe the birth and death of roots (Roberts, 1976), and so many studies rely on indirect methodologies for assessing turnover in the root system (Nadelhoffer et al., 1985). Harris et al. (1977) suggested that the ratio of root production to root turnover ($\text{kg ha}^{-1} \text{yr}^{-1}/\text{kg ha}^{-1} \text{yr}^{-1}$) as an estimate of longevity, but this estimate produces a unitless value and longevity must be measured in temporal units. The ratio of standing biomass to the production rate of biomass yields an estimate of the 'residence time' of a unit of biomass in a biomass 'pool' which is analogous to mean lifespan (Nadelhoffer et al., 1985). Such estimates should be viewed with caution however, since few authors explicitly separate live roots from dead roots and mycorrhizae are generally omitted or ignored (Persson, 1980; Fogel, 1983; Albaugh et al., 1998). In addition, since production is generally estimated from sequential measurements of biomass such estimates are necessarily correlated.

We were unable to obtain direct estimates of v_R for loblolly pine fine roots (≤ 2 mm in diameter). The only direct measurement available for fine root longevity was that of Roberts (1976), who observed that the root tips (≤ 1 mm) of Scots pine lasted between 2 and 9 weeks with a mean of 4 weeks, or 0.77 years. We estimated v_R indirectly from the ratio of fine root biomass (≤ 2 mm) to fine root production ($\text{mg ha}^{-1}/\text{mg ha}^{-1} \text{yr}^{-1}$) from data presented in Albaugh et al. (1998). We found that fine root longevity, measured in this way, was sensitive to irrigation and fertilization treatments, so that fine root longevity increased with greater soil amendment (Albaugh et al., 1998). Thus parametrization of v_R requires an understanding of the relationship between changes in root allocation, root biomass and turnover in reference to environmental conditions. Although Albaugh et al. (1998) show an inverse relationship between site quality and productivity there is also considerable evidence in the literature to suggest otherwise (Nadelhoffer et al., 1985). We estimated fine root longevity assuming that

unfertilized irrigated plots (Albaugh et al., 1998) most closely resembled the conditions of our model site and estimated $v_R = 1.05(0.21)$ mg ha⁻¹/2.13 (0.67) mg ha⁻¹ yr⁻¹ = 0.478(0.161) years. Note that the large variation in the value of v_R comes from large differences in biomass and production estimates between years, within a site-type (Albaugh et al., 1998). Hence even when site-specific relationships are accounted for there is still a high degree of natural uncertainty in the mean life-expectancy of fine roots.

4.5. Carbon allocation

Our review of carbon allocation in plant communities revealed a wide variation in short-term allocation, which is species dependent and highly sensitive to surrounding environments (Ågren et al., 1980; Koch and Mooney, 1996). Long-term effects are undocumented. Pine stands in general allocate a large portion of their carbon to above ground biomass when compared to other plant communities (Caldwell, 1987). Carbon allocation in a loblolly pine is largely determined by its underlying genetic characteristics, which are modified by environmental feedback (Drew and Ledig, 1980). Loblolly pine is intolerant and intra-specific competition is high. Loblolly pine also grows in areas where fire is common. These factors cause loblolly pine to preferentially allocate carbon to above ground biomass, particularly terminal shoot growth. Even within this species, regional populations can be quite different, however (Zobel and Talbert, 1984).

4.6. λ -Carbon allocation parameter

In *Pipistem*, available carbon substrate is allocated to the elongation of pipes ($\delta L/\delta t$) and the addition of new active pipes ($\delta A^+/\delta t$). The parameter λ is the proportion of available carbon substrate allocated to the production of new active pipes, foliage and feeder roots, and $1 - \lambda$ is the proportion allocated to the elongation of existing pipes, which leads to the relationships:

$$\frac{\delta A^*}{\delta t} \propto \frac{\lambda A}{(z^* + L)} \quad (3)$$

$$\frac{\delta L}{\delta t} \propto 1 - \lambda \quad (4)$$

when z^* is calculated as:

