

FLORAL SEX ALLOCATION AT INDIVIDUAL AND BRANCH LEVELS IN *BETULA PLATYPHYLLA* VAR. *JAPONICA* (BETULACEAE), A TALL, WIND-POLLINATED MONOECIOUS TREE SPECIES¹

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Floral sex allocation at the individual and first-order branch levels and the relation between these levels were examined in *Betula platyphylla* var. *japonica*, a wind-pollinated monoecious tree. Floral sex allocation at the individual level varied with resource availability in a pattern similar to that predicted by the Masaka and Takada model (*Journal of Theoretical Biology* 240: 114–125). Thus, individual trees with few reproductive resources produced only female or male inflorescences, whereas individuals with many resources rarely had a high male ratio (i.e., number of male inflorescences/total number of inflorescences). Furthermore, the number of male inflorescences tended to reach an upper limit, whereas the number of female inflorescences increased monotonically with increasing reproductive investment. The patterns of floral sex allocation at the first-order branch level were analogous to those at the individual level. Thus, each first-order branch of *B. platyphylla* var. *japonica* behaves like an individual, and the floral sex allocation of a given branch does not necessarily represent the individual tree. The effect of the individual-level floral sex ratio on branch-level floral sex allocation indicates that branch behavior is controlled by the individual.

Key words: first-order branch; floral sex allocation; individual; reproductive resources; wind-pollinated monoecy.

Monoecious plants can adjust gender expression to maximize fitness by changing the number or amount of female and male flowers at the level of the individual (Wilson, 1983). The manner of fitness gain differs greatly between female and male functions, and consequently, plants are expected to have various gender patterns according to their fecundity (Charnov, 1982; Klinkhamer and de Jong, 1997). For example, wind-pollinated monoecious species often have different gender patterns among individuals within a population (reviewed in Sakai and Sakai [2003] and Masaka and Takada [2006]). To explain this effect of fecundity, researchers have proposed two major hypotheses: the size-dependent fecundity and height-advantage hypotheses (Klinkhamer and de Jong, 1997; Klinkhamer et al., 1997; Sakai and Sakai, 2003). Both hypotheses predict that individual maleness should increase with increasing plant size (height) because the pollen vector, wind, is not saturated by pollen transportation, while female fitness is expected to be a decreasing function of seed number as a result of the strong local resource competition among offspring (Charnov, 1982; Charlesworth and Charlesworth, 1981; Klinkhamer and de Jong, 1997). Alternatively, the hypotheses predict that both pollen dispersal distance by wind and mating potential will increase with plant height (Willson and Ruppel, 1984; Burd and Allen, 1988; Aizen and Kenigsten, 1990; Klinkhamer and de Jong, 1997; Sakai and Sakai, 2003). However, plant size and maleness are negatively correlated in some wind-pollinated monoecious species and not correlated at all in other species (Burd and Allen, 1988; Murakami and

Maki, 1992; Bickel and Freeman, 1993; Fox, 1993; Dajoz and Sandmeier, 1997; Klinkhamer and de Jong, 1997). It follows that the size-related hypotheses do not explain the gender variation in wind-pollinated monoecious species.

Masaka and Takada (2006) proposed a realistic theoretical model that explained floral sex ratio strategy in wind-pollinated monoecious species in evolutionary terms (cf. Regal, 1982). Their model postulates two situations: competitive sharing among male flowers (CSM; Lloyd, 1984) and wind-pollination efficiency (WPE). CSM is defined as the share of female flowers among male flowers within the local breeding population. Wind-pollinated species seem to form the local breeding population because airborne pollen does not reach distant individuals (e.g., Nilsson and Wästljung, 1987; Allison, 1990; Kawashima et al., 2002). In the population, there is a trade-off between the number of female flowers and the number of male flowers. Female flowers should decrease if male flowers increase in a population. Then competition over female flowers among males would be much stronger. WPE, on the other hand, is defined as the frequency of fertilized seeds by an individual via wind. Because the relationship between the probability of a pollen grain contacting a female and pollen density in the air can be described by a Poisson distribution (Feller, 1968; Sarvas, 1968; Smith et al., 1990), WPE can be described by a Poisson distribution function. Using CSM and WPE, Masaka and Takada (2006) developed an *n*-persons game model (Fig. 1). Their model predicts that individuals with the fewest reproductive resources will produce only female flowers and that those with slightly more resources will produce only male flowers; the model also predicts that, with further resource increases, male flower production will remain constant (i.e., there is an upper limit to male flowers, and remaining reproductive resources are directed to female flower production). This tendency was clearly observed in certain tall, wind-pollinated monoecious tree species (e.g., Smith, 1981; Linhart and Mitton, 1985; Arista and Talavera, 1997; Goubitz, 2001; Kimura et al., 2003) but not in species with other reproductive systems. With insect-pollinated monoecy, for example, individuals with the fewest reproductive resources

