Aboveground productivity of an unsuccessful 140-year-old Cryptomeria japonica plantation in northern Kyushu, Japan

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Aboveground productivity of an unsuccessful 140-year-old *Cryptomeria japonica* plantation in northern Kyushu, Japan

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Abstract

We measured the aboveground biomass, biomass increment and litterfall production of a 140-year-old, abandoned *Cryptomeria japonica* plantation in order to infer the effects of topography on biomass production. The plantation was unsuccessful and the naturally regenerated broad-leaved trees contributed 93.4% (374.2 Mg ha^{-1}) of the total aboveground biomass (400.2 Mg ha^{-1}). Comparing between different slope positions, aboveground biomass decreased downslope corresponding to the decrease in broad-leaved tree biomass. The biomass of *C. japonica* did not vary with slope position. Biomass increment and litterfall production of the broad-leaved trees also decreased downslope. However, litterfall production per unit biomass and aboveground net primary production per unit biomass increased downslope. Results of a path analysis showed that biomass increment of *C. japonica* decreased with increasing topographical convexity, whereas biomass and litterfall production of broad-leaved tree increased. Litterfall production of broad-leaved tree decreased with increasing biomass of *C. japonica*, suggesting that, despite their small biomass, the presence of residual *C. japonica* may have negative effects on the distribution and productivity of the broad-leaved trees. Our results indicated that total aboveground biomass of the study site was comparable to that of old-growth *C. japonica* plantations. We inferred that the variation in aboveground biomass of the broad-leaved trees was largely determined by the topography, while their productivity was affected by interactions with

planted *C. japonica*.

Keywords: biomass, litterfall, mixed forest, unsuccessful plantation, topography

Introduction

Old growth forests are usually carbon sinks (Luyssaert et al. 2008), though forest growth declines with stand age (Kira and Shidei 1967; Gower et al. 1996, Ryan et al. 2004). In Japan, the area of mature plantations that have passed harvesting age is increasing, because under the current economic and social situation, timber prices cannot cover the harvesting cost and clearcutting areas have been reduced. As a result, many conifer plantations are shifting to long-rotation forestry, but it is not clear whether the aging plantations will continue to be productive. Some studies indicate that growth is maintained in *Cryptomeria japonica* D. Don plantations up to 200 years (Takeuchi 2005; Masaki et al. 2006；Watanabe and Mogi 2007) and in 84-year-old *Chamaecyparis obtusa* Sieb. et Zucc plantation (Kondo et al. 2001). Variable results have been reported for age-related changes in litterfall production, which is correlated with stand productivity. Litterfall production decreased with increasing stand age for *C. japonica*, while it did not change for *C. obtusa* (Inagaki et al. 2004; Ichikawa et al. 2006). In contrast, an increase in litterfall production with stand age has also been reported for *C. japonica* (Shutou and Nakane 2004). Because various factors such as stand density, site index, and management influence stand productivity, more data from various old-aged plantations are needed to understand the age-related changes in stand productivity of Japanese plantation forests.

Conifer growth is especially low in heavy snowfall regions (Yokoi and Yamaguchi 2000;

Masaki et al. 2004) and in high-altitude areas (Sato et al. 1995; Kominami et al. 2004). Plantations in these areas were often unsuccessful and eventually abandoned. In abandoned, unsuccessful conifer plantations, broad-leaved trees often regenerate naturally resulting in a mixed conifer-broadleaf forest (Imada et al. 1991; Hasegawa and Taira 2000; Masaki et al. 2004; Kodani 2006). In natural, mixed conifer-broadleaf forests, stand basal area tends to be greater than that of forests comprising only broadleaved trees (Midgley et al. 2002; Aiba et al. 2007). This suggests that, although the unsuccessful plantations may be unsuitable for timber production, stand productivity may not be low. However, we are aware of no previous studies documenting the primary production of unsuccessful Japanese conifer plantations.