$$z^* \approx \frac{z_F(1 + c_F) + z_R(1 + c_R)}{z_W(1 + c_W)} \quad (5)$$

Estimating the carbon allocation parameter, λ requires an understanding of the tradeoff between height growth and lateral growth at the stand level. Since $\lambda + (1 - \lambda) = 1$, elongation and lateral growth are defined in the model as competing processes. Mäkela and Sievänen (1992) developed a model which analyzes height growth as a compromise between maximizing functional crown size and reducing the maintenance cost of non-photosynthetic tissues which must support the crown. In their model, foliar biomass is proportional to height raised to an exponent, u :

$$P \propto H^u \quad (6)$$

where P = kilograms of foliar biomass and H = average tree height in meters; u , estimated by least squares regression, ranged from 2 to 3 with most values around 2.5 (Mäkela and Sievänen, 1992). This represents a tree growing in the open when this relationship should be optimized because light is not limiting.

We assume the relationship $u \approx \lambda/(1 - \lambda)$, because foliar biomass P in Eq. (5) is equivalent to F in *Pipistem* which is proportional to changes in active pipe area A^+ and λ (Eq. (3)), and $(1 - \lambda)$ is proportional to changes in height (H and $\delta L/\delta t$ in Eq. (5)). We relate u to $\lambda/(1 - \lambda)$ by relating Eq. (3) to Eq. (4) to obtain:

$$\frac{\lambda}{1 - \lambda} \propto \frac{\delta A^* (z^* + L)}{\delta L \quad A} \quad (7)$$

Hence $u \approx \lambda/(1 - \lambda)$, when z^* is a small constant.

We averaged estimates of u reported by Mäkela and Sievänen (1992) solving the relationship $u = \lambda/(1 - \lambda)$ for λ , to obtain $\lambda = 0.713$ (0.014). Although this value corresponds to what we would for open grown trees, we used this same value of λ for the model stand (Table 1.), because a pipe-model stand, can also be viewed as a single large tree (Shinozaki et al., 1964a.). For a very intolerant tree, self-shading may not be any more important than the shading effects of neighboring trees.

Thus the stand should optimize the relationship between the foliar biomass it can support and height growth in the same way that an individual does. In this sense, both branches and stems can as such be considered, singly or collectively, as autonomous units (Horne, 1993) which can either maintain their sapwood connection or not.

5. Discussion

Our investigations of the physiological and morphological parameters of a forest process model revealed a great deal of uncertainty in both empirical estimates and in the opinions of experts regarding potential parameter values. We used probability distributions to capture this uncertainty in a formal mathematical statement regarding each parameter's value, because it reflects what is known about them. While the use of these 'stochastic' parameters must ultimately be evaluated in terms of model predictions, it is an important first step to determine if the parameters make sense in light of accumulated knowledge (Vanclay and Skovsgaard, 1997); after all, isn't that the point of process-modelling? The methodology we present here not only follows the inherent logic of process modelling (i.e. it incorporates what is known about forest processes), but also provides a useable quantity, in light of recent advances in model evaluation (Raftery et al., 1995; Poole and Raftery, 1998; Green et al., 1999).

Estimating probability distributions from published information led us to develop 'generic' parameter values, which may be useable in other similar models. However, generic parameters may not be appropriate in some cases. For example, respiration parameters are poorly represented by generic values since they are highly temperature dependent and variable between locations and stand types (Lavigne, 1996; Lavigne and Ryan, 1997). Hence 'uncertainty' in the measured value of a constant parameter can be separated from more predictable fluctuations in a variable parameter, because the latter can be reduced by reformulating the model, while the former remains intractable without new methodology or data.

