

Article

Application of the 3-PG Model for Gross Primary Productivity Estimation in Deciduous Broadleaf Forests: A Study Area in Japan

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Abstract: The physiological principles predicting growth (3-PG) model is generally used to estimate gross primary productivity (GPP) in forest plantations. All existing parameter values in the 3-PG model for GPP estimation have been set as the standard values for eucalyptus and pine plantations. We propose that the 3-PG model can be applied to deciduous broadleaf forests dominated by *Betula platyphylla* via appropriate parameterization of their structure and functions. The allometric relationships between stem biomass and stem diameter, and between foliage biomass and stem biomass, were determined for the biomass partitioning ratio. Additionally, a temperature modifier was considered appropriate because it affected canopy quantum efficiency. After parameterization, the model showed a good correlation between the estimated results and the data from experimental plots in central and northern Japan. At both sites, GPP peaked around August and was 0 during the winter, when the canopy is bare of leaves. Furthermore, a sensitivity analysis was conducted to determine the most influential parameter relative to the output. GPP was sensitive to changes in canopy quantum efficiency and optimum temperature. Among the meteorological data used, solar radiation and temperature had great impacts on GPP, therefore, these parameters should be carefully considered to produce accurate results.

Keywords: the 3-PG model; GPP; deciduous broadleaf forest; parameterization; sensitivity analysis

1. Introduction

Process-based models, which were created in response to studies examining changes in environmental factors or management interventions [1,2], have the potential to reflect the nonlinear relationships between physiological processes and environmental factors. In forests, environmental factors affect the canopy structure, canopy density, biomass partitioning, and physiological processes. Intensive studies of the effects of environmental factors improve researchers' understanding of processes influencing forest growth [3].

Among process-based models, the physiological principles predicting growth (3-PG) model is often used to estimate forest properties in fast-growing forests and forest plantations [3-7]. The 3-PG model has been used to bridge the gap between conventional empirical, mensuration-based growth and yield models, and process-based carbon balance models [8]. The 3-PG model is primarily used for forest plantations or even-aged, relatively homogeneous forests, but this type of model can also be applied to various environments and species. However, parameterization is needed for individual species [9]. *Eucalyptus globulus* and *E. grandis* were initially parameterized by Sands and Landsberg [10] and Almeida *et al.* [11]. For other species, parameter values were adjusted to fit the output based on *in situ* measurements. Dye [7] and Dye *et al.* [12] used the 3-PG model to predict the growth and water use of *Pinus patula* and eucalyptus plantations. This model has been applied to analyses of forest productivity of various species in countries such as Australia, Brazil, Canada, New Zealand, South Africa, and the U.S. [3,4,13-16]. However, parameterizations are still lacking, especially for natural forests which can act as carbon sinks. To develop parameter values for natural forests, *in situ* measurements are required.

Forest ecosystems in middle and high latitudes of the northern hemisphere have large effects on the carbon cycle, because leaf phenological processes of forests in these regions, such as deciduous broadleaf forests, correspond to carbon sequestration. In this paper we attempted parameterization of the 3-PG model for deciduous broadleaf forests in Japan. We focused on parameters related to biomass production because biomass related to outputs as GPP provides valuable information that will aid in understanding the carbon status of the biosphere. The objective of this study was to assign standard parameter values for deciduous broadleaf forests in the 3-PG model that the original model and previous studies have not calibrated. Our results should make the 3-PG model more applicable to additional species. Moreover, sensitivity analyses were conducted to investigate the parameters with the most influence on output. Parameters identified as sensitive could then be carefully parameterized to calculate output with higher accuracy.

2. The 3-PG Model

2.1. Overview

Landsberg and Waring [8] initiated the 3-PG model as a simple process-based model, on the stand level, for forest growth. The model is composed of five sub-models: assimilation of carbohydrates; biomass partitioning to foliage, stem, and roots; determination of stem number; soil water balance; and the conversion of biomass into variables of interest to forest managers.

2.2. Data Inputs

The main input parameters required are site factors and species-specific data of the species of interest (Table 1). The site factors include latitude, maximum available soil water (ASW_x : mm), soil texture (sandy, sandy loam, clay, or clay loam), and fertility rating (FR). Species-specific parameter values are adjusted for each species. If the parameter values for a species do not exist, parameterization of the new site-specific parameter is necessary. Another input is meteorological variables, including mean air temperature (T_a : °C), mean solar radiation (SR : $\text{MJ m}^{-2} \text{day}^{-1}$), total precipitation (R : mm), frost days (d_F : days per month), and vapor pressure deficit (VPD : mbar). If VPD is not available, it can be calculated from the maximum and minimum temperatures (T_x and T_n : °C) as half the difference between the saturated vapor pressure at T_x and T_n . The meteorological inputs can be actual monthly data or long-term monthly averages.

Table 1. List of all parameters of species specific with descriptions, symbols and unit.

Description of parameter	Symbol	Units
Biomass partitioning and turnover		
Allometric relationships & partitioning		
Ratio of foliage:stem partitioning at $B = 2$ cm	p_2	—
Ratio of foliage:stem partitioning at $B = 20$ cm	p_{20}	—
Constant in stem mass v diam. relationship	a_s	—
Power in stem mass v diam. relationship	n_s	—
Maximum fraction of NPP to roots	R_x	—
Minimum fraction of NPP to roots	R_n	—
Litterfall & root turnover		
Litterfall rate at $t = 0$	F_0	month^{-1}
Litterfall rate for mature stands	F_1	month^{-1}
Age at which litterfall rate has median value	t_F	month
Average monthly root turnover rate	R	month^{-1}
Growth modifiers		
Temperature modifier		
Minimum temperature for growth	T_n	°C
Optimum temperature for growth	T_{opt}	°C
Maximum temperature for growth	T_x	°C
Frost modifier		
Number of days production lost for each frost day	kF	days

Table 1. Cont.

