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Individual resource allocation to vegetative growth and reproduction in subgenus *Cyclobalanopsis* (*Quercus*, Fagaceae) trees

Abstract The resource allocation for vegetative growth and female reproduction in three tree species of subgenus *Cyclobalanopsis* (*Quercus*, Fagaceae), i.e., *Q. salicina*, *Q. sessilifolia*, and *Q. acuta*, were examined on a per-individual basis in two consecutive reproductive seasons, in order to test whether these trees fit the predictions of the masting hypotheses about resource matching versus resource switching. Since the three *Quercus* species have a biennial fruiting habit, it takes 3 years for the observation of two reproductive events. Female flower and acorn production per tree were investigated by using a seed-trap method and a numerical analysis of seed dispersal. The net production of each individual was estimated as the sum of the annual increase in the dry mass of vegetative organs and reproductive investment per tree. In the data analyses, the three species were pooled, since all 12 sample trees of the subgenus apparently showed masting in the same year, with no exceptions. Female flower and acorn production per individual tree changed considerably between years. The net production per tree increased with tree size, but did not differ between years. Therefore, the reproductive allocation (proportion of a plant's annual assimilated resources which are used for reproduction) differed dramatically between years. On the other hand, within a year, the reproductive allocation increased with increasing net production per tree. These results suggest that the switching of resource allocation between years within an individual are occurring in subgenus *Cyclobalanopsis* species, and the intensity of the switching increases with increasing tree size.

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Introduction

Many forest trees show intermittent synchronous production of large seed crops within the population (e.g., Janzen 1971; Silvertown 1980; Kelly 1994). This habit is commonly termed masting, and is observed in many trees, including the *Quercus* species (Sork et al. 1993; Kelly and Sork 2002). There have been two hypotheses about the cause of masting; resource matching and economies of scale (Norton and Kelly 1988; Koenig et al. 1994). The resource matching hypothesis states that the reproductive output of each plant tracks the available resources, being higher during favorable conditions (Kelly and Sork 2002). The economy of scale hypothesis states that the masting results from resource switching, that is, the reallocation of resources over the years in order to increase reproductive success (Janzen 1971; Sork 1983; Smith et al. 1990; Koenig et al. 1994). To test whether tree species fit the predictions of the masting hypotheses about resource matching versus resource switching, the knowledge of resource allocation for the vegetative growth and reproduction of a plant is essential. The proportion of a plant's annual assimilated resources which are used for reproduction is usually defined as the reproductive allocation (Silvertown and Charlesworth 2001), and is one of the most important parameters in plant reproductive ecology. In discussing the reproductive allocation of plants, individual-based reproductive variables such as flower and fruit productions per individual are necessary. However, with regard to tree species, few studies have clarified the reproductive variables on the basis of individual trees because most trees are large and produce flowers and fruits at the top of their canopies, which are too tall for direct observation of the reproductive phenomena (Herrera 1991; Nakashizuka et al. 1997; Hirayama et al. 2004). In

order to overcome this difficulty, a method without requiring access to the canopy is required.

In our previous study, we successfully examined the flower and seed production of a tall tree species *Lindera erythrocarpa* Makino (Lauraceae) on an individual tree basis by adopting both the seed-trap method for plant litter sampling and a proposed numerical approach for the analysis of seed dispersal (Hirayama et al. 2004). In the study, the spatial distribution pattern of dispersed reproductive organs was expressed using a mathematical model with a probability density function. This new approach is effective for investigating the reproductive investment of individual trees, particularly in the case of very large trees wherein a direct count of all reproductive organs is not actually possible.

In this study, we used the above mentioned novel approach to examine the reproductive allocation of three evergreen oak species of subgenus *Cyclobalanopsis* of genus *Quercus* (Fagaceae), i.e., *Q. salicina*, *Q. sessilifolia*, and *Q. acuta*, at the Kasugayama Forest Reserve, Japan. The species of subgenus *Cyclobalanopsis* are often found as dominant components of broad-leaved evergreen forests in temperate East Asia (Govaerts and Frodin 1998). The acorn production of the *Quercus* species has a demonstrable influence on the population dynamics of many wildlife species and forest regeneration (Koenig et al. 1994; Wolff 1996; Greenberg and Parresol 2002). Despite its ecological importance, there are few studies on the female reproductive investment of the evergreen oak species of subgenus *Cyclobalanopsis*.