Many conifer plantations in Japan have been established on steep slopes with complicated topography. In the plantations, topographic heterogeneity is a major factor affecting stand dynamics and productivity through its effects on edaphic conditions (Hirobe et al. 1998; Tokuchi et al. 2000; Nishina et al. 2009), tree growth (Tange et al. 1989; Enoki et al. 1996; Kohama et al. 2006; Tsuji et al. 2007) and litterfall production (Enoki et al. 1997). The occurrence of naturally regenerated broad-leaved species also varies depending on topography (Ito et al. 2003, 2006), indicating that topography may also affect the regeneration pattern of the broad-leaved trees, as well as the competition between the planted conifer trees and the naturally regenerated broadleaved trees.

In the present study, we estimated the aboveground biomass and aboveground net primary

production (ANPP) of a 140-year-old, unsuccessful *C. japonica* plantation to infer the effects of topography on biomass and productivity. We attempted to answer the following questions: 1) Is an abandoned, old-growth plantation more or less productive than managed plantations? 2) How does the topography influence biomass and productivity of the plantation? 3) How do topography and the planted tree influence biomass and productivity of broad-leaved trees?

Methods

Study site

This study was carried out in Kasuya Research Forest of Kyushu University located in Fukuoka prefecture southwestern Japan (33°39'N, 130°32'E). The mean annual temperature and precipitation were 16.1℃ and 1499mm, respectively in 1999-2003 (Kasuya Research Forest, Kyushu University). The study site was located on a steep slope (mean inclination = 36.0 degrees) within an elevation range from 400 to 500m asl. The study site is a *C. japonica* plantation that was established about 140 years ago. No records are available that indicate any silvicultural treatments (e.g., pruning and thinning). The present study site is inferred to be an unsuccessful plantation, in which planted *C. japonica* could not form a closed canopy and broad-leaved trees regenerated naturally (Table 1). Dominant canopy trees include, *Quercus saliciana* Blume and *Carpinus tschonoskii* Bl.,on the upper part of the slope, and *Swida controversa* Sojak and *Acer palmatum* Thunb on lower part of the slope.

Camellia japonica L. are dominant in the subcanopy layer. Details of the study site have been reported in Inoue et al. (2008).

Tree census

A 100 m×100 m study plot, including a ridge top and a valley bottom, was established on a north-facing slope (Fig.1). The plot was divided into 100 cells, each measuring 10 m×10 m. All trees larger than 15cm in girth at breast height were tagged and mapped. We measured the height and diameter at breast height (DBH) in April 2006. The DBH was measured again in October 2007.

Litterfall collection

Litterfall was collected with 0.25m^2 circular traps. The traps consisted of a metallic hoop and nylon net and were positioned 1m above the ground with plastic stakes. A total of 100 traps were placed in the plot, one in the center of each cell. Litterfall was collected at monthly intervals from August 2006 to August 2007. The samples were separated into *C. japonica*, broad-leaved trees and miscellaneous litter and then oven-dried at 70ºC for 48 hours for measurement of dry mass.

Data analysis

The above-ground dry mass (Wt;kg) of an individual tree was the sum of mass of stem (Ws;kg), branches (Wb;kg) and leaves (Wl;kg):

$$Wt = Ws + Wb + Wl.$$

The mass of each part of the individual tree (Wi) was estimated by the following allometric equation:

$$\log(Wi) = a \times \log(D) - b$$

where D is DBH (cm), and a and b are the coefficients whose values were obtained from Ando et al. (1968) for *C. japonica* and Ando et al., (1977) for broad-leaved trees (Table 2).