Description of parameter	Symbol	Units
Fertility modifiers		
Value of m when $FR = 0$	m_0	—
Value of f_N when $FR = 0$	f_{N0}	—
Power of $(1-FR)$ in f_N	n_{fN}	—
VPD modifier		
Defines stomatal response to VPD	k_D	mbar
Soil water modifier		
Moisture ratio deficit which gives $f_\theta = 0.5$	c_θ	—
Power of moisture ratio deficit in f_θ	n_θ	—
Age modifier		
Maximum stand age used to computer relative age	t_x	yr
Power of relative age in f_{age}	n_{age}	—
Relative age to give $f_{age} = 0.5$	r_{age}	—
Conductance		
Maximum canopy conductance	g_{Cx}	m s^{-1}
Canopy LAI for maximum canopy conductance	L_{Cx}	$\text{m}^2 \text{m}^{-2}$
Canopy boundary layer conductance	g_B	m s^{-1}
Canopy structure and processes		
Specific leaf area		
Specific leaf area at stand age 0	σ_0	$\text{m}^2 \text{kg}^{-1}$
Specific leaf area for mature aged stands	σ_1	$\text{m}^2 \text{kg}^{-1}$
Age at which specific leaf area = $\frac{1}{2}(\sigma_0 + \sigma_1)$	t_σ	yr
Rainfall interception		
Maximum fraction of rainfall intercepted by canopy	i_{Rx}	—
LAI for maximum rainfall interception	L_{ix}	$\text{m}^2 \text{m}^{-2}$
Light interception, production and respiration		
Extinction coefficient for PAR absorption by canopy	k	—
Age at full canopy cover	t_c	yr
Maximum canopy quantum efficiency	α_{Cx}	—
Ratio NPP/GPP	Y	—
Wood and stand properties		
Basic density		
Minimum basic density—for young trees	ρ_0	t m^{-3}
Maximum basic density—for older trees	ρ_1	t m^{-3}
Age at which $\rho = \frac{1}{2}$ density of old and young trees	t_ρ	yr
Conversion factors		
Intercept of net radiation and solar radiation relationship	Q_a	W m^{-2}
Slope of net radiation and solar radiation relationship	Q_b	—
Molecular weight of dry matter		g mol^{-1}
Conversion of solar radiation to PAR		mol MJ^{-1}

Source: Sands and Landbergs [10].

2.3. Data Outputs

The outputs are primarily foliage, root, and stem biomass (W_F , W_R , and W_S : t ha^{-1}), gross primary productivity (GPP: t ha^{-1}), and net primary productivity (NPP: t ha^{-1}). Other stand-level outputs can be leaf area index (LAI), specific leaf area (SLA), stem volume (V : $\text{m}^3 \text{ha}^{-1}$), stem number (N : trees ha^{-1}), average stem diameter at breast height (B : cm), and mean annual stem-volume increment (MAI: $\text{m}^3 \text{ha}^{-1} \text{year}^{-1}$). 3-PG outputs can be estimated monthly or annually, as well as over longer periods.

2.4. Major Elements of the 3-PG Model for Parameterization

In this study, we focused on parameterization of deciduous broadleaf forests for GPP. The species-specific parameters involved in estimating GPP are part of biomass partitioning and biomass production. Biomass partitioning is related to biomass allocation to the stem, foliage, and roots, each of which is influenced by the GPP. Biomass partitioning is controlled by the ratio of foliage to stem biomass allocation. Root biomass allocation is influenced by soil nutrition and available soil water. However, root data were not available in this study. The partitioning ratio between foliage biomass and stem biomass (pFS) is a function of stem diameter, as shown in the allometric relationship in Equation (1):

$$pFS = a_p B^{n_p} \quad (1)$$

where B is diameter at breast height (DBH), $a_p = a_F n_F / a_s n_s$, and $n_p = n_F - n_s$. Both a_p and n_p are expressed in terms of pFS_2 and pFS_{20} . Generally, pFS_2 and pFS_{20} are extracted for B values of 2 and 20 cm, respectively [10].

To obtain a_s and n_s (Equation (2)), we determine the relationship between W_s and B by fitting the allometric relationship from the observed data. a_F and n_F (Equation (3)) are from the allometric relationship between W_F and B .

$$W_s = a_s B^{n_s} \quad (2)$$

$$W_F = a_F B^{n_F} \quad (3)$$

In biomass production, growth modifiers directly influence GPP. This modification accounts for environmental conditions affecting forest growth. The six growth modifiers are temperature (f_T), frost day (f_F), site nutrition (f_N), available soil water (f_θ), vapor pressure deficit (f_D), and stand age (f_{AGE}). The value of each modifier ranges from 0 to 1. As a modifier approaches 0, it has a stronger influence on forest growth [8,10]. Temperature and frost effects control biomass production in this study area. The equations describing each modifier are as follows. The other modifiers have been reported by Landsberg and Waring [8].

2.5. Temperature Modifier

This parameter is given by the expression:

$$f_T = [(T_a - T_n) / (T_{opt} - T_n)] [(T_x - T_a) / (T_x - T_{opt})]^{(T_x - T_{opt}) / (T_{opt} - T_n)} \quad (4)$$

where T_a is monthly mean temperature (the actual value for each month), and T_n , T_{opt} , and T_x are the minimum, optimum, and maximum temperatures for forest growth, respectively. If $T_a \leq T_n$ or $T_a \geq T_x$, f_T becomes 0.

2.6. Frost Day Modifier

This parameter is calculated by the expression:

$$f_F = 1 - k_F(d_f/30) \quad (5)$$

where k_F is the number of days of production lost for each frost day, and d_f (day month⁻¹) is the mean number of frost days per month. If frost does not occur at the site, then $f_F = 1$. Note that the number shown above as 30 changes according to the number of days in each month.

GPP is calculated as shown in Equation (6), by converting absorbed photosynthetically active radiation (APAR, ϕ_{pa}) to GPP using the canopy quantum efficiency (α_C), which is constrained by the growth modifiers [8,10]:

$$\alpha_C = \alpha_{Cx} \varphi f_T f_F f_N \quad (6)$$

where α_{Cx} is the maximum canopy quantum efficiency, and f_T , f_F , and f_N are the temperature, frost day, and site nutrition modifiers, respectively. φ (Equation (7)) is a physiological modifier that is determined by the minimum vapor pressure deficit (f_D) and available soil water modifiers (f_θ) multiplied by the stand age modifier (f_{age}):

$$\varphi = f_{age} \min\{f_D, f_\theta\} \quad (7)$$

Then, GPP is estimated using Equation (8):