The objectives of this study are as follows: (1) to clarify female reproductive investment on an individual tree basis; (2) to examine the relationship between the vegetative growth and female reproductive investment per tree; and (3) to test whether subgenus *Cyclobalanopsis* trees fit the predictions of the masting hypotheses about resource matching versus resource switching by comparing the reproductive allocation between two consecutive years of high and low acorn production.

Methods

Study species

Q. salicina, *Q. sessilifolia*, and *Q. acuta* are evergreen tall tree species. They are monoecious and wind pollinated. They usually begin to bloom in May and June, and they fruit in the second autumn after flowering. This fruiting habit is known as biennial fruiting (Borgardt and Nixon 2003). In biennial fruiting species, fertilization does not occur immediately after pollination; it occurs in the following spring, after the quiescent period. Thus, resource allocation for the maturation of acorns occurs during the second autumn after the flowering (Sork et al. 1993).

We have studied the annual variation in acorn production of the biennial fruiting species of subgenus *Cyclobalanopsis* at the forest stand level from 1989 to 2001, and the results clearly show that the trees exhibit a 2-year cycle of masting, synchronized across species (Hirayama et al. unpublished data).

Study forest

A series of observations and measurements were carried out in a 13-ha research plot demarcated in a warm-temperate evergreen forest, which covers the Kasugayama Forest Reserve of 243 ha in area, Nara City (34°41′N, 135°51′E), western Japan. Since the forest has been protected for 1,100 years as the sacred forest of the Kasuga Shinto shrine, it is densely covered by the original vegetation with oak-laurel dominants (Mizuno et al. 1999; Hirayama et al. 2004). According to the Nara Meteorological Station (104 alt.), which is about 2.5 km northwest of the study forest, from 1985 to 2001, the mean annual temperature is 14.9°C and the mean monthly temperature ranges from 4.2°C (January) to 26.9°C (August). The mean annual precipitation is 1,331.5 mm, and the mean monthly rainfall ranges from 40.7 mm (December) to 216.3 mm (June). Frost is common in winter, but a snow cover greater than 10 cm is unusual.

Forest inventory and sample collection

All of the trees larger than and equal to 20 cm in DBH in the 13-ha study plot were labeled, mapped, identified to species, and measured by DBH by Mizuno and his colleagues at Osaka City University in 1991 (Mizuno et al. 1999). The number of living individuals of *Q. salicina*, *Q. sessilifolia*, and *Q. acuta* found in the study plot in 1998 was 265, 120, and 200, respectively. The DBHs of all of the trees in the plot were measured every April from 1998 to 2002, and their annual DBH growth was calculated.

In 1998, four or five sample trees of each study species were chosen in order to cover a full range of DBH to permit the evaluation of the effect of tree size on their flower and seed production. Four to eight traps (trap area = 0.25 m²) were linearly established under the canopy of each sample tree at an interval of 2.0 m in 1998. We assumed no directional bias in the dispersion of the reproductive organs, although this method might result in potential error of the estimation. The traps were made of nylon cloth. The female organs (female flowers and fruits) and leaves that fell in the traps were collected every month from January 1999 until late December in 2001.

The sorting of flowers and fruits

The reproductive organs collected from the traps were brought to the laboratory of Osaka City University and sorted into the following categories: (1) immature acorns and (2) mature acorns. In this study, according to the definition of Matsuda (1982), mature acorns were de-

fined as the acorns the width of which is larger than the cup width, and the length of which is twice as long as that of the cup. Immature acorns were defined as female reproductive organs that fell into traps before growing to mature acorns. This immature fraction includes aborted flowers.