The aboveground biomass in each cell (W, kg ha^{-1}) was calculated as the sum of the biomass of all trees in the cell. The biomass increment was calculated as the difference in the biomass between 2006 and 2007. Above-ground net primary production, ANPP (kg ha^{-1} $year^{-1}$), was estimate by the summation method as

$$ANPP = \Delta Wt + \Delta L$$

where ΔWt (kg ha^{-1} $year^{-1}$) is biomass increment, and ΔL is litterfall production (kg ha^{-1} $year^{-1}$). As an indicator of relative growth and production, we calculated the annual biomass increment, litterfall production and ANPP relative to aboveground biomass (ΔWt_r, ΔL_r and $ANPP_r$, respectively, %), as follows:

$$\Delta Wt_r = \Delta Wt / W$$

$$\Delta L_r = \Delta L / W$$

$$ANPP_r = ANPP / W$$

The study plot was divided into three areas (ridge, mid-slope and valley) to compare aboveground biomass and productivity in relation to slope position (Fig. 1). We compared the Wt, ΔWt, ΔL, ANPP, ΔWt_r, ΔL_r and $ANPP_r$ among the three areas to infer the effects of slope position on stand productivity.

The microtopography of each of the 100 cells was evaluated by calculating the slope inclination and relief of each cell from the topographic survey data obtained by Inoue et al. (2008). The slope inclination and relief of each cell were calculated following methods described in Yamakura et al. (1995). The slope inclination (SI) was calculated based on the coefficients of the following linear equation of the regression plane obtained using coordinates of the four corners of each cell:

$$Z = b_0+b_1X+b_2Y,$$

where Z is the vertical elevation, and X and Y are the horizontal coordinates within the research plot (Fig 1). The b_0, b_1, and b_2 are coefficients obtained using linear least-squares regression.

SI was calculated as,

$$SI = \arccos\left(1/\sqrt{b_1^2 + b_2^2}\right).$$

The relief was evaluated using the index of convexity (IC),

$$IC = Ec - Es$$

where Ec is the mean elevation of the four corners of a given cell and Es is the mean elevation of the 12 outer corners of the surrounding eight cells. Larger SI indicates steeper slope. Positive IC indicates convex relief, whereas negative IC indcates concave relief. The mean and range of SI and IC in the study plot are shown in Table 3. The slope and relief were relatively gentle on the ridge compared with the mid-slope and valley.

Path analysis, a kind of structural equation modeling (SEM) was used to infer the causal relationships among biomass, biomass increment, litterfall production, and microtopography. Path analysis, by way of correlation and partial regression coefficients, can be used to estimate direct and indirect contributions between the standardized predictor and criterion variables (Sokal and Rohlf 1995). We used the values obtained in each 10m x10m cell for the analysis (n=100). To infer the effect of microtopography on biomass and productivity, we hypothesized that the variation in biomass of *C. japonica* (Bc) and broad-leaved trees (Bb), biomass increment of *C. japonica* (Gc) and broad-leaved trees (Gb), and litterfall production of *C. japonica* (Lc) and broad-leaved trees (Lb) in each cell is caused by SI and IC. To infer competitive interactions between *C. japonica* and the broad-leaved trees, we hypothesized that Bc causes the variation among cells in Bb, Gc, Lc, Gb, and Lb and that Bb causes the variation among cells in Gc, Lc, Gb, and Lb. The fit of the hypothesized model was assessed using the maximum likelihood chi-squared statistic (χ^2) and non significant

paths ($p > 0.10$) were eliminated to derive the best fit model to the observed data. The model fit was assessed using Akaike's information criterion (AIC). To investigate whether causal relationships varied among topographic types, separate models were fit for groups of cells in the ridge, mid-slope and valley positions, respectively. All path analyses were performed using the SPSS statistical package, AMOS 17.0 (SPSS Japan Inc., Tokyo).

Results

Total biomass of the study plot was 400.7 Mg ha^{-1}, of which the broad-leaved trees contributed 93.4% (Table 4). Biomass increment and litterfall production of *C. japonica* was markedly lower than those of the broad-leaved trees. Total biomass increment, litterfall production, and ANPP of the study plot were 11.5, 5.2 and 16.6 Mg ha^{-1} yr^{-1}, respectively, of which the broad-leaved trees contributed 96, 90 and 95%, respectively.

