A Process-Based Growth Model for the Grass Stage Pine Seedlings

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A carbon- and nitrogen-balance model, applying pipe model theory and a modification of functional balance as growth-guiding rules, is presented for the grass stage pine seedlings. Three populations of *Pinus merkusii* Jungh. et de Vriese, originating from northern and northeastern Thailand, were grown under controlled environment for 47 weeks to obtain parameter information, to evaluate the model performance and to investigate genotypic variation in various characteristics among the populations. Monte Carlo simulations were used to evaluate the sensitivity of the model behaviour to varying parameter values and to calibrate the model for each population.

With given sets of parameter values, the simulated biomass development fitted rather well the observed one during the experiment. The two most important parameters determining model performance were within-shoot shading and specific nitrogen uptake rate of fine roots. The fit of simulated versus measured fine roots had a major effect on acceptable model performance in Monte Carlo simulations. Significant variation in biomass growth, nitrogen use efficiency, height, stem diameter, total carbon concentrations of stem and fine roots, and total nitrogen concentrations of needles, transport roots and fine roots was found among the populations. The observed genotypic variation in seedling biomass and stem diameter was consistent with the geographical distribution of the populations while the variation in the rest of the measured characteristics was not. It seems that *P. merkusii* populations in Thailand are adapted to more site specific conditions rather than climatic conditions alone, and that the variation in biomass growth may result from variation in internal carbon and nitrogen dynamics among the populations.

Keywords grass stage, *Pinus merkusii*, allocation, Monte Carlo simulation, dynamic model

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1 Introduction

Grass stage is an exceptional juvenile growth pattern occurring in several pine species, e.g. *Pinus montezumae* Lamb. and *P. michoacana* Mart. in Mexican highlands (Perry 1991), *P. palustris* Mill. in southeastern United States (Brown 1964), and *P. merkusii* Jungh. et de Vriese in mainland Southeast Asia (Cooling 1968). Following germination subsequently, the grass stage is an initial period of slow shoot growth with inhibited internodal elongation, and it ends when a period of rapid shoot growth with normal internodal elongation begins (Sirikul 1990). In field conditions, the grass stage may last three to five years (*P. merkusii*) (Cooling 1968) or even up to 15 years (*P. palustris*) (Brown 1964) before the rapid shoot growth initiates.

The slowly-developing terminal bud is well protected by long secondary needles and the seedlings also develop a thick secondary cortex in their short, branchless stem. Hence the grass stage has been considered as an adaptation to withstand fire in a seasonal climate (e.g. Cooling 1968). The grass stage increases the probability of the seedlings to survive after a ground fire but it also prolongs the time period the seedlings are susceptible to ground fires. In addition, the grass stage pine seedlings have to compete with ground layer vegetation for several years. Thus this juvenile growth period is a critical phase while regenerating forests of the given pine species.

In fire-dominated environment, nitrogen cycling is strongly affected by fire in several ways of which one is nitrogen loss through volatilisation (Raison 1979, Rundel 1981). Among other functions, nitrogen has an important role in the structural growth of plants (e.g. Kramer and Kozlowski 1979), and nitrogen deficiency decreases the demand for carbohydrates, causing starch accumulation (Birk and Matson 1986). Cooling (1968) reported numerous starch grains in the cells of a secondary cortex of *P. merkusii* seedlings. Adequate carbohydrate storage in the thick secondary cortex may be required before the seedlings emerge from the grass stage since Koskela et al. (1995) observed that shoot length increased as soon as the stem and taproot reached a certain volume. It is unknown to what extent the carbohydrate storing in the grass stage seedlings is under genetic control and what is the role of possible imbalance between carbon intake and nitrogen uptake in the fire-dominated sites.

Sirikul (1990) reported genotypic variation in shoot morphology and in the duration of the grass stage among mainland Southeast Asian populations of *P. merkusii* whereas the insular populations had no grass stage. He found that high-altitude mainland populations exhibit a pronounced and low-altitude ones less pronounced grass stage. It is not known, however, whether possible genotypic variation in biomass growth or allocation during the grass stage among the populations is also related to geographical distribution of the populations.

An analysis of growth during the grass stage should combine i) photosynthesis, ii) nitrogen uptake, and iii) dynamics of non-structural carbon and nitrogen. Process-based modelling approach provides means to combine various physiological processes which result in structural growth. A process-based growth model can be used as a research tool allowing the investigation of the underlying mechanisms of growth (Bossel 1991), and to answer management questions while considering the dynamic nature of biological processes (Battaglia and Sands 1998). In this approach, a plant is seen as a system consisting of state variables which represent different parts of the plant, and which interact with the environment and each other through material flows (e.g. Nikinmaa 1992). Hence, growth results from differences of material flows in and out of different parts of the plant. Resource acquisition from the surrounding environment and the need to transport water from roots to leaves have major effects on these material flows (e.g. Cannell and Dewar 1994).

The aims of this study were (1) to formulate a process-based growth model for the grass stage pine seedlings, (2) to obtain parameter information for the model with a controlled experiment, (3) to analyse the sensitivity of the model behaviour to varying parameter values with Monte Carlo simulations, and (4) to investigate whether possible genotypic variation in biomass growth, structural properties and total carbon and nitrogen concentrations among three populations of *P. merkusii* is consistent with the geographical distribution of the populations.

2 Material and Methods

2.1 The Growth Model

A grass stage seedling is considered to be a dynamic system consisting of state variables such as biomass compartments (needles, branchless stem including wood and bark, transport roots and fine roots), and soluble carbon and nitrogen pools at plant-level. Photosynthesis, respiration, nitrogen uptake, and utilisation of soluble carbon and nitrogen in structural growth were included as physiological processes affecting the rate at which the seedling grows. Carbon and nitrogen flows for structural growth of the different biomass compartments is assumed to take place so that an adequate amount of nitrogen is taken up, and that transpiring biomass and woody structure are in balance. Changes in the state variables were calculated on daily basis.

