

## Article

# Biometric-Based Net Primary Production (NPP) and the Effects of a Masting Event on Production Allocation in a Secondary Lucidophyllous Forest in Central Japan

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**Abstract:** Lucidophyllous (evergreen broad-leaved) forests are the dominant forests in human-dominated subtropical/warm-temperate regions in East Asia. Biometric-based estimates of net primary production (NPP) were conducted in a secondary lucidophyllous forest on Mt. Kinka (35°26' N, 136°47' E) near the northern limit of their distribution in central Japan for three years, including the masting event. The forest stand mainly consists of *Castanopsis cuspidata* (Thunb.) Schottky and *Cleyera japonica* Thunb. in the canopy and sub-tree layers, respectively. In 2018, the total NPP of the masting year was  $14.53 \pm 2.03 \text{ ton ha}^{-1} \text{ yr}^{-1}$ , including woody NPP (above:  $2.63 \pm 0.35 \text{ ton ha}^{-1} \text{ yr}^{-1}$ ; below:  $0.57 \pm 0.08 \text{ ton ha}^{-1} \text{ yr}^{-1}$ ), foliage NPP ( $4.07 \pm 0.23 \text{ ton ha}^{-1} \text{ yr}^{-1}$ ), reproductive NPP ( $4.81 \pm 0.77 \text{ ton ha}^{-1} \text{ yr}^{-1}$ ), and fine root production ( $P_{fr}$ ) ( $2.46 \pm 1.84 \text{ ton ha}^{-1} \text{ yr}^{-1}$ ).  $P_{fr}$  and belowground production comprised 16.9% and 20.9%, respectively, of the total NPP. The nut production of *C. cuspidata* in 2018 ( $4.31 \pm 0.75 \text{ ton ha}^{-1} \text{ yr}^{-1}$ ) was significantly higher than that in 2017 ( $0.77 \pm 0.13 \text{ ton ha}^{-1} \text{ yr}^{-1}$ ) and 2019 ( $0.23 \pm 0.06 \text{ ton ha}^{-1} \text{ yr}^{-1}$ ). No significant change was observed for the three years of foliage NPP and total NPP without  $P_{fr}$ . However, the woody NPP in 2018 ( $3.20 \pm 0.43$ ) was lower than in 2017 ( $5.37 \pm 0.33 \text{ ton ha}^{-1} \text{ yr}^{-1}$ ) and 2019 ( $4.71 \pm 0.38 \text{ ton ha}^{-1} \text{ yr}^{-1}$ ). This suggests that nut production in the masting years compensated by decreasing woody production in the *Castanopsis* forest.

**Keywords:** *Castanopsis cuspidata*; evergreen broad-leaved forest; fine root production; reproductive production; stand increment; woody production



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## 1. Introduction

Studies on forest net primary production (NPP) have been conducted since the 1960s. The “summation method” was developed to estimate forest NPP to facilitate standardization without complex instruments under field conditions [1] to consider the biological basis of productivity and human welfare. As global warming has become a more significant issue since the 1980s, considerable attention has been paid to the carbon (C) sequestration of forests because the forest ecosystem is an essential terrestrial carbon sink [2]. Forest NPP studies are becoming increasingly important as basic information for estimating carbon sequestration in terrestrial ecosystems (e.g., [3]). In particular, woody biomass increments of stems and branches in tree species are essential components of carbon sequestration in forest ecosystems.

Early forest NPP studies focused on comparing the organic products among various ecosystems in the biosphere and their environmental controlling factors [4]. However, little attention has been paid to yearly variations and allocation to belowground parts, partly due to methodological difficulties. In contrast, recent studies have shown significant annual variations in forest NPP [5,6] and analyzed how and where carbon accumulates in forest ecosystems, including belowground parts, using biometric methods (e.g., [7,8]). These studies suggested that estimating belowground production is inevitable for forest carbon sequestration. Thus, the current requirement of inventory-based carbon dynamics led to the development of the summation method as an improved “biometric method” [9,10] used to measure the yearly change of NPP and C sequestration, including belowground.

Evergreen broad-leaved forests are distributed widely in the subtropical and warm-temperate regions of East Asia [11]. These lucidophyllous forests can be correlated with the tropical lower montane forests mainly dominated by evergreen Fagaceae, and the northern latitudinal limit reaches sea level at 35° N in central Japan [12]. *Castanopsis cuspidata* (Thunb.) Schottky (*C. cuspidata*) and *Castanopsis sieboldii* (Makino) Hatus. ex T.Yamaz. et Mashiba subsp. *sieboldii* (*C. sieboldii*) are typical dominant species in Japanese lucidophyllous forests from the coastal area of central Japan to southwestern Japan [13]. Some pioneering production studies in subtropical lucidophyllous forests are based on the “summation method” [14–16]. However, information on the contribution of underground components and annual variation is inadequate. Moreover, masting events, which reproduce flowers and nuts heavily in some years at the population level, also occur in many Japanese Fagaceae species [17,18]. There is a trade-off between tree growth and seed production for resources [19,20]. Still, few studies on the impact of seed production on NPP allocation, particularly for subtropical lucidophyllous forests, exist.

