

## Masting in *Fagus crenata* and its influence on the nitrogen content and dry mass of winter buds

QINGMIN HAN,<sup>1,2</sup> DAISUKE KABEYA,<sup>3</sup> ATSUHIRO IIO<sup>4</sup> and YOSHITAKA KAKUBARI<sup>4</sup>

<sup>1</sup> Department of Plant Ecology, Forestry and Forest Products Research Institute (FFPRI), 1 Matsunosato, Tsukuba, Ibaraki 305-8687, Japan

<sup>2</sup> Corresponding author (qhan@ffpri.affrc.go.jp)

<sup>3</sup> Kiso Experimental Station, FFPRI, 5473-8 Kisofukushima, Nagano 387-0001, Japan

<sup>4</sup> Faculty of Agriculture, University of Shizuoka, Ohya 836, Shizuoka 422-8529, Japan

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**Summary** In *Fagus*, full-mast seeding years are invariably followed by at least one non-mast year. Both flower and leaf primordia develop during the summer within the same winter buds. Flower bud initiation occurs when the N content of developing seeds is increasing rapidly. We hypothesized that competition for nitrogen (N) between developing seeds and buds limits flower primordium formation in mast years and, hence, limits seed production in years following mast years. We tested this hypothesis in three *Fagus crenata* Blume forests at elevations of 550, 900 and 1500 m. Bud N concentration ( $N_{\text{con}}$ ), amount of N per bud ( $N_{\text{bud}}$ ) and dry mass per bud (DM) were compared between a mast year (2005) and the following non-mast year (2006), and between winter buds containing both leaf and flower primordia ( $B_{\text{F}}$ ), which were formed during the non-mast year, and winter buds containing leaf primordia only ( $B_{\text{L}}$ ), which were formed in both mast and non-mast years. In addition, leaf numbers per shoot corresponding to the analyzed buds were counted, and the effect of masting on litter production was analyzed by quantifying the amounts of litter that fell in the years 2004 to 2007. The dry mass and N content of  $B_{\text{F}}$  formed in 2006 by trees at both 550 and 1500 m were 2.1–3.4-fold higher than the corresponding amounts in  $B_{\text{L}}$ , although the numbers of leaves per current-year shoot in 2007 that developed from the two bud types in the same individuals did not differ significantly. These results indicate that more N and carbohydrate are expended in producing  $B_{\text{F}}$  than in producing  $B_{\text{L}}$ . The amount of litter from reproductive organs produced in the mast year was similar to the amount of leaf litter at 900 and 1500 m, but three times as much at 550 m. Leaf numbers per shoot were significantly lower at all elevations in the mast year than in the non-mast years (and the amount of leaf litter at 550 and 1500 m tended to be lower in the mast year than in the non-mast years). In conclusion, preferential allocation of resources to seeds in the mast year reduced the availability of resources for flower primordium formation, and this may have accounted for the poor seed production in the following non-mast year.

**Keywords:** bud mass, elevation, flower bud, Japanese beech, leaf bud, litter, reproductive shoot.

### Introduction

Among temperate tree species, including members of the genus *Fagus*, annual shoot growth is predetermined in the winter bud (Eschrich et al. 1989, Kimura et al. 1998, Uemura et al. 2000). There have been many studies of the effects of winter bud morphology, anatomy, morphogenesis and organogenesis in relation to shoot growth, branching architecture, tree size, and ecological niche (MacDonald and Mothersill 1983, Nitta and Ohsawa 1998, Costes 2003). However, less attention has been paid to the relationship between bud chemical composition and its relationship with shoot development, including flower and seed production.

Mast seeding or masting, i.e., synchronous seeding within plant populations, with high inter-year variability, is characteristic of many species, including tropical trees, temperate forest trees, and temperate herbs (Kelly 1994, Kelly et al. 2001, Kelly and Sork 2002). According to the resource allocation hypothesis (Kelly and Sork 2002), which has been widely invoked to account for synchronous seeding, trees take several years to recover from the large expenditure of internal resources required in the production of seeds in a mast year. This idea has been tested with the aid of several models in which carbohydrate is the main limiting internal resource (Isagi et al. 1997). However, recent studies have demonstrated that carbohydrate contents of fruit are more dependent on current-year photosynthates than on internal stores of carbohydrates (Miyazaki et al. 2002, Hoch et al. 2003, Hoch 2005). Therefore, if mast seeding is dependent on resource availability, it is likely regulated by resources other than carbohydrate. A candidate for such a limiting resource is nitrogen (N) for the following reasons. Leaf photosynthesis is closely correlated to leaf N concentration because of the large proportion of leaf N