As already mentioned, the three study species exhibit a biennial fruiting behavior. Thus, the samples collected from each trap may have reproductive organs borne in the current year and previous year, and these organs were distinguishable by their shape and size. Of the total female reproductive organs which were collected by a trap, we used only the samples that were borne in 1999 and 2000 for the data analyses. The samples comprise the following fractions: (1) immature acorns borne in 1999; (2) mature acorns borne in 1999; (3) immature acorns borne in 2000; and (4) mature acorns borne in 2000. The number of collected reproductive organs was recorded in terms of a fraction, trap location, and the collection date. All of the reproductive organs were dried at 80°C for 1 week and then weighed.

The number of organs in each fraction per tree was expressed as $N(i)$, where i is the identification number of each fraction. The i for female flowers and immature acorns was 2, while that for mature acorns was 3. $N(1)$ represents the total number of initial flowers or the sum of two fractional samples per tree, i.e., $N(1) = N(2) + N(3)$. The fruit set, FS, i.e., the ratio of mature acorns to the total reproductive organs, was expressed by $N(3)/N(1)$. The observed values of FS were used to estimate the total quantity of mature acorns produced by an individual tree.

Flower and seed production per tree

In order to estimate the total production of reproductive organs per tree, we adopted the numerical method of Hirayama et al. (2004). Using this method, the dispersal pattern of the reproductive organs around a sample tree is represented by the density of the dispersed reproductive organs (i.e., the number of organs per unit land area) along the line of the seed traps. The following model of the Weibull distribution is tentatively applicable to the observed spatial distribution of reproductive organs, provided that the density of the organs is sufficient and continuous with respect to the dispersal distance:

$$\rho_i(x) = N_i \cdot \left(\frac{1}{a_i}\right)^{m_i} \cdot m_i \cdot x^{m_i-1} \cdot \exp\left(-\left(\frac{x}{a_i}\right)^{m_i}\right) \qquad (1)$$

where x is the distance between the trap position and the center of the distribution of the dispersed reproductive organs of a sample tree on the forest floor in meters (m); i is the identification number of the reproductive organ of interest; $\rho_i(x)$ with a unit of m^{-2} is the density of the dispersed reproductive organ i at point x; and a_i (m), m_i (m^{-2}), and N_i are coefficients specific to organ i and the mother tree. The estimates of coefficients a_i, m_i, and N_i

were adopted for the estimation of the reproductive organs per tree as described below.

Assuming the absence of a directional bias in the sampling of the dispersed reproductive organs, the total production of reproductive organs per tree was obtained by the arcwise integration of Eq. 1 over distance x:

$$N^*(i) = 2\pi \int_0^\infty x \cdot \rho_i(x)\mathrm{d}x$$
$$= 2\pi \int_0^\infty x \cdot N_i \cdot \left(\frac{1}{a_i}\right)^{m_i} \cdot m_i \cdot x^{m_i-1} \cdot \exp\left(-\left(\frac{x}{a_i}\right)^{m_i}\right)\mathrm{d}x$$
$$= 2a_i \cdot \pi \cdot N_i \cdot \Gamma\left(1 + \frac{1}{m_i}\right) \qquad (2)$$

where Γ is the gamma function, $N^*(i)$ is the per-tree production of the organ of interest, i, and π is the circular constant. When $i = 1$, $N^*(1)$ corresponds to the total female flower production per tree. By substituting the coefficients a_i, m_i, and N_i with $i = 1$ into Eq. 2, the value of $N^*(1)$ was calculated for each sample tree.

The value of $N^*(i)$ can be calculated for a given i if the coefficients a_i, m_i, and N_i are explicitly known for the corresponding i. However, these coefficients were not always available for every i, owing to the paucity of the $\rho_i(x)$ values. Therefore, the $N^*(3)$ values were calculated by multiplying $N^*(1)$ with the corresponding ratio FS, and the $N^*(2)$ values were calculated by the differences between $N^*(1)$ and $N^*(3)$.

Dry matter investments in reproduction

The investment in reproduction was evaluated on the basis of dry matter of the reproductive organs because this was more feasible as compared to the determination of nitrogen and phosphorus. The dry matter investment in reproduction by each tree was calculated as the number of reproductive organs per tree (calculated as described above) multiplied by the dry matter mass per organ. The total mass of the two fractions (immature acorns and mature acorns) represents the female reproductive investment per tree.