The model is based on a mass balance approach (e.g. Thornley 1972, de Wit 1978) where the soluble carbon pool, C_p (g C), is determined by daily photosynthesis, P (g C d^{-1}), respiration, R (g C d^{-1}), and carbon utilisation in structural growth, C_g (g C d^{-1}) (Fig. 1):

$$C_p(t) = P - R - C_g + C_p(t-1) \tag{1}$$

The soluble nitrogen pool, N_p (g N), is determined by daily nitrogen uptake, N_d (g N d^{-1}), and nitrogen utilisation in structural growth, N_g (g N d^{-1}):

$$N_p(t) = N_d - N_g + N_p(t-1) \tag{2}$$

Initial sizes of C_p and N_p depend on soluble carbon and nitrogen concentrations, Cs_i and Ns_i (g C or N g^{-1} dry matter (DM)), and sizes of the biomass compartments, W_i (g DM) (i = needles (n), stem (s), transport roots (tr) and fine roots (fr)) :

$$C_p = \sum Cs_i \, W_i \tag{3}$$

$$N_p = \sum Ns_i \, W_i \tag{4}$$

Daily photosynthesis is assumed to be proportional to the daily photosynthesis of unshaded needles, P_d (g C g^{-1} DM d^{-1}), within-shoot shading, s (unitless), and needle biomass, W_n

$$P = P_d \, s \, W_n \tag{5}$$

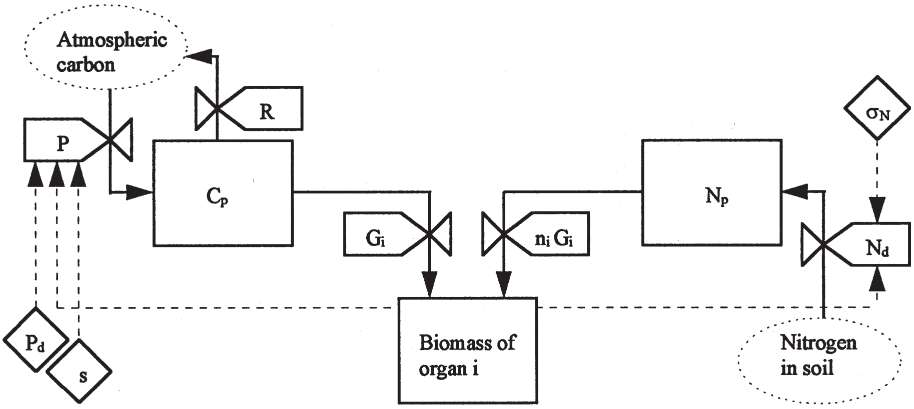

Fig. 1. A schematic presentation of the structure of the growth model. For the sake of clarity only state variables (boxes), material flows (solid lines), and selected information flows (dotted lines) are presented. P and R denote daily photosynthesis and respiration, P_d and s are daily photosynthesis of unshaded needles and within-shoot shading, N_d and σ_N are daily nitrogen uptake and specific nitrogen uptake rates, C_p and N_p are soluble carbon and nitrogen pools, and G_i and $n_i \, G_i$ are carbon and nitrogen used for structural growth of different biomass compartments (i = needles, stem, transport roots and fine roots).

Respiration is divided into maintenance respiration, R_m (g C d^{-1}), and growth respiration, R_g (g C d^{-1}), (e.g. Mäkelä 1986):

$$R = R_m + R_g \tag{6}$$

The amount of daily maintenance respiration is proportional to respiring biomass in each compartment:

$$R_m = \sum r_i W_i \tag{7}$$

where the r_i are compartment specific parameters (g C g^{-1} DM d^{-1}). Growth respiration is proportional to the amount of carbon used for growth:

$$R_g = r_g C_g \tag{8}$$

where r_g is a parameter (g C g^{-1} C). The daily amount of carbon used for growth is assumed to be proportional to C_p:

$$C_g = b\, C_p \tag{9}$$

where b is a parameter (unitless). Nitrogen uptake is proportional to fine root biomass W_{fr} and specific nitrogen uptake rate σ_N (g N g^{-1} DM d^{-1}):

$$N_d = \sigma_N\, W_{fr} \tag{10}$$

Size of a biomass compartment at a certain moment is:

$$W_i(t) = W_i(t-1) + \Delta W_i(t) \tag{11}$$

in which ΔW_i is a compartment specific change in dry matter:

$$\Delta W_i = Ctot_i^{-1}\, \eta_i\, C_g \tag{12}$$

where $Ctot_i$ are the total carbon concentrations of biomass compartments and η_i are the proportions of C_g which are allocated to each biomass compartment. Considering the time scale of the present study, it was assumed that no senescence took place during the experiment.

Stem biomass is derived using the geometric dimensions (e.g. Mäkelä 1986):

$$W_s = \phi\, \rho\, h\, A_s \tag{13}$$

where ϕ (unitless) is an empirical stem form coefficient, ρ (g DM mm^{-3} DM) the wood density, h is the seedling height, and A_s (mm^2) is the sapwood cross sectional area below the needles. According to the pipe model theory (Shinozaki et al. 1964) which implies functional interconnections between different parts of a tree (e.g. Kaipiainen and Hari 1985, Hari et al. 1986, Mäkelä 1986), the sapwood area at a certain height and needle mass above this point can be related using a constant ratio ε_s (mm^2 g^{-1} DM):

$$A_s = \varepsilon_s\, W_n \tag{14}$$

Applying the same principle, transport root mass and needle mass can also be related using a constant ratio ε_{tr} (g DM g^{-1} DM):

$$W_{tr} = \varepsilon_{tr}\, W_n \tag{15}$$

In addition, it is assumed that height of a seedling during the grass stage is proportional to needle mass:

$$h = h_0 + \beta\, W_n \tag{16}$$

where h_0 (mm) is initial height after germination is completed and β (mm g^{-1} DM) is a height growth parameter.

The total amount of carbon used for structural growth, C_g can be written as a sum of carbon allocated to the different biomass compartments, G_i (g C d^{-1}):

$$C_g = G_n + G_s + G_{tr} + G_{fr} \tag{17}$$

and the total amount of nitrogen used in growth, N_g depends on the amounts of carbon allocated to different biomass compartments:

$$N_g = n_n G_n + n_s G_s + n_{tr} G_{tr} + n_{fr} G_{fr} \tag{18}$$

where n_i (g N g^{-1} C) are organ specific nitrogen requirements in structural growth. The concept of functional balance (Brouwer 1962, Davidson 1969), which implies that carbohydrates are distributed between shoot and root growth so that the internal nutrient concentration remains stable, has been used as a growth-guiding rule in tree growth models (e.g. Mäkelä 1986, Nikinmaa 1992). It can be assumed that the metabolically active organs of a tree, needles and fine roots, take first priority in the utilisation of carbohydrates (e.g. Cannell and Dewar 1994), and that carbohydrates are distributed for fine root and needle growth so that the ratio of soluble nitrogen and carbon pools (N_p:C_p) remains stable (cf. Thornley 1972, Reynolds and Thornley 1982, Mäkelä and Sievänen 1987). Hence the assimilation of carbon and the acquisition of nutrients should be in balance with the utilisation of these elements in growth (i.e. a tree maintains the amount of fine roots which is required for sufficient nitrogen uptake).