in the photosynthetic machinery (Evans 1989) and the limited amounts of available N in soils of most regions (Niinemets et al. 2001, Han et al. 2003). In addition, early season leaf growth after bud burst is more dependent on N supplied by remobilization from internal stores than on N uptake by roots (Grassi et al. 2002, Frak et al. 2006, Millard et al. 2006). Furthermore, compared with small juvenile trees, large mature trees rely on the remobilization of stored N for growth each spring more than on N uptake by roots (Millard 1996).

Large proportions of the N in trees can be allocated to reproductive organs in masting events. In *Fagus crenata* Blume, for instance, the N contents of reproductive organs account for 22–57% of total N in annual litterfall in mast years (Kawada and Maruyama 1986, Yasumura et al. 2006). Therefore, masting events may reduce the internal storage pool of N, and thus the amount of N that can be remobilized. Periodic fertilization of *F. crenata* forests has been shown to reduce the interval of masting events and to diminish the reduction in diameter growth in mast years (Hashizume 1991). Large individuals have a shorter mast interval than small individuals (Takeda 1992), and the former have a larger potential internal storage pools than the latter. These results suggest that masting can affect internal N dynamics in trees in the following year. If so, the nitrogen status of winter buds may provide a useful and easily measured early index of masting events. Yasaka et al. (2001) tried to predict masting events of *F. crenata* based on the numbers of flower buds in winter buds. To our knowledge, however, there have been no studies on the relationships between masting and N in winter buds.

In both *F. sylvatica* and *F. crenata*, observations spanning two centuries and 12 years, respectively, show that little or no seed production occurs following a full-mast seeding year, although the intervals between full masting events varied from 2 to 20 years (Hilton and Packham 2003, Suzuki et al. 2005). The flower primordia of *F. crenata* trees differentiate in the same winter buds as the leaf primordia beginning in June and July when, in mast years, the protein contents of concurrently developing seeds are increasing rapidly (Hashizume and Fukutomi 1978, Hashizume 1983). We, therefore, hypothesized that the effect of full masting on bud N is the factor responsible for poor masting the following year. We tested this hypothesis in three *F. crenata* forests at elevations of 550, 900 and 1500 m by (1) examining the effects of masting on the N concentration ( $N_{\text{con}}$ ), amount of N ( $N_{\text{bud}}$ ) and dry mass (DM) in individual buds, (2) analyzing the differences in  $N_{\text{con}}$ ,  $N_{\text{bud}}$  and DM between leaf buds ( $B_L$ ) and flower buds ( $B_F$ ), (3) examining the difference in leaf numbers per reproductive and

non-reproductive shoots that formed from the corresponding  $B_L$  and  $B_F$  in the previous year and (4) analyzing the effect of masting on litter production.

## Materials and methods

### Study site

The study area was located in the Naeba Mountains in southern Niigata Prefecture, Japan (36°51' N, 138°46' E), where *F. crenata* forests are found over an altitudinal range from 550 to 1500 m. Eight permanent plots along the altitudinal gradient were established in 1970 for long-term ecological monitoring within the framework of the International Biological Program (Kakubari 1977). The bedrock is predominantly andesite and basalt, on which moderately water-retentive brown forest soil has formed. During the period 1979–2006, mean annual precipitation and temperature at a nearby meteorological station (36°56' N, 138°49' E, 340 m a.s.l.; Japanese Bureau of Meteorology) were 2225 mm and 11.5 °C, respectively. Around 3–4 m of snow accumulates during the winter. Three of the eight permanent plots with elevations of 550, 900 and 1500 m were chosen for study. General characteristics of the selected stands and trees are shown in Table 1. Further details about the sites are presented in Kakubari (1977) and Kubota et al. (2005).