Biomass (Wt), biomass increment (ΔWt), litterfall production (ΔL), and ANPP of the study plot decreased downslope from ridge to valley (Fig.2). The broad-leaved trees contributed to this trend, while the Wt, ΔWt, ΔL, and ANPP of *C. japonica* did not vary with slope position. In contrast to the downslope decrease in Wt, ΔWt, ΔL, and ANPP, relative biomass increment (ΔWt_r) of the broad-leaved trees did not vary with slope position, and relative litterfall production (ΔL_r) and relative ANPP ($ANPP_r$) increased downslope. The relative growth and production of *C. japonica*

did not vary with slope position.

Effects of microtopography on stand structure and productivity

The results of path analysis showed a negative correlation between IC and SI (Fig. 3). IC had positive effects on Bb and Lb, and a negative effect on Gc. Bc had positive effects on Gc and Lc, and a negative effect on Lb. Bb had a positive effect on Gb.

Discussion

The biomass of old-growth *C. japonica* plantations (77 to 126 years old) range, 210.5−515.0 Mg ha^{-1} (Tange et al. 1987, Nishimura et al. 1992, Watanabe and Mogi 2007). Although the biomass of *C. japonica* in our study plot was only 26.5 Mg ha^{-1}, the total biomass of 400.7 Mg $ha^{-1}$was comparable to that of old-growth plantations, suggesting that the regenerated broad-leaved trees complemented the decrease in *C. japonica* biomass. The total biomass was also comparable to that of an old-growth warm-temperate laurel forest in southern Kyushu, Japan (323.4 Mg ha^{-1}, Kimura 1960).

The broad-leaved trees contributed a substantial amount of the aboveground net primary production (ANPP) of the study plot. More than 90% of the biomass increment and litterfall production was attributed to the broad-leaved trees. The ANPP of the stand (16.8 Mg ha^{-1} yr^{-1}) was

comparable to those of 11- to 49-year-old *C. japonica* plantations (8.9-16.7 Mg ha^{-1} yr^{-1}, Tadaki et al. 1965) and that of the old growth warm-temperate laurel forest (21.6 Mg ha^{-1} yr^{-1}, Kimura 1960).

Aboveground biomass in the study plot decreased downslope. This is in contrast to several previous studies, which reported downslope increase in stand biomass in both plantations (Enoki et al. 1997, Tokuchi et al. 1999, Tsuji et al. 2007) and natural forest (Tateno et al. 2004). In our study plot, the slope inclination was relatively gentle and the relief was mild on the ridge. Relatively stable topographic conditions on the ridge may have promoted regeneration and establishment of the broad-leaved trees (Inoue et al. 2008). In contrast, unstable topographic conditions (steeper slope and concave relief) may have prohibited broad-leaved tree regeneration at lower slope positions.

Although biomass increment, litterfall production and ANPP of the broad-leaved trees decreased downslope, litterfall production and ANPP relative to the aboveground biomass increased downslope. The downslope increase in relative litterfall production suggested that trees on lower slope allocated their photosynthetic production more into leaves and branches, in part because of low stem density. The downslope increase in the relative production might be partly due to a gradient in nutrient and water availability along the slope. Nutrient availability generally increases downslope both in plantations (Hirobe et al. 1998; Tokuchi et al. 2000; Nishina et al. 2009) and natural forest (Vitousek et al. 2003; Porder et al. 2005; Takyu et al.2002; Tateno and Takeda 2003). In a cool

temperate deciduous forest in Kyoto Prefecture, Japan, the downslope increase in ANPP was attributed to the increase in the rate of soil nitrogen mineralization (Tateno et al. 2004).

In addition to the gradient in nutrient and water availability along the slope, tree distribution may be another possible explanation for the downslope increase in relative production. The downslope decrease in tree density and above-ground biomass may have reduced the effects of neighborhood competition among trees. Various factors influence the relationships among biomass, production, and neighborhood competition, such as species, tree size, and disturbances (Uriarte et al. 2004). In our study plot, we observed that frequent ground disturbances at midslope, where the slope inclination was steepest resulted in accumulation of various rock and woody debris at lower slope positions. This may have prevented tree establishment and resulted in lower tree density and aboveground biomass downslope.