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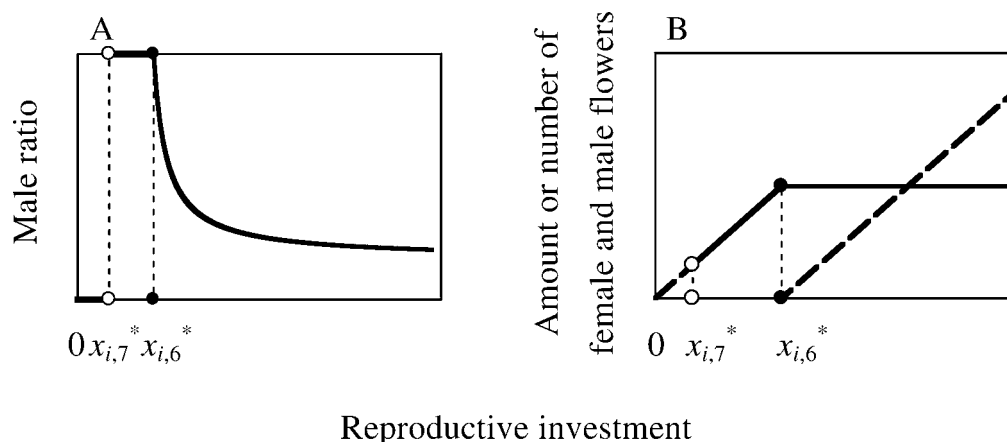


Fig. 1. Theoretical model proposed by Masaka and Takada (2006) to explain floral sex allocation in wind-pollinated monoecious species. (A) Relationship between floral sex ratio (male ratio) and reproductive investment. The switching point from female phase to male phase is indicated by $x_{i,7}^*$ and from male phase to constant male phase by $x_{i,6}^*$. (B) Relationship between number of flowers and reproductive investment. Solid and dashed lines indicate amount or number of male and female flowers, respectively. Also see Introduction.

produce male flowers and those with more resources produce female flowers, presumably because it costs less to produce males than females (Lovett Doust and Cavers, 1982; Bierzychudek, 1984). In the case of wind-pollinated androdioecy, individual gender expression is often stable (Liston et al., 1990; Pannell, 1997, 2000). In addition, an individual that does not release a large quantity of pollen into the air will have a reduced probability of having its pollen land on a stigma (Masaka and Takada, 2006), while a stigma could receive several pollen grains as long as other plants produce high pollen density in the air (Streiff et al., 1999). Under these conditions, wind-pollinated monoecious species would have no advantage in producing male flowers when the individual has little reproductive resources. Therefore, wind-pollinated monoecious species should produce female flowers when the individual has little reproductive resources (Masaka and Takada, 2006).

Because of the difficulty in investigating all of the flowers in a large tree crown, some researchers have used the branch as representative of the individual (Freeman et al., 1981; Allen and Antos, 1988, 1993; Antos and Allen, 1999). However, knowledge of flower arrangement within the crown is scanty (but see Koike et al., 1990). Both reproductive and vegetative first-order branches sometimes co-occur within the crowns of some tree species (here, we define a first-order branch as a branch directly attached to the main stem). Suzuki (2005) reported that the reproductive investment at the individual level differed from that at the branch level in a dioecious shrub. However, there are few studies of other reproductive systems (e.g., wind-pollinated monoecy) or reproductive strategies. Thus, the relationship between the reproductive system of the individual and that of each branch is still unknown for tree species. Verifying the relationship may increase our understanding of the physiology of resource allocation for reproduction (e.g., Umeki and Kikuzawa, 2000; Umeki and Seino, 2003; Umeki et al., 2006).

A plant is sometimes seen as an assemblage of repetitive subunits (modules), and the branch is regarded as one of the modules (Harper, 1981; White, 1979). Under this modular concept, the floral sex allocation of each first-order branch is analogous to that of the individual. Thus, each first-order

branch should have a female phase, a male phase, and then a constant male phase with increasing reproductive resources. The modular concept, however, does not indicate that each first-order branch adopt the optimal strategy for the floral sex ratio. The optimal floral sex ratio is often assumed to be achieved at the individual level by the control of branches. Although researchers have reported that much of the photosynthate necessary for fruit maturation on a branch is provided by the branch itself (Watson and Casper, 1984; Tuomi et al., 1988; Hasegawa et al., 2003), the idea presented here is different from the concept of branch autonomy (Watson and Casper, 1984; Sprugel et al., 1991), which posits that reproduction in each branch corresponds to its carbon budget (e.g., Koike et al., 1990).

In the present study, the gender expression of a tall, wind-pollinated monoecious tree species, *Betula platyphylla* var. *japonica* (Miq.) Hara, at the individual and first-order branch levels was evaluated in Hokkaido, northern Japan. Three questions were considered. Can the floral sex allocation pattern in *B. platyphylla* var. *japonica* at the individual level be explained by the theoretical model of Masaka and Takada (2006)? Does floral sex allocation at the first-order branch level reflect that at the individual level? And to what extent are floral sex allocation at the individual and branch levels related?