### Bud sampling and nitrogen analysis

At all elevations in the Naeba Mountains, *F. crenata* fully fruited in 2005, which was followed by a non-fruiting year in 2006. Three to five trees that fully fruited around a scaffolding tower in each plot were selected for study. Samples were collected from the same individuals at 550 and 1500 m in both years. At 900 m, however, the sampled individuals differed between the two years because the tower collapsed under heavy snow and the boughs of some individuals selected in 2005 were broken. Three of the four selected individuals at 550 m and all of the selected trees at 1500 m produced flower buds in 2006 and fruited in 2007, but all of the selected individuals at 900 m formed only leaf buds in 2006. At elevations of both 900 and 1500 m, an additional individual that did not fruit in 2005 was selected, as a reference, but the data acquired from these additional trees were not pooled with the data from the fruiting trees in the following statistical analyses.

Two branches were sampled from each tree in November after leaf fall. In each case, the branching system representing the previous 5 years of growth was retained, and all of the buds

Table 1. General information on the plots and selected individuals of *Fagus crenata* at three elevations in the Naeba Mountains in 2005.

Elevation (m)	Slope aspect (°)	Age (years)	Density (trees ha <sup>-1</sup> )	Stand leaf area index	Tree leaf area index	Tree height (m)	Diameter at breast height (cm)
550	0 N	150–200	238	5.1	4.0	26.7–36.7	36.7–77.6
900	13 NE	83–84	1190	4.9	3.6	17.2–22.8	20.5–38.1
1500	8 NE	190–260	248	5.5	2.7	19.2–21.6	34.1–62.6

on the branching system were collected. Branch order was not taken into account, but because all branches were located in the upper parts of the tree crowns, the selected branching systems were assumed to be comparable in the environmental conditions (especially light regime) to which they had been exposed.

All buds were dried to constant mass at 70 °C. Bud N concentration was determined by gas chromatography (GC-8A, Shimadzu, Kyoto, Japan) after combustion with circulating O<sub>2</sub> from an NC analyzer (Sumigraph NC-900, SCAS, Osaka, Japan). Six to twelve B<sub>L</sub> and B<sub>F</sub> from each sampled branch were used for N analysis.

#### *Leaf number per shoot*

In 2007, we counted leaf numbers per current-year shoot sampled from eight branches of each selected tree at all elevations, based on the same 5-year-old branching system mentioned above. Leaf numbers formed on 1- to 3-year-old shoots were counted from the petiole scars.

#### *Litter-trap samples*

Litter from 10 litter-traps placed at each elevation was collected monthly. The litter traps had a mouth of 0.25 m<sup>2</sup> and were fixed about 1 m above the ground. Litter that fell from species other than *F. crenata* was discarded, and the *F. crenata* litter was sorted into fractions of leaves, woody organs (bark, bud scales and branches) and reproductive organs (flowers, husks and nuts), and dried to constant mass at 70 °C.

#### *Statistical analyses*

Effects of all independent variables (i.e., bud type, masting year and study site) on all measured potentially dependent variables were evaluated by fitting generalized linear mixed models (GLMMs) by restricted maximum likelihood. The GLMMs provide a flexible way to model traits that do not satisfy the assumptions of a standard linear model, allowing fixed and random factors to be distinguished in the model (Verbeke and Molenberghs 1997). Their use in this case is justified by the normal or Poisson distribution of dependent variables under consideration and the inclusion of random sources of variation (i.e., individuals and branches). First,  $N_{\text{con}}$ ,  $N_{\text{bud}}$  and DM in single buds of trees that fruited in 2005 were treated as dependent variables. The fixed effects of bud type (B<sub>L</sub> in 2005, B<sub>L</sub> in 2006 and B<sub>F</sub> in 2006) and study site on those parameters were tested assuming a normal error distribution of dependent variables. The variances derived from selected individuals, inter-annual changes in individuals (year), and sampled branches in each individual were included in the GLMM model as random factors. Second, the fixed effects of reproduction and study site on leaf number per current-year shoots of 2007 within trees that fruited were tested assuming a Poisson error distribution with a log link function. The variance derived from individuals was treated as a random factor. Data collected from reproductive and nonreproductive shoots of the three individuals that fruited in both 2005 and 2007 were pooled. Third, the fixed effects of masting and study site on leaf number per shoot were tested for all individuals that

fruited in 2005, assuming a Poisson error distribution with a log link function. The variances derived from individuals, branches within individuals, and twig age classes within branches were included in the model as random factors. Data discriminated from petiole scars of all individuals that fruited in 2005 were used, and Satterthwaite's method was used to approximate the degrees of freedom of the denominator to prevent overestimation of the above mentioned random effects (Verbeke and Molenberghs 1997). All random effects were relatively minor compared with the residual error (see Tables 1–4).