The portion of C_g which is first distributed between the metabolically active organs is denoted as C_a (g C d^{-1}) This is an auxiliary term and it is reduced from the equations when solving allocation coefficients. Thus the amounts of carbon allocated to fine root and needle growth are:

$$G_{fr} = z\ C_a \tag{19}$$

$$G_n = (1-z)\ C_a \tag{20}$$

where the multiplier z varies according to changes in N_p:C_p ratio. The amount of carbon allocated to stem is

$$G_s\ =\ \phi\,\rho\,(\Delta A_s h + \Delta h A_s) \tag{21}$$

As sapwood and height growth are proportional to growth of needle mass, ΔA_s and Δh are

$$\Delta A_s = \varepsilon_s\, G_n \tag{22}$$

$$\Delta h = \beta\, G_n \tag{23}$$

and the amount of carbon allocated to transport roots is

$$G_{tr} = \varepsilon_{tr}\, G_n \tag{24}$$

Allocation coefficients, η_i, can be solved including equations 19, 20, 21 and 24 into the carbon balance (equation 17):

$$\eta_n = \frac{1}{1+\phi\,\rho\left(\varepsilon_s\ h+\beta A_s\right)+\varepsilon_{tr}+\dfrac{z}{1-z}} \tag{25}$$

$$\eta_s = \frac{\phi\,\rho\left(\varepsilon_s\ h+\beta A_s\right)}{1+\phi\,\rho\left(\varepsilon_s\ h+\beta A_s\right)+\varepsilon_{tr}+\dfrac{z}{1-z}} \tag{26}$$

$$\eta_{tr} = \frac{\varepsilon_{tr}}{1+\phi\,\rho\left(\varepsilon_s\ h+\beta A_s\right)+\varepsilon_{tr}+\dfrac{z}{1-z}} \tag{27}$$

$$\eta_{fr} = \frac{z}{(1-z)+(1-z)\phi\,\rho\left(\varepsilon_s\ h+\beta A_s\right)+\varepsilon_{tr}(1-z)+z} \tag{28}$$

It is known that the root proportion of total plant biomass increases almost linearly when nitrogen availability decreases to sub-optimal levels (e.g. Ingestad 1979, Ingestad and Lund 1979), and that nitrogen deficiency affects decreasingly the ratio between non-structural nitrogen and carbon substrates (e.g. Green et al. 1994). In this study, it is assumed that the multiplier z depends on the N_p:C_p ratio as follows (Fig. 2):

$$z\ =\ \begin{cases} 1 & if\ N_p\!:C_p \le 0.015 \\ -38.4\left(N_p\!:C_p\right)+1.6 & if\ \ 0.015 < N_p\!:C_p < 0.04 \\ 0.04 & if\, N_p\!:C_p \ge 0.04 \end{cases} \tag{29}$$

The more detailed assumptions and calculations to determine z and the initial values of N_p and C_p at the beginning of the simulations are given in Appendix 1. The presented process-based growth model, applying pipe model theory and a modification of functional balance as growth-guiding rules, includes totally 34 parameters and one multiplier.

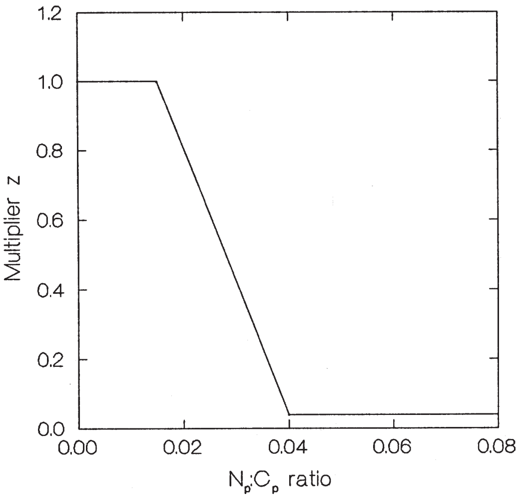

Fig. 2. Dependence of multiplier *z* on N_p:C_p ratio which controls carbon allocation between needles and fine roots.

2.2 Plant Material

Seeds of three Thai populations of *P. merkusii* (Table 1) were germinated in containers filled with a sand-peat mixture (1:1) in a walk-in growth chamber. The Huey Bong (HB) population from northern Thailand represented the high-altitude populations with pronounced grass stage pattern whereas the Khong Chiam (KC) and Sangkha (S) populations from northeastern Thailand represented the low-altitude populations with intermediate pattern (cf. Sirikul 1990). Germinated seedlings were transplanted into 40 cm-long PVC tubes (5.5 litres) filled with homogenized sand (grain size 0.1–0.6 mm) and thereafter fertilized once a week by applying 50 ml of a nutrient solution with a 0.1 % concentration of a nitrogen poor fertilizer (9-25-20, N-P_2O_5-K_2O). Irrigation was arranged through small holes at the bottom of the pots which were kept in continuous contact with water. Soil water potential was measured with standard jet-fill tensiometers (model 2725, Eijkelkamp, Giesbeek, The Netherlands) at depths of 15 and 30 cm in four pots. Soil water potential remained fairly constant throughout the growing period at both depths, approximately at 600 and 400 Pa, respectively.

The daily photoperiod consisted of 11 hours with a constant irradiance level of approximately 200 µmol m^{-2} s^{-1} and one-hour transition periods at the beginning and the end of the constant period. Air temperature during the photoperiod was kept at 26 °C ± 1 °C and during the dark period, at 18 °C ± 1 °C. Relative air humidity was set to 60 % ± 10 % and 70 % ± 10 %, during the light and dark periods, respectively.

At the age of 23, 29, 35, 41, and 47 weeks, four seedlings per population were harvested and separated into needles, stems, transport roots, and fine roots (defined as nonwoody, unsuberized or suberized roots with a diameter of 1 mm or less, cf. Kramer and Kozlowski 1979). While harvesting the seedlings, height, stem and sapwood diameters and length of the taproot were measured. Biomass compartments were dried to a constant mass at 105 °C (24 h) and weighed.

Total carbon and nitrogen concentrations were measured from samples of homogenised needles, stem, and transport roots per seedling with an elemental analyser (CHN-900, Leco CO., St Joseph, MI, USA) whereas all fine roots per seedling, due to the small dry mass, were composited and analysed using an another elemental analyser (CNS-1000) which requires less sample material.

Table 1. Seed origin of the three populations of *Pinus merkusii* from Thailand used in the study.