It must be noted that individual size (volume, height, or trunk diameter) is not necessarily a useful predictor of reproductive allocation in trees because trees often show periodic abundant flower production called masting or mast behavior (Norton and Kelly, 1988; Mizui, 1993; Koenig and Knops, 1998; Kelly and Sork, 2002; Shibata et al., 2002). Even if a tree produces flowers and seeds in a quantity corresponding to its size in a mast year, it may produce few flowers and seeds in a nonmast year. A resource budget model can be used to explain masting behavior (Isagi et al., 1997; Masaka and Maguchi, 2001; Ranta et al., 2005; Kon et al., 2005). Therefore, the resources available for reproduction in an individual or a branch should be delineated by its own fecundity at a given time, i.e., by the number of flowers.

MATERIALS AND METHODS

Materials—*Betula platyphylla* var. *japonica* is the major tall tree species in Hokkaido, northern Japan. Birch is a wind-pollinated monoecious species, widely distributed in cool-temperate and boreal forests in the northern hemisphere (Krüssmann, 1976). In Japan, tall birch are typical pioneer species and often regenerate in a site after disturbance (Kikuzawa, 1983; Koike, 1988), such as fire, landslide, or artificial soil scarification for silviculture (Kikuzawa, 1987, 1988). Regeneration after disturbance often produces even-aged stands (Kikuzawa, 1987, 1988; Shibuya, 1994).

Two to three male inflorescences develop together at the tip of each long shoot and are exposed to the environment during winter, whereas female inflorescences develop singly in a bud on a short shoot and winter within the bud (Maillette, 1982; Caesar and Macdonald, 1983, 1984; Macdonald and Mothersill, 1983; Macdonald et al., 1984). A short shoot bud rarely produces two female inflorescences. Theoretically, female and male flowers should have equal reproductive cost in a self-incompatible, wind-pollinated species (Lemen, 1980; Charnov, 1982). *Betula platyphylla* var. *japonica* is a self-incompatible species, and the reproductive cost (as measured by dry mass) is similar between a fruit and a set of male inflorescences (Masaka, 2006).

Data sampling—The study was carried out in three locations: Dohoku Branch Station arboretum, Hokkaido Forestry Research Institute (HFRI) in Nakagawa (44°48' N, 142°3' E, 20 m a.s.l.), northern Hokkaido; two shelterbelts in Iwamizawa (43°13' N, 141°44' E, 15 m a.s.l.); and a stand established at a road-cut in Bibai (43°16' N, 141°50' E, 40 m a.s.l.), central Hokkaido. *Betula platyphylla* var. *japonica* was planted in the HFRI arboretum in 1976 (Nakagawa cohort), and the trees were investigated in 1999. The shelterbelts were planted in 1993 (Iwamizawa-1 cohort) and 1997 (Iwamizawa-2 cohort) and were investigated in 2001 and 2002, respectively. The trees at the Bibai road-cut (Bibai cohort) were about 14 yr old, based on counts of annual rings at the tree base, when they were investigated in 2005. Thus, all stands were even-aged cohorts. The height of the largest trees was 17–18 m in the Nakagawa cohort, 6–7 m in the Iwamizawa-1 cohort, 4–5 m in the Iwamizawa-2 cohort, and 8–9 m in the Bibai cohort.

The randomly selected samples included 11 individuals from the Nakagawa cohort, 15 each from the Iwamizawa-1 and Iwamizawa-2 cohorts, and 12 from the Bibai cohort. In 2002, five trees were added to the Iwamizawa-2 cohort sample to replace five trees from the original sample that died during the winter (total sample, 15 trees), and six trees were added to the Iwamizawa-1 cohort sample (total sample, 21 trees). The Nakagawa and Bibai trees were felled, and the inflorescences on each first-order branch were counted. Binoculars were used to count the inflorescences in the two Iwamizawa cohorts. The Nakagawa and Bibai trees were used to analyze floral sex allocation at the first-order branch level.

Because two or three male inflorescences develop together at the tip of long shoots in *B. platyphylla* var. *japonica*, a set of long shoot male inflorescences was counted as a “male set.” Gender expression was described by the proportion of males (male ratio), which was calculated as $x/(x+y)$, where y and x are the number of female inflorescences and male sets, respectively. Although Fox (1993) and Klinkhamer et al. (1997) recommend using x/y to describe the proportion of males, $x/(x+y)$ is a better expression because x/y becomes infinite when $y=0$, as does y/x when $x=0$. Wind-pollinated monoecious species often have individuals with only female or male flowers (Abul-Fatih et al., 1979; Smith, 1981; Gleason, 1982; Linhart and Mitton, 1985; McKone and Tonkyn, 1986; Jordano, 1991; Arista and Talavera, 1997; Goubitz, 2001; Kimura et al., 2003); thus, $x/(x+y)$ is more appropriate than x/y . Male ratio was expressed as R at the individual level and R_B at the first-order branch level.