## Results

#### *Effects of masting on bud nitrogen*

The amounts of N in single buds ( $N_{\text{bud}}$ ) were significantly affected by bud type, but not by study site (Table 2). In 2006,  $N_{\text{bud}}$  values were 2.1-fold higher in B<sub>F</sub> than in B<sub>L</sub> at 550 m, and 3.4-fold higher at 1500 m (Figure 1a). Values of  $N_{\text{bud}}$  in B<sub>L</sub> in the mast year were similar to those of corresponding buds in the non-mast year at 1500 m, but at 550 and 900 m  $N_{\text{bud}}$  values were significantly lower in the mast year than in the non-mast year (Figure 1a). Bud N concentration ( $N_{\text{con}}$ ) was significantly affected by bud type but not by study site (Table 2). In 2006,  $N_{\text{con}}$  was significantly higher in B<sub>F</sub> than in B<sub>L</sub> at 1500 m, but not at 550 m (Figure 1b). Masting did not lead to a reduction in  $N_{\text{con}}$  in B<sub>L</sub> at any of the studied sites. In contrast,  $N_{\text{con}}$  in B<sub>L</sub> formed in the mast year was higher than  $N_{\text{con}}$  in B<sub>L</sub> formed in the following non-mast year at 550 m.

#### *Effects of masting on bud dry mass*

The DM of single buds was significantly affected by bud type but not by study site (Table 2). In 2006, the DM of B<sub>F</sub> was 2.0- and 2.4-fold higher than the DM of B<sub>L</sub> at 550 and 1500 m, respectively (Figure 1c). The DM of B<sub>L</sub> buds at 550 m, but not at 900 and 1500 m, was significantly lower in the mast year than in the following non-mast year (Figure 1c). The DM of individual buds (both B<sub>L</sub> and B<sub>F</sub>) from all sites varied widely (Figures 2a and 2b).

#### *Relationships between bud dry mass and nitrogen*

Because both flower and leaf primordia develop in the same winter buds and share the same N source, we analyzed the relationship between bud DM and N independently of bud type. Bud nitrogen concentration was not correlated with DM in either the mast or non-mast year (Figure 3a). However,  $N_{\text{bud}}$  was closely related to the corresponding DM in both the mast and non-mast years (Figure 3b). In addition, the slope of the linear regression between  $N_{\text{bud}}$  and their DMs was higher in the non-mast year than in the mast year (ANCOVA,  $P < 0.05$ ).

#### *Effects of masting on number of leaves per shoot*

Within individual trees that fruited in 2007, the numbers of leaves per current-year shoot did not differ significantly between reproductive shoots and non-reproductive shoots at either 550 or 1500 m (Figure 4, Table 3). Therefore, we exam-

Table 2. Summary statistics for the Type III test of fixed effects and the estimated random effects in the generalized linear mixed model, with dependent variables of winter bud nitrogen amount per bud ( $N_{\text{bud}}$ ), nitrogen concentration ( $N_{\text{con}}$ ) and bud dry mass (DM) in *Fagus crenata* between  $B_L$  buds in the mast year 2005,  $B_L$  and  $B_F$  buds in the following non-mast year 2006, at elevations of 550, 900 and 1500 m. The degrees of freedom of the denominator (den df) were calculated by general Satterthwaite approximation.

Effect	df	$N_{\text{bud}}$			$N_{\text{con}}$			DM		
		den df	<i>F</i>	<i>P</i>	den df	<i>F</i>	<i>P</i>	den df	<i>F</i>	<i>P</i>
<i>Fixed factors</i>										
Bud type	2	8.53	67.97	< 0.0001	4.74	10.18	0.019	6.04	70.69	< 0.0001
Study site	2	10.3	0.23	0.798	7.91	1.07	0.388	10.2	1.18	0.345
Interaction	3	9.0	3.43	0.066	4.74	14.41	0.008	6.16	4.48	0.055
<i>Random factors</i>										
Individual		6.59E-03			7.89E-03			6.23E+01		
Year		4.01E-03			1.27E-03			1.76E+01		
Branch		0			2.50E-04			0		
Residual		1.95E-02			1.07E-02			1.57E+02		

ined whether masting affected leaf number per shoot by counting petiole scars (on both reproductive and non-reproductive shoots) of individuals that fruited for each year from 2004 to 2007. We found that numbers of leaves per shoot were significantly lower in the masting year than in the non-masting years

(Figure 5, Table 4). In addition, the number of leaves per shoot in the non-fruited trees examined at both 900 and 1500 m were higher than in the trees that fruited in 2005.

