



## Structure, allometry, and biomass of plantation *Metasequoia glyptostroboides* in Japan

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### Abstract

We quantified structural features and the aboveground biomass of the deciduous conifer, *Metasequoia glyptostroboides* (Hu and Cheng) in six plantations in central Japan. In order to derive biomass estimates we dissected 14 *M. glyptostroboides* trees into three structural components (stem wood, branch wood and foliage) to develop allometric equations relating the mass of these components and of the whole tree to diameter at breast height (DBH). We found robust relationships at the branch and whole tree level that allow accurate prediction of component and whole tree biomass. Dominant tree height was similar within five older (>40 years) plantations (27–33 m) and shorter in a 20-year-old plantation (18 m). Average stem diameter varied from 12.8 cm in the youngest stand to greater than 35 cm in the oldest stand.

*Metasequoia* have relatively compact crowns distributed over the top 30% of the tree although the youngest stand had the deepest crown relative to tree height (up to 38%). At the individual tree level in older stands, 87% of the aboveground biomass was allocated to the stem, 9% to branch wood and 4% to foliage. We found little difference in the relative distribution of above ground biomass among the stands with the exception of lower foliage biomass in larger diameter trees. Total aboveground biomass of the older stands varied twofold, ranging from a maximum of 450 Mg ha<sup>-1</sup> in a 42-year-old stand to a minimum of 196 Mg ha<sup>-1</sup> in a 48-year-old stand. Total above ground biomass of the 20-year-old stand was 176 Mg ha<sup>-1</sup>.

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### 1. Introduction

*Metasequoia glyptostroboides* (Hu and Cheng), is a rare deciduous conifer of the redwood family (Taxodiaceae) with a natural range limited to small areas of western Hubei, northern Hunan and eastern Sichuan

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provinces in central China (Chu and Cooper, 1950; Bartholomew et al., 1983). It was known initially from fossil material (Miki, 1941) and it was not until 1948 that extant *M. glyptostrobooides* was described in the scientific literature as a species (Hu and Cheng, 1948). The native population of *M. glyptostrobooides* is isolated in a region of ca. 800 km<sup>2</sup> within which small stands are scattered along ravines between 750 and 1500 m elevation (Chu and Cooper, 1950). Following the formal description of *M. glyptostrobooides* as a new species, seed was collected from several populations in China and these were distributed worldwide in an effort to prevent its extinction (see Merrill, 1948). Seedlings from this seed lot have been planted throughout the world and trees are growing in botanical gardens and arboreta from as far north as Scandinavia to as far south as New Zealand (Satoh, 1999). The growth of solitary *M. glyptostrobooides* has been well studied from a horticultural perspective and periodic measurement of solitary *M. glyptostrobooides* over the past 50 years indicates that it is capable of sustained growth in a broad array of climates (Hendricks and Søndergaard, 1998; Kuser, 1999). In contrast, relatively little is known regarding the growth of *M. glyptostrobooides* growing in stands. Chu and Cooper (1950) completed a limited study of the ecology of *M. glyptostrobooides* within its native range. Although their primary objective was to document the environmental conditions and floristic composition of *M. glyptostrobooides* stands, they made limited measurements of tree size and age that indicated *M. glyptostrobooides* was capable of attaining heights up to 50 m and diameter at breast height (DBH) in excess of 2 m. We know of no other studies of the forest ecology of *M. glyptostrobooides* within its native range.

Whereas relatively little is known about the ecology of *M. glyptostrobooides* in China, the situation is somewhat better for planted *M. glyptostrobooides* stands. For example, in Japan, *M. glyptostrobooides* was introduced in 1950 with a limited number of seedlings established from the Chinese seed lot collected in 1948. Clonal plantations from rooted cuttings were established at multiple locations to evaluate the growth and performance of the species for reforestation and as a forest product. Early reports indicated good growth and biomass accumulation rates in young Japanese plantations (i.e., 9–20-year-old; Saito et al., 1970; Satoo, 1974). Similar data exist for young

plantations (6–14-year-old) in China and the Czech Republic (Pokorný, 1981; Fang et al., 1995). *Metasequoia* introduced to southern Switzerland fared worse in trial plantings where mortality was high and tree growth was poor (tree height averaged only 3.5 m after 18 years) apparently due to insufficient growing season precipitation (Buffi, 1987; P. Rotach, personal communication, 1999).

Recent analysis of *M. glyptostrobooides* wood suggests that it has merit as a potential source of wood for forest products (Jin and Hua, 1997; Polman et al., 1999). However, there are no published reports of biomass and productivity for older *M. glyptostrobooides* and little information is available on the variation of aboveground biomass with stand age and location. Furthermore, existing allometric equations (Satoo, 1974) were developed using young trees and have limited use in predicting aboveground biomass of trees in older stands with larger diameters and heights. This leads to difficulty in assessing the performance and managing older *M. glyptostrobooides* plantations. We sought to develop a set of general allometric equations to estimate aboveground biomass of *M. glyptostrobooides* plantations in Japan. The general objective of this study was to describe and quantify the structure and aboveground biomass of *M. glyptostrobooides* plantations in central Japan. In order to achieve this objective, we (1) made dimensional measurements of individual *M. glyptostrobooides* in plantations; (2) developed general allometric equations to estimate stem, branch and foliar biomass of *M. glyptostrobooides*; (3) determined the relative distribution of aboveground biomass at the stand level; and (4) compared the aboveground biomass of different plantations in Japan.

## 2. Methods

### 2.1. Site descriptions

We analyzed six *M. glyptostrobooides* stands in four experimental forests on Honshu Island, Japan. The plantations are all located in the warm-temperate climate zone of Japan. At the Tokyo University Forests, Tanashi Experimental Station, near Tokyo, Japan (35°44'N, 139°32'E), two small stands of differing age and initial planting density were analyzed. The stands are located on a flat area derived from volcanic parent

material at approximately 60 m elevation. The mean annual temperature at this site is 13.7 °C and mean annual precipitation is ca. 1400 mm. One stand (hereafter referred to as “Tanashi-A”) was established in 1953 from the rooted cuttings of two parent trees. Trees were established on a 2 m square grid pattern and the original plot size was ca. 600 m<sup>2</sup>. Five trees were removed from the plot in 1970 as part of a study by Satoo (1974). Otherwise, the stand has received no silvicultural treatment. A second stand (hereafter referred to as “Tanashi-B”) was established in 1980 from rooted cuttings taken from Tanashi-A trees. The cuttings were planted on a 1 m square grid pattern adjacent to the Tanashi-A stand and the entire stand is ca. 420 m<sup>2</sup>. Both stands are growing on an Andisol soil (Kanto-loam). The pH of the upper 10 cm is 5.7.