Geographical location	Latitude	Longitude	Elevation (m)	Annual rainfall (mm)
Khong Chiam, Ubon Ratchatani 1)	15°28' N	105°30' E	150	2100
Sangkha, Surin 1)	14°41' N	103°46' E	160	1300
Huey Bong, Hot 2)	18°10' N	98°25' E	800	1300

Seed source: 1) Danida Forest Seed Centre, Denmark 2) Royal Forest Department, Thailand

Table 2. List of symbols used in the growth model.

Name	Notation	Unit
Soluble carbon pool	C_p	g C
Daily photosynthesis	P	g C d^{-1}
Respiration	R	g C d^{-1}
Maintenance and growth respiration	R_m, R_g	g C d^{-1}
Carbon utilisation in structural growth	C_g	g C d^{-1}
Carbon used for growth of biomass compartments, i = needles, stem, transport roots and fine roots	G_i	g C d^{-1}
The portion of C_g for needles and fine roots	C_a	g C
The proportion of C_a for fine roots	z	unitless
Allocation coefficients	η_i	unitless
Biomass compartments	W_i	g DM
Soluble nitrogen pool	N_p	g N
Daily nitrogen uptake	N_d	g N d^{-1}
Nitrogen utilisation in structural growth	N_g	g N d^{-1}
Initial height	h_0	mm
Height	h	mm
Sapwood cross sectional area	A_s	mm^2

2.3 Sensitivity Analysis of the Growth Model

List of symbols used in the growth model is presented in Table 2. The Monte Carlo simulation method (e.g. Spear and Hornberger 1980, Hornberger and Spear 1981, Hornberger and Cosby 1985) was applied for calibration and sensitivity analysis of the growth model. One Monte Carlo simulation consisted of 500 runs for a population. The behaviour of the model is determined by 14 parameters (Table 3) which were varied stochastically in each run, while other parameters of lesser importance (Table 4) were assigned constant values. For each run, values of these 14 parameters were randomly assigned from *a priori* uniform distributions which were selected based on the results of the present experiment and the literature. The model was run using the selected parameter values, and the resulting model output and the parameter values were stored. The initial state of the model was fixed to correspond to the amount of biomass at the age of 23 weeks in each run.

After 500 runs, the results were classified according to a performance criterion into accepted or rejected subsets. As a performance criterion, it was required that model output simultaneously explain 85 % or more of the variances in needle, stem and transport root biomasses, and 65 % or more of the variance in fine root biomass during the experiment. In case of fine roots, the lower criterion was selected due to the identifying problems, which introduced additional variation in the measured fine root biomass. The fine root biomass values of five seedlings were considered to be outliers and excluded from the data before the calibration of the model, as recommended by Janssen and Heuberger (1995).

The two subsets were used to examine the importance of the parameters to model performance. Accepted and rejected subsets of the parameters do not differ from each other for non-important parameters. The more important a parameter is to model performance, the more the accepted and rejected parameter distributions differ from each other. The sensitivity analysis was based on the comparison of the cumulative distributions of the two subsets with Kolmogorov-Smirnov two-sample test. If the accepted and rejected parameter sets differed ($P \leq 0.05$), the *a priori* distribution was narrowed according to the results, and a new Monte Carlo simulation was conducted. This was repeated until no differences were found between the accepted and rejected parameter sets.

Table 3. Parameters of the model which were varied in the Monte Carlo simulations.

The parameter	Notation	Unit	Initial range	Source
Daily photosynthesis of unshaded needles	P_d	g C g^{-1} DM d^{-1}	0.023–0.036	Estimated, Koskela et al. 1999
Shading	s	unitless	0.4–1.0	Estimated, Stenberg 1995
Daily utilisation of carbon pool	b	d^{-1}	0.01–0.25	Estimated
Growth respiration	r_g	g C g^{-1} C	0.2–0.3	Estimated, Sprugel et al. 1995
Maintenance respiration:				
needles	r_n	g C g^{-1} DM d^{-1}	0.005–0.01	Estimated, Koskela et al. 1999
stem	r_s	g C g^{-1} DM d^{-1}	0.0005–0.001	Estimated, Ryan et al. 1994
transport roots	r_{tr}	g C g^{-1} DM d^{-1}	0.0005–0.001	Estimated, Ryan et al. 1994
fine roots	r_{fr}	g C g^{-1} DM d^{-1}	0.005–0.05	Estimated, Ryan et al. 1994
Specific nitrogen uptake rate	σ_N	g N g^{-1} DM d^{-1}	0.001–0.01	Estimated
Stem form coefficient	ϕ	unitless	1.8–3.0	This study
Wood density	ρ	kg DM m^{-3} DM	440–460	This study
Sapwood area: needle mass ratio	ε_s	mm^2 g^{-1} DM	3.4–4.1	This study
Transport root : needle mass ratio	ε_{tr}	g DM g^{-1} DM	0.46–0.52	This study
Shoot growth per new foliage	β	mm g^{-1} DM	18.0–22.0	This study

Table 4. Parameters of the model which were assigned constant values in the Monte Carlo simulations.

The parameter	Notation	Unit	Value	Source
Total carbon content:				
needles	$Ctot_n$	g C g^{-1} DM	0.47	This study
stem	$Ctot_s$	g C g^{-1} DM	0.47	This study
transport roots	$Ctot_{tr}$	g C g^{-1} DM	0.30	This study
fine roots	$Ctot_{fr}$	g C g^{-1} DM	0.27	This study
Soluble carbon content:				
needles	Cs_n	g C g^{-1} DM	0.035	Estimated, Chung and Barnes 1977
stem	Cs_s	g C g^{-1} DM	0.028	Estimated, Chung and Barnes 1977
transport roots	Cs_{tr}	g C g^{-1} DM	0.028	Estimated, Chung and Barnes 1977
fine roots	Cs_{fr}	g C g^{-1} DM	0.028	Estimated, Chung and Barnes 1977
Total nitrogen content:				
needles	$Ntot_n$	g C g^{-1} DM	0.02	This study
stem	$Ntot_s$	g C g^{-1} DM	0.01	This study
transport roots	$Ntot_{tr}$	g C g^{-1} DM	0.006	This study
fine roots	$Ntot_{fr}$	g C g^{-1} DM	0.008	This study
Soluble nitrogen content:				
needles	Ns_n	g C g^{-1} DM	0.0017	Estimated, Chung and Barnes 1977
stem	Ns_s	g C g^{-1} DM	0.0008	Estimated, Chung and Barnes 1977
transport roots	Ns_{tr}	g C g^{-1} DM	0.0008	Estimated, Chung and Barnes 1977
fine roots	Ns_{fr}	g C g^{-1} DM	0.0008	Estimated, Chung and Barnes 1977
Nitrogen used in structural growth:				
needles	NC_n	g N g^{-1} C	0.042	Estimated
stem	NC_s	g N g^{-1} C	0.021	Estimated
transport roots	NC_{tr}	g N g^{-1} C	0.023	Estimated
fine roots	NC_{fr}	g N g^{-1} C	0.030	Estimated

2.4 Statistical Analysis

Variation in the size of the biomass compartments and structural properties (i.e. root:shoot ratio, nitrogen use efficiency (NUE) of the whole seedling, height, stem diameter, taproot length), and total carbon and nitrogen concentrations among the populations were analysed using two-way analysis of variance. The arcsin transformation was made for root:shoot ratios before the test. The hypothesis was that the populations do not differ in any of these characteristics from each other during the experiment. If a test rejected the hypothesis, Tukey's HSD-test was used for pairwise comparisons.