#### Effects of masting on litter fall

Litter from reproductive organs accounted for 72, 53 and 43% of the total amount of *F. crenata* litter that fell in 2005 at 550, 900 and 1500 m, respectively (Figure 6). Compared with the mean value for annual leaf litter per tree over the four monitored years, the amount of leaf litter that fell in the masting

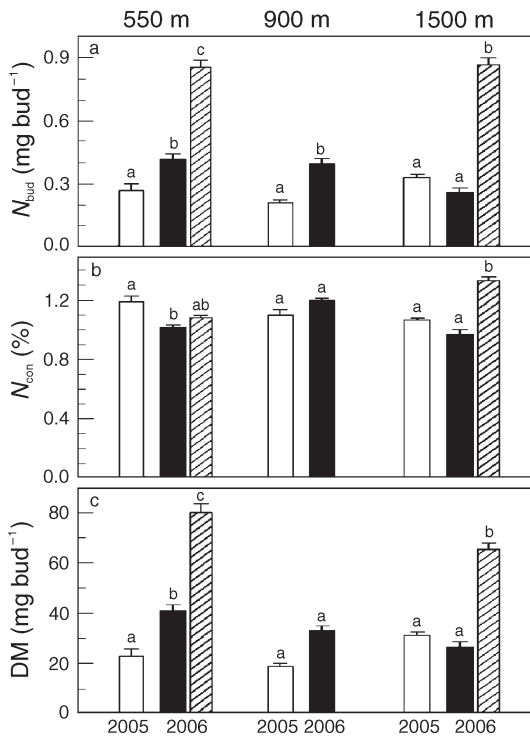


Figure 1. Mean (a) nitrogen content ( $N_{\text{bud}}$ ), (b) nitrogen concentration ( $N_{\text{con}}$ ) and (c) dry mass (DM) of leaf buds in the mast year 2005 (open bars) and the following non-mast year 2006 (closed bars) at elevations of 550, 900 and 1500 m from the upper crowns of three to five fruited trees. Hatched bars represent corresponding values of the flower buds in the non-mast year 2006. Values shown are means  $\pm$  SE estimated from individual-averaged data. Different letters indicate significant differences in the corresponding values of buds from the same elevation ( $P < 0.05$ ).

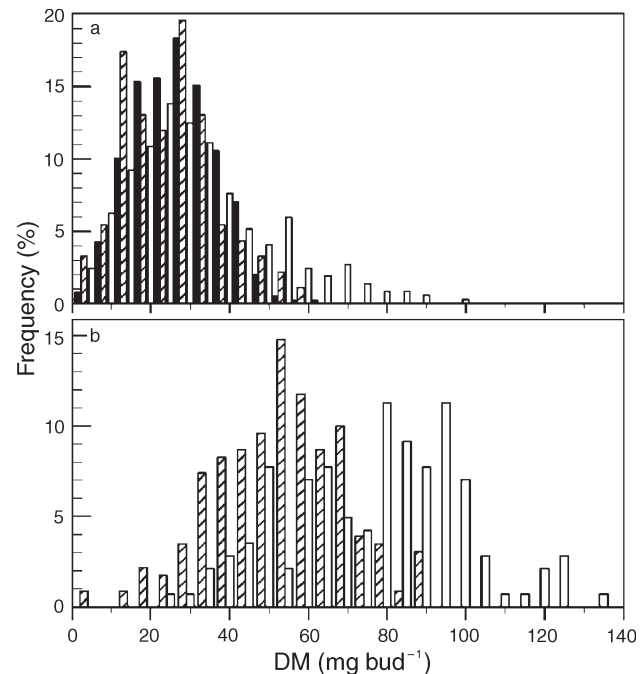


Figure 2. Frequency distributions of dry mass (DM) of (a) leaf buds and (b) flower buds collected from the upper crowns of three to five individuals at elevations of 550 m (open bars), 900 m (closed bars) and 1500 m (hatched bars) in November 2006, a non-mast year ( $n = 110\text{--}398$ ). No flower buds were observed in trees at 900 m.