Evergreen broad-leaved species (mainly *C. cuspidata*) were recruited after World War II as secondary forests ca. 70 years old on Mt. Kinka, central Japan [21]. The stand's basal area increased significantly due to the growth of *C. cuspidata*. At the same time, the stem density of *C. cuspidata* decreased due to intraspecific competition during the last 30 years [21]. The evergreen broad-leaved forests on Mt. Kinka are relatively well developed, with a maximum dbh of 63.9 cm of *C. cuspidata* and no direct human impact recently. Such forests are ideal sites for studying the carbon cycle and long-term variability of the NPP for lucidophyllous forests, which are typical vegetation in East Asia. This study's objective is to estimate NPP in a subtropical broad-leaved evergreen forest, mainly to clarify production allocation above- and belowground, including fine roots, using the biometric method. The study also aims to explain the three-year variation in NPP allocation, including masting events.

## 2. Materials and Methods

### 2.1. Study Site

The study site is located on Mt. Kinka, central Japan. The area surrounding Mt. Kinka is an ancient populated town built around the Gifu castle, which has sat on Mt. Kinka since the 11th century. The forests on Mt. Kinka have been used historically. However, evergreen broad-leaved tree species (mainly *C. cuspidata*) have been recruited as secondary forests after forest harvesting was prohibited in 1947 [21]. The topography of the area is hilly, with young soil, and the bedrock is composed of sedimentary rock on a chert layer [22]. Almost all areas of Mt. Kinka consist of secondary natural forests (93%), primarily lucidophyllous forests dominated by *C. cuspidata* and artificial coniferous forests (2%) [21]. The study area has a subtropical/warm-temperate climate. The annual mean temperature is 16.2 °C, with the mean temperature in the coldest month, January, and the hottest month, August, being 4.6 °C and 28.3 °C, respectively. The average annual precipitation was 1861 mm. The climatic data between 1991 and 2020 were collected at a weather station situated approximately 4 km from the study plot.

## 2.2. Field Methods

In 2016, a 0.7 ha study plot (70 m × 100 m) was established on the lower slopes of Mt. Kinka (ca. 60 m a.s.l., 35°26' N, 136°47' E). The forest of the permanent plot consists mainly of *C. cuspidata* (87.8% of the total basal area) in a canopy layer, *Cleyera japonica* Thunb. (4.5%), and *Eurya japonica* Thunb. (1.4%) in a subtree layer [21]. There were a few canopy trees other than *C. cuspidata*, with some pioneer deciduous trees reaching the canopy (such as *Ilex micrococca* Maxim. and *Magnolia obovata* Thunb.), and only one stem of an evergreen tree, *Quercus glauca* Thunb. All tree stems taller than 1.3 m high were tagged and mapped as x–y coordinates, identified to the species level. A number tag was attached to each trunk at 1.3 m height using a stapler. In January 2017, all diameters of the stems at breast height (dbh) were measured directly under the number tag. All tree stems with a dbh ≥ 10 cm were re-measured in February 2018, January 2019, and February 2020 at the exact position of the trunks, with those of newly recruited stems over 10 cm and dead stems during the intervals as annual mortality.

Litterfall production was estimated using nine litter traps (1 m<sup>2</sup> in area) set in the study plot in December 2016. Litterfall was collected monthly and divided into foliage (evergreen and deciduous leaves), reproductive organs (flowers and seeds), woody materials (bark and twigs), and others (e.g., insect excrement). These materials were oven dried to a constant mass and weighed.

## 2.3. Biometric-Based NPP

The summation method [23] has been widely used for estimating NPP in forest ecosystems and was generally expressed by the following equation:

$$\text{NPP} = \Delta y + L + G,$$

where  $\Delta y$  is the biomass increment during  $t_1$  and  $t_2$ , and  $L$  is lost due to the death of plants and their parts.  $G$  is loss due to animal grazing, although the item is usually omitted because herbivore loss by grazing is assumed to be negligible in healthy forest stands [15,24]. However, there is conceptual confusion about the summation method, and thus, the method developed into the “biometric method” during the global warming issue in the 1990s [10]. Biometric-based NPP estimates are conceptually defined as the total amount of new organic matter produced during an interval per unit area as follows:

$$\text{NPP} = SI + L_{an} + P_{fr},$$

where  $SI$  is the stand increments of woody biomass,  $L_{an}$  is newly produced aboveground litter, and  $P_{fr}$  is fine root production. The allometric regression between dbh and dry weights of each organ (stem, branch, and foliage) was derived from the result of destructive sampling in a subtropical lucidophyllous forest at the Yona Experimental Forest belonging to the University of the Ryukyus, southwestern Japan (26°45' N, 128°05' E). The forests consist mostly of secondary growth of evergreen broad-leaved trees dominated by *C. sieboldii*, *Distylium racemosum* Siebold et Zucc., and *Styrax japonicus* Siebold et Zucc. [16]. The allometric equations were as follows:

$$\log_{10} W_f = 1.77 \log_{10} D - 1.591 \quad (R^2 = 0.88, n = 11)$$

$$\log_{10} W_s = 2.04 \log_{10} D - 0.710 \quad (R^2 = 0.95, n = 13)$$

$$\log_{10} W_b = 2.53 \log_{10} D - 1.852 \quad (R^2 = 0.84, n = 13)$$

where  $D$  is the dbh (cm), while  $W_f$ ,  $W_s$ , and  $W_b$  are the dry weights (kg) of the foliage, stems, and branches, respectively. A single allometric equation reliably predicted root biomass from shoot biomass for forests and woodlands was shown in a review paper by Mokany et al. [25]. The belowground biomass of the coarse root ( $W_{cr}$ ) was estimated using an equation, as follows:

$$W_{cr} = 0.489 (W_f + W_s + W_b)^{0.890} (R^2 = 0.93)$$

The *SI* during the measurement interval (yearly) can be estimated as follows [26]:

$$SI = \Sigma BI_s + \Sigma BI_i,$$

where  $BI_s$  represents annual woody biomass increments of surviving trees in the plot, while  $BI_i$  represents increments in ingrowth trees that reached the minimum diameter (10 cm) during the study period.  $BI_s$  were calculated as the difference between the estimated biomass ( $W_s$ ,  $W_b$ , and  $W_{cr}$ ) at the beginning and end of the measuring intervals using allometric equations. The increment in ingrowth trees ( $BI_i$ ) was calculated as the difference between the estimated biomass at the end of the interval and the biomass of a tree with a minimum measured diameter (10 cm). We defined stand increment (*SI*) as the net woody biomass increase that contributed to annual woody NPP but excluded foliage. This is because foliage mass initially increases with forest age and reaches equilibrium after closing the canopy [27]. Thus, we regarded foliage mass as being stable in the mature evergreen forest in the permanent plot.

$L_{an}$  includes the fine litter of leaves, flowers, and fruits (mainly nuts and cupules of *C. cuspidata*), excluding woody parts because fallen branches were primarily produced during previous years. Annual leaf litterfall in evergreen forests may include production from the current and previous years because the leaf longevity of evergreen trees in the lucidophyllous forests of central Japan is longer than one year [28]. In this study, the current and previous years of leaf litter were included to estimate annual foliage NPP to accommodate mass balance considerations where foliage mass was stable. The annual production of reproductive organs (reproductive NPP) was estimated using the annual litter production of flowers and seeds.

Fine root production ( $P_{fr}$ ) was estimated using a sequential core sampling method [29,30]. Fine root biomass and necromass were estimated using monthly core sampling ( $\phi = 5$  cm and 15 cm depth,  $n = 9$ ) from February 2018 to January 2019.  $P_{fr}$  was calculated using the following equation:  $P_{fr} = \sum_{i=1}^{12} P_i$ , where  $i$  is the month, while  $P_i$  is the monthly change in fine root biomass ( $\Delta L$ ) and fine root necromass ( $\Delta D$ ).  $P_i$  was calculated using the following rules: when both  $\Delta L$  and  $\Delta D$  are positive,  $P_i = \Delta L + \Delta D$ ; when  $\Delta L$  is positive, and  $\Delta D$  is negative,  $P_i = \Delta L$ ; when  $\Delta L$  is negative,  $P_i = 0$ .