Data analyses—No statistical analysis can be used to simultaneously evaluate data on the female, male, and constant male phase. However, the relation between the number of male sets and reproductive investment (= total number of inflorescences) can be approximately fitted to a saturated curve. Then, the relationship can be fitted to a Gompertz curve as

$$N_M = b_0 \exp[-b_1 \exp(-b_2 N_T)], \quad (1)$$

where b_i ($i=0, 1, 2$), N_T , and N_M are regression coefficients, the total number of inflorescences, and the number of male sets on the individual, respectively. Reproductive investment at the individual and first-order branch levels was expressed as the total number of inflorescences at the individual and first-order branch levels, respectively. The relationship between the number of female

inflorescences and reproductive investment can be approximately fitted to a linear curve in the range where the Gompertz curve approaches an asymptote (i.e., >90% of the asymptote).

Male ratio at the branch level (R_B) may be strongly affected by that at the individual level (R) because if $R=0$ or 1 for an individual, then $R_B=0$ or 1 for all branches on that individual. Because the relation between male ratio and reproductive resources is reciprocal in the range of the constant male phase (Masaka and Takada, 2006), the effect of R on R_B is evaluated as

$$R_B = b_0 + b_1 \ln N_i + b_2 R, \quad (2)$$

where b_i ($i=0, 1, 2$) and N_i are regression coefficients and reproductive investment at first-order branch level, respectively. This equation indicates that the deviation in the $R_B - \ln N_i$ relationship can largely be explained by R . Branches with only female flowers ($R_B=0$) were excluded from the analysis because of the statistical analysis difficulty mentioned earlier. However, this did not present a problem because of the small sample size (see Masaka and Takada, 2006). Statistically significant variables were selected with a forward stepwise regression.

RESULTS

Floral sex allocation at the individual level—Each cohort expressed various genders. The relation between male ratio (R) and the total number of inflorescences is shown for all four cohorts (Fig. 2). In the Iwamizawa-1 and Iwamizawa-2 cohorts, several individuals had only female inflorescences ($R=0$; $N=3$ in 2001, $N=2$ in 2002) or male sets ($R=1$; $N=0$ in 2001, $N=8$ in 2002). In the Bibai cohort, one individual produced only male sets. The total number of inflorescences on these individuals tended to be small. In the Nakagawa cohort, no individuals had only female inflorescences or male sets. The largest R value for any individual within the cohort was 0.978, with a total of 20 female and 871 male flowers. In all four cohorts, few individuals with high reproductive investment had a large male ratio. For all four cohorts, the number of male sets tended to reach an upper limit when reproductive investment was large, whereas the number of female inflorescences increased monotonically with increasing reproductive investment (Fig. 3).

Floral sex allocation at the first-order branch level—The relationships between male ratio (R_B) and the total number of inflorescences at the first-order branch level in the Nakagawa and Bibai cohorts are shown in Fig. 4. Gender expression at the first-order branch level was similar to that at the individual level. Thus, several branches had only female inflorescences (Nakagawa, $N=3$; Bibai, $N=51$) or male sets (Nakagawa, $N=167$; Bibai, $N=49$). The reproductive resources in these branches tended to be few. Few branches with large reproductive investment had a large male ratio.

In both the Nakagawa and Bibai cohorts, the number of male sets tended to reach an upper limit when reproductive investment was large (Fig. 5). Although female production tended to depart slightly from the graphical model shown in Fig. 1, the number of female inflorescences increased monotonically with increasing reproductive investment in both the Nakagawa and Bibai cohorts (Fig. 5).

Relationship between individual and branch level floral sex allocation—A statistically significant relationship between floral sex allocation at the individual and branch levels was demonstrated by the following stepwise regression analysis: Nakagawa cohort