The linear relationships of sapwood cross sectional area, transport root mass and height to needle mass was tested with analysis of regression. In addition, it was also tested, using analysis of covariance, whether the regression coefficients differed among the populations.

3 Results

3.1 Biomass Growth and Structural Properties

Biomass growth during the experiment is presented in Fig. 3. There was statistically significant variation in all biomass compartments among the populations (Table 5). In case of needles, stem and transport roots, the northern HB had more biomass than the two northeastern populations ($P < 0.05$) while KC and S differed in fine root biomass ($P < 0.01$). No statistically significant interactions (population × time) were found in the biomass compartments.

There was no statistically significant variation in root:shoot ratio or in taproot length among the populations (Table 6). At the end of the experiment, mean root:shoot ratio varied from 0.43 to 0.48, and mean taproot length from 39.0 to 40.6 cm. The formation of deep taproot was distinct in

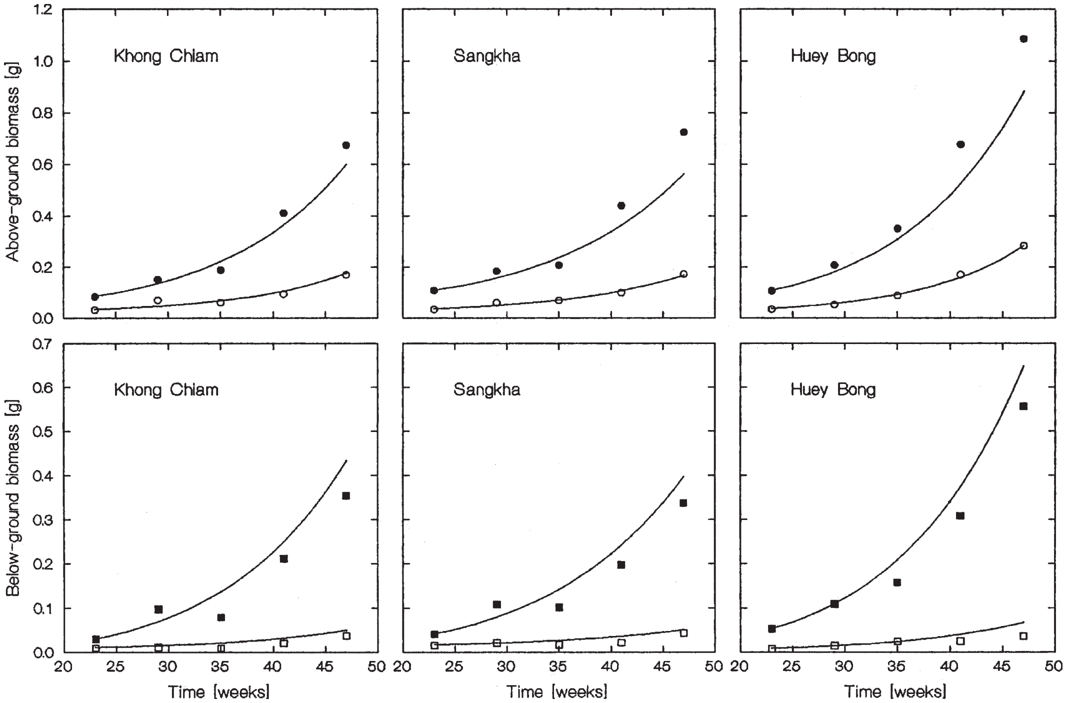

Fig. 3. Measured (● needles, ○ stem, ■ transport roots, □ fine roots) and simulated (continuous lines) biomass of three populations of *Pinus merkusii* seedlings as a function of time during the experiment. Mean parameter values for each population (Table 8) were used in the simulations.

Table 5. Analysis of variance for biomass compartments.

Source	SS	DF	MS	F-ratio	P
Needle biomass					
Population	0.386	2	0.193	8.071	0.001
Time	4.235	4	1.059	44.282	<0.001
Population × time	0.255	8	0.032	1.336	0.251
Error	1.076	45	0.024		
Stem biomass					
Population	0.021	2	0.011	6.001	0.005
Time	0.228	4	0.057	32.291	<0.001
Population × time	0.029	8	0.004	2.084	0.057
Error	0.079	45	0.002		
Transport root biomass					
Population	0.088	2	0.044	4.437	0.017
Time	1.061	4	0.265	26.812	<0.001
Population × time	0.074	8	0.009	0.936	0.497
Error	0.445	45	0.010		
Fine root biomass					
Population	0.001	2	0.001	5.307	0.009
Time	0.004	4	0.001	9.859	<0.001
Population × time	0.002	8	<0.001	2.018	0.066
Error	0.005	45	<0.001		

all populations already at the first harvesting time when mean tap root length was 34.0–35.8 cm.

Statistically significant variation in nitrogen use efficiency (NUE), height and stem diameter was found among the populations (Table 6). KC and HB differed in NUE and height ($P < 0.05$), and HB and the other two populations in stem diameter ($P < 0.05$). At the end of the experiment, mean NUE ranged from 68.7 to 72.9 g DM g^{-1} N, height from 7.4 to 8.3 cm, and stem diameter from 3.2 to 4.2 mm among the populations.

There were clear linear relationships between sapwood cross sectional area and needle mass, and between transport root mass and needle mass (Table 7). The linear regression models resulted high proportions of explained variance ($r^2 = 0.91$ or higher) for both relationships in all populations. Sapwood cross sectional area:needle mass ratio, ε_s, varied from 3.47 to 3.97 mm^2 g^{-1} DM, and transport root mass:needle mass ratio, ε_{tr}, varied from 0.47 to 0.51 mm^2 g^{-1} DM. No statistically significant variation in ε_s or ε_{tr} was found among the populations.