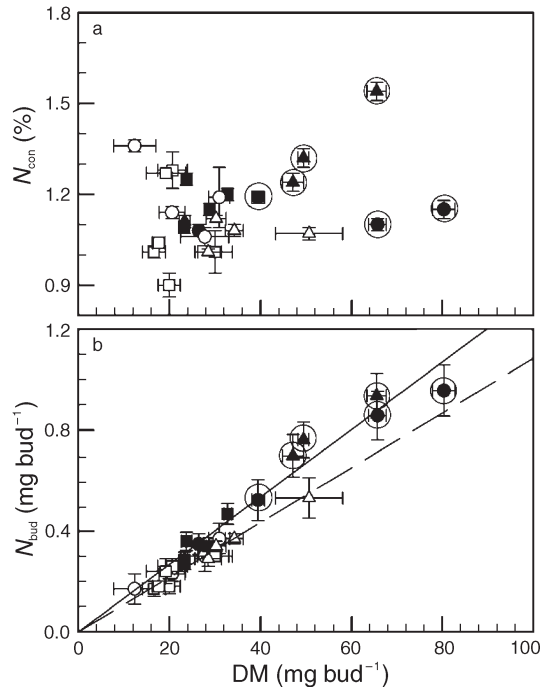


Figure 3. Relationships between winter bud dry mass (DM) and (a) nitrogen concentration ( $N_{con}$ ) and (b) nitrogen content per bud ( $N_{bud}$ ) when individual-averaged data from all elevations were pooled:  $N_{bud} = 0.0108DM$ ,  $r^2 = 0.95$ ,  $P < 0.001$  (open symbols and the broken line indicate data from the mast year, 2005);  $N_{bud} = 0.0134DM$ ,  $r^2 = 0.95$ ,  $P < 0.001$  (closed symbols and the solid line indicate data from the non-mast year, 2006). Values shown are means  $\pm$  SE. Circles, squares and triangles represent individuals at elevations of 550, 900 and 1500 m, respectively. Encircled symbols represent flower buds.

year of 2005 was about 30% lower at 550 m, and there were lesser reductions at elevations of 900 and 1500 m. Leaf litter was significantly higher in 2007 than in 2005 at all elevations.

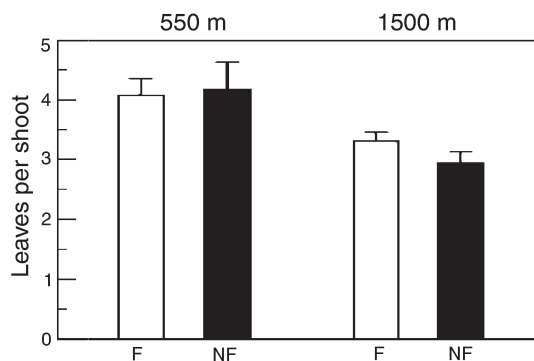


Figure 4. Comparison of mean numbers of leaves per current-year fruit-bearing shoots (F) and non-fruiting shoots (NF) developed from winter buds produced in 2006 sampled from the upper crowns of trees that fruited at elevations of 550 and 1500 m. Values shown are means  $\pm$  SE estimated from individual-averaged data of three trees that fruited in both 2005 and 2007. Results of the statistical analysis of the factors affecting this parameter are shown in Table 3.

Table 3. Summary statistics for the Type III test of fixed effects and the estimated random effects in the generalized linear mixed model for leaf numbers in current-year shoots in 2007 within the three *Fagus crenata* trees that fruited in both 2005 and 2007 at elevations of 550 and 1500m. The degrees of freedom of the denominator (den df) were calculated by general Satterthwaite approximation.