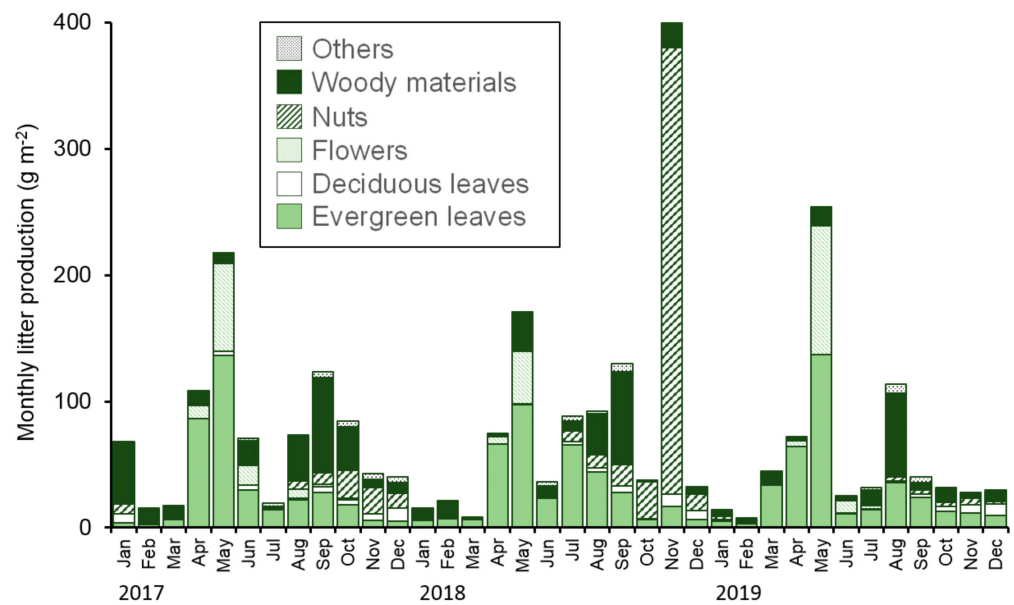
#### 2.4. Statistical Analysis

The study plot was divided into five subplots of 140 m<sup>2</sup> (70 m × 20 m) along a topographic position to calculate the average annual woody NPP and their estimated error (SE). We calculated the average annual foliage and reproductive NPP and their estimated error (SE) using nine replicated litter traps. In addition, the error of  $P_{fr}$  was estimated using replicated nine cores of monthly samplings. The total uncertainty of the added values (e.g.,  $S_1 \pm \varepsilon_1$  and  $S_2 \pm \varepsilon_2$ ) is shown by the following equation:  $(S_1 \pm \varepsilon_1) + (S_2 \pm \varepsilon_2) = (S_1 + S_2) \pm \sqrt{\varepsilon_1^2 + \varepsilon_2^2}$ . Significant tests of the annual variation of NPP for three years were assessed using univariate analysis of variance (ANOVA) and post hoc Tukey HSD tests.

### 3. Results

#### 3.1. Aboveground Litter Production

The aboveground litter production in the lucidophyllous forest varied seasonally for three years (Figure 1). Leaf litterfall events normally occurred during the spring, between April and May, for three years. The flowering of *C. cuspidata* occurs yearly in early spring, and the flowers mainly shed in May. Annual foliage litter production for the three-year study period was  $4.00 \pm 0.28$  ton ha<sup>-1</sup> yr<sup>-1</sup> in 2017,  $4.06 \pm 0.15$  ton ha<sup>-1</sup> yr<sup>-1</sup> in 2018, and  $3.89 \pm 0.15$  ton ha<sup>-1</sup> yr<sup>-1</sup> in 2019 (Table 1). No significant differences in annual foliage litter production were observed for the three years.



**Figure 1.** Monthly litter production ( $\text{g m}^{-2}$ ) in a lucidophyllous forest dominated by *C. cuspidata* using nine litter traps for three years.

**Table 1.** Interannual variation in NPP components in a lucidophyllous forest. Superscript letters represent significant differences ( $p < 0.05$ ) among the years based on one-way ANOVA followed by Tukey's test.

	2017		2018		(*) *	2019	
	( $\text{ton ha}^{-1} \text{yr}^{-1}$ )	(%)	( $\text{ton ha}^{-1} \text{yr}^{-1}$ )	(%)		( $\text{ton ha}^{-1} \text{yr}^{-1}$ )	(%)
Woody NPP (Stand Increments)							
Aboveground	$4.39 \pm 0.27^a$	39.2	$2.63 \pm 0.35^b$	21.8	(18.1)	$3.85 \pm 0.31^{ab}$	38.5
Belowground	$0.97 \pm 0.06^a$	8.7	$0.57 \pm 0.08^b$	4.8	(4.0)	$0.86 \pm 0.07^{ab}$	8.5
Subtotal	$5.37 \pm 0.33^a$	47.9	$3.20 \pm 0.43^b$	26.5	(22.0)	$4.71 \pm 0.38^{ab}$	47.0
Foliage NPP							
Evergreen	$3.59 \pm 0.26^a$	32.0	$3.75 \pm 0.17^a$	31.0	(25.8)	$3.63 \pm 0.15^a$	36.3
Deciduous	$0.42 \pm 0.06^a$	3.7	$0.32 \pm 0.06^a$	2.6	(2.2)	$0.26 \pm 0.07^a$	2.6
Subtotal	$4.00 \pm 0.28^a$	35.7	$4.06 \pm 0.15^a$	33.6	(27.9)	$3.89 \pm 0.15^a$	38.8
Reproductive NPP							
Flower	$1.07 \pm 0.07^a$	9.5	$0.50 \pm 0.04^b$	4.2	(3.5)	$1.19 \pm 0.09^a$	11.9
Fruits	$0.77 \pm 0.13^a$	6.9	$4.31 \pm 0.75^b$	35.7	(29.6)	$0.23 \pm 0.06^a$	2.3
Subtotal	$1.84 \pm 0.13$	16.4	$4.81 \pm 0.77$	39.8	(33.1)	$1.42 \pm 0.11$	14.2
Fine root production	–	–	$2.46 \pm 1.84$	–	(16.9)	–	–
Total NPP	$11.21 \pm 0.45$	100.0	$12.07 \pm 0.89$	100.0		$10.02 \pm 0.42$	100.0
(with fine root)	–	–	$14.53 \pm 2.05$	–	(100.0)	–	–

\* % including fine root production.