Plant mass of vegetative organs

The mass of the vegetative organs was not measured directly in this study because harvesting is not permitted in the study plot. Therefore, the mass of the trees was calculated by using the DBH data of the sample trees and the allometric equations determined by Ogawa and Saito (1965) for hardwood tree species in broad-leaved evergreen forest in the Kagoshima Prefecture, southwest Japan. The allometric equations are not species-specific, but we applied the equations to the study species following Naka and Yoneda (1984). The height–diame-

ter relationship determined by Naka (1982) in canopy trees at our study forest was used for the estimation of the height of the sample trees from the observed DBH. The total mass of three different organs, i.e., stems $W(S)$ in kg, branches $W(B)$ in kg, and leaves $W(L)$ in kg, were calculated for the individual sample trees as follows:

$$\frac{1}{H} = \frac{1}{1.26 \cdot D} + \frac{1}{25.8}$$

$$W(S) = 0.0396 \times \left(D^2 H\right)^{0.9326}$$

$$W(B) = 0.00602 \times \left(D^2 H\right)^{1.027}$$

$$\frac{1}{W(LF)} = \frac{26}{W(S) + W(B)} + 0.02$$

where D is the stem DBH in cm and H is the tree height in m (Naka 1982).

The amount of annual leaf-fall of each individual was estimated by the same method as the estimation of the flower and acorn production per tree. The model of the Weibull distribution (Eq. 1) was applicable to the observed spatial distribution of the leaf-fall density of an individual, but, in this case, the variable $\rho_i(x)$ in Eq. 1 was replaced by $\rho_L(x)$ with the unit of g m^{-2}, and the coefficient N_i was replaced by W with the unit of g. In the estimation of the total amount of leaf-fall per tree $W(LF)$, Eq. 2 was used, but the variable $N^*(i)$ and the coefficient N_i were replaced by $W(LF)$ and W, respectively.

Statistical methods

Least squares regression analysis and the non-linear least squares method for mathematical models with non-linear parameters were used for the data analysis. Wilcoxon's signed ranks test was used for examining differences in the flower and acorn production per tree between years and differences in the net production per tree between years. Spearman's rank correlation test was used for examining the relationship between the net production per tree and the reproductive allocation (see Sokal and Rohlf 1995).

Results

Flower and seed production per tree

We were unable to collect the reproductive organs for two sample trees, *Q. salicina* C and D, using the traps in 1999, as the traps had broken several times due to typhoon visits in the year. Therefore, for the two sample trees, we were unable to estimate the total number of reproductive organs borne in 1999. The Weibull distribution model fitted the data satisfactorily. The coefficients of determination (r^2) between the observed $\rho_i(x)$ and the calculated $\rho_i(x)$ of Eq. 1 ranged from 0.335 to 0.999.

Figure 1 shows the estimated numbers of reproductive organs per tree. The female flower and acorn production per tree were highly variable between the years. The per-tree number of female flowers borne in 2000 was 1.8 to 85.1 times greater than that borne in 1999. The acorn production per tree ranged from 7.403×10^2 to 1.400×10^5 in 2001 (flowering in 2000), while six trees did not produce any mature acorns in 2000 (flowering in 1999) (Fig. 1). In the data analyses, the three species were pooled, since all 12 sample trees apparently showed mast year in the same year (2001), with no exceptions. The annual differences in flower and acorn production of all sample trees were statistically significant (Wilcoxon's signed ranks test, $n = 12$, $P < 0.01$).

Vegetative growth and net production per tree

The results of the estimation of vegetative growth in 2000 and 2001 are listed in Table 1. The annual increase of woody organs per tree $\Delta W(C)$ (kg/year) is defined as the sum of the increase in the branches and stem. The sum of the annual leaf-fall ($W(LF)$), the annual increase in the amount of leaves ($\Delta W(L)$), and $\Delta W(C)$ provide an estimate of the total annual investment in vegetative growth per tree, i.e., $\Delta W(VG)$ (kg/year). As already mentioned, the resource allocation for the maturation of acorns occurs during the second year after flowering. Thus, the value of the total dry mass of per-tree reproductive organs borne in 1999 represents the approximate reproductive investment in 2000, and that of organs borne in 2000 represents the approximate reproductive investment in 2001.