$$GPP = f_T f_F f_N \alpha_{Cx} \varphi \phi_{pa} \quad (8)$$

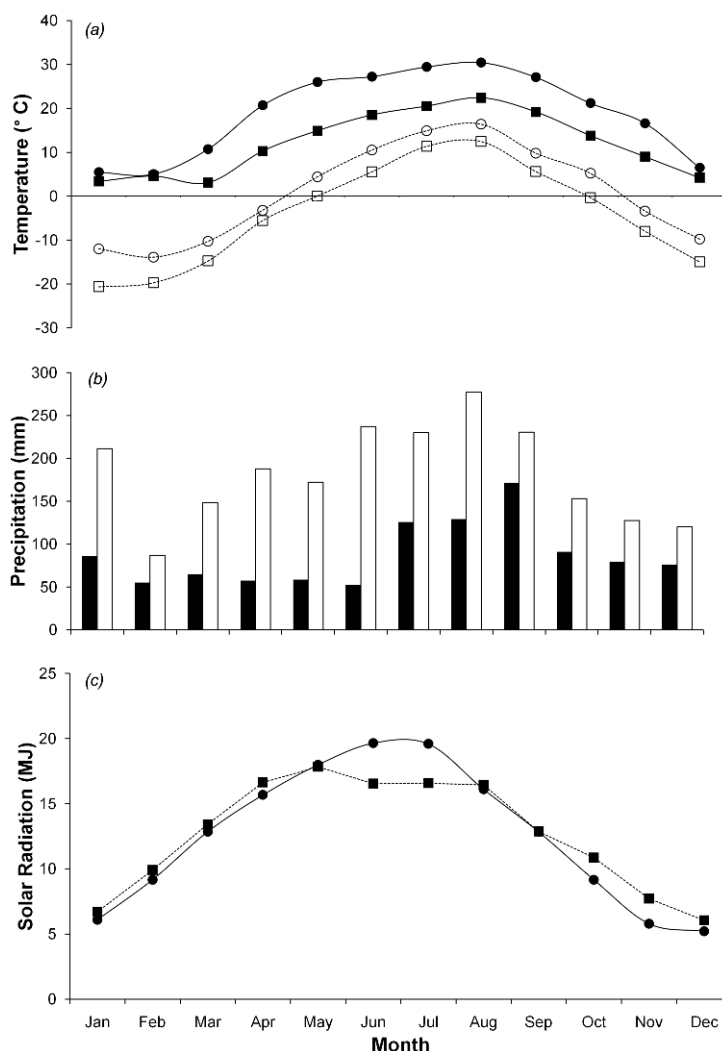
where ϕ_{pa} is APAR calculated using Beer's Law using intercepted solar radiation based on LAI for photosynthesis. NPP is a constant fraction of GPP multiplied by 0.47 ± 0.4 [17,18].

3. Materials and Methods

3.1. Site Description

We collected data at two study sites, Hitsujigaoka and Takayama. Hitsujigaoka is located in northern Japan at 42°59'13" N and 141°23'7" E and is 180 m above sea level. Takayama is in central Japan at 36°8'46" N and 137°25'23" E and is 1,420 m above sea level. At each site, a flux tower collected meteorological data and ecological characteristics. Averaged over five years, from 2001 to 2006 (Figure 1), the maximum temperatures at Hitsujigaoka and Takayama were 24.9 ± 1.8 °C and 22.4 ± 1.6 °C in August, while the minimum temperatures were -12.4 ± 1.7 °C and -11.7 ± 2.1 °C in February, respectively. The mean annual precipitation and mean annual solar radiation at Hitsujigaoka were $1,047 \pm 174$ mm and 12.25 ± 0.4 MJ m⁻² day⁻¹, respectively, whereas at Takayama they were $2,275 \pm 165$ mm and 12.43 ± 0.3 MJ m⁻² day⁻¹, respectively. Both sites experience snow cover in the winter (December to April) to a depth of 1 m.

Figure 1. Average monthly meteorological data from 2001–2006 as **(a)** temperature in terms of minimum temperature at Hitsujigaoka (open rectangular and dashed line) and Takayama (open circle and dashed line), and maximum temperature at Hitsujigaoka (solid rectangular and solid line) and Takayama (solid circle and solid line); **(b)** precipitation at Hitsujigaoka (solid bar) and Takayama (open bar); and **(c)** solar radiation at Hitsujigaoka (solid rectangular and dashed line) and Takayama (solid circle and solid line).



The main vegetation type was deciduous broadleaf natural forest, and the dominant species was *Betula platyphylla*. The stand basal area for this species accounted for around 81% and 63% of the total basal area at Hitsujigaoka and Takayama, respectively. Tree height ranged from 14 to 28 m. Overstory trees at Hitsujigaoka (around 100 years) were older than those at Takayama (around 50 years; [19,20]). The mean DBH was larger at Hitsujigaoka (23.0 cm) than at Takayama (11.4 cm; [19]). We note that the flux tower at Hitsujigaoka was compromised and the forest around the flux tower was severely damaged by a typhoon in 2003. Data from Takayama were used for calibration, while data from Hitsujigaoka were used for validation. The different locations did not significantly influence the model output because the two sites are located in the same climatic zone and are characterized by the same canopy species. Site data is summarized in Table 2.

Table 2. Summary of the site description at Takayama and Hitsujigaoka.

	Takayama	Hitsujigaoka
Latitude	36 8'46" N	42 59'13" N
Longitude	137 25'23" E	141 23'7" E
Maximum Temperature (°C)	22.4	24.9
Minimum Temperature (°C)	−11.7	−12.4
Precipitation (mm)	2,275	1,047
Solar Radiation (MJ m ^{−2} day ^{−1})	12.43	12.25
Dominant Species	<i>Betula platyphylla</i>	<i>Betula platyphylla</i>
Average Canopy Age (year)	50	100
Mean DBH (cm)	11.4	23
Mean Tree Height (m)	22	24

3.2. Flux Tower Measurements

Each site has two flux towers. The first tower continuously monitored meteorological data. The second monitored only ecological properties. Meteorological data, including air temperature, precipitation, global solar radiation, humidity, wind speed, and soil temperature were collected every 30 min. The 3-PG model requires data on air temperature, precipitation, and solar radiation. Figure 1 shows monthly meteorological data, which were used as input parameters, for Hitsujigaoka and Takayama from 2001–2006. Vapor pressure deficit was calculated based on maximum and minimum temperatures. Days when the temperature was below 2 °C were counted as frost days. CO₂ flux was measured by the eddy covariance method [21]. These data were collected in 30-min increments and used to validate the results. CO₂ flux was used to estimate net ecosystem exchange (NEE). Then, GPP was estimated by NEE and ecosystem respiration. Canopy respiration was not observed in the study, therefore NPP is not available.

3.3. Parameterization for Deciduous Broadleaf Forests

3.3.1. Biomass Partitioning

Tree canopy properties were measured in a 100 m × 100 m permanent plot near the flux tower at Takayama [19]. Within the plot, 24 trees (comprising several species) were selected to measure DBH, height, and tree density. Trees with DBH from 1.7 to 29.0 cm were selected to represent the different stand ages, because the actual stand age was not identified. Nine of the 24 sampled trees were *B. platyphylla*, with a range of small to large DBH. The different DBHs can be used to predict forest growth. The trees were harvested for biomass calculation using the dry mass of the stem and the foliage. Data for *B. platyphylla* were used for parameterization in biomass partitioning. Figure 2a shows the allometric relationship between DBH and stem biomass. Figure 2b shows the allometric relationship between DBH and foliage biomass. The allometric parameters gave an excellent fit to the trend lines, with $r^2 = 0.97$ and 0.98 for stem and foliage biomass, respectively. The equations in Figure 2 were used to re-estimate stem and foliage biomass at Hitsujigaoka for validation. The results are shown in Figure 3, where the plots of estimated versus observed stem and foliage biomass were

close to one-to-one linear relationships. Stem biomass was underestimated by around 3%, whereas foliage biomass was overestimated by about 15%.