The linear relationship between height and needle mass was not as clear as the above mentioned relationships (Table 7). In this case, the linear regression model resulted in considerably smaller proportions of explained variance ($r^2 = 0.32$–0.63). The height growth parameter b varied from 19.5 to 22.8 mm g^{-1} DM among populations but the variation was insignificant.

3.2 Carbon and Nitrogen Concentrations

Total carbon concentrations in needles and stems were rather constant throughout the experiment whereas the concentrations in roots showed variation (Fig. 4). Mean carbon concentration in needles varied between 46.0–48.2 % of dry mass, and the differences were not statistically significant among the populations. At the age of 35 weeks, carbon concentration in needles was higher than at the first two harvesting time ($P < 0.01$). In stems, mean carbon concentration ranged from 45.8 to 47.6 % and statistically significant variation among populations ($P < 0.01$) and among

Table 6. Analysis of variance for structural properties.

Source	SS	DF	MS	F-ratio	P
Root:shoot ratio					
Population	0.012	2	0.006	0.559	0.575
Time	0.057	4	0.014	1.273	0.295
Population × time	0.082	8	0.010	0.918	0.511
Error	0.501	45	0.011		
NUE					
Population	940.953	2	470.477	4.634	0.015
Time	567.029	4	141.757	1.396	0.251
Population × time	2031.400	8	253.925	2.501	0.024
Error	4568.390	45	101.520		
Height					
Population	566.306	2	283.153	4.614	0.015
Time	2333.005	4	583.251	9.504	<0.001
Population × time	544.112	8	68.014	1.108	0.376
Error	2761.603	45	61.369		
Stem diameter					
Population	2.433	2	1.217	5.289	0.009
Time	36.912	4	9.228	40.112	<0.001
Population × time	1.872	8	0.234	1.017	0.437
Error	10.353	45	0.230		
Taproot length					
Population	4364.933	2	2182.467	2.322	0.110
Time	20547.767	4	5136.942	5.466	0.001
Population × time	876.233	8	109.529	0.117	0.998
Error	42291.250	45	939.806		

Table 7. Regression equations for relatioship between sapwood cross sectional area [mm^2] and needle mass [g], transport root mass [g] and needle mass, and height [mm] and needle mass in three populations of *Pinus merkusii*.

Variable	Population	Equation	r^2
Sapwood area	Khong Chiam	$A_s = 3.97\ W_n$	0.95
	Sangkha	$A_s = 3.97\ W_n$	0.96
	Huey Bong	$A_s = 3.47\ W_n$	0.97
Transport root mass	Khong Chiam	$W_{tr} = 0.51\ W_n$	0.96
	Sangkha	$W_{tr} = 0.47\ W_n$	0.99
	Huey Bong	$W_{tr} = 0.49\ W_n$	0.91
Height	Khong Chiam	$h = 55.3 + 22.8\ W_n$	0.32
	Sangkha	$h = 59.5 + 21.6\ W_n$	0.22
	Huey Bong	$h = 60.2 + 19.5\ W_n$	0.63

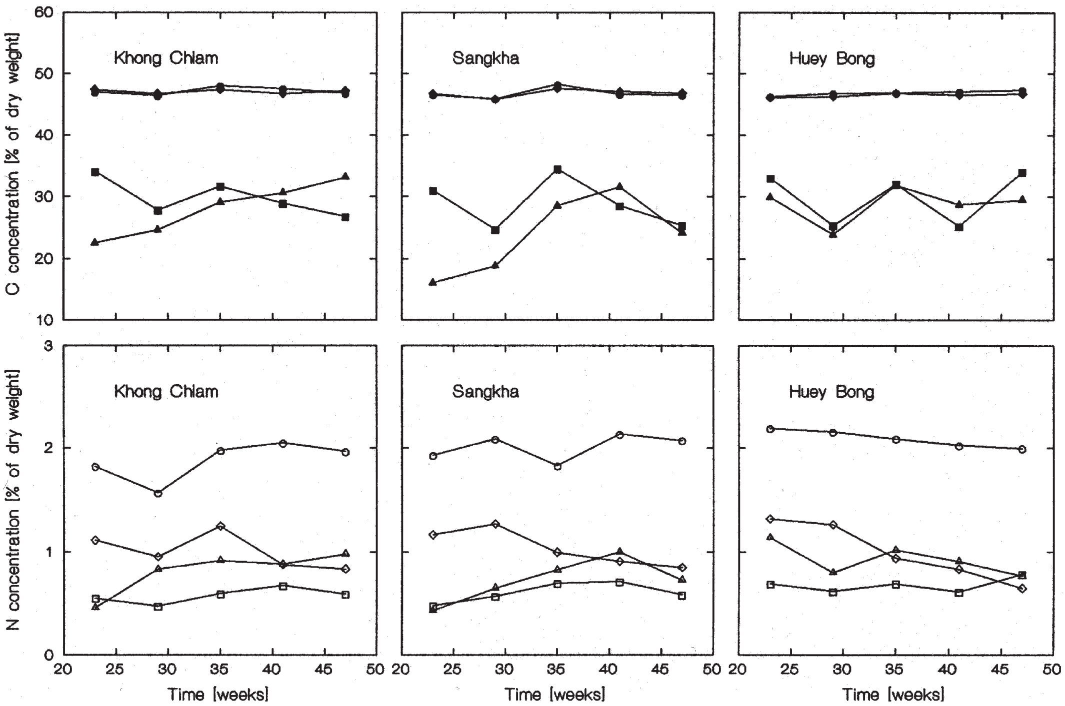

Fig. 4. Carbon (filled symbols) and nitrogen (open symbols) concentrations of biomass compartments (● needles, ◆ stem, ■ transport roots and ▲ fine roots) as a function of time during the experiment in three populations of *Pinus merkusii*.

harvesting times ($P < 0.001$) was found. However, only KC and HB had different carbon concentration in their stems. At the age of 29 weeks, carbon concentration in stem was lower than six weeks later, and at the end of the experiment.

Total carbon concentrations in transport and fine roots were considerably lower than in the above-ground biomass. Mean carbon concentrations in transport roots ranged from 24.8 and 34.5 %, and the differences were not statistically significant among the populations. Time had significant effect on carbon concentration in transport roots ($P < 0.001$). In fine roots, mean carbon concentration varied from 16.1 to 33.1 %, and the variation among populations was statistically significant ($P < 0.01$). S had lower concentration than other populations ($P < 0.05$). Time also had significant effect on the carbon concentration in fine roots ($P < 0.001$).