The sum of $\Delta W(VG)$ and the reproductive investment represents the approximate total of the resources acquired per tree, or the net production per tree. Figure 2 shows the relationships between the tree size and the net production per tree in the 2 years. The net production per tree of the subgenus *Cyclobalanopsis* trees did not differ between the 2 years, with each species showing a similar pattern. The annual differences in the net production per tree of the total sample trees were not significant (Wilcoxon's signed ranks test, $n = 12$, $P \geq 0.05$). The dependency of the net production per tree ($P(n)$, kg) in the 2 years on the tree size (DBH) was expressed by using the following allometric equation:

$$P(n) = 0.117 \cdot D^{1.713} \tag{5}$$

where D is the DBH in cm (Fig. 2). The coefficient of determination (r^2) was 0.730.

Reproductive allocation per tree

As already mentioned, the reproductive allocation per tree is defined as the ratio of the reproductive investment to the net production in each tree. Although the net

Fig. 1a, b Variations in the quantities of produced reproductive organs per tree between years. The female flower production per tree (**a**) and acorn production per tree (**b**) were highly variable between the years. *NA* represents unavailable data because the traps had broken several times due to typhoon visits in the year. The differences in flower and acorn production of all sample trees between years were statistically significant (Wilcoxon's signed ranks test, $n = 12$, $P < 0.01$)
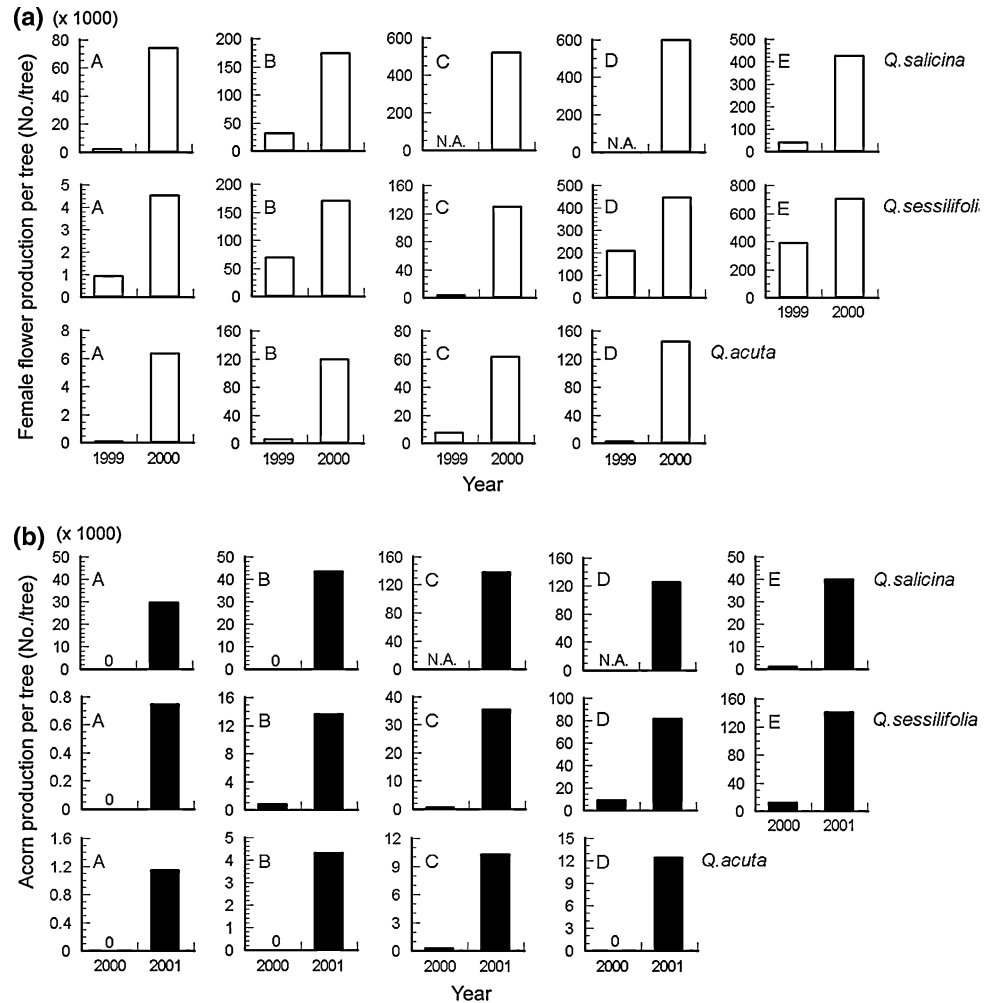
production values of a given sized individual were similar between years 2000 and 2001, the reproductive allocation values of each individual varied considerably between the 2 years (Table 1). The values of reproductive allocation per tree ranged from 0.01% to 8.39% (2.65% mean) in the year of 2000, and 5.76% to 79.80% (56.65% mean) in the year of 2001. On average, *Q. salicina*, *Q. sessilifolia*, and *Q. acuta* allocated 0.62%, 4.46%, and 0.24% of their net production to the reproductive structures in 2000, and 68.25%, 55.50%, and 28.00% in 2001 (Table 1).