The masting event of 2018 was demonstrated in three years of litter production monitoring in the forest (Figure 1). The nuts of *C. cuspidata* shed yearly in autumn. However, nut production fluctuated significantly annually. The nut production in 2018 ( $4.31 \pm 0.75 \text{ ton ha}^{-1} \text{yr}^{-1}$ ) was significantly higher than that in 2017 ( $0.77 \pm 0.13 \text{ ton ha}^{-1} \text{yr}^{-1}$ ) and 2019 ( $0.23 \pm 0.06 \text{ ton ha}^{-1} \text{yr}^{-1}$ ). Conversely, the litterfall of flowers in 2018 ( $0.50 \pm 0.04 \text{ ton ha}^{-1} \text{yr}^{-1}$ ) was significantly lower than that of 2017 ( $1.07 \pm 0.07 \text{ ton ha}^{-1} \text{yr}^{-1}$ ) and 2019 ( $1.19 \pm 0.09 \text{ ton ha}^{-1} \text{yr}^{-1}$ ). The ratio of reproductive NPP to total NPP increased significantly to 39.8% in 2018, while the ratio of foliage NPP remained relatively constant (Table 1).

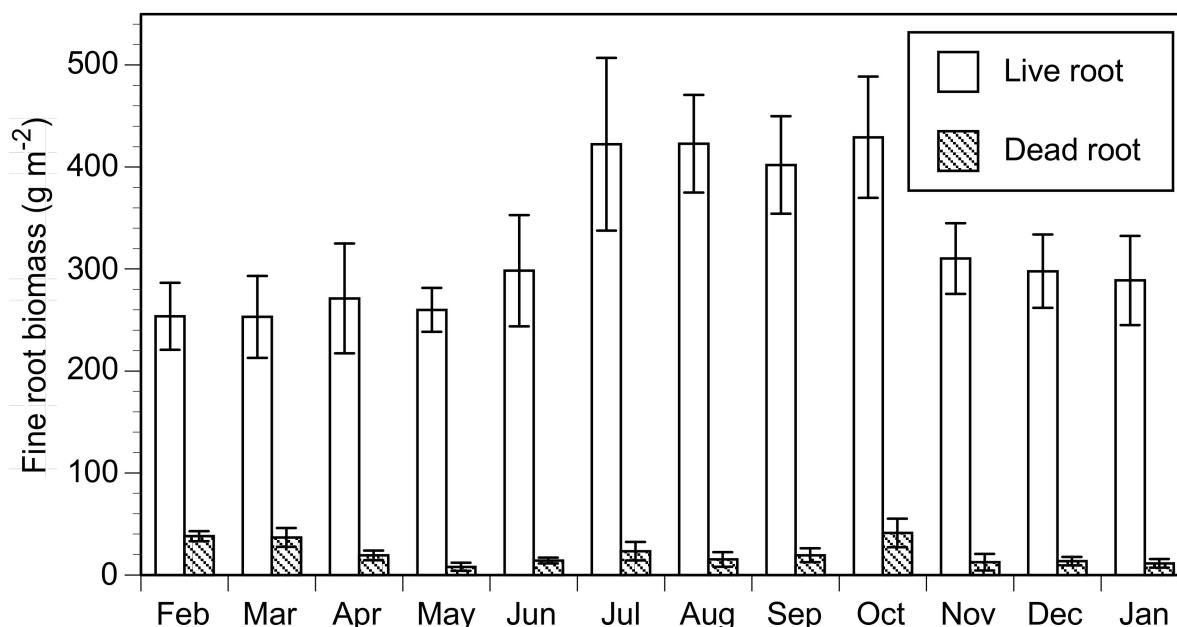
### 3.2. Forest Structures and Stand Increments

We examined the forest structure and species composition in each subplot at the end of the study period: February 2020 (Table 2). There were 11 species with a dbh  $\geq 10$  cm. The number of stems per subplot and basal area ranged 471–586 stems  $\text{ha}^{-1}$  and 39.5–47.9  $\text{m}^2 \text{ha}^{-1}$ , respectively. The mean dbh of the tree stems in each subplot is roughly 30 cm. *C. cuspidata* had the highest number of stems, and the dominance based on the basal area was over 86% in all the subplots.

Annual woody NPP, including coarse roots of the lucidophyllous forests, varied annually, ranging from  $3.20 \pm 0.43$  to  $5.37 \pm 0.33$   $\text{ton ha}^{-1} \text{yr}^{-1}$  (Table 1). The annual woody NPP of 2018 was the lowest for the three years and significantly decreased from 2017. The ratio of belowground coarse root production to total woody NPP was fairly constant, from 17.8% to 18.9% for the three years, although the ratio of woody NPP to total NPP in 2018 (26.5%) was lower than in 2017 (47.9%) and 2019 (47.0%). The mean total NPP for the three years from 2017 to 2019, excluding the fine root production, was  $11.21 \pm 0.45$   $\text{ton ha}^{-1} \text{yr}^{-1}$ ,  $12.07 \pm 0.89$   $\text{ton ha}^{-1} \text{yr}^{-1}$ , and  $10.02 \pm 0.42$   $\text{ton ha}^{-1} \text{yr}^{-1}$ , respectively (Table 1). No apparent differences in the total NPP were observed among the three years, while the total NPP in 2018 was slightly higher than in the other years.