In the study plot, IC had a negative effect on Gc indicating that growth of *C. japonica* decreased with increasing convexity. Many studies have been reported that, near the upper part the slope, growth of *C. japonica* is low on convex topography where water and nutrient availability are low (Tange et al. 1989, Tokuchi et al. 1999). In contrast, IC had positive effects on Bb and Lb suggesting that the broad-leaved trees could establish and be productive on stable convex topography on and around the ridge of the study plot.

The lack of correlation between Bc and Bb suggested that *C. japonica* seemed to have no

effect on the distribution of the broad-leaved trees. However, Bc had a negative effect on Lb, indicating that the productivity of the broad-leaved trees decreased with increasing *C. japonica* biomass. This suggested a competitive relationship and/or spatial segregation between *C. japonica* and the broad-leaved trees. In *C. japonica* and broad-leaved mixed forests on Yakushima Island, the additive basal area of *C. japonica* increased stand-level litterfall production (Aiba et al. 2007). They proposed that the emergent status of *C. japonica* above the canopy of the broad-leaved trees contributed to additive basal area of mixed forests compared with broad-leaved forests. In the present study site, however, there was little difference in tree height between *C. japonica* and broad-leaved trees, suggesting that competitive interaction and/or spatial segregation may have resulted in the negative correlation between Bc and Lb. We inferred that the lack of vertical stratification made the basal areas of two different crown forms exclusive rather than additive.

The results of our study suggested that in the unsuccessful, old-growth *C. japonica* plantation, variation in aboveground biomass might be determined by the distribution pattern of the naturally regenerated broad-leaved trees, which was largely affected by the topography. On the other hand, ANPP of the broad-leaved trees was affected by slope position and spatial distribution relative to the residual *C. japonica* trees, which may have resulted from competitive interaction or spatial segregation .

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Figure legends

Fig. 1 Topographic map of the study plot (100 x100 m) indicating the classification of each cell (10 x 10 m) by slope position.

Fig. 2 Biomass, biomass increment, litterfall production and aboveground net primary production (ANPP) of *Criptomeria japonica* (filled bars) and broad-leaved trees (open bars) in ridge, slope and valley slope positions. Biomass increment, litterfall production and ANPP relative to the aboveground biomass (%) are shown as black and white circles for *C. japonica* and broad-leaved trees, respectively.

Fig. 3 A path diagram of the relationships among index of convexity (*IC*), slope inclination (*SI*), biomass of *Cryptomeria japnica* (*Bc*) and broad-leaved trees (*Bb*), biomass increment of *C. japponica* (*Gc*) and broad-leaved trees (*Gb*), and litterfall production of *C. japonica* (*Lc*) and broad-leaved trees (*Lb*) obtained for each slope position: **a)** ridge, **b)** mid-slope, **c)** valley. All path coefficients represent standardized partial regression coefficients. *P <0.05, ** P <0.01, *** P <0.001.

Table 1 Tree density (stems ha^{-1}), basal area (m^2 ha^{-1}) and maximum tree height (m) of each species with stem girth larger than 15 cm in the study plot.

Species	Tree density (stems ha^{-1})	Basal area (m^2 ha^{-1})	Maximum tree height (m)
Cryptomeria japonica D. Don	46	7.4	26.8
Quercus salicina Blume	90	8.6	18.4
Carpinus tschonoskii Bl.	66	7.0	14.7
Camellia japonica L.	474	4.4	9.7
Quercus acuta Thunb. ex Murray	22	4.2	14.3
Cinnamomum japonicum Sieb. ex Nakai	139	4.1	13.5
Swida controversa Sojak	23	3.9	20.5
Machilus thunbergii Sieb. Et Zucc	29	2.2	14.5
Diospyros japonica Sieb. et Zucc.	17	1.3	17.1
Acer palmatum Tunb.	15	1.1	16.2
Machilus japonica Sieb. et Zucc.	46	1.0	12.1
Others	352	6.8	20.3
Total	1319	52.0	26.8

Data are from Inoue et al. 2008.