Figure 3 shows the relationships between the net production and reproductive allocation per tree in the years 2000 and 2001. The relationship changed drastically between the two years (Fig. 3). In 2001, almost all individuals showed extremely high values of reproductive allocation compared to that of year 2000 (Fig. 3). Furthermore, including the three species, the values of reproductive allocation increased with increasing net production per tree (Spearman's rank correlation test, $P < 0.05$), although it appeared that the values of the reproductive allocation were different among species.

Discussion

Individual-based reproductive variables

In this study, we estimated the reproductive allocation of subgenus *Cyclobalanopsis* species on an individual tree basis. The effectiveness of our approach was already discussed in our previous study (Hirayama et al. 2004). The individual-based reproductive variables have been measured mainly for herbs and grasses (Ohlson 1988; Horvitz and Schemske 1988; Armstrong and Irvine 1989). For tree species, the variables have been assessed in relative terms on a per-inflorescence or per-branch basis (e.g., fruit set) (McCarthy and Quinn 1989; Herrera 1991). However, as suggested by Herrera (1988, 1991), broad differences in size and fecundity among individuals often exceed, and, thus, can offset the comparatively minor differences in the relative measures of reproductive investment. In our previous study, we examined the flower and seed production of a tall tree species *Lindera erythrocarpa* on an individual tree basis, and we showed that the relative measures,

Table 1 Variables of vegetative growth and reproduction in the sample trees. RI and RA represent the female reproductive investment (kg/year) and reproductive allocation (%), respectively. On an average, the RA of *Q. salicina*, *Q. sessilifolia*, and *Q. acuta* were 0.62%, 4.46%, and 0.24% in 2000, and 68.25%, 55.50%, and 28.00% in 2001. The sum of ΔW(VG) and RI represents the net production per tree (kg/year)

(a) 2000 (the year of low acorn production)

	DBH (cm)	W(LF) (kg/year)	ΔW(L) (kg/year)	ΔW(C) (kg/year)	ΔW(VG) (kg/year)	RI (kg/year)	RA (%)
Q. salicina A	25.60	24.86	0.302	11.57	36.73	0.004	0.01
Q. salicina B	40.72	47.71	0.293	19.87	67.88	0.224	0.33
Q. salicina C	54.31	41.11	0.141	17.01	58.26	NA	NA
Q. salicina D	70.70	81.49	0.133	32.11	113.73	NA	NA
Q. salicina E	84.25	145.86	0.053	21.60	167.52	1.475	0.87
Q. sessilifolia A	29.98	15.24	0.353	15.75	31.34	0.007	0.02
Q. sessilifolia B	53.80	149.95	0.320	38.10	188.37	1.815	0.95
Q. sessilifolia C	59.68	87.37	0.106	16.17	103.65	0.477	0.46
Q. sessilifolia D	84.00	272.81	0.097	39.47	312.37	14.838	4.53
Q. sessilifolia E	99.90	238.77	0.057	40.53	279.36	25.596	8.39
Q. acuta A	25.48	4.60	0.362	13.84	18.80	0.010	0.05
Q. acuta B	44.10	63.64	0.262	20.51	84.41	0.227	0.27
Q. acuta C	48.25	212.01	0.207	19.28	231.49	0.758	0.33
Q. acuta D	59.48	114.71	0.262	39.82	154.79	0.188	0.12