Mean nitrogen concentration in needles ranged from 1.6 to 2.2 %, and variation in the concentration was statistically significant among populations ($P < 0.01$). HB had significantly higher concentration than KC ($P < 0.01$), and there was also significant interaction (population × time) ($P < 0.05$). Mean nitrogen concentration in stem was 0.6–1.3 %, and no statistically significant variation was found among the populations. Time had significant effect on nitrogen concentration in stem ($P < 0.001$).

In transport roots, mean nitrogen concentration varied between 0.5–0.8 %, and both population ($P < 0.01$) and time ($P < 0.05$) had statistically significant effect on it. Only HB and S differed significantly ($P < 0.01$). The interaction was also significant ($P < 0.05$). In fine roots, mean nitrogen concentration ranged from 0.4–1.1 %. Both population and time had significant effect on the nitrogen concentration in fine roots ($P < 0.01$). HB had higher concentration than S ($P < 0.01$). The interaction also had significant effect on the nitrogen concentration in fine roots ($P < 0.001$).

3.3 Sensitivity Analysis of the Growth Model

The results of the Monte Carlo simulations are presented in Table 8, and the fit of the simulated to measured biomass growth during the experiment is presented in Fig. 3 (using mean parameter values from Table 8). Using the given *a priori* distributions, the two most important parameters determining model performance were within-shoot shading (s) and specific nitrogen uptake rate (σ_N). After these, with varying ranking among the populations, were daily utilisation of the carbon pool (b), daily photosynthesis of unshaded needles (P_d), maintenance respiration of transport roots (r_{tr}), and transport root mass:needle mass ratio (ε_{tr}). The ranking was calculated as a ratio between the initial and final range of a given parameter. The rest of the parameters were not important in determining performance of the model within the given parameter ranges. It should be kept in mind, however, that the results of the sensitivity analysis depend on the selected *a priori* distributions of the parameters.

The Monte Carlo simulations with 500 runs were repeated four times in KC, three in S, and six in HB before no differences were observed between the accepted and rejected subsets of the parameters. The simulated needles, stem, and transport roots often fulfilled the performance criteria for acceptance, while the simulated fine roots caused a rejection. Thus, the final parameter ranges in the last simulation resulted in rather low proportions of accepted runs; 19.2, 8.6 and 18.8 % in KC, S and HB, respectively. The considerable low proportion of accepted runs in case of S was due to a slightly higher variation in the measured fine root biomass as compared with the other populations.

There was obvious negative correlation in the final parameter sets of all populations between shading (s) and daily photosynthesis of unshaded needles (P_d) (Spearman rank correlation coefficients were –0.59, –0.64 and –0.76 for KC, S and HB, respectively), while the correlations between other parameters were less significant. Linear regression analyses showed that P_d explained ca. 34, 42 and 56 % of the variation in s. When the correlations were included into the stochastic parameter input, the acceptance percentages increased to 27.4, 12.8, and 43.2 % in KC, S and HB, respectively.

Table 8. Results of the Monte Carlo simulations (see Table 2 for the definitions of the parameters).

	Final distributions														
	Khong Chiam					Sangkha					Huey Bong				
Parameter	Min.	Max.	Mean	Comparison with initial		Min.	Max.	Mean	Comparison with initial		Min.	Max.	Mean	Comparison with initial	
				%	Rank				%	Rank				%	Rank
P_d	0.024	0.035	0.029	85	4	0.023	0.035	0.029	92	4	0.024	0.036	0.029	92	6
s	0.69	0.98	0.83	41	1	0.68	0.97	0.81	41	1	0.66	0.96	0.81	43	2
b	0.02	0.15	0.09	93	5	0.02	0.13	0.07	79	3	0.06	0.14	0.10	57	3
r_g	0.20	0.30	0.25	100		0.20	0.30	0.25	100		0.20	0.30	0.25	100	
r_n	0.005	0.010	0.008	100		0.005	0.010	0.008	100		0.005	0.010	0.007	100	
r_s	0.0005	0.0010	0.0007	100		0.0005	0.0010	0.0008	100		0.0005	0.0010	0.0007	100	
r_{tr}	0.0005	0.0009	0.0007	80	3	0.0005	0.0010	0.0007	100		0.0005	0.0009	0.0007	80	4
r_{fr}	0.005	0.050	0.027	100		0.005	0.050	0.031	100		0.005	0.050	0.027	100	
σ_N	0.003	0.010	0.006	78	2	0.003	0.010	0.007	78	2	0.008	0.010	0.009	22	1
ϕ	1.8	3.0	2.4	100		1.8	3.0	2.4	100		1.8	3.0	2.4	100	
ρ	440	460	450	100		440	460	450	100		440	460	450	100	
ε_s	3.4	4.1	3.8	100		3.4	4.1	3.7	100		3.4	4.1	3.7	100	
ε_{tr}	0.46	0.52	0.49	100		0.46	0.52	0.49	100		0.46	0.51	0.48	83	5
β	18.0	22.0	20.0	100		18.0	22.0	20.1	100		18.0	22.0	20.1	100	

4 Discussion

The presented process-based growth model for the grass stage pine seedlings was calibrated for three population of *P. merkusii* grown under controlled environment. With given sets of parameter values, the simulated growth of the biomass compartments fitted rather well the observed biomass growth during the experiment. The simulated height development, however, did not fit the observed one as well as biomass development. This was because the linear regression model did not explain well enough the relationship between height and needle mass. Thus this relationship requires more attention while improving and testing the model with field data.

The results indicate that the two most critical parameters for acceptable model performance were within-shoot shading and specific nitrogen uptake rate of fine roots. The two parameters have major effects on simulated photosynthesis and nitrogen uptake; processes that largely determine the ratio between soluble nitrogen and carbon pools which regulate carbon allocation according to the present model structure. Hence Monte Carlo simulations identified the most critical component in the model structure affecting acceptable model behaviour. Excess water and nitrogen supply allowed seedlings to exhibit steady-state growth during the experiment. Therefore, the accepted parameter combinations, especially shading and specific nitrogen uptake rate, were those which kept the N_p:C_p ratio high enough.

One of the major problems in calibrating models is the imbalance between the complexity of the model and the availability of the data (Janssen and Heuberger 1995). In the present study, the complexity of the model was low and the experiment was purposely planned to produce relevant data to enable the sensitivity analysis with quantitative misfit measures. The analysis as applied here is more concerned with parameter estimation than testing the model structure (e.g. Fedra et al. 1981). Therefore, it remains to be tested how well the model performance will fit biomass data under low nitrogen availability. In that case, the amount of simulated fine roots would increase at the expense of needles, subsequently decreasing carbon allocation to stem and transport roots. This is realistic behaviour according to the present knowledge of tree growth dynamics.