### 3.3. Fine Root Production in 2018

Fine root biomass was sampled monthly in 2018. Fine root biomass changed insignificantly between February and June, then increased abruptly in July and remained relatively high until October (Figure 2). Then, it decreased again from November onwards. Based on these changes in the biomass, the estimated fine root production for the year was estimated to be  $2.46 \pm 1.84$   $\text{ton ha}^{-1} \text{yr}^{-1}$  on a dry weight basis. The total annual NPP in 2018, including fine root production, was estimated to be  $14.53 \pm 2.05$   $\text{ton ha}^{-1} \text{yr}^{-1}$ . The belowground production (fine roots and coarse woody roots) of the lucidophyllous forest in 2018 was  $3.03 \pm 2.29$ , amounting to 20.9% of the total NPP.



**Figure 2.** Monthly changes in fine root biomass ( $\text{g m}^{-2}$ ) in a lucidophyllous forest dominated by *C. cuspidata* in February 2018 to January 2019.

**Table 2.** Floristic composition (dbh  $\geq$  10 cm) and forest structures in each subplot (1400 m<sup>2</sup>) in the lucidophyllous forest at the end of the study period (February 2020).

Species	Subplot 1			Subplot 2			Subplot 3			Subplot 4			Subplot 5		
	Number of Stems (ha <sup>-1</sup> )	Basal Area (m <sup>2</sup> ha <sup>-1</sup> )	Mean dbh (cm)	Number of Stems (ha <sup>-1</sup> )	Basal Area (m <sup>2</sup> ha <sup>-1</sup> )	Mean dbh (cm)	Number of Stems (ha <sup>-1</sup> )	Basal Area (m <sup>2</sup> ha <sup>-1</sup> )	Mean dbh (cm)	Number of Stems (ha <sup>-1</sup> )	Basal Area (m <sup>2</sup> ha <sup>-1</sup> )	Mean dbh (cm)	Number of Stems (ha <sup>-1</sup> )	Basal Area (m <sup>2</sup> ha <sup>-1</sup> )	Mean dbh (cm)
<i>Castanopsis cuspidata</i> (Thunb.) Schottky	371	41.6	36.5	414	45.6	35.9	329	34.3	35.2	450	43.4	33.6	436	40.6	32.9
<i>Ilex micrococca</i> Maxim.	7	1.4	49.5	7	0.8	37.9	7	1.2	45.7	7	1.7	54.5	0	-	-
<i>Cleyera japonica</i> Thunb.	36	0.4	12.3	71	0.9	12.7	64	1.0	13.7	71	0.8	11.8	50	0.6	12.0
<i>Magnolia obovata</i> Thunb.	7	0.5	30.8	7	0.3	23.1	14	0.4	19.5	7	0.2	20.7	7	0.9	40.0
<i>Ilex macropoda</i> Miq.	36	0.7	15.1	14	0.2	13.6	14	0.1	10.5	50	0.7	12.9	29	0.4	13.4
<i>Chengiopanax sciadophylloides</i> (Franch. et Sav.)	0	-	-	0	-	-	0	-	-	0	-	-	14	1.7	37.4
C. B. Shang et J. Y. Hunag															
<i>Toxicodendron trichocarpum</i> (Miq.) Kuntze	14	0.5	19.9	7	0.1	13.0	19.9	0.5	19.9	0	-	-	0	-	-
<i>Quercus serrata</i> Murray subsp. <i>serrata</i> var. <i>serrata</i>	0	-	-	0	-	-	7	0.8	38.8	0	-	-	0	-	-
<i>Quercus glauca</i> Thunb.	0	-	-	0	-	-	7	0.8	37.8	0	-	-	0	-	-
<i>Padus grayana</i> (Maxim.) C. K. Schneid.	0	-	-	0	-	-	7	0.3	24.2	0	-	-	0	-	-
<i>Eurya japonica</i> Thunb.	21	0.2	11.3	0	-	-	7	0.1	12.7	0	-	-	0	-	-
Total	493	45.3	31.7	521	47.9	31.7	471	39.5	30.3	586	46.8	29.3	536	44.2	30.1

## 4. Discussion

### 4.1. Biometric-Based NPP Estimates in Forest Ecosystems

The summation method [23] has been widely used to estimate NPP in forest ecosystems. For example, Kira & Yabuki [31] estimated the NPP in an evergreen oak forest at Minamata predominated by *C. cuspidata* (17.17–19.41 ton ha<sup>-1</sup> yr<sup>-1</sup>), including coarse roots, using the summation method. They calculated  $\Delta y$  using a four-year forest survey and estimated  $L$  using the litterfall method, including big wood litter, such as twigs and branches. In contrast with the summation method, we measured NPP in the lucidophyllous forest using the biometric method. The biometric method focuses only on new biomass accumulation between  $t_1$  and  $t_2$  (usually one year), and  $SI$  is considered the annual woody biomass increments of surviving trees. Moreover,  $L_{an}$  only included fine litter, such as leaves, flowers, and seeds, which are the newly produced organic matter, mainly in the current year. Since  $SI$  and  $\Delta y$  and  $L_{an}$  and  $L$  are conceptually different items, we must carefully consider intercomparisons with past and present NPP data for forest ecosystems, particularly for carbon allocation.

However, there is conceptual confusion about both methods. For example, early studies often used a single forest survey to estimate  $\Delta y$  [14,16], although two biomass measurements at  $t_1$  and  $t_2$  were originally needed to estimate  $\Delta y$ . Kawanabe [16] estimated  $\Delta y$  using an allometric regression between annual stem weight increment and dbh in sample trees (stem analysis) in a mixed secondary forest dominated by *C. sieboldii*, Okinawa Island. Here, the estimated annual stem weight increment as a substitute for  $\Delta y$  is similar to  $SI$ , but is essentially different because this  $\Delta y$  is a long-term average biomass increment and cannot account for the growth of dead trees during the study period. Moreover,  $L$  included leaf litter and woody litter in the original summation method. However, there also seems to be some confusion about whether to apply the whole litter production (as  $L$ ) or only fine litter as  $L_{an}$  as part of the forest NPP.

It is necessary to evaluate the amount of organic matter fixed in the current year and to estimate yearly variations of NPP compared with the eddy-covariance method to estimate C sequestration in forest ecosystems [9,32]. Therefore, the biometric method was proposed to estimate the components of  $SI$ ,  $L_{an}$ , and  $P_{fr}$  based on the contribution of newly produced organic matter to forest ecosystems. It is important to note that measuring all newly produced organic matter in the current year is impossible under field conditions, as the biometric method always underestimates the actual organic production [26].

### 4.2. Importance of Belowground NPP in Forest Ecosystems

The summation method is rarely used for belowground production, partly due to methodological difficulties. Kimura [14] estimated the NPP in a warm-temperate laurel forest in the southern part of the Osumi Peninsula, Kyushu, Japan, mainly dominated by *Distylium racemosum*, as 21.61 ton ha<sup>-1</sup> yr<sup>-1</sup>, including coarse root production (1.84 ton ha<sup>-1</sup> yr<sup>-1</sup>). However, the coarse root biomass was tentatively estimated at 25% of the stem and branch biomass and was excluded from fine root production. The allometry of belowground biomass has become widely known (e.g., [33]), and the  $SI$  of coarse roots can be estimated using allometric regressions [7,8,34]. These studies suggested that the contribution of belowground parts (coarse roots) is approximately 15–25% of woody NPP, which is comparable with the results of this study (ca. 18%, Table 1).

Additionally, the contribution of fine root production to the total forest NPP is higher than coarse root production. Simultaneously, few studies have measured all components of the biometric method, including  $P_{fr}$ , particularly for broad-leaved evergreen forests [35,36]. The allometric regression cannot be used for fine roots with fast biomass turnover. Thus, another method is needed to estimate  $P_{fr}$ . Do et al. [35] recently examined the NPP in detail in a warm-temperate old-growth evergreen broad-leaved forest in southwestern Japan using the biometric method. The forest was dominated by evergreen trees, including *D. racemosum*, *Machilus thunbergii* Siebold et Zucc., and *Quercus acuta* Thunb. They estimated that  $SI$  was 4.63 ton ha<sup>-1</sup> yr<sup>-1</sup>,  $L_{an}$  was 6.57 ton ha<sup>-1</sup> yr<sup>-1</sup>, and  $P_{fr}$  was 5.66 ton ha<sup>-1</sup> yr<sup>-1</sup>,



a total of 16.96 ton ha<sup>-1</sup> yr<sup>-1</sup> in this forest.  $P_{fr}$  contributed 33%, and belowground parts, including coarse roots, contributed 36% of the total NPP. In our previous study,  $P_{fr}$  contributed 17%, and belowground parts contributed 21% of the total NPP in 2018 (Table 1). Thus, the contribution of belowground parts, especially for fine roots, is so high that it is an essential measurement item for biometric methods in forest ecosystems.

However, no standardized method for  $P_{fr}$  is easy to use under field conditions, and various new techniques are still being developed [36–38]. For example, Do et al. [35] used the continuous inflow method [39] to estimate fine root production in the lucidophyllous forest. This method needs sequential core sampling to evaluate biomass increment and the root litter bag technique to estimate the decomposition ratio of dead fine roots. The sequential core method was used in this study to estimate fine root production. This simple method cannot quantify the fine roots that decompose during the sampling interval. Moreover, error estimation is vital for assessing the C sequestration of forest ecosystems compared with the eddy-covariance method. In this study, the estimated error of fine root production is relatively high compared with the other NPP components (Table 1) because monthly core sampling has a substantial individual sample variation (Figure 2). There is a trade-off between the accuracy and continuity of field measurements. Standardized simple methods (e.g., [38]) to compare fine root production among forest ecosystems and to measure yearly variations of forest NPP are needed.

#### 4.3. Effects of Masting Events on NPP

Masting events are known for many Fagaceae species (especially deciduous species, such as *Fagus crenata* Blume and *Quercus crispula* Blume var. *crispula*) in Japan [17,18,40]. They reproduce flowers and nuts heavily in some years at the population level and cease reproduction in subsequent years. It has been thought that these species need to store a certain amount of carbohydrate resources in trees for masting events [41]. However, it has been revealed in recent studies that *F. crenata* produced inflorescences using carbon resources assimilated mainly in the year when the flower buds were formed [42]. Thus, storing carbohydrate resources might not be a limiting factor in the flowering frequency for deciduous Fagaceae species. The evergreen Fagaceae species mainly consist of lucidophyllous forests and also have masting events. For example, the subgenus *Cyclobalanopsis* produces more nuts every two years, primarily because it takes two years for nuts to mature [43]. *C. cuspidata* also takes two years for nuts to mature, and Saito [44] studied the annual reproductive production in a *C. cuspidata* stand over eight years. Saito [44] revealed that the annual mean reproductive NPP was 1.68 ton ha<sup>-1</sup> yr<sup>-1</sup>, ranging from 0.61 to 3.03 ton ha<sup>-1</sup> yr<sup>-1</sup>, and that masting events occur every three years. In the current studies, the annual reproductive NPP in 2018 was 4.81 ton ha<sup>-1</sup> yr<sup>-1</sup>, and more than 2.5 times compared with the other two years (Table 1), while the cycle of nut production in this study was unclear only in the three-year study.

Growth reductions in the masting years are reported in evergreen forests, such as Norway spruce [20] and Bornean tropical rainforest [19]. After three years of monitoring the forest NPP, the changes in NPP allocation during masting events in forest ecosystems were examined in this study. If the annual NPP does not vary significantly, masting events should be compensated by reducing resources for other components. In this study, nut production in 2018 was more than five times higher than in any other year (Table 1). Conversely, foliage NPP was reasonably constant for the three years, and woody NPP in 2018 was lower than in 2017 and 2019; thus, nut production in the masting year can be considered compensated by reduced woody production. These phenomena suggest that masting species have substantial trade-offs, as their reproductive strategy is characterized by highly variable allocation to reproduction [19]. The considerable trade-off between tree growth and reproduction in this lucidophyllous forest cannot be buffered by stored carbohydrate resources alone, hence the corresponding reduction in woody material production.

## 5. Conclusions

Annual net primary production (ANPP) in the lucidophyllous forests dominated by *C. cuspidata* amounted to  $14.53 \pm 2.05$  ton ha<sup>-1</sup> yr<sup>-1</sup> in 2018, in which fine root production ( $P_{fr}$ ) was measured. The NPP was allocated to woody NPP ( $3.20 \pm 0.43$  ton ha<sup>-1</sup> yr<sup>-1</sup>), foliage NPP ( $4.06 \pm 0.15$  ton ha<sup>-1</sup> yr<sup>-1</sup>), reproductive NPP ( $4.81 \pm 0.77$  ton ha<sup>-1</sup> yr<sup>-1</sup>), and  $P_{fr}$  ( $2.46 \pm 1.84$  ton ha<sup>-1</sup> yr<sup>-1</sup>). Underground production (coarse woody roots and fine roots) accounts for more than 20% of the ANPP and is a critical component. Excluding fine root production, the three-year variation in ANPP was small, ranging from 10.02 to 12.07 ton ha<sup>-1</sup> yr<sup>-1</sup>. However, the allocation of ANPP varied significantly annually, with seed production accounting for more than 1/3 of ANPP in the masting year of 2018. In contrast with 2018, seed production allocation was only 6.9% in 2017 and 2.3% in 2019. Conversely, the allocation of woody NPP in 2018 was the smallest (26.5%) compared with those in 2017 (47.9%) and 2019 (47.0%). A substantial trade-off in resource allocation between seed and woody production during the masting year is suggested by these phenomena. Differences in carbon partitioning have a significant impact on the fate of carbon. The turnover of carbon fixed as trunk growth is much different from that of carbon dispersed to the ground as nut production. Since only a few nuts recruit and most of them die within a year, the turnover is short because of feeding and decomposition. Such a partitioning cannot be measured using the eddy-covariance method, indicating the importance of inventory data in estimating carbon sequestration.

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