A third site was located on the Izu Peninsula (34°42'N, 138°51'E) at the Aono Forest of the Arboricultural Research Institute, Minamiizu, Japan. The mean annual temperature at this site is 15.0 °C and mean annual precipitation is ca. 2300 mm. Trees were established on a 1.8 m square grid pattern within a 1600 m<sup>2</sup> area. The stand we analyzed was located at 180 m elevation with a northwest aspect. This stand was on a 15% slope and surrounded by forest vegetation on all sides. The stand is growing in an Alfisol soil.

The fourth stand we analyzed was located at the Kyoto University, Kamigamo Experimental Forest (35°04'N, 135°45'E), near Kyoto, Japan. The mean annual temperature is 15.3 °C and mean annual precipitation is ca. 1700 mm. One-year-old rooted cuttings were established in 1956 within a 0.41 ha area at approximately 2 m spacing. The stand is located at ca. 140 m elevation. This stand spans a 20% slope with a northwest aspect. The stand is growing on an argillaceous Alfisol.

The fifth and sixth plantations are both located at the Kyoto University, Ashiu Experimental Forest (35°18'N, 135°43'E), near Miyama, Japan. The mean annual temperature at Ashiu is 12.3 °C and mean annual precipitation is ca. 2375 mm. Soils are Alfisols with a clay loam texture and pH of 4.3 in the upper 10 cm (Ueda et al., 1993). The Naisugi stand is a 0.1 ha, 41-year-old plantation located at 420 m elevation with a northeast aspect. Koyomogi is a 0.43 ha, 44-year-old plantation located at 435 m elevation with a southeast aspect. Both plantations were established from rooted cuttings at initial planting densities of

2000 stems ha<sup>-1</sup> at Naisugi and 2093 stems ha<sup>-1</sup> at Koyomogi.

## 2.2. Stand measurements

We established sample plots at Tanashi, Izu, and Kamigamo. Each plot was established so that all border trees were excluded from our analysis with the boundary of each sample plot passing midway between the outmost and first row of trees. We measured the diameter at 1.4 m above the ground (DBH) on all trees at Tanashi, Izu and Kamigamo. In June 2001 we established sample plots at Ashiu. We measured DBH in both plantations at Ashiu. In all plantations, heights of non-destructively sampled trees were determined using a Blume-Leiss altimeter or geometrically using a Suunto clinometer and distance tape.

## 2.3. Tree selection and sampling

In June 2000, 14 *M. glyptostroboides* differing in stem diameters (minimum 8.9 cm, maximum 50.1 cm) were selected for destructive sampling. We selected three sample trees that were above and below the stand average diameter for each stand from Tanashi-A, Tanashi-B, Izu, and Kamigamo. No trees were destructively sampled in the Ashiu stands. For each sample tree, DBH (1.4 m) was determined using a DBH tape prior to felling. Once the tree was felled a measuring tape was laid along the stem axis from tip to base and tree height was recorded. The distances of all living and dead branches were tallied from the tip downward along with branch diameter at the point at which it joins the stem. Five to six live branches were selected from the canopy of each tree and the length, fresh foliage weight, and fresh branch wood weight were measured. These data were used to develop regressions between branch diameter and both branch wood and foliage biomass. The basal branch diameters measured on each tree were used to estimate foliar and branch biomass using these regressions. Dry weight determination of these fractions was based on the fresh/dry weight ratios determined on oven-dried (65 °C until constant weight) sub-samples. Stems were cut into logs (1–2 m long). Fresh weights and dimensions of the logs were recorded and sample discs ca. 20 cm thick were cut from the logs near the base, middle and top of each tree for dry weight determination. Dry weights of

logs were calculated from the log fresh weights and disc fresh/dry ratios.

#### 2.4. Estimation of biomass

All measured values were transformed using natural logarithms to normalize their probability distributions. Branch wood and foliage dry weights were regressed against branch basal diameter using ordinary least-squares regression to predict branch and foliar biomass. These regressions were then applied to the basal diameters of all non-weighed branches and the results summed to estimate the dry weight of branch wood and foliage in the entire canopy of each sample tree. Summed estimates of total-canopy branch wood and foliage dry weights for each tree were used to develop regressions between DBH and total-canopy component dry weight. We also developed regressions between DBH and stem biomass. Bole wood dry weights were calculated by wet/dry conversion of bole field weights. Bark was not removed from bole sections and was incorporated in the dry weight estimates.

Measured weights were related to diameters using ordinary least-squares regressions with the standard allometric formula

$$Y = \alpha x^\beta,$$

where  $\alpha = e^{\gamma+\varepsilon}$  and  $\beta$  is the regression slope,  $\gamma$  the regression intercept and  $\varepsilon$  the error term equal to 1/2

the mean squared error from the regression analysis. The error term is included to compensate for a downward bias introduced during back-transformation of regression estimates due to the fact that the mean of a logarithmic value is equal to the median of the untransformed value (Bell et al., 1984; Niklas and Buchman, 1994). We employed Tukey's jackknife technique (Sokal and Rohlf, 1995) to assess the regression sensitivity to removal of individuals (15 random individuals recalculated 30 times) in the case of branch level equations and the removal of single samples for the tree level allometric equations. Statistical analyses were completed using the statistical program JMP 4.0 (SAS Institute, Raleigh, NC). We also assessed the precision of the whole tree regression equations by defining the relative dispersion of sample points about the regression lines by computing an estimate of relative error (sensu Whittaker and Woodwell, 1968).

### 3. Results

#### 3.1. Stand structure

Current stem density ranged from a low of 816 stems ha<sup>-1</sup> in Tanashi-A to a high of 2767 stems ha<sup>-1</sup> in Tanashi-B (Table 1). We compared original and present stem densities to assess mortality

Table 1  
Structural variables and estimated aboveground biomass of six *M. glyptostroboides* stands in central Japan

Variable	Tanashi-A	Tanashi-B	Izu	Kamigamo	Ashiu, Koyomogi	Ashiu, Naisugi
Age (years)	48	20	48	47	41	44
Initial planting density (trees ha <sup>-1</sup> )	2500	10,000	3086	2500	2000	2093
Current density (trees ha <sup>-1</sup> )	816	2,767	1706	1000	1630	884
Dominant tree height (m)	30.7	18.0	31.1	28.6	27.3	31.5
DBH (cm)	34.3	12.4	25.1	24.4	27.1	35.5
DBH range (minimum, maximum)	19.8, 50.6	1.5, 30.5	2.8, 53	6.2, 52.0	9.6, 54.4	23.4, 58.0
Basal area (m <sup>2</sup> ha <sup>-1</sup> )	81	48.63	96.6	53.3	114.7	93.4
Longest branchless span (m)	7.5	8.5	24.3	14	nm <sup>a</sup>	nm
Length of canopy (m)	10	6.5	9.5	8.3	nm	nm
Aboveground biomass						
Foliage (Mg ha <sup>-1</sup> )	8.8	6.1	11.3	6.3	13.5	11.0
Branch (Mg ha <sup>-1</sup> )	30.7	15.5	37.2	19.7	48.6	41.4
Stem (Mg ha <sup>-1</sup> )	318.0	154.8	313.8	170.4	387.5	322.5
Total aboveground (Mg ha <sup>-1</sup> )	357.5	176.4	362.3	196.4	449.6	375.0

<sup>a</sup> Not measured.

in each plantation. Excluding the mechanically thinned Naisugi stand, mortality was lowest in the Koyomogi stand (19%) followed by Izu (45%), Kamigamo (60%), Tanashi-A (67%), and Tanashi-B (72%). Although mortality was greatest at the highest planting density, there was no significant correlation between initial planting density and mortality ( $R = 0.55$ ;  $P = 0.3117$ ).