Figure 2. Allometric relationship between **(a)** stem biomass and DBH (open circle); and **(b)** foliage biomass and DBH (solid rectangular) at Takayama. The allometric equation of stem biomass and DBH is $y = 0.049x^{2.64}$, while foliage biomass and DBH is $y = 0.002x^{2.56}$. The values from the allometric equation were used to calculate the parameter values in the biomass partitioning.

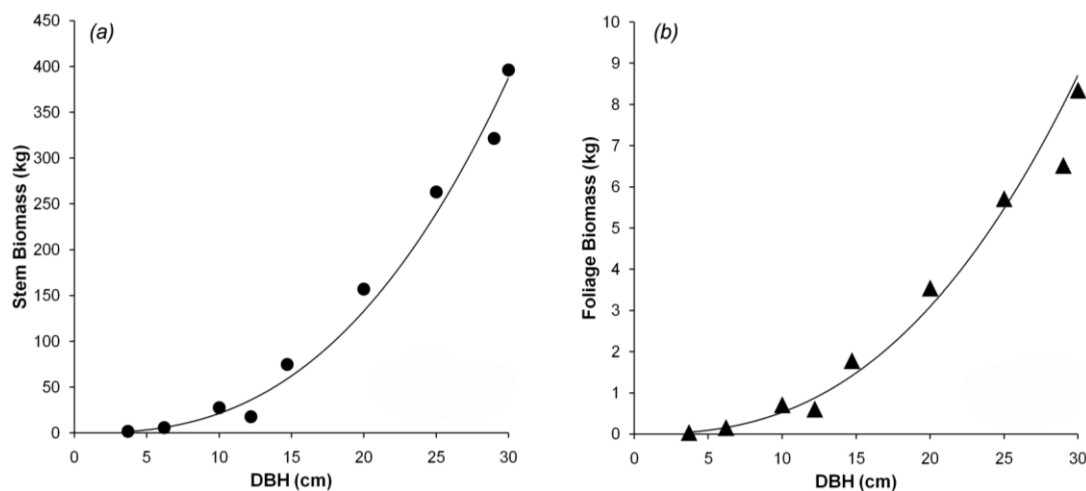
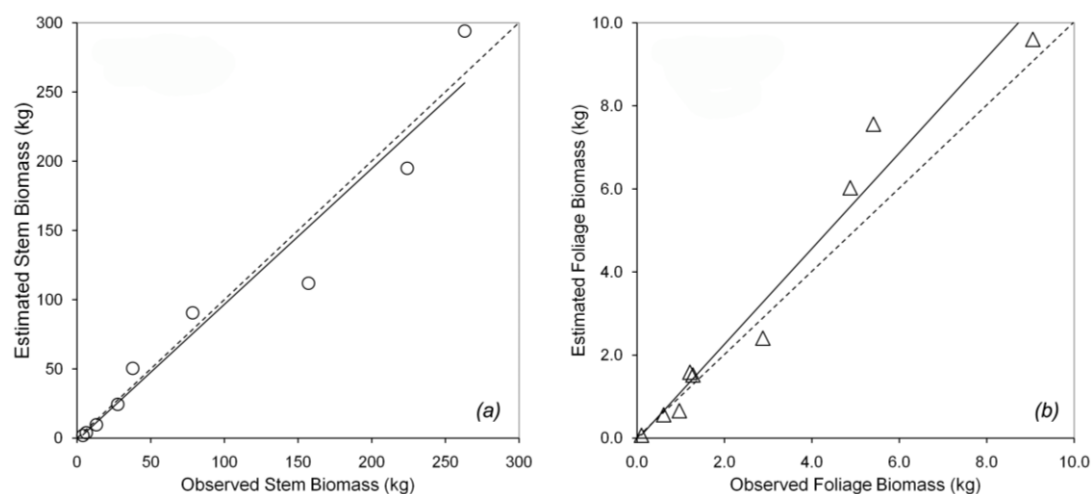


Figure 3. The estimated biomass versus the observed biomass at Hitsujigaoka for validation, the estimated values equal the observed values, **(a)** stem biomass (open circle); and **(b)** foliage biomass (open triangle). The linear regression showed $y = 0.98x - 1.60$ for stem biomass, and $y = 1.15x - 0.04$ for foliage biomass, respectively.



From those relationships, a_s , n_s , a_F , and n_F were calculated as 0.049, 2.64, 0.002, and 2.56, respectively ($r^2 = 0.97$ for stem biomass and 0.98 for foliage biomass). Based on the allometric relationships, a_P and n_P were computed by substituting a_s , n_s , a_F , and n_F , to retrieve a_P and n_P . $pFS2$ and $pFS20$ were 0.03 and 0.02, respectively, in these deciduous broadleaf forests of *B. platyphylla*.

3.3.2. Growth Modifiers

GPP was influenced by LAI and solar radiation, as well as environmental conditions, especially temperature. Figure 4a plots observed GPP with average temperature, solar radiation, and LAI throughout the year. GPP occurred from May to October and was highest in July. Conversely, there was no GPP from November to April. GPP responded to leaf phenology, with leaves emerging in May and falling in November. Solar radiation and LAI peaked in July, resulting in high levels of intercepted solar radiation (Figure 4b) and maximum GPP. The temperature modifier affected quantum efficiency. Figure 5 shows the relationship between mean annual temperature and the temperature modifier to determine T_n , T_{opt} , and T_x for growth. Thus, in this study, T_n , T_{opt} , and T_x were 8.5 °C, 24.5 °C, and 36 °C, respectively. If the mean temperature was less than T_n or greater than T_x , α_C was 0 and caused GPP to also be 0.

Figure 4. Comparison among (a) monthly gross primary productivity (solid bar) with mean monthly temperature (solid line), monthly solar radiation (small dashed line) and monthly LAI (big dashed line); (b) monthly gross primary productivity (solid bar) with monthly intercepted radiation (dashed line).