(b) 2001 (the year of high acorn production)

	DBH (cm)	W(LF) (kg/year)	ΔW(L) (kg/year)	ΔW(C) (kg/year)	ΔW(VG) (kg/year)	RI (kg/year)	RA (%)
Q. salicina A	26.06	3.46	0.278	10.83	14.57	28.08	65.84
Q. salicina B	41.17	6.95	0.255	17.63	24.84	42.72	63.24
Q. salicina C	54.60	9.10	0.188	23.07	32.37	127.84	79.80
Q. salicina D	71.10	21.84	0.128	31.33	53.30	102.22	65.73
Q. salicina E	84.48	19.62	0.046	18.95	38.61	51.03	56.93
Q. sessilifolia A	30.50	2.87	0.347	15.76	18.97	1.16	5.76
Q. sessilifolia B	54.43	63.00	0.227	27.74	90.97	19.28	17.49
Q. sessilifolia C	59.93	21.28	0.110	16.92	38.31	49.57	56.41
Q. sessilifolia D	84.41	126.93	0.109	45.10	172.14	161.32	48.38
Q. sessilifolia E	100.25	35.23	0.047	33.97	69.24	254.62	78.62
Q. acuta A	26.03	0.54	0.293	11.39	12.22	1.67	12.02
Q. acuta B	44.53	5.81	0.336	26.88	33.02	8.49	20.45
Q. acuta C	48.62	3.43	0.232	22.02	25.68	12.68	33.06
Q. acuta D	60.08	19.56	0.221	34.41	54.19	25.82	32.27

such as fruit set and seed set, are not reliable predictors of individual differences in the absolute seed production (Hirayama et al. 2004). Suzuki (2005) examined the reproductive investment in male and female *Eurya japonica* (Theaceae) at the tree and branch levels, and showed that the magnitude of sexual difference at the tree level was much lower than that at the branch level. These reports offer support for the assertion that the fecundity of a tree species should be measured on an individual tree basis.

The individual-based estimates of fecundity have another merit of leading to the straightforward approach to the investigation of the life history of trees. For many years, the plant mass of vegetative organs has been estimated on an individual tree basis by using allometric approaches for many tree species (Ogawa et al. 1965; Nagano and Kira 1978; Kawaguchi and Yoda 1986; Yoneda et al. 1995). Therefore, the individual-based estimates of reproductive investment enabled us to examine the relationships between vegetative growth and reproduction at the individual tree level.

Reproductive allocation of subgenus *Cyclobalanopsis* trees

In this study, the female flower and acorn production per tree changed considerably between years within an individual (Fig. 1). The net production per tree increased with increasing tree size, but did not differ significantly between years within an individual (Fig. 2). Therefore, the reproductive allocation differed dramatically between years within an individual (Fig. 3). If the reproductive output in the study species results from resource matching, the values of the reproductive investment should not change significantly because the net production per tree were similar for the two years. These results suggest that the reproductive output of the subgenus *Cyclobalanopsis* species was not determined by the resources acquired in the year.