Effect	df	den df	F	P
<i>Fixed effects</i>				
Reproduction	1	64.63	1.78	0.187
Study site	1	4.17	6.05	0.067
Interaction	1	64.63	0.38	0.540
<i>Random effects</i>				
Individual		1.62E+02		
Residual		1.46E+00		

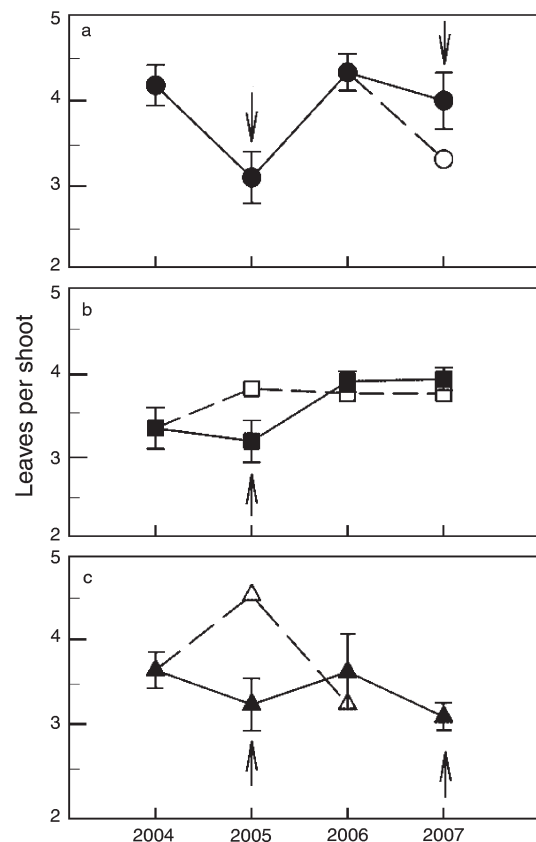


Figure 5. Interannual variations in numbers of leaves per current-year shoots sampled from 2004 to 2007 at elevations of (a) 550, (b) 900 and (c) 1500 m from three to five trees that fruited in 2005 (closed symbols). Open symbols represent corresponding values obtained from single individuals that did not fruit in 2005 and/or 2007. Arrows represent the years when fruiting occurred at the respective elevations. Results of the statistical analysis of the factors affecting this parameter are shown in Table 4.

Table 4. Summary statistics for the Type III test of fixed effects and the estimated random effects in the generalized linear mixed model for leaf numbers in current-year shoots during 2004 and 2007 in *Fagus crenata* trees sampled at elevations of 550, 900 and 1500 m ( $n = 3-5$ ). The degrees of freedom of the denominator (den df) were calculated by general Satterthwaite approximation.

Effect	df	den df	<i>F</i>	<i>P</i>
<i>Fixed effects</i>				
Masting	1	43.48	11.28	0.002
Study site	2	12.88	1.98	0.178
Interaction	2	43.12	0.04	0.959
<i>Random effects</i>				
Individual		2.55E-03		
Branch		1.42E-03		
Twig age		1.16E-02		
Residual		1.56E+00		

## Discussion

The numbers of leaves per shoot did not differ significantly between reproductive and non-reproductive shoots within individuals that fruited in 2007 at either 550 or 1500 m (Figure 4), in agreement with the results of an earlier study of *Styrax obassia* Sieb. et Zucc. (Miyazaki et al. 2002); however, both  $N_{\text{bud}}$  and DM of the winter buds from which they originated were higher in  $B_F$  than in  $B_L$  in 2006 (Figures 1a and 1c). In *Fagus* trees, all leaves are completely preformed in winter buds, so the numbers of leaves (and even the numbers of cell layers in palisade tissues within the leaves) are predetermined in the preceding year (Eschrich et al. 1989, Kimura et al. 1998, Uemura et al. 2000). In addition, a recent study has demonstrated that masting in 2005 did not significantly decrease leaf

N in trees at 550 and 1500 m (Wang et al. 2008). Because both flower and leaf primordia develop within the same winter buds (Hashizume 1983), the differences in  $N_{\text{bud}}$  and DM between  $B_F$  and  $B_L$  may indicate the nitrogen and carbohydrate expenditures for developing flower primordia. Thus, 2.0–3.4-fold more N and carbohydrate may be required to differentiate flower primordia in a  $B_F$  (while maintaining the same number of leaf primordia) than in a  $B_L$ .