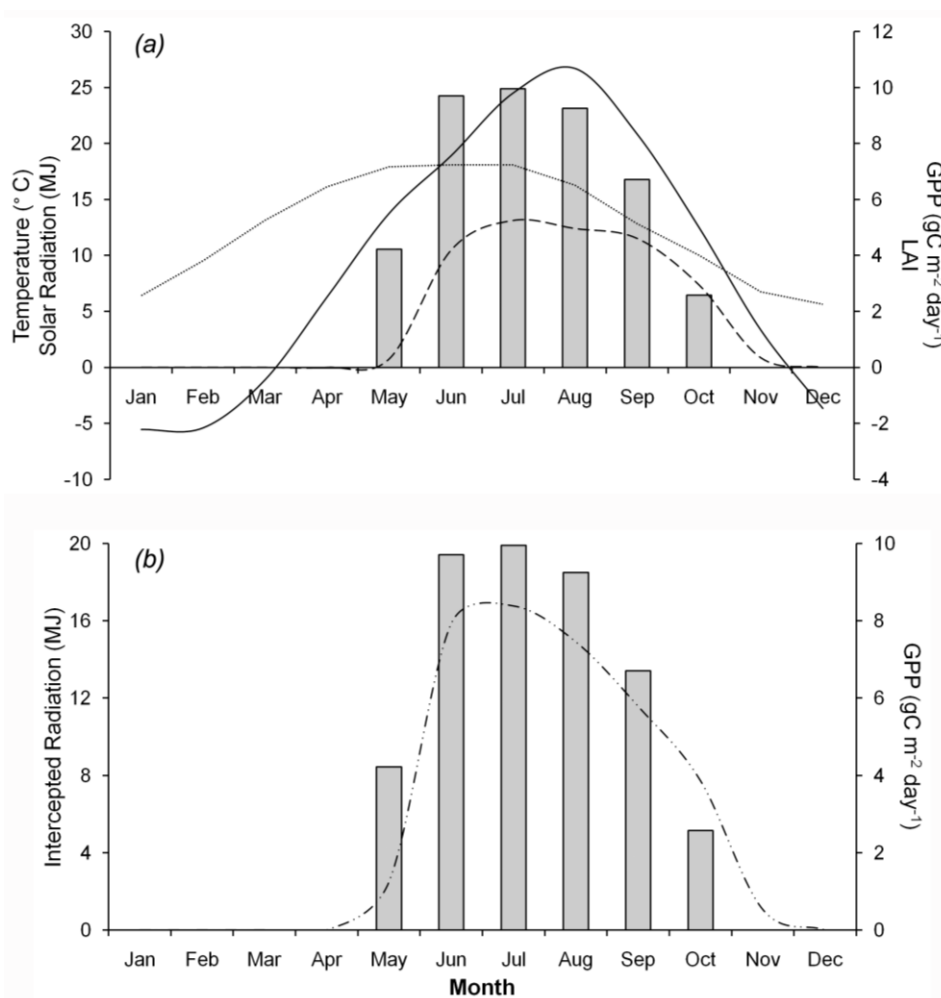
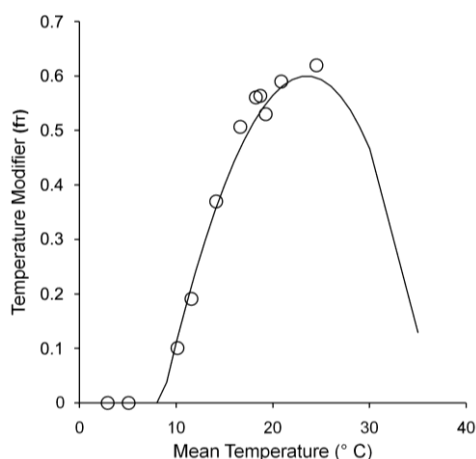


Figure 5. Appearance of the temperature modifier (f_T). Point fitted (open circle) were determined by fitting 3-PG to data from Takayama. The line observed (solid line) is a fit of the data to the equation of temperature modifier.



3.3.3. Other Parameters

Other parameters related to biomass production were assigned values based on direct field measurements. If data were not available for parameterization, a best-fit method was applied by tuning the parameter to obtain an output that corresponded with observed data.

LAI data were obtained using the fish-eye camera method with a Nikon CoolPix camera fitted with a fish-eye lens (Nikon FC-E8). Photos were automatically taken every 2 min during the day and those from 2004 to 2006 were used [22]. Clear sky condition photographs were selected to calculate LAI. LAI data were used to initialize specific leaf area. Litterfall data were collected using 14 traps in a 100 m × 100 m area. Each trap was 1 m² and was set up for the entire growing season. Tree canopy density was counted based on the amount of tree canopy within the permanent plot. The ratio of NPP/GPP was used to convert GPP to NPP [23]. Note that sites were not constrained by site nutrition or available soil water factors. Parameter values not available for biomass partitioning and biomass production were set as the default values based on the original 3-PG model and did not significantly affect output. All parameter values derived in this study are presented in Table 3.

3.4. Sensitivity Analysis

A sensitivity analysis was carried out to examine how parameter values influenced the output. The parameters examined were a_s and n_s , biomass partitioning ratio at B = 2 and 20 cm, maximum canopy quantum efficiency (α_{Cx}), T_n , and T_{opt} . These are the main parameters of biomass partitioning and biomass production, and the most influential for GPP estimation. We determined the effects of changes in these parameters on W_s , W_f , and GPP. Additionally, sensitivity to meteorological data was analyzed with the GPP results. The parameter values changed by −20%, −10%, +10%, and +20% from the default values, except for temperature, which was changed to degrees Celsius (−2 °C, −1 °C, +1 °C, and +2 °C) since changes in degrees Celsius usually showed a more significant effect than those in percentage.

Table 3. List of parameter values as used in 3-PG for deciduous broadleaf forest. Most data are observed (O) from the experimental plot data and the others were obtained from the literature (L).

Description of parameter	Symbol	Units	Default Value	O/L
Allometric relationships & partitioning				
Ratio of foliage:stem partitioning at $B = 2$ cm	pFS_2	—	0.03	O
Ratio of foliage:stem partitioning at $B = 20$ cm	pFS_{20}	—	0.02	O
Constant in stem mass v diam. relationship	a_S	—	0.06	O
Power in stem mass v diam. relationship	n_S	—	2.6	O
Litterfall & root turnover				
Litterfall rate at $t = 0$	F_0	month ⁻¹	0.083	O
Litterfall rate for mature stands	F_1	month ⁻¹	0.083	O
Age at which litterfall rate has median value	t_F	month	24	O
Average monthly root turnover rate	R	month ⁻¹	0.083	L
Temperature modifier				
Minimum temperature for growth	T_n	°C	8.5	O
Optimum temperature for growth	T_{opt}	°C	24.5	O
Maximum temperature for growth	T_x	°C	36	O
Frost modifier				
Number of days production lost for each frost day	k_F	days	1	O
VPD modifier				
Defines stomatal response to VPD	k_D	mbar	0.05	O
Stem Number				
Basic density	ρ	t m ⁻³	0.6	O
Maximum tree stem mass for 1,000 trees ha ⁻¹	$w_{S \times 1000}$	kg tree ⁻¹	180	O
Conductance				
Maximum canopy conductance	g_{Cx}	m s ⁻¹	0.02	O
Canopy LAI for maximum canopy conductance	L_{Cx}	m ² m ⁻²	3.33	O
Specific leaf area				
Specific leaf area at stand age 0	σ_0	m ² kg ⁻¹	16	L
Specific leaf area for mature aged stands	σ_1	m ² kg ⁻¹	16	L
Age at which specific leaf area = $\frac{1}{2}(\sigma_0 + \sigma_1)$	t_σ	yr	2.5	L
Light interception, production and respiration				
Extinction coefficient for PAR absorption by canopy	k	—	0.565	O
Maximum canopy quantum efficiency	a_{Cx}	—	0.012	O
Ratio NPP/GPP	Y	—	0.422	O

4. Results

Because the study site was a mature forest we do not present an age-series analysis. In this study, we were interested in biomass production because biomass directly relates to the amount of carbon stored by the tree canopy. Our results were validated with the observed data, and a linear regression was applied to investigate accuracy.