Of course there are limitations to how much we can gain from investigating parameters in this way. An obvious problem is that time constraints may simply preclude this type of parameter investigation for every model, although there is no clear point of diminishing returns. Sometimes specific data from which parameter values can be directly estimated are simply unavailable (Gertner et al., 1999), however, this does not imply that we know nothing. Some parameters have known co-dependency which may be used to transform knowledge regarding one parameter to an informed distribution for another. As an example, we were able to estimate fine root biomass per unit of sapwood, z_R , from foliage biomass estimates, z_F , as a function of fine root to foliage ratios (Fine root to foliage ratios also have a known dependence on site quality, although the exact nature of this relationship remains in question, see Nadelhoffer et al., 1985; Albaugh et al., 1998). We were, however, unable to obtain useable information for parameters s and ρ , which were assigned uniform distributions, leaving the problem of effectively infinite uncertainty (the method of Green et al. (1999) is designed, in part, to mitigate this uncertainty). Finally, any such investigations are limited by the bias of the investigator, who may weigh the opinion of one expert over that of another, or be ignorant of relevant studies. However, if this bias is specifically characterized as a component of parameter uncertainty, it can become an insight, rather than a hidden flaw, to the model user.

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Appendix A. Conversion factors and sample calculations

A.1. Biomass conversions

1 g biomass = 0.5 g C (Chung and Barnes, 1977; Cropper and Gholz, 1991).

1 g glucose contains 0.4 g of C by molecular weight.

1 mg CO₂/g biomass/h = 4.78 kg C/kg C/year.

1 g CO₂ = 12/44 g C.

Specific gravity measured in grams of biomass/cm³ greenwood = 500 kg C/m³

A.2. Constructive respiration(c_i)

$c_i = (1/Y_g) - 1$; $i = F, R, W$ $Y_g = 1/(1 + c_i)$ = grams of biomass produced per gram of substrate consumed = conversion efficiency.

Conversions to c_i : Chung and Barnes (1977) reported that it takes 1.577 g glucose to produce 1 g of needle biomass, or $1/(1 + c_F) = 1/1.577$. For *Pipistem*, we must convert to units of C. Using the conversion factors above, 1.577 g gluc. \times 0.4 g C/g gluc. = 0.631 g C biomass consumed to produce 1 g biomass. 1 g of biomass contains 0.5 g C, so $Y_g = 0.5$ g C/0.631 g C = 1.262. Thus, $c_F = (1/Y_g) - 1 = (1/1.262) - 1 = 0.262$ for this value.

A.3. Maintenance respiration (m_i)

m_i ; $i = F, R, W$.

r_t = total respiration = $m_i + c_i$.

The ratio of maintenance respiration to total respiration (m_i/r_t) was calculated as follows:

$m_i = r_t - c_i$, when $c_i \sim 0.25 \times \text{NPP}$ for the whole plant.

Kinerson et al. (1977) reported $r_t = 2068 \text{ g C m}^{-2} \text{ year}^{-1}$ and $\text{NPP} = 2056 \text{ g C m}^{-2} \text{ year}^{-1}$. Thus, $m_i = r_t - c_i = 2068 - (0.25 \times 2056) = 1554 \text{ g C m}^{-2} \text{ year}^{-1}$, so $m_i/r_t = 0.75$.

For loblolly pine roots, m_R/r_R was calculated as follows:

r_R = total root respiration = $m_R + c_R \propto r_d$.

r_i = annual respiration rates, $i = d$, g for dormant and growing season rates, respectively. Boyer (1971) found $r_d = 14.80$ (5.37) and $r_g = 17.65$ (3.32) for loblolly pine roots in winter and

spring, respectively. Maintenance respiration was assumed proportional to winter respiration, (i.e. $r_d \propto m_R$), and total respiration was assumed proportional to total respiration (maintenance respiration plus constructive respiration).

Thus, $r_d/r_t \propto m_R/m_R + c_R$, so $r_d/r_t = 14.80/(5.37)/17.65$ (3.32) = 0.82 (0.15)^a, where subscript a stands for S.D. calculated in Mood et al. (1974).

Using the ratio of maintenance respiration to total respiration r_d/r_t , maintenance respiration of fine roots, m_R , and foliage, m_F were calculated as follows from data reported in Cropper and Gholz (1991):

r_i = annual respiration rates, $i = R, F$, fine roots and foliage, respectively.