Table 2 Parameters applied to calculation for the biomass of *Cryptomeria japonica* and broad-leaved trees by the following allometric equations: $\log(Wi) = a \times \log(D) - b$, where D is DBH (cm), and a and b are the coefficients dependent on the species and the part of the trees. The weight of each part of the individual tree (Wi: kg) was weight of stem (Ws), branch (Wb) and leaf (Wl), respectively. The values of a and b are from Ando et al. (1968) for *C. japonica* and Ando *et al*., (1977) for broad-leaved trees.

Trees	Part	a	b
	Ws	2.3478	1.2406
Cryptomeria japnica	Wb	1.5945	-0.9894
	Wl	1.0963	-0.1329
	Ws	2.5857	-1.2268
Broad-leaved trees	Wb	2.6560	-1.8546
	Wl	1.7433	-1.6735

Table 3 Mean and range (minimum – maximum) of index of convexity (IC) and slope inclination (SI) for each slope position.

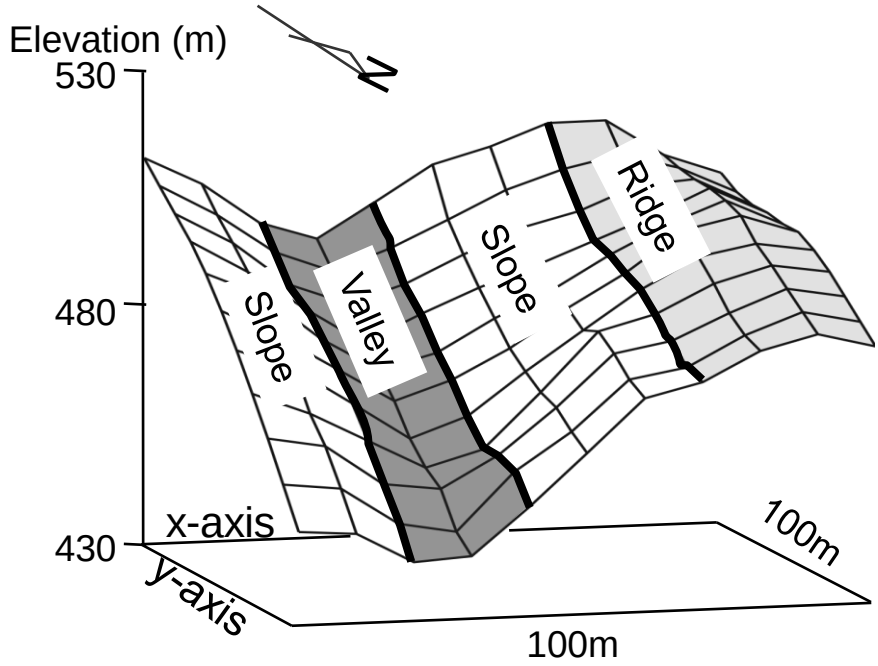
	Ridge	Mid-slope	Valley
IC (m)	2.3	0.3	-4.4
	(-1.4 – 4.9)	(-3.2 – 2.9)	(-6.7 – -2.7)
SI (degree)	28.4	40.2	37.0
	(17.1 – 39.2)	(17.7 – 50.2)	(26.7 – 50.4)

Data are from Inoue et al. 2008.