Stand height was similar among plantations with the exception of the youngest stand, which was approximately 14 m shorter than the tallest stand (Table 1). The Naisugi ( $31.5 \pm 1.19$  m), Tanashi-A ( $30.7 \pm 0.35$  m), and Izu ( $31.7 \pm 1.15$  m) stands had the tallest canopy dominant individuals followed by Kamigamo ( $28.5 \pm 0.95$  m), Koyomogi ( $27.3 \pm 1.04$  m), and Tanashi-B ( $16.9 \pm 0.62$  m).

Average stem diameters varied among stands. The largest diameter trees were found at Naisugi (mean = 35.5 cm, S.E. =  $\pm 2.7$ ) and Tanashi-A ( $34.4 \pm 1.90$

cm). At Koyomogi ( $27.1 \pm 2.5$  cm), Izu ( $25.3 \pm 0.9$  cm) and Kamigamo ( $24.4 \pm 1.2$  cm) stem diameters were similar to each other but smaller than the trees at Naisugi and Tanashi-A. Trees in the youngest stand, Tanashi-B, were on average the smallest diameter trees ( $12.4 \pm 0.9$  cm). Fig. 1 illustrates the stem diameter distribution for each plantation. The Tanashi-A and Kamigamo stem diameters were more normally distributed whereas the other stands were skewed right with higher percentages of stems in the smaller size classes. The Naisugi stem size distribution shows the effect of an improvement cutting where small diameter trees were removed early in stand development. Mean stem diameter was strongly correlated with present tree density ( $R = 0.90$ ;  $P = 0.0139$ ).

Stand basal areas for the oldest stands were high and varied substantially between stands. The maximum basal area was found in the Koyomogi stand

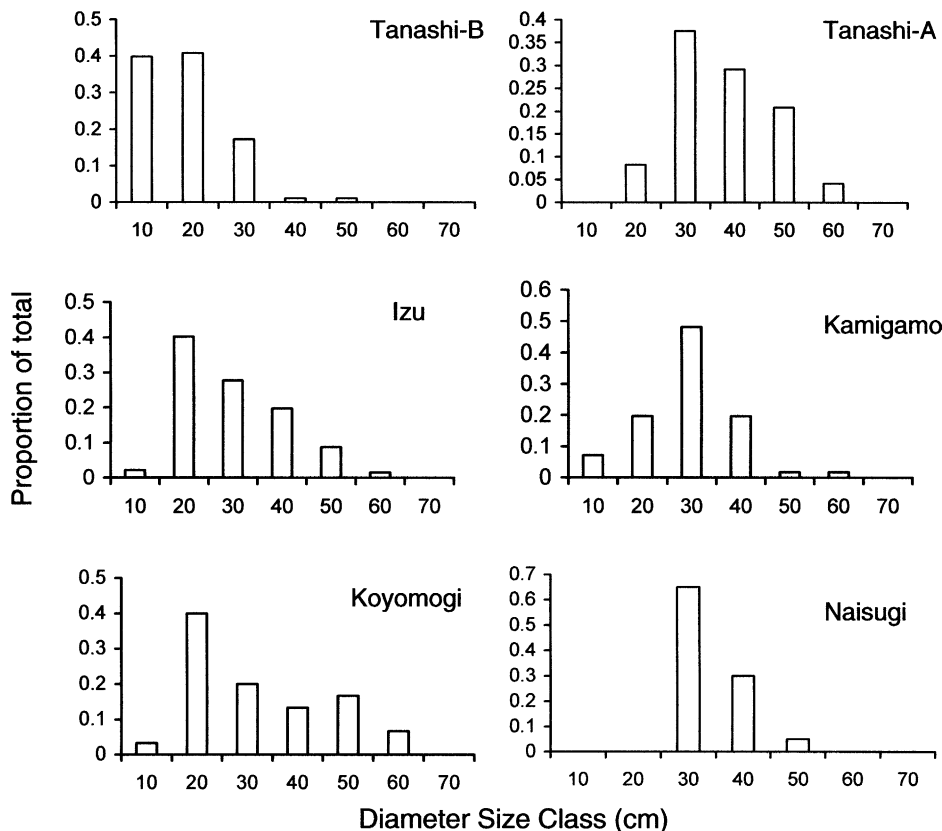


Fig. 1. Stem diameter-frequency distribution for six *M. glyptostroboides* plantations in central Japan.

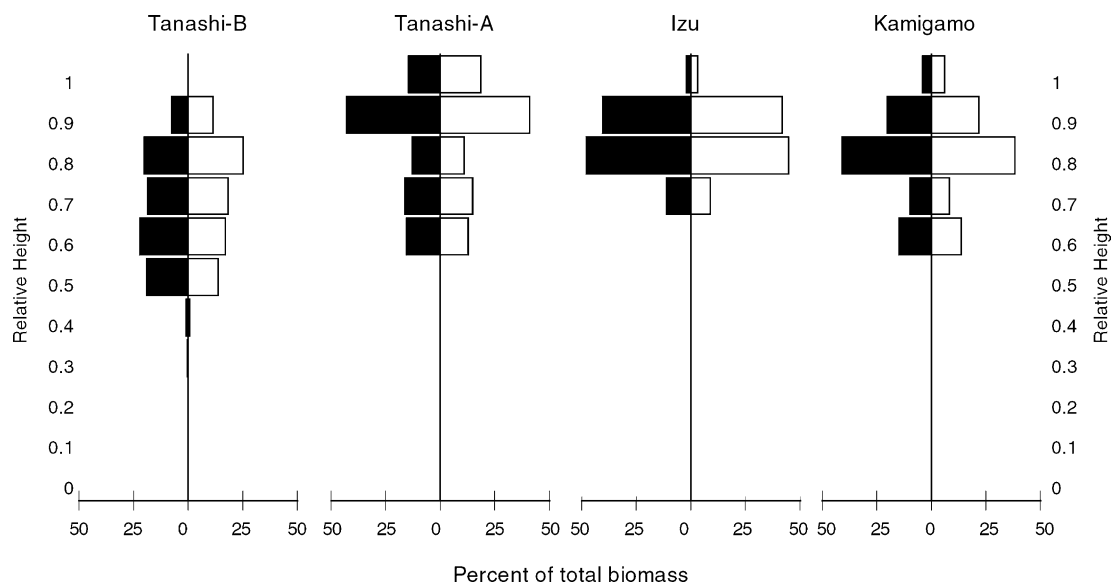


Fig. 2. Vertical distribution of branch wood (patterned bar) and foliage (hollow bar) biomass in relation to relative tree height for four canopy dominant *M. glyptostrobooides* trees from plantations in Japan.