(1) Initial measurements

Needle respiration in *P. elliotii*, at $\sim 20^\circ\text{C}$, reported as $r_F = 0.28$ (0.08) mg CO₂/g biomass h^{-1} , and fine root respiration was $r_R = 0.42$ (0.12) mg CO₂/g biomass h^{-1}

(2) Covert to kg C kg C⁻¹ year⁻¹ (see Biomass Conversions above).

$r_F = 1.34$ (0.38) kg C kg C⁻¹ year⁻¹ and $r_R = 2.01$ (0.57) kg C kg C⁻¹ year⁻¹ at 20°C .

(3) Temperature conversions

All temperature dependent variables were calculated assuming a mean temperature equal to 15°C for the stand. If data used in calculations was reported at temperatures other than 15°C , they were transformed using the following equation from Lavigne and Ryan (1997): $r_T = r_{15}Q_{10}^{(T-15)/10}$, where r_T is the respiration rate at a reference temperature T and r_{15} is the respiration rate at 15°C . Q_{10} values were estimated from Cropper and Gholz (1991), Ryan et al. (1994); Q_{10} foliage = 2.08 (0.13), Q_{10} fine roots = 1.61 (0.32), and Q_{10} wood = 2.14 (0.31).

The temperature difference between the *P. elliotii* stands of Cropper and Gholz (1991) and our model stand was 5°C . We converted estimates to 15°C from 20°C using Q_{10} foliage ~ 1.44 , (calculated as $r_{15} = r_{20}/1.44$) to obtain r_F (15°C) = 0.931 (0.264) g C g C⁻¹ year⁻¹ and r_R (15°C) = 1.59 (0.452) g C g C⁻¹ year⁻¹ using Q_{10} fine roots ~ 1.26 .

(4) Convert to maintenance rates

Use $m_F = r_d/r_t \times r_F$ (15°C) to convert r_F (15°C) to m_F ($r_d/r_t = 0.75$ from above), so $m_F = r_d/r_t \times r_F$

$(15^\circ\text{C}) = 0.75 \times 0.913 (0.317) = 0.698(0.198)$. Similarly, we convert r_R (15°C) to m_R using $r_d/r_t = 0.868(0.132)$ instead, to obtain, $m_R = r_d/r_t \times r_R$ (15°C) = 0.868×1.33 (0.253) = 1.38 (0.445)^a, where subscript a stands for S.D. calculated as described in Section 3; see Mood et al. (1974).

Longevity

v_i = Longevity (years), $i = F, R$.

$v_i \approx \text{residence time} = \text{biomass ha}^{-1}/\text{biomass ha}^{-1} \text{ year}^{-1}$.

Appendix B. Parameter and variable definitions

c_F	Units of C substrate consumed in constructive respiration for production of a unit of foliar dry matter
c_R	Units of C substrate consumed in constructive respiration for production of a unit of fine-root dry matter
c_W	Units of C substrate consumed in constructive respiration for production of a unit of woody dry matter
m_F	Units of C substrate consumed in maintenance respiration per unit foliar dry matter per unit time
m_R	Units of C substrate consumed in maintenance respiration per unit fine-root dry matter per unit time
m_W	Units of C substrate consumed in maintenance respiration per unit live woody dry matter per unit time
s	Units of C substrate produced per unit of unshaded foliar dry matter per unit time
z_F	Units of foliar dry matter per unit cross-sectional area of active pipes
z_R	Units of fine-root dry matter per unit cross-sectional area of active pipes
z_W	Units of dry matter per unit wet volume of woody tissue
v_F	Longevity of foliage
v_R	Longevity of fine roots
ρ	Scaling parameter of the C substrate production rate
λ	Proportion of available substrate allocated to the production and constructive respiration of new active pipes, and foliar and fine-root dry matter.

A	Active pipe area (m^2/ha)
X	Disused pipe area (m^2/ha)
L	Average pipe length (m)
C	Average height to a live crown (m)
D	Average intertree distance (m)
N	Number of trees per hectare (N/ha)
H	Tree height (m)
P, F	Foliar biomass (kg)
R	Fine root biomass (kg)
W	Woody biomass (kg)
W^*	Live wood biomass (kg)

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