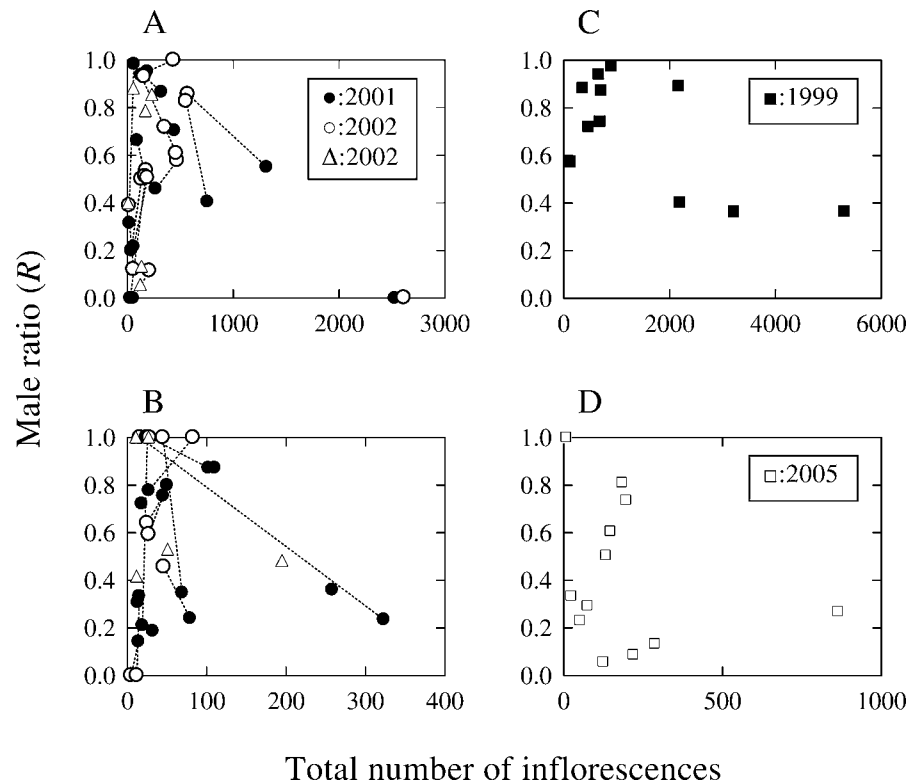


Fig. 2. Floral sex allocation at the individual level in *Betula platyphylla* var. *japonica*. (A) Iwamizawa-1 cohort. (B) Iwamizawa-2 cohort. (C) Nakagawa cohort. (D) Bibai cohort. When a closed circle (●) is connected to an open circle (○) by a dotted line in A or B, the data represent the same individual. Δ indicates R of individual added to the sample trees in 2002.

$$R_B = 0.575 - 0.073 \ln N_t + 0.641R$$

(adjusted $R^2 = 0.654$, $N = 302$, $P < 0.001$)

(3)

Bibai cohort

$$R_B = 0.501 - 0.117 \ln N_t + 0.715R$$

(adjusted $R^2 = 0.644$, $N = 127$, $N < 0.001$)

(4)

No variables were eliminated in the procedure. The $\ln N_t$ regression coefficient was significantly smaller in the Bibai cohort than in the Nakagawa cohort, although the intercept and R regression coefficient of the two cohorts were similar. In both cases, R_B decreased reciprocally with the increase in the total number of inflorescences (N_t), and R_B at a given N_t increased as R increased (Fig. 6). Thus, the first-order branch of individuals with large R values tended to have greater R_B values than did branches from individuals with small R values.

DISCUSSION

Floral sex allocation in *B. platyphylla* var. *japonica* at the individual level varied with resource availability as predicted by the theoretical model of Masaka and Takada (2006) (Fig. 1). Thus, individuals with few reproductive resources produced

female or male inflorescences, and individuals with abundant reproductive resources usually produced many more females than males (Fig. 2). Other hypotheses, such as height-advantage and size-dependent fecundity, have been invoked widely in studies of floral sex allocation in wind-pollinated monoecious species (Klinkhamer and de Jong, 1997; Sakai and Sakai, 2003). Both of these hypotheses posit an adaptive advantage of larger individuals producing more male flowers. Thus, a positive relation between individual size, especially stem height, and number of male inflorescences should be observed in floral sex allocation. However, these hypotheses do not explain the patterns observed in *B. platyphylla* var. *japonica* in the present study. Furthermore, Masaka (2006) also reported that there was no relation between individual size (height, trunk diameter, or volume) and maleness. Maleness should also increase with individual growth under the size-related hypotheses, but the male ratio decreased greatly for two consecutive years in some individuals (Fig. 2A, B). In contrast, the patterns predicted by Masaka and Takada (2006) have been observed in several other tree species (reviewed in Masaka and Takada, 2006), suggesting that the assumptions of the floral sex ratio strategy of their model are likely to be more appropriate in wind-pollinated monoecious species than the assumptions of size-related hypotheses.