(114.7 m<sup>2</sup> ha<sup>-1</sup>) although basal areas at the Izu and Naisugi stands were also considerable (96.6 and 94.3 m<sup>2</sup> ha<sup>-1</sup>, respectively). The low density of trees in combination with the smaller stem diameters resulted in a relatively low basal area at Kamigamo (53.3 m<sup>2</sup> ha<sup>-1</sup>). The minimum stem basal area was found at the Tanashi-B stand (48.6 m<sup>2</sup> ha<sup>-1</sup>).

The vertical distribution of foliage and branch biomass was similar for canopy dominant trees in different stands. Maximum canopy biomass occurred within the upper 20% of the tree (Fig. 2). Absolute canopy lengths are given in Table 1 and ranged from a maximum of 10 m in Tanashi-A to a minimum of 6.5 m in Tanashi-B. Expressed as live crown ratios (i.e., the ratio of live crown length to tree height), canopy dominant trees averaged 33% across all plantations but at the stand level ranged from an individual to a low of 25% at Izu to a high of 38% at Tanashi-B. The shallow canopy depth and the self-pruning of branches in all plantations resulted in variable lengths of branch-free wood. The largest average branch-free spans were recorded for trees in Izu (24.5 m) and the shortest at Tanashi-A (7.5 m). It should be noted that smaller (<10 mm diameter) epicormic branches were occasionally found on the lower stems of trees that had self-pruned larger branches.

### 3.2. Allometric relationships

#### 3.2.1. Limb analysis

Individual branch observations on dry branch wood and foliage mass were conducted on 80 branches. Table 2 presents the coefficients and standard errors for equations using branch diameters to predict dry weight of branch wood and foliage. Foliage and branch dry mass increased with increasing basal branch diameter. We found a good relationship between basal branch diameter and branch dry weight ( $R = 0.98$ ) and foliage dry weight ( $R = 0.95$ ; Fig. 3). Both equations proved insensitive to removal of multiple individuals and the jackknife analysis resulted in no significant change in the correlation coefficient for either the branch wood mass equation ( $R = 0.98$ , 95% CI: 0.9842–0.9863,  $n = 65$ ) or the foliage dry mass equation ( $R = 0.95$ , 95% CI: 0.9490–0.9559,  $n = 65$ ).

#### 3.2.2. Whole tree analysis

Table 2 presents the coefficients and errors for canopy regressions as well as bole and whole tree regressions on DBH. We found strong correlations between DBH and total estimated dry branch wood and foliage weight (Figs. 4 and 5). Foliage and branch biomass both increased with DBH and were strongly

Table 2

Parameters, model mean square error (MSE), standard error of the estimate (SEE) and coefficients of determination ( $R^2$ ) for the standard allometric model of the power-form:  $y = \alpha x^\beta$ , where  $y$  is the branch component dry weight or whole tree component dry weight,  $x$  the branch diameter or stem DBH in cm,  $\alpha$  the  $\alpha = e^{\gamma+\varepsilon}$ , where  $\gamma$  is the intercept from the regression and  $\varepsilon$  the error term equal to 1/2 the MSE from the regression analysis and  $\beta$  the slope of regression

Dependent variable	$\alpha$	$\beta$	MSE	SEE	$R^2$
Branch level components ( $n = 80$ ) <sup>a</sup>					
Foliage dry mass (g)	17.16	1.9974	0.194	0.44	0.91
Branch dry mass (g)	23.82	2.7188	0.108	0.329	0.97
Whole tree level ( $n = 14$ ) <sup>b</sup>					
Foliage dry mass (kg)	0.0095	1.9787	0.092	0.303	0.934
Branch dry mass (kg)	0.0039	2.5622	0.112	0.335	0.952
Stem dry mass (kg)	0.0701	2.4074	0.023	0.152	0.988
Whole tree dry mass (kg)	0.0787	2.4086	0.0155	0.124	0.992

<sup>a</sup> Sample branch diameter range: 0.5–5.0 cm.

<sup>b</sup> Sample trees DBH range: 8.4–50.9 cm.

correlated with DBH (Table 2). We used Tukey's jackknife procedure to assess regression sensitivity to removal of individual values. For canopy components, jackknife equations differed little from the

whole sample regressions. The jackknife correlation coefficient for branch wood regression is 0.98 (95% CI: 0.9785–0.9810,  $n = 13$ ). There was a high correlation between tree DBH and foliage mass as well

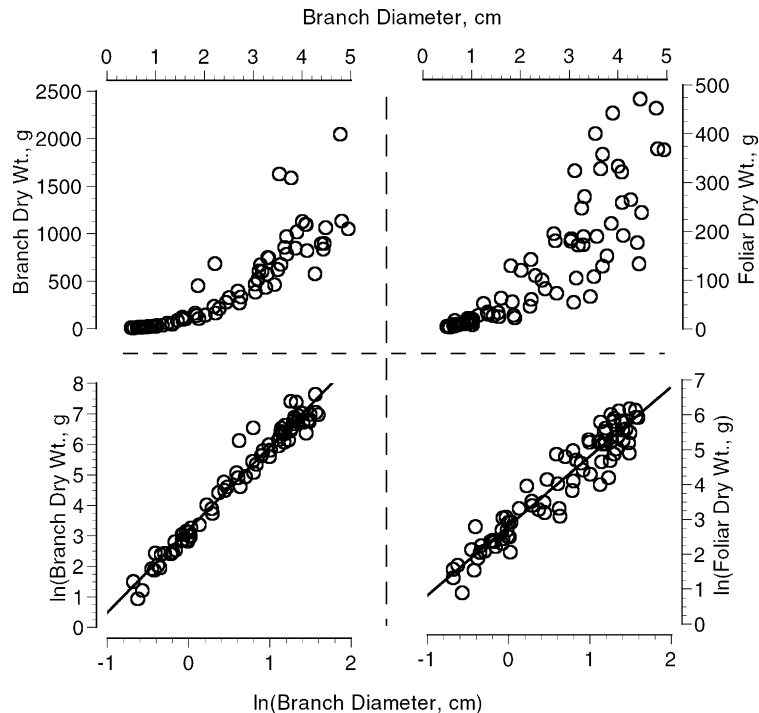


Fig. 3. Branch diameter versus branch weight; branch diameter versus foliage weight for *M. glyptostroboides* in Japan. Branch component (branch wood and foliage) dry weight regressed on basal branch diameter. Regression statistics presented in Table 2.