According to Kelly and Sork (2002), the key evidence that disproves the resource matching hypothesis is the presence of switching, where in successive years plants move resources into, then away from, reproduc-
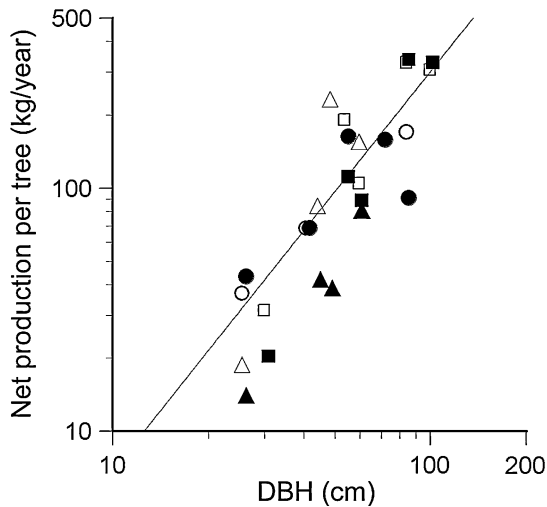
Fig. 2 Relationship between net production per tree and tree size (DBH) in three species of subgenus *Cyclobalanopsis*. The symbols indicate year (*open symbols* = 2000, *solid symbols* = 2001) and species (*Q. salicina* = circles, *Q. sessilifolia* = squares, *Q. acuta* = triangles). The differences in the net production per tree of all sample trees between years were not significant (Wilcoxon's signed ranks test, *n* = 12, *P* ≥ 0.05). The *line* shows the calculated trajectory of Eq. 5
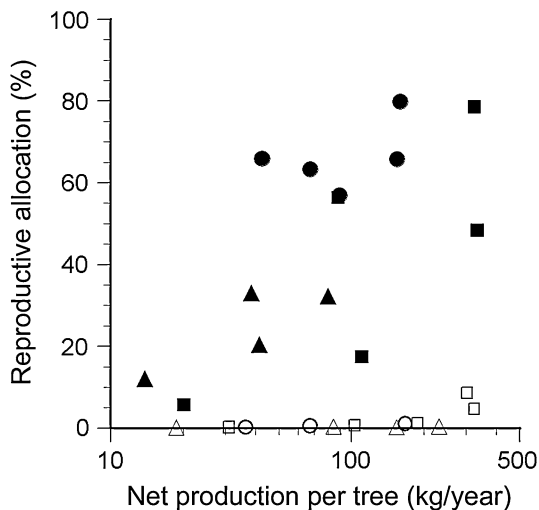

Fig. 3 Relationships between the reproductive allocation and the net production per tree. The symbols indicate year (*open symbols* = 2000, *solid symbols* = 2001) and species (*Q. salicina* = circles, *Q. sessilifolia* = squares, *Q. acuta* = triangles). The relationship changed drastically between the two years. In 2001, almost all individuals showed extremely high values of reproductive allocation compared to that of year 2000. The values of reproductive allocation increased with increasing net production per tree (Spearman's rank correlation test, *P* < 0.05)

tion (Norton and Kelly 1988; Kelly and Sork 2002). The values of the reproductive allocation of the *Cyclobalanopsis* trees in the two years in this study might support resource switching. The switching of resource allocation to vegetative growth and reproduction between years has been documented for several genera

of trees, including *Abies*, *Pseudotsuga*, *Dacrydium*, *Tsuga*, and *Nothofagus* (Eis et al. 1965; Norton and Kelly 1988; Woodward et al. 1994; Monks and Kelly 2006).

Furthermore, several papers, including Sork et al. (1993) and Kelly and Sork (2002), talk about negative relationships within trees of acorn production one year and the next. The negative correlation implies that masting causes resource depletion and is another form of evidence in favor of the resource switching to mast years. Our data of the considerable change of acorn production per tree in two consecutive years might support this point.

On the other hand, in the year of high acorn production (2001), the values of reproductive allocation increased with increasing net production per tree (Spearman's rank correlation test, *P* < 0.05, Fig. 3). The bigger trees put a greater fraction in female reproductive allocation in the mast year. These results suggest that the intensity of the switching of resource allocation between years within an individual is dependent on the tree size and increases with increasing tree size. However, it appeared that the values of the reproductive allocation were different among species in 2001 (Fig. 3). The differences among species should be examined using more detailed analyses with larger samples in future studies. Furthermore, not only female but also male reproductive allocation should be measured in future studies.

The tree size or production-dependent reproductive allocation has been discussed by several studies (e.g., Nakashizuka et al. 1997; Niklas and Enquist 2003), but there is still little information about the reproductive allocation at the whole-tree level. The individual variation in the reproductive allocation of tree species cannot be cleared by conventional methods, in which the reproductive output was investigated at the population level. Thus, in the present study, we confirmed the usefulness of the approach and the importance of the individual-based estimates of the reproductive variables in tall tree species.

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