Litter from reproductive organs accounted for about 43–72% of the total *F. crenata* litter falling in 2005 (Figure 6). In addition, the amount of N in litter from reproductive organs accounted for 47–67% of the total N content of the litter in 2005 (data not shown); values that were close to, or exceeded, maximum values (22–57%) previously reported for *F. crenata* (Kawada and Maruyama 1986, Yasumura et al. 2006). These results support the conclusion that the N contents of reproductive organs are substantial in masting years. Flower primordia of *F. crenata* start to differentiate in winter buds in June and July, months in which protein contents of developing seeds (N allocation) rapidly increase in a mast year (Hashizume and Fukutomi 1978, Hashizume 1983). Both seeds and winter buds have the same N sources (N absorption by roots or remobilization of internally stored N, or both), and assuming that N absorption by roots did not differ significantly between 2005 and 2006, these results imply that a large proportion of the available N was supplied to seeds in the masting year, resulting in a shortage in the supply of N to buds. The limited N supply to buds (in conjunction with the larger expenditure of N required to develop a  $B_F$  than a  $B_L$ ) may, in turn, have impeded the differentiation of flower primordia in winter buds in the masting year (Figures 1a and 3). These speculations are consistent with the N limitation hypothesis and may explain why masting years are always followed by non-masting years in both European beech (Hilton and Packham 2003) and Japanese beech (Suzuki et al. 2005).

Leaf numbers per shoot were significantly lower in the full masting year than in the other years (Figure 5, Table 4), in accordance with the annual variations in leaf litter (Figure 6). However, the buds from which the leaves originated developed in the preceding non-masting year (2004), in which there was no competition from seeds for N and carbohydrate resources during flower differentiation. Therefore, it is likely that the observed reduction in leaf number per shoot may be caused by the large N expenditure for  $B_F$ . Decreases in total bud numbers per individual when  $B_F$  developed, or the possibility that smaller leaves with less DM were produced in the reproductive shoots, as found in *S. obassia* (Miyazaki et al. 2002), or both, may also have contributed to the reductions in annual leaf litter. The extent to which leaf numbers per shoot and leaf litter decrease in a mast year may be related to the total numbers of  $B_F$  per individual, based on the differences in the ratio of litter originating from reproductive organs and leaves between different sites, given that the effects of study sites on leaf number per shoot were not significant (Figures 5 and 6, Tables 3 and 4).

Trees at 900 m did not fruit in 2007, unlike the trees at 550 and 1500 m, even though the amount of seeds produced per

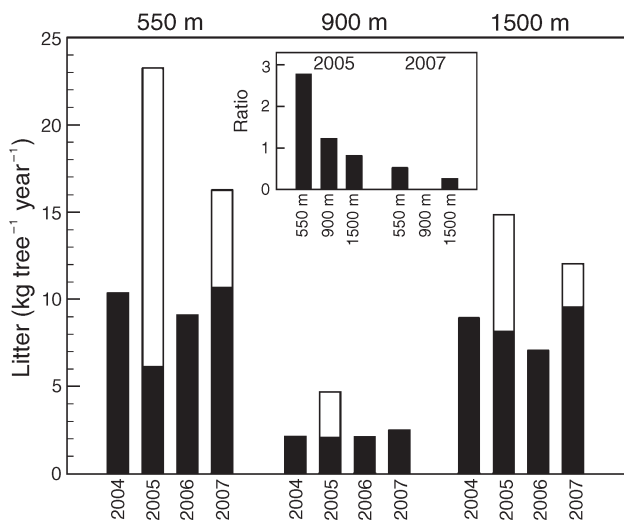


Figure 6. Interannual variations in litterfall of leaves (black bars) and reproductive organs (white bars) averaged at the individual level from 2004 to 2007 at elevations of 550, 900 and 1500 m. The inset shows ratios of reproductive organ to leaf litter in the mast years 2005 and 2007.

unit leaf mass was much lower at 900 m than at 550 m, and the effects of study site on  $N_{\text{con}}$ ,  $N_{\text{bud}}$  and DM were not significant (Figure 6, Tables 2–4). Although our data provide no definitive explanation for these altitudinal differences, the observed differences may be related to: (1) non-synchronized reproductive behavior among the individuals at 900 m (Healy et al. 1999); (2) differences in tree size (for example, Takeda (1992) found that large trees tend to fruit more frequently than smaller trees (cf. Table 1)); (3) differences in internal storage pool size reflecting differences in tree sizes; and (4) differences in secondary metabolites (Selås et al. 2001).

In conclusion, masting reduced dry mass and amount of nitrogen in winter buds of *Fagus crenata*, a species that produces buds with predetermined numbers of leaves and shoots. Preferential allocation of resources to seeds in the mast year will have reduced the availability of resources for flower primordium formation, and may have accounted for the poor seed production in the following non-masting year.

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