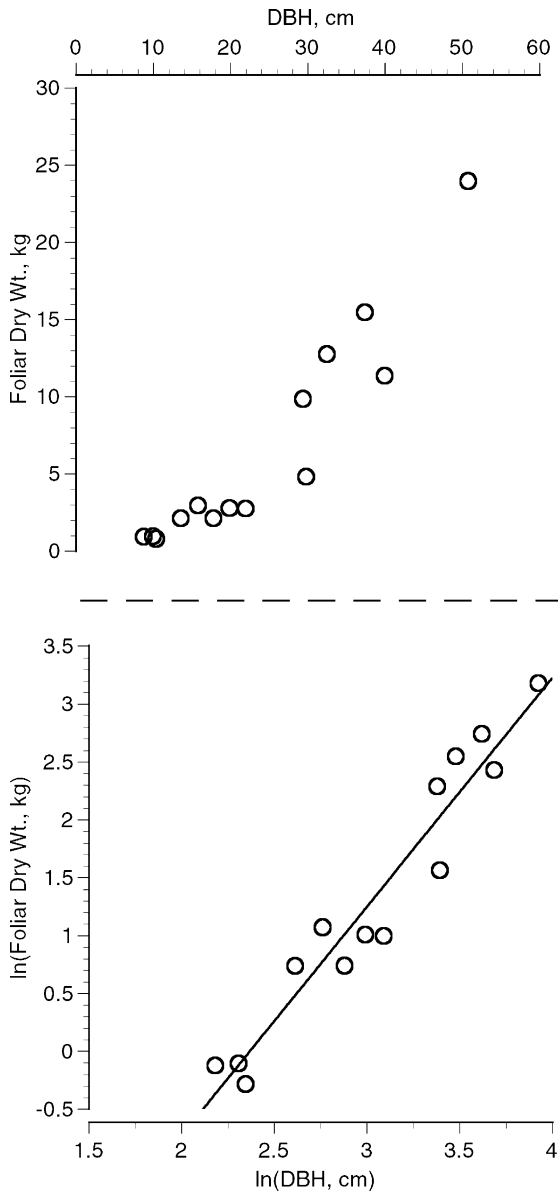


Fig. 4. Data and regressions shown for dry weight of canopy foliage against bole DBH for plantation *M. glyptostroboides* in Japan. Regression statistics are presented in Table 2.

( $R = 0.97$ , 95% CI: 0.9720–0.9752,  $n = 13$ ). Stem mass and whole tree biomass increased with increasing stem diameter. DBH and stem mass were strongly correlated (Fig. 6) ( $R = 0.985$ ) and whole tree biomass (i.e. sum of foliage, branch and stem dry mass) was strongly correlated with DBH (Fig. 7;  $R = 0.99$ ).

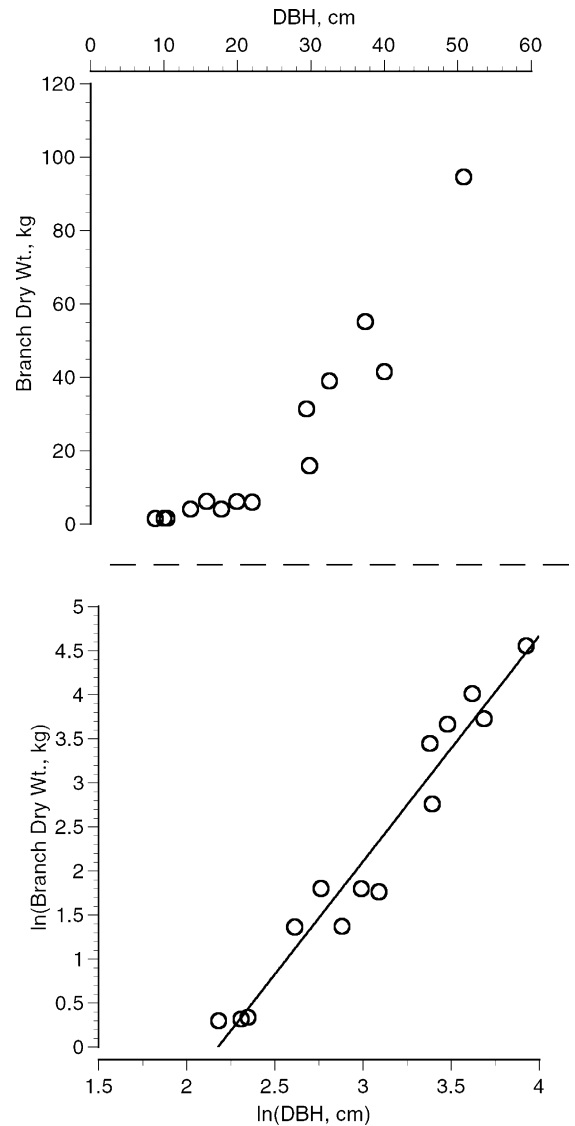


Fig. 5. Data and regressions shown for dry weight of canopy branch wood against bole DBH for plantation *M. glyptostroboides* in Japan. Regression statistics are presented in Table 2.

Jackknife analysis resulted of both equations resulted in little change in the coefficients of determinations (DBH versus bole mass:  $R = 0.985$ , 95% CI: 0.981–0.991,  $n = 13$ ; DBH versus whole tree mass:  $R = 0.991$ , 95% CI: 0.989–0.994,  $n = 13$ ).

Estimates of relative error for equations using DBH as the independent variable suggest that prediction of canopy components is less accurate than

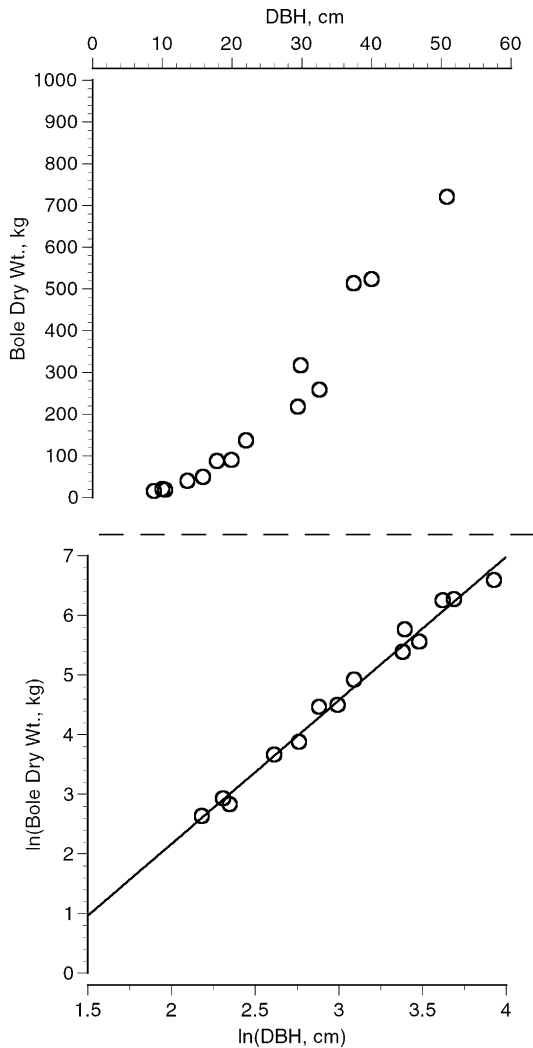


Fig. 6. Data and regressions shown for dry weight of bole wood against bole DBH for plantation *M. glyptostroboides* in Japan. Regression statistics are presented in Table 2.