4.1. Biomass Calculation

Biomass can be divided into three parts: stem, foliage, and root biomass. We did not examine root biomass because empirical data were not available. Figure 6 shows the estimated stem and foliage biomass *versus* the observed biomass at each site. Both relationships were close to one-to-one linear relationships. Linear regression showed a high correlation between the estimated and observed values ($r^2 = 0.89$ and 0.94 for stem and foliage biomass, respectively). These values were close to the one-to-one line, in which the estimated values should be equal to the observed values. Foliage and stem biomass at Takayama were slightly overestimated compared to those at Hitsujigaoka. This difference was likely because the canopy at Takayama is younger than that at Hitsujigaoka. A summary of regression statistics is given in Table 4.

Figure 6. Validation of **(a)** estimated stem biomass *versus* observed stem biomass at Hitsujigaoka (open circle) and Takayama (solid circle); and **(b)** estimated foliage biomass *versus* observed foliage biomass at Hitsujigaoka (open triangle) and Takayama (solid triangle). The estimated values equal the observed values.

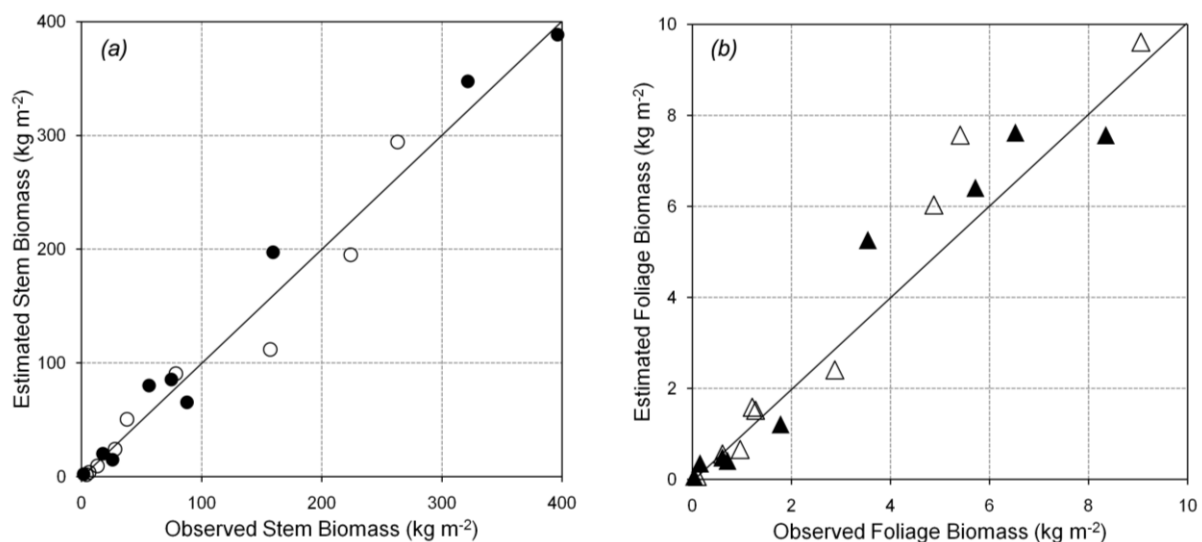


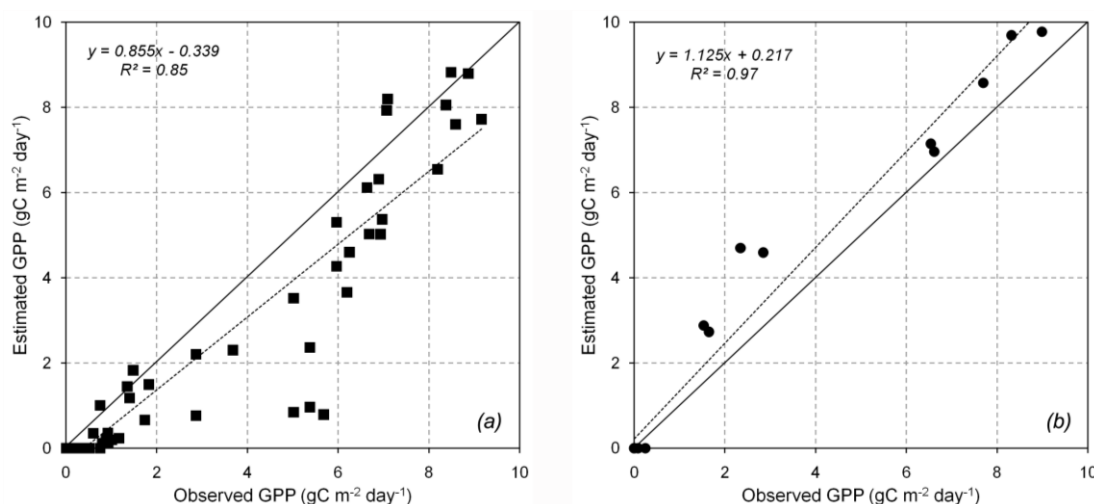
Table 4. Summary of linear regression statistics of estimated *versus* observed values of stem biomass (W_s), foliage biomass (W_F) and GPP at Hitsujigaoka (HTJ) and Takayama (TKY). The error terms were presented as the standard deviation values.