The most stringent subcriteria for an acceptable model output during the sensitivity analysis was the fit of the simulated fine root growth to observed growth. This highlights the importance of the selection of the performance criteria so that they are relevant from a model structure point of view. In addition, data for a performance criterion should be accurately measurable. In case of fine roots, more inaccuracy will always remain in measured data than in other biomass compartments, even in a laboratory study. This should be taken into account when selecting the performance criteria.

In the present model, nitrogen acquisition, and ultimately the N_p:C_p ratio, depends not only specific uptake rate, but also the amount of fine roots. Thus it is logical that calibration of the growth model is highly dependent on the fit between simulated and measured fine roots. If only the above-ground biomass growth had been selected as a performance criterion, lower values of specific nitrogen uptake rate would have been accepted provided that enough carbon was available for more intensive fine root growth.

Under natural conditions in northern Thailand, the grass stage *P. merkusii* seedlings have been observed to form a deep taproot (Koskela et al. 1995). Despite the excess water availability, the formation of the deep taproot was also distinct in this study. All seedlings allocated most of their biomass into needles and transport roots while less biomass was allocated into stem and fine roots. In an another grass stage pine, *P. palustris*, Prior et al. (1997) found that low nitrogen availability increased root:shoot ratio due to increased allocation to taproots and fine roots, whereas water stress had little effect on the ratio. The same authors concluded that soil nitrogen availability was the overall controlling resource concerning the growth of *P. palustris* seedlings. This statement may also be true in *P. merkusii* since both species are adapted to frequent fire occurrence and low nitrogen availability in their natural environment. The deep taproot growth habit of the grass stage pine seedlings seems to be independent of water availability, and thus it is obviously under a genetic control.

It is likely that fine root growth was slow due to high nitrogen availability during the experiment. The rather low values of NUE (cf. Sheppard and Cannell, 1985) also indicate this since NUE decreases as nitrogen availability increases (Birk and Vitousek, 1986). High nitrogen availability also explains why the seedlings allocated a rather low proportion of total biomass into the stem. No thick secondary cortex, characteristic of field-grown seedlings, was formed during the experiment. This suggests that no large carbohydrate storage was accumulated into the stem since there was sufficiently nitrogen available for structural growth.

Sirikul (1990) reported that *P. merkusii* populations from northern Thailand exhibited slower shoot development during the grass stage than the northeastern ones. In this study, however, the northern population (HB) did not exhibit the slowest height growth of all populations. Thus the classification of the mainland Southeast Asian *P. merkusii* populations into short- and long-lasting grass stage populations solely based on altitude or geographical distribution may not always hold.

Genotypic variation was observed in biomass growth, NUE, height, stem diameter, total carbon concentrations of stem and fine roots, and total nitrogen concentrations of needles, transport roots and fine roots among the populations during the experiment. The northern HB population had more biomass and larger stem diameter than the two northeastern populations. In case of other characteristics, the variation was not consistent with the geographical distribution of the populations. Considering the parameter distributions, the final ranges of the parameter b and σ_N were somewhat narrower in HB than in other populations after Monte Carlo simulations. Thus it seems that *P. merkusii* populations in Thailand are adapted to more site specific conditions rather than climatic conditions alone, and that the variation in growth may result from variation in internal carbon and nitrogen dynamics among the populations.

In conclusion, first-year simulated biomass development, produced by the presented process-based growth model with certain parameter sets, fitted rather well with the observed biomass development in three *P. merkusii* populations. Monte Carlo simulations revealed that the most important parameters affecting model behaviour were within-shoot shading and specific nitrogen uptake rate of fine roots. The observed genotypic variation in seedling biomass and stem diameter among *P. merkusii* populations was consistent with the geographical distribution of the populations while the variation in the rest of the measured characteristics was not.

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Appendix 1

Estimation of Initial Soluble Carbon and Nitrogen Pools

Estimation of the initial amount of soluble carbon and nitrogen pools of the whole seedling is based on chemical compositions of *Pinus taeda* L. shoots (Chung and Barnes 1977). The soluble nitrogen pool was assumed to consist of amino acids and nucleic acids (0.86 % of dry needle biomass (DNB) and 0.38 % of dry axis biomass (DAB)), and the soluble carbon pool was assumed to consist of sucrose, reducing sugars and organic acids (making totally 8.8 % of DNB and 6.9 % of DAB). Proteins and starch were considered as non-structural insoluble components (Chung and Barnes 1977).

The above mentioned values of soluble nitrogen and carbon concentration in DAB were applied for stems, transport roots, and fine roots. The amount of nitrogen and carbon (% of dry mass) in soluble pools was calculated assuming that the average nitrogen concentration of the soluble nitrogen substrates is 20 % and that the average carbon concentration of the soluble carbon substrates is 40 %. This implies that the concentration of soluble nitrogen is 0.17 % of dry mass in needles and 0.08 % in other biomass compartments and the concentrations of soluble carbon are 3.5 % and 2.8 %, respectively. These values were then used for calculating the initial sizes of total soluble nitrogen (N_p) and carbon (C_p) pools and the dependence of the multiplier z on the N_p:C_p ratio.

Calculation of the Dependence of z on the N_p:C_p Ratio

As the seedlings were grown under adequate nitrogen availability throughout the experiment, it was assumed that seedlings would minimize the amount of carbon allocated to fine roots while still taking up sufficient amount of nitrogen to keep the N_p:C_p ratio in balance. Values of the N_p:C_p ratio were calculated for each harvesting time and the ratio was rather constant and similar in each population, approximately 0.04. The proportion of fine roots, z, of the metabolically active biomass was then calculated for each population and harvesting time, resulting in an average value of 0.04. It was assumed that this value of z describes the minimum fine root proportion of metabolically active biomass which is required for adequate nitrogen uptake when the N_p:C_p ratio is 0.04 or higher.

When $z = 1$, i.e. when all carbon available for growth is allocated to fine roots, it was assumed that the total needle nitrogen concentration should be approximately 0.5 % which generally indicates very poor growing site in terms of nitrogen availability (cf. Ågren 1983, Birk and Matson 1986). Assuming that the relationship between the soluble carbon pool and structural carbon remains the same, this decrease in total needle nitrogen concentration would decrease the concentration of soluble nitrogen from 0.17 % to 0.04 %. It was further assumed that the concentration of soluble nitrogen in other biomass compartments decreases from 0.08 % to 0.05 % and that C_p is more or less constant. This gives a value of 0.015 for the N_p:C_p ratio when $z = 1$. When the N_p:C_p ratio varies between 0.015 and 0.04, z was assumed to depend linearly from the ratio, i.e. increasing constantly with the decreasing N_p:C_p ratio (Fig. 2).