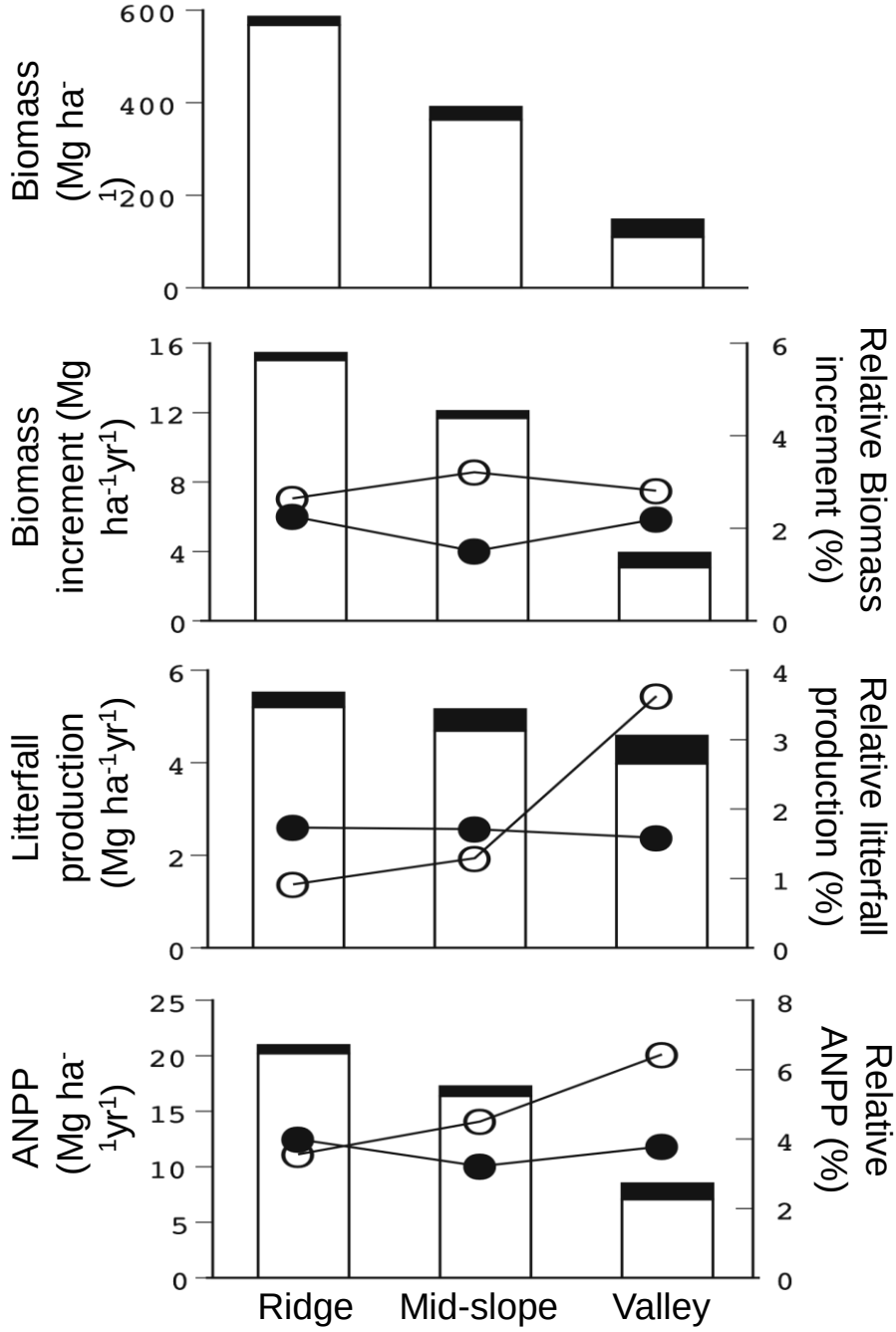
Table 4 Biomass, biomass increment, litterfall mass and aboveground net primary production (ANPP) of *Cryptomeria japonica* (CJ) and broad-leaved trees (BL) in the study plot. The relative values of biomass increment, litterfall and ANPP per unit biomass (%) are given in the parentheses.

	CJ	BL	Total
Biomass ($Mg\ ha^{-1}$)	26.5	374.2	400.7
Biomass increment ($Mg\ ha^{-1}\ yr^{-1}$)	0.49 (0.57)	11.0 (3.88)	11.5 (3.30)
Litterfall ($Mg\ ha^{-1}\ yr^{-1}$)	0.45 (0.37)	4.7 (5.08)	5.2 (8.04)
ANPP ($Mg\ ha^{-1}\ yr^{-1}$)	0.94 (0.95)	15.7 (8.99)	16.6 (7.48)

Enoki et al. Fig. 1



Enoki et al. Fig. 2



Enoki et al. Fig. 3