Parameters	Site	N	Equation	RMSE	Standard deviation
W_s	HTJ	9	$0.98X - 1.59$	0.95	14.40
	TKY	9	$1.02X + 3.79$	0.96	12.66
	All	18	$1.01X + 0.02$	0.94	16.22
W_F	HTJ	9	$1.15X - 0.04$	0.96	0.25
	TKY	9	$1.04X - 0.07$	0.94	0.26
	All	18	$1.09X + 0.02$	0.89	0.28
GPP	HTJ	24	$1.13X + 0.22$	0.97	3.21
	TKY	60	$0.86X - 0.34$	0.85	4.01

4.2. Gross Primary Productivity

The GPP estimation at Hitsujigaoka and Takayama is presented in Figure 7a and 7b, respectively. The monthly estimated GPP was compared with the observed GPP from 2000 to 2004. The results for both locations showed a good correlation in terms of the linear regression, with $r^2 = 0.85$ and 0.97 at Takayama and Hitsujigaoka, respectively. The 3-PG model indicated that inter-annual GPP peaked around July and August and was 0 in winter (November to April). GPP was lower at Takayama than at Hitsujigaoka because of the smaller LAI at Takayama. Thus, the interception of radiation was lower at Takayama. The GPP at Takayama was underestimated because of the mixed age of the trees in the plot and the influence of the temperature modifier. The low value of the latter at the beginning of the growing season resulted in the low estimate for GPP (low points in the graph). At Hitsujigaoka, the GPP was overestimated because the large tree leaves could absorb more solar radiation for photosynthesis. The average GPP over 5 years was $973.30 \text{ g C m}^{-2}$ (Takayama) and $1255.21 \text{ g C m}^{-2}$ (Hitsujigaoka). Table 4 compares the estimated and observed values of GPP in terms of root mean square error.

Figure 7. Comparison of estimated GPP and observed GPP from flux tower at (a) Takayama and (b) Hitsujigaoka, respectively. The dash line is the linear regression between the estimated and observed value. At Takayama, the linear equation is $y = 0.855x - 0.339$, and at Hitsujigaoka is $y = 1.125x + 0.217$, respectively.



4.3. Sensitivity Analysis

Changing selected parameter values from -20 to 20% had different effects on the estimated output. Figure 8 shows the effects of changes in a_s , n_s , $pFS2$, $pFS20$, α_{Cx} , T_n , T_{opt} , W_F , and W_s . Changes in a_s (Figure 8a) and n_s (Figure 8b) primarily affected W_F ; when a_s and n_s were changed by -20% , W_F differed by around 16% and 6% , respectively. However, the selected outputs were less sensitive to changes in $pFS20$ (Figure 8d) than $pFS2$ (Figure 8c). GPP was highly sensitive to α_{Cx} (Figure 8e) and to T_{opt} (Figure 8f). W_s was also sensitive to both of those parameters, but not as sensitive as GPP. T_n (Figure 8g) most affected GPP when it was changed by 20°C . From these results, we recommend that α_{Cx} , T_{opt} , and T_n be carefully measured if accurate results are desired, especially in GPP calculations.

Figure 8. Sensitivity analysis of selected 3-PG outputs by changed the value of **(a)** stem constant: a_s ; **(b)** stem power: n_s ; **(c)** biomass partitioning ratio at DBH = 2 cm: $pFS2$ and **(d)** DBH = 20 cm: $pFS20$; **(e)** maximum canopy quantum efficiency: α_{Cx} ; **(f)** optimum temperature: T_{opt} ; and **(g)** minimum temperature: T_{min} . The effect on the following output as stem biomass (black bar), foliage biomass (grey bar) and GPP (open bar) by changed the parameter value differed from -20 to 20% , with 10% interval. For both of T_{opt} and T_{min} , they were changed in degree Celsius as $-2\text{ }^{\circ}\text{C}$, $-1\text{ }^{\circ}\text{C}$, $+1\text{ }^{\circ}\text{C}$, and $+2\text{ }^{\circ}\text{C}$.

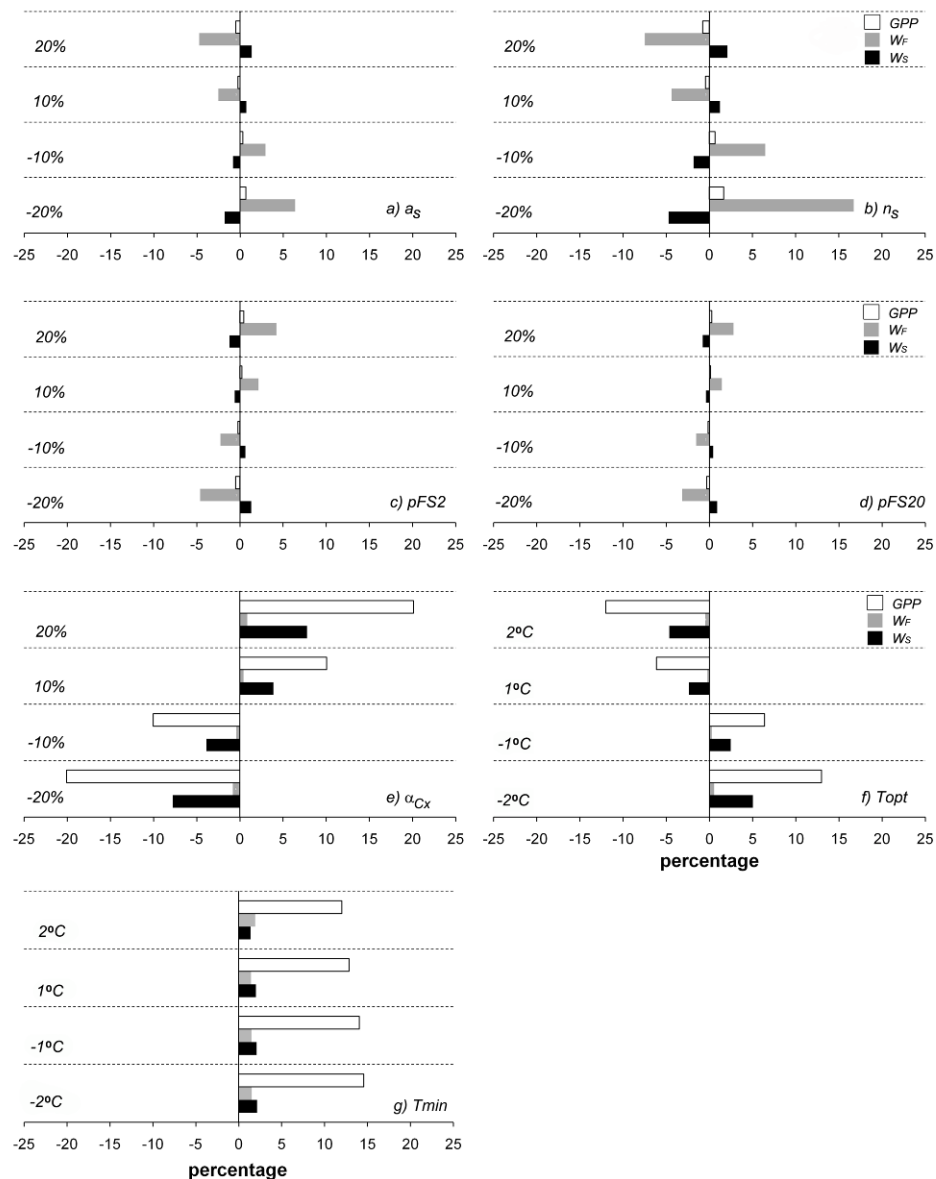
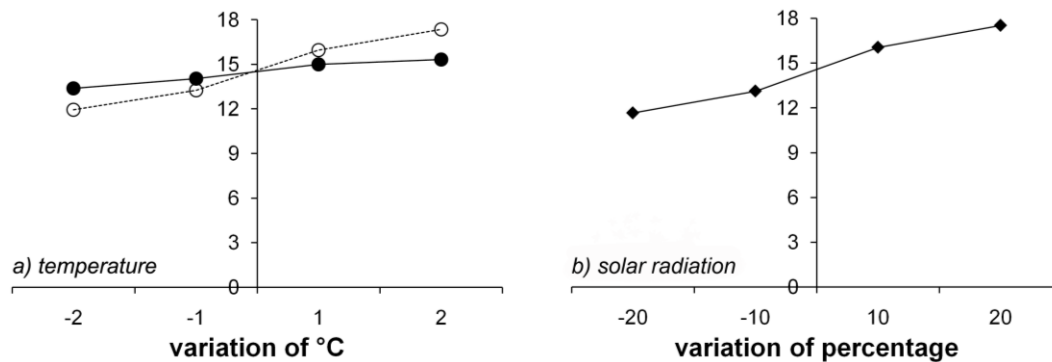