The pattern of floral sex allocation was similar at the level of the first-order branch and at the level of the individual (Figs. 4 and 5); branches with few reproductive resources produced only female or male inflorescences, and branches with abundant reproductive resources produced a relatively constant

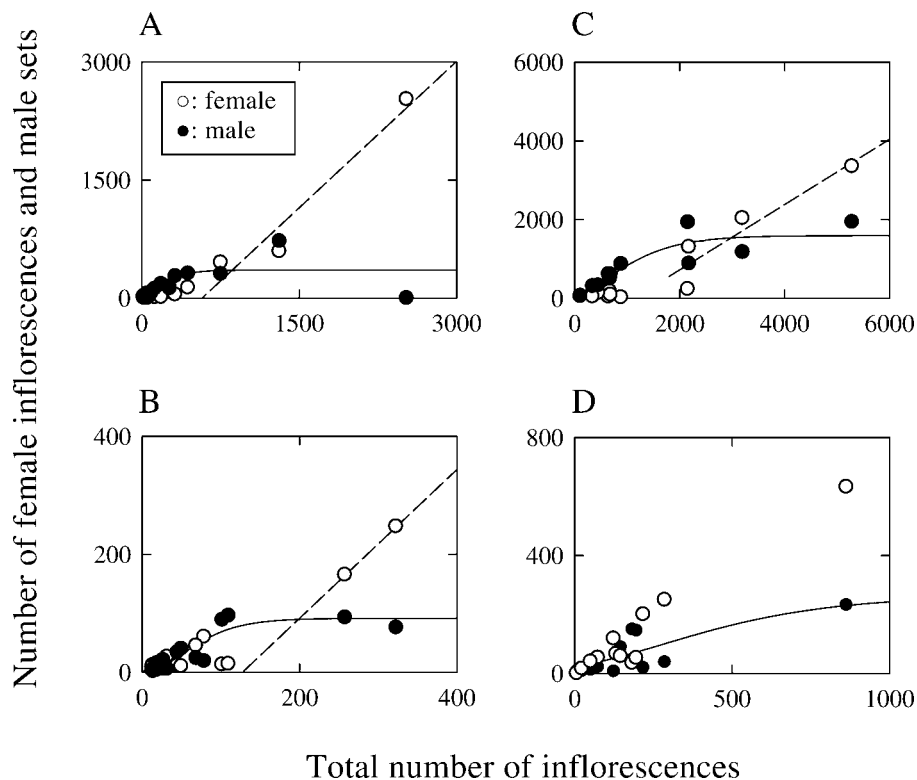


Fig. 3. Number of female inflorescences (N_F) and male sets (N_M) with respect to reproductive investment (N_T = total no. of inflorescences) at the individual level. (A) Iwamizawa-1 cohort. (B) Iwamizawa-2 cohort. (C) Nakagawa cohort. (D) Bibai cohort. Solid line is regression curve between N_M and N_T (Gompertz curve): $N_M = 346.403 \exp(-3.609 \exp[-0.007N_T])$, $R^2 = 0.488$, $P < 0.01$ for Iwamizawa-1 cohort; $N_M = 90.429 \exp(-4.464 \exp[-0.027N_T])$, $R^2 = 0.810$, $P < 0.01$ for Iwamizawa-2 cohort; $N_M = 1596.016 \exp(-2.721 \exp[-0.001N_T])$, $R^2 = 0.779$, $P < 0.01$ for Nakagawa cohort; $N_M = 264.670 \exp(-2.539 \exp[-0.003N_T])$, $R^2 = 0.600$, $P < 0.01$ for Bibai cohort. Dashed line indicates the relationship between N_F and N_T . Spearman's rank correlation coefficient was $r_s = 1.000$ ($P < 0.01$) for both the Iwamizawa-1 and the Nakagawa cohorts. The relationship between N_F and N_T is fitted to a linear curve in the range where the Gompertz curve approaches an asymptote (i.e., $>90\%$ of the asymptote). No statistical values could be shown for Iwamizawa-2 and Bibai cohorts, because sample size was too small.

number of male inflorescences and an increased number of female inflorescences as total reproductive effort increased. Thus, each first-order branch of *B. platyphylla* var. *japonica* behaved like an individual, but the floral sex allocation of a given branch did not necessarily represent that of the individual

because different branches had different reproductive resources. The behavior of the branch reflects individual modular characteristics. If the branch produced flowers autonomously, i.e., in response to the resource budget within the branch itself, the individual clearly could not achieve an optimal floral sex

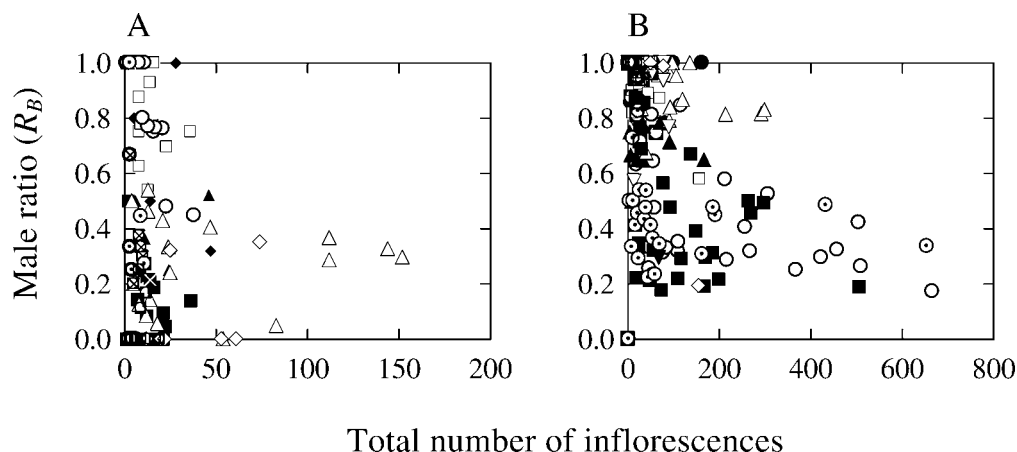


Fig. 4. Floral sex allocation at the first-order branch level in *Betula platyphylla* var. *japonica*. (A) Bibai cohort. (B) Nakagawa cohort. The same symbol indicates the branches on the same individual in each cohort.

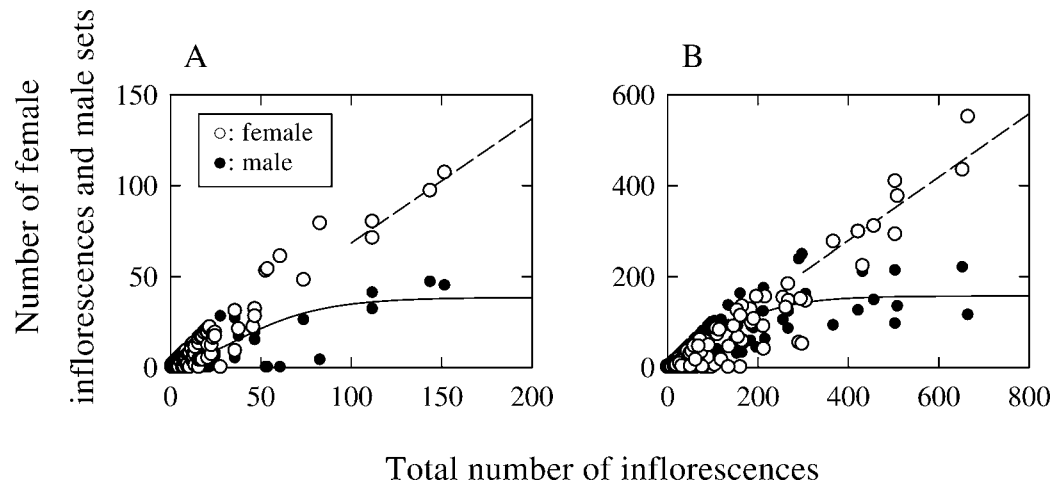


Fig. 5. Number of female inflorescences (N_f) and male sets (N_m) with respect to reproductive investment (N_t = total no. of inflorescences) at the branch level. (A) Bibai cohort. (B) Nakagawa cohort. Solid line is the regression curve between N_m and N_t : $N_m = 38.076 \exp(-3.604 \exp[-0.036N_t])$, $R^2 = 0.724$, $P < 0.01$ for Bibai cohort. $N_m = 155.675 \exp(-2.881 \exp[-0.011N_t])$, $R^2 = 0.775$, $P < 0.01$ for Nakagawa cohort. Dashed line indicates the relationship between N_f and N_t . Spearman's rank correlation coefficient was $r_s = 0.881$ ($P < 0.001$) for Nakagawa cohort and $r_s = 0.948$ ($P = 0.051$) for Bibai cohort. The relationship between N_f and N_t is fitted to a linear curve in the range where the Gompertz curve approaches an asymptote (i.e., $>90\%$ of the asymptote).

ratio. In fact, branch autonomy has recently been criticized in studies of branch demography (e.g., Novoplansky et al., 1989; Takenaka, 2000; Sprugel, 2002; Umeki and Seino, 2003; Umeki et al., 2006). In birch, male inflorescences are induced in early May, before bud burst (Macdonald et al., 1984), indicating that male inflorescence induction is controlled at the individual rather than the branch level. Generally, resources for leaf flush in deciduous trees are stored mainly in the root and not in the branches and stem during winter (Larcher, 1994). Thus, a birch branch cannot control flower induction in spring, even though the branch provides much of the photosynthate necessary for fruit maturation on the branch during the growing season (Watson and Casper, 1984; Tuomi et al., 1988; Hasegawa et al., 2003). In addition, the branch autonomy concept cannot explain the floral sex ratio at the branch level (Fig. 6). If the floral sex ratio at the branch level were

controlled by the branch itself, the floral sex ratio at the branch level should be similar to the floral sex ratio at the individual level. However, the branches of individuals with large R values always tended to have greater R_B values than did branches of individuals with small R values. The relationship between the floral sex ratio at the branch and individual levels indicates that branch behavior is controlled at the level of the individual.

The relation between the floral sex ratio at the individual and branch level was quite different in the Nakagawa and Bibai cohorts (Fig. 6). In the older Nakagawa cohort, most branches produced only male inflorescences (167 of 305 reproductive branches; 54.8%), and only a few produced only female inflorescences (3 of 305 reproductive branches; 0.98%). In the younger Bibai cohort, the number of branches that produced only female inflorescences (51 of 178 reproductive branches; 30.5%) or only male inflorescences (49 of 178 reproductive

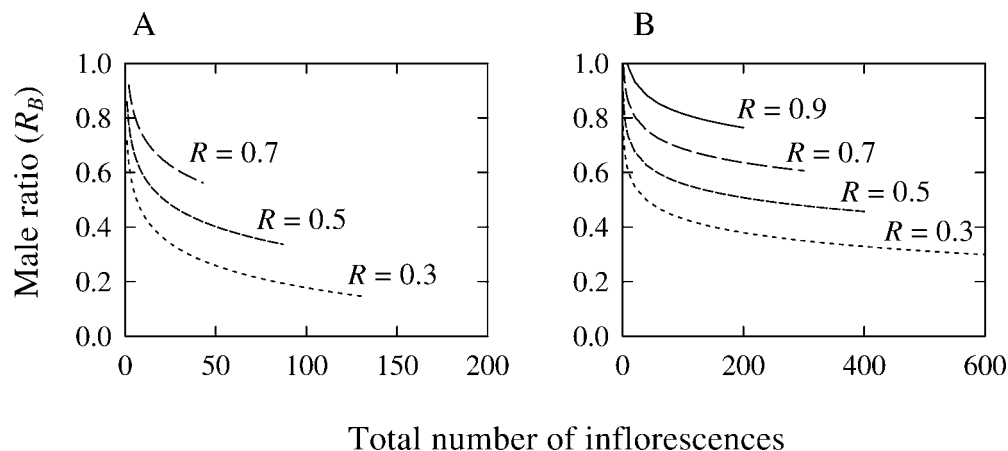


Fig. 6. Simulation of the relationship of the reproductive investment (N_t) to male ratio (R_B) at the first-order branch level for different male ratios at the individual level (R). The curves were drawn using Eqs. 3 and 4. (A) Bibai cohort. Curves for $R = 0.3, 0.5$, and 0.7 . (B) Nakagawa cohort. Curves for $R = 0.3, 0.5, 0.7$, and 0.9 .

branches; 29.3%) was similar. This difference in the occurrence of unisexual reproductive branches suggests that younger birches tend to have fewer male branches and more female branches than older birches. Moreover, the regression coefficient ($\ln N_i$) was smaller in the Bibai cohort than in the Nakagawa cohort (Eqs. 3 and 4), suggesting that the floral sex ratio of a Bibai cohort branch (R_B) is always lower than that of a Nakagawa cohort branch at a given N_i and R .

One possible explanation for the difference between the cohorts is that birch is a typical pioneer species (Kikuzawa, 1983; Koike, 1988), and a young tree must invest in vegetative growth rather than in reproduction. In birch, long shoots contribute to crown development (Maillette, 1982; Fujimoto and Miyakawa, 1991), and male organs are produced on long shoots (Caesar and Macdonald, 1984; Macdonald et al., 1984). However, the production of male organs prevents long shoots from further elongation because the organs develop at the tip. Consequently, the production of abundant male inflorescences would be maladaptive for young birch. Hasegawa and Takeda (2001) reported that young *Alnus hirsuta* var. *sibirica* (Betulaceae), in which long shoots contribute to crown development, also tend not to produce flowers. On the other hand, many small, first-order branches form in the crown of young birch (data not shown), but these branches soon die as the tree grows taller (Sumida and Komiyama, 1997). Because short shoots gain photosynthate with minimal investment in vegetative structure, the production of short rather than long shoots should be adaptive for shaded branches (Maillette, 1982). Ishihara and Kikuzawa (2004) reported on the plasticity of such shoot bifurcation in birch. Because birch female organs are produced on short shoots (Caesar and Macdonald, 1983; Macdonald and Mothersill, 1984), small, shaded branches would tend to produce only female inflorescences. Thus, younger birches should have fewer male and more female branches than older birches. These birch-specific shoot bifurcation and reproduction systems would also affect floral sex allocation among branches. Because I investigated only two cohorts, further study is necessary to verify this explanation.

In conclusion, individual gender expression in *B. platyphylla* var. *japonica* agrees with the floral sex allocation strategy of wind-pollinated, monoecious species proposed by Masaka and Takada (2006). Within the birch crown, the floral sex ratio of each first-order branch was analogous to that of the individual, but the gender expression of a given branch did not represent the individual. The relationship between floral sex ratio at the individual and branch level suggests that the individual strongly integrates branch behavior. Thus, the floral sex allocation of *B. platyphylla* var. *japonica* cannot be explained using the concept of branch autonomy. However, Umeki and Kikuzawa (2000) observed autonomous branch behavior in birch growth and mortality. Understanding the extent to which modules are physiologically integrated in an individual plant is