that of stem wood or whole tree biomass as has been found for other species (e.g., Whittaker et al., 1974; Vann et al., 1998). The foliage equation is likely to predict the true mean foliage biomass at the stand level to within  $\pm 16\%$ . Prediction of branch wood biomass was somewhat more accurate yielding an estimate of relative error of  $\pm 10\%$ . Stem biomass and whole tree biomass predictive equations had similar estimate of relative error values and suggest that predicted values are likely to vary about the true mean by  $\pm 3\%$ .

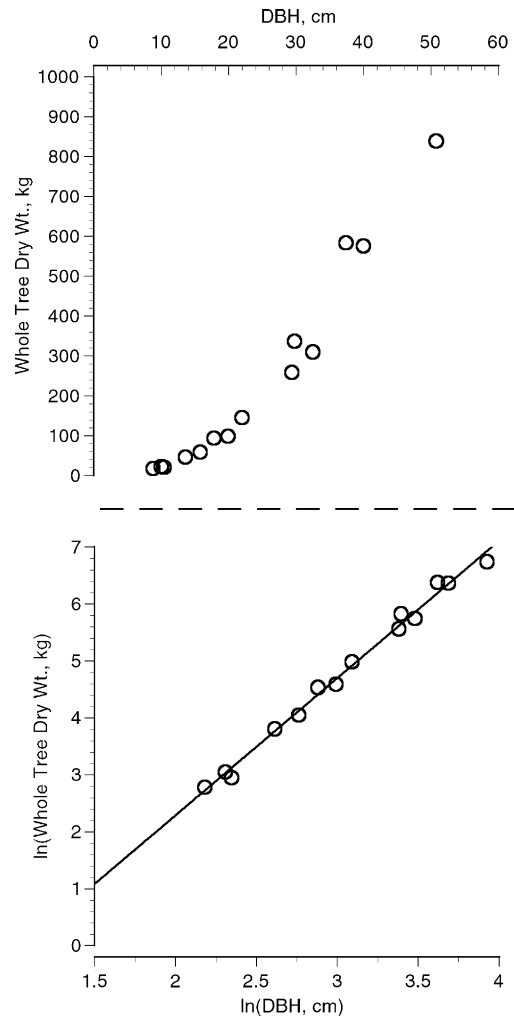


Fig. 7. Data and regressions shown for dry weight of whole tree against bole DBH for plantation *M. glyptostroboides* in Japan. Regression statistics are presented in Table 2.

### 3.2.3. Biomass distribution

Biomass distribution among the aboveground tree components was similar across the sample of harvested trees. Averaged across all sampled trees, the largest amount of biomass was in stem wood (average 87%) followed in order by branch wood (9%) and foliage (4%). Across the size range (8.9–50.1 cm DBH) of sample trees we found no significant relationship between DBH and the proportion of biomass in either the stem wood ( $F_{13,1} = 0.0722$ ,  $P < 0.7923$ ) or branch wood ( $F_{13,1} = 1.5869$ ,  $P < 0.2299$ ) biomass

components. There was a significant negative relationship between DBH and the proportion of aboveground biomass in the foliage component ( $F_{13,1} = 5.3804$ ,  $P < 0.0428$ ) with larger diameter trees having a smaller proportion of biomass in foliage.

#### 3.2.4. Stand biomass

Table 1 presents the total aboveground biomass for the three different biomass components for each stand derived using the tree level allometric equations in Table 2. Owing to a relatively high stem density, total aboveground biomass of the Koyomogi stand was the greatest ( $450 \text{ Mg ha}^{-1}$ ). Aboveground biomass in the Naisugi and Izu stands was of similar magnitude to each other ( $375$  and  $362 \text{ Mg ha}^{-1}$ , respectively) but lower in magnitude than Koyomogi stand. Tanashi-A was of intermediate aboveground biomass ( $358 \text{ Mg ha}^{-1}$ ), whereas the Kamigamo ( $196 \text{ Mg ha}^{-1}$ ) and Tanashi-B ( $176.4 \text{ Mg ha}^{-1}$ ) stands accumulated the smallest amounts of aboveground biomass across all the stands we surveyed.

## 4. Discussion

### 4.1. Stand structure

With the exception of the Naisugi plantation, which was thinned at age 15, the stands that we studied received no silvicultural treatment. When initial and present tree densities are compared, it is evident that mortality claimed trees in all of the untreated stands. Previous investigations at a few of the stands we studied indicate that self-thinning took place in the early stages of stand development. However, mortality varied with original planting density in a complex manner. By age 17, 67% of the trees in the Tanashi-A stand had died (Satoo, 1974). In comparison, the Izu stand, planted at a higher initial density than Tanashi-A (3086 versus  $2500 \text{ stems ha}^{-1}$ ), suffered lower mortality (50%) during the first 20 years of stand development (Ikeda, 1980). Trees planted at the highest density had the highest mortality (72%). Mortality is most frequent among the smallest suppressed individuals in each stand, some of which we observed to be suffering from heart rot (at Izu and Tanashi-B) or occasional snow or animal damage (Ando et al., 1991). Nevertheless, a comparison of the tree densities

we measured at Tanashi-A and Izu with previously collected data indicates no further reduction in tree density following the early self-thinning that occurred in the first 20 years of stand development. This pattern is consistent with the development of pure, even-age, single-canopied stands in which plant to plant competition is most intense in the early stages of canopy closure (Oliver and Larson, 1990).

Across all of the stands we studied, on average, the largest diameter trees occurred in the lowest density stands and there was a strong negative correlation between these variables ( $R = -0.90$ ). Maximum density-yield or density size relationships are well established for even-age monospecific stands (Yoda et al., 1963; Gorham, 1979) and our data suggest that *M. glyptostroboides* conforms to these relationships. A density related depression in stem size is apparent when the Tanashi-A and -B plantations are compared. These stands are replicate clonal plantations growing at the same location and on the same soils but with different initial stem densities. Average stem diameters in Tanashi-B are significantly smaller (12.4 cm) than those measured in Tanashi-A (20.2 cm) when it was of a similar age (Satoo, 1974). A similar comparison of the thinned Naisugi stand and the unthinned Koyomogi stand also indicates larger stem diameters at lower stem densities and is consistent with the results of others that suggests better growth of *M. glyptostroboides* in thinned (i.e. lower density) versus unthinned stands (Zhou et al., 1998).

Our measurements of tree height reveal that *M. glyptostroboides* can attain average stem lengths greater than 30 m in less than 50 years in Japan. The height of canopy dominant individuals was similar among the older study sites and differed by only four meters. These tree heights are similar to those reported by Haupthoff (1998) for 40-year-old *M. glyptostroboides* growing in Germany but taller than similar age trees growing in the Czech Republic, The Netherlands, and Denmark (Goudzwaard and Schmidt, 1992; Hendricks and Søndergaard, 1998; Liao and Podráský, 2000). Most of the height growth apparently occurs early in stand development with vertical extension slowing through time. For example, Satoo (1974) reported the average tree height of the Tanashi-A stand at age 17 to equal 14.7 m with dominant trees as tall as 16.8 m. This is equivalent to an average annual height increment of 86 cm per

year. This stand was measured again at 25 years of age and vertical growth had decreased to 66 cm per year (T. Tange, unpublished data). Our measurements suggest that between 25 and 48 years of age, vertical growth decreased to 56 cm per year. Trends in vertical growth at the Izu stand follow a similar pattern decreasing from a rate of 103 cm per year up to age 20 (Ikeda, 1980) to a rate of 48 cm per year from age 20 to 48 years.

These rates of vertical growth tend to be slightly higher than European *M. glyptostroboides*. For example, Goudzwaard and Schmidt (1992) reports height growth rates of 40 to 60 cm per year for 22–30-year-old trees in The Netherlands. Haupthoff (1998) reports vertical rates of extension for a *M. glyptostroboides* plantation in Germany of 93 cm per year during the first 28 years of stand development and then a decrease to 31 cm per year between 28 and 40 years. Similar rates are also noted for *M. glyptostroboides* in the Czech Republic by Liao and Podráský (2000), who report growth rates of 67 cm per year from 4 to 22-year-old and then a decrease to a current rate of ca. 30 cm per year. In general, the height growth of *M. glyptostroboides* is about twofold greater than that of *Cryptomeria japonica* grown in Japanese plantations (Ando et al., 1991).

#### 4.2. Branch and stem allometry

On *M. glyptostroboides*, the amount of foliage and branch dry mass was closely related to basal branch diameter (Table 2 and Fig. 3); the larger the branch diameter, the greater the foliage and branch biomass it bore. These allometric relationships result from biomechanical principles that govern the structural design of branches (Morgan and Cannell, 1987; Bertram, 1989). Of the few studies of branch allometry that exist, most report a good relationship between branch diameter and foliage and/or branch dry mass (e.g., Gilmore and Seymour, 1997; Vann et al., 1998). We found that the predictive equation describing foliage biomass on the basis of branch diameter to have a higher standard error and lower coefficient of determination than the branch biomass equation. The larger error associated with the foliage biomass prediction equation probably results from a greater sensitivity of foliage production to yearly variation in growing environment and age related changes in canopy structure

particularly when compared to evergreen species whose biomass sums several years of foliar growth. On the other hand, branch dry mass accumulation is cumulative and less likely to vary from year to year depending on the canopy light environment. Others have also found foliage equations to have higher associated errors than branch wood equations across different tree types (Vann et al., 1998; Monserud and Marshall, 1999). Unfortunately, we know of no published branch level allometric equations for other deciduous conifers making it difficult to compare the branch allometry of *M. glyptostroboides* to other deciduous conifers.

We found DBH to be a good predictor of *M. glyptostroboides* component and whole tree biomass (Figs. 4–7). This is expected given that the excurrent stem form of *M. glyptostroboides* leads to a consistent stem shape among trees of different diameters. Because wood constitutes the majority of total tree mass and is concentrated within the stem, mass and stem diameter closely related and this relationship has been found by many others for a wide variety of different sized trees (Whittaker et al., 1974; Tritton and Hornbeck, 1982; Siccama et al., 1994).

All of our DBH versus component mass equations differed slightly from the equations developed by Satoo (1974) for the 17-year-old Tanashi-A plantation suggesting changes in the allometry of stem diameter and mass have occurred with aging of the stand (Fig. 8). The slopes of our DBH versus component biomass equations were statistically indistinguishable from Satoo's (1974) equations suggesting proportionally similar scaling of diameter and mass with increasing age. However, the y-intercepts of all three equations differed statistically from Satoo's. Our equations predicted greater stem mass and lower branch and foliage mass for a given diameter than did Satoo's equations.

The difference in predicted stem mass for the two sets of equations probably reflects age related differences in tree height with Satoo's 17-year-old trees being shorter, and thus having less stem mass than older trees of the same diameter. In contrast, at age 17, the trees Satoo measured had more branch and foliage biomass for a given diameter than the trees we measured. At age 17 this stand had a greater canopy exposure and as a consequence was able to support a larger branch and foliage biomass than a tree of

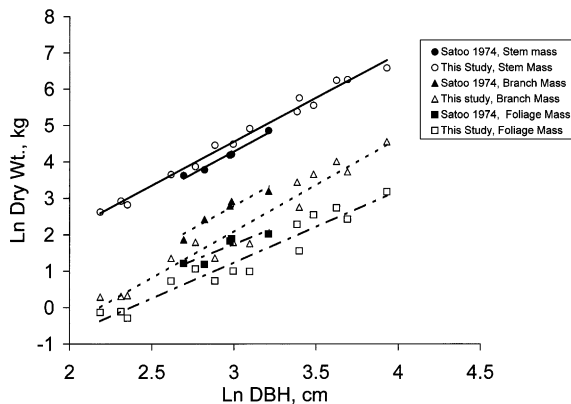


Fig. 8. Comparison of published allometric equations for the Tanashi-A, *M. glyptostrobooides* stand at age 17 (Satoo, 1974) with those generated from this study.

similar diameter at age 48 growing in a more developed canopy. With increasing stand age, the canopy has receded upward resulting in a compaction of the canopy. This is also supported by the higher live crown ratios in the Tanashi-B stand as compared to the other older stands. Bartelink (1996) reported a similar trend for Douglas-fir in a chronosequence study in The Netherlands. A difference in predicted stem mass for the two sets of equations may also arise as a consequence of our application of generalized allometric equations across several stands with slightly different morphology; hence, allometry would also vary. Finally, there tends to be an upward bias in the equations as larger trees are added to the regression.

#### 4.3. Tree level biomass distribution

Our analysis showed that at the individual tree level, on average, stems accounted for 87%, branches 9%, and foliage 4% of whole tree (aboveground) biomass. These percentages varied little over the DBH range of the trees we measured. Aside from the age related changes in allometry discussed above, there is other evidence from previous studies suggesting that stand age influences the relative proportion of biomass in each of the three components. For *M. glyptostrobooides* planted at 2500 trees ha<sup>-1</sup> in China, Fang et al. (1995) found that from age 6 to 14 the distribution of biomass in the stem increased (from 54 to 66%) and foliage biomass decreased (from 19 to 9%). Surprisingly,

Fang et al. (1995) report a nearly uniform proportion of biomass in the branch component irrespective of age (mean 24%; range 23–27%). This proportion of branch wood is greater than what others have reported for both younger and older *M. glyptostrobooides* (Saito et al., 1970; Satoo, 1974).

Our measurements suggest that an age related shift in the proportion of biomass in each of the aboveground biomass compartments occurred in the Tanashi-A plantation. Satoo (1974) found aboveground biomass of the Tanashi-A plantation distributed in the following manner: 77% stem, 17% branches and 6% foliage. We measured the stem, branch and foliage biomass of trees in the same stand to be 85, 12 and 3%, respectively. This pattern is not unexpected in light of the fact that stem mass is cumulative and cannot decline with age (without mortality) where self-pruning of shaded branches and changes in foliage production can alter the proportion of biomass in the canopy. Following canopy closure, the amount of foliage that can be maintained in the canopy is often limited due to increased shading. This trend has been noted for other species as well (Kellomaki et al., 1980; Bartelink, 1996; Mäkelä and Vanninen, 1998). At Kamigamo we measured the distribution of biomass in the stem, branches, and leaves to be 89, 8, and 3%, respectively. This is nearly identical to estimates made by Nakai and Nakane (1994) 8 years earlier.

The pattern of aboveground biomass distribution in the *M. glyptostrobooides* we studied appears to be typical of most trees, where stem wood makes up the largest biomass component followed by branch biomass and foliage. The aboveground dry matter distribution of the plantation *M. glyptostrobooides* we studied was similar to that of the closely related deciduous conifer *Taxodium disticum*. Using aboveground biomass data presented by Mitsch and Ewel (1979) for *T. disticum* from a size range similar to that of the *M. glyptostrobooides* we studied, we found that for *T. disticum*, 90% of the aboveground biomass was allocated to the stem, 7% to branch wood and 3% to foliage, nearly identical to the *M. glyptostrobooides* we studied. *Larix leptolepis*, another deciduous conifer, also has aboveground biomass distributed in a similar manner in similar proportions (Satoo, 1970).

In general, it appears that the overall pattern of biomass distribution is the most variable in young *M. glyptostrobooides*, probably up to, or just following, the

point of canopy closure when branches begin to become shaded out by competitors and self-pruning of branches occurs. Early differences most likely arise due to differences in stand density. After this point, the changes in the distribution of aboveground biomass reflect, for the most part a reduction in foliage biomass relative to branch wood biomass as the tree crown recedes upward and foliage is concentrated on the end of longer branches with increased canopy closure.

#### 4.4. Stand biomass

Our estimates of stem wood, branch wood and foliage biomass for stands older than 40 years of age averaged 294, 36, and 10 Mg ha<sup>-1</sup>, respectively. Among these plantations, total aboveground biomass differed by 56% between the highest (Koyomogi) and lowest (Kamigamo) biomass stands. These values are greater than those reported for younger stands of *M. glyptostroboides*. For example, Saito et al. (1970) reported a total aboveground biomass of 52 Mg ha<sup>-1</sup> (40 in stem, seven in branches, and 5 Mg ha<sup>-1</sup> in foliage) for a 9-year-old stand in central Japan. Fang et al. (1995) estimated a total aboveground biomass of 84 Mg ha<sup>-1</sup> for a 14-year-old stand in China. Our estimate of aboveground biomass for the 20-year-old Tanashi-B stand (179 Mg ha<sup>-1</sup>) is also higher than reported values. Satoo (1974) estimated the total biomass of the Tanashi-A stand at age 17 to be on the 74.7 Mg ha<sup>-1</sup> with 58 Mg ha<sup>-1</sup> in stem wood, 12.7 Mg ha<sup>-1</sup> in branch wood, and 4.3 Mg ha<sup>-1</sup> in foliage. Thus, over the 31-year period that separates our study from Satoo's, the Tanashi-A stand accumulated approximately 300 Mg ha<sup>-1</sup>, which is equivalent to a mean annual stem biomass increment of 9 Mg ha<sup>-1</sup> per year. Of the oldest plantations, we found that the Kamigamo forest had the lowest aboveground total biomass (196 Mg ha<sup>-1</sup>) and the smallest mean annual biomass increment (3.6 Mg ha<sup>-1</sup> per year). Our results corroborate the findings of Nakai and Nakane (1994), who estimated the biomass of a portion of this stand at age 40 (142 Mg ha<sup>-1</sup>) and determined that this stand has lower productivity rates (3.8 Mg ha<sup>-1</sup> per year) than the other *M. glyptostroboides* stands in central Japan. Aside from the study of Nakai and Nakane (1994), we know of no other studies of *M. glyptostroboides* for comparison. These values are within the range of aboveground biomass and

annual biomass production for naturally established stands of another deciduous redwood, *T. disticum* growing in Florida, USA (Brown, 1981). Our estimates of stand biomass and productivity for *M. glyptostroboides* tend to be slightly higher than values reported for the common Japanese plantation tree *C. japonica* (Cannell, 1982 and references therein).

Maximum total biomass was achieved in the Koyomogi and Naisugi stands, despite being slightly younger in age. In general, we found the highest mean annual biomass increments at sites with the greatest precipitation. As noted by others, the performance of *M. glyptostroboides* appears to be tightly coupled with water availability (Pokorny, 1981; Buffi, 1987; Kuser, 1999; Xie et al., 1999). Both Izu and Ashiu receive nearly twice the mean annual precipitation of the other sites and this may account in part for higher biomass accumulation at these sites. This, in combination with larger accumulated heat sums, may also explain the better growth of Japanese *M. glyptostroboides* in comparison to those growing in Europe (e.g., Goudzwaard and Schmidt, 1992). Japan's monsoonal climate results in enhanced precipitation during the growing season in Japan and greater mean annual precipitation. In contrast *M. glyptostroboides* growing in the continental climate of Europe experiences between one-fourth to one-half the mean annual precipitation of Japan which may lead to lower growing season water availability and hence, lower biomass accumulation. Likewise, Japan also experiences warmer temperatures than continental Europe and accumulated heat sums are on the order of 5000 growing degree days per year in contrast to central Europe (e.g. Germany, Czech Republic) which typically accumulate less than 2600 growing degree days per year (NOAA NCEP CPC Global Monthly data set available from: <http://iridl.ldeo.columbia.edu/index.html>). Thus, both temperature and growing season water availability probably play an important role in regulating biomass accumulation and primary productivity in *M. glyptostroboides* stands.

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