Figure 9 shows the effects of meteorological data on GPP. Solar radiation (Figure 9b) and T_n (Figure 9a) had significant impacts on GPP, with differences around $\pm 3\text{ g C m}^{-2}$, but T_x had only a slight effect (Figure 9a). Increased solar radiation and T_n increased GPP. However, GPP was not sensitive to frost days or precipitation, since the study sites are not limited by water. Snow melt increases the soil water content in the summer. The effect of frost days on GPP was large in the winter, as large as the effect of temperature. However, frost days did not affect GPP in the summer, during which GPP was most affected by temperature and solar radiation.

Figure 9. Effect of meteorological data on GPP as following **(a)** minimum temperature (open circle and dashed line) and maximum temperature (solid circle and solid line); **(b)** solar radiation. The parameter values were changed -20% , -10% , $+10\%$, and $+20\%$, except for temperature, which was changed in degrees Celsius ($-2\text{ }^{\circ}\text{C}$, $-1\text{ }^{\circ}\text{C}$, $+1\text{ }^{\circ}\text{C}$, and $+2\text{ }^{\circ}\text{C}$).



5. Discussion

This study determined the 3-PG model parameter values for a deciduous broadleaf forest dominated by *B. platyphylla*. The original parameter values were proposed for *Eucalyptus* forest plantations in Australia [10]. Some authors have directly applied these available parameters to other tree species or indirectly applied tuning methods [12,13,16,24]. The parameter values determined in this study corresponded to mature forest, focusing on biomass production. Data from young forests were not available, so we could not investigate forest growth rate or complete an age-series analysis with the 3-PG model.

An allometric analysis was performed to parameterize biomass partitioning between W_S and W_F . Our model results were in agreement with empirical data (Figure 6) after parameterization. Even though some default parameter values were used, doing so did not cause significant errors in the output [17]. $pFS2$ and $pFS20$ values were moderately different from previous studies [7,10,11]. Deciduous broadleaf forests have annual leaf cycles, and biomass is typically stored in stems and branches throughout the year. However, DBH growth is small due to the short growing season in cool-temperate forests [25,26]. Even though age-series data were not available, trees with different DBH were present, and were assumed to represent different tree ages; these trees were used to find the relationship between relative annual growth rate and above-ground biomass. The relative annual growth rate of estimated above-ground biomass had a trend similar to the observed one. Foliage biomass was highly responsive to leaf phenology (*i.e.*, leaf growth, maturation, senescence, and leaf fall). Litterfall was calculated as a constant fraction of foliage biomass corresponding to leaf growing conditions.

In parameterization, growth modifiers are the main factors affecting GPP calculations [8]. Among the growth modifiers, the temperature modifier had the most effect on α_{Cx} . Because our study site was constrained by temperature, the 3-PG model was run so that $\text{GPP} = 0$ when the temperature was lower than T_n or higher than T_x . The temperature at both study sites never reached T_x because it is a cool-temperate area; thus, T_x had no effect on GPP calculations. However, the temperature in the

winter was always lower than T_n , and this affected the number of frost days. Thus, the 3-PG model generated GPP values of 0 at Hitsujigaoka and Takayama during winter. GPP is a function of environmental factors and the interception of radiation for photosynthetic processes. Thus, solar radiation (Figure 9b) increased GPP in relation to leaf area. Soil water may be limited at other forest sites, as found in *Eucalyptus* forest plantations by Esprey *et al.* [27]. In that case, increased precipitation resulted in increased stand volume, which is relevant to stem biomass. However, our study sites were not limited by water stress because they were located in an Asian monsoon climate region with high precipitation [28]. Additionally, snow melt increases the amount of soil water in the summer. Therefore, precipitation had no effect on GPP.

Biomass production, especially W_s and GPP, was controlled by α_{Cx} and T_{opt} (Figure 8). α_{Cx} can be highly sensitive, relative to other input parameters [16,27], and directly affects the calculation of GPP. Changes in α_{Cx} result in significant differences in GPP. T_{opt} had an inverse relationship with GPP, such that lower temperatures resulted in higher GPP. T_n influenced GPP in the deciduous broadleaf forest examined here, but had no effect in previous studies [27,29]. The large differences in a_s and n_s had strong influences on W_F . Almeida *et al.* [11] also reported the effect of a_s and n_s on W_F for *E. grandis*. Increased n_s resulted in increased W_F partitioning. However, it is important to note that the various output types had different sensitivity to changes in each parameter.

Even though the growing cycle of deciduous broadleaf forests differs from that of other forest types, such as tropical forest, the set of parameter values indicates that it is not necessary to use a different ratio. Since the parameter values were determined over the entire growing season and there were no leaves in the winter, 3-PG will calculate a GPP of 0 if LAI equals 0. Therefore, there were not increases or losses of biomass during winter. One caveat regarding this study is that root biomass was not included because root data were unavailable at the study site.

The 3-PG model can be applied to estimate biomass production for the deciduous broadleaf tree *B. platyphylla*. However, long-term empirical data are needed for better understanding parameterization, validating models, and making further improvements in the performance of the 3-PG model.

6. Conclusions

After parameterization, the 3-PG model is applicable to mature, non-water limited deciduous broadleaf forests. The main parameters affecting biomass production are assigned appropriate values from a set of standard parameter values. Some parameters are determined based on empirical data such as the allometric relationships between stem biomass and stem diameter, or between foliage biomass and stem diameter, as well as growth modifiers. Parameters for which empirical data are not available are determined by fitting the output to the observed data. The parameterization in this study emphasized biomass production. Default values were used for parameters that are not involved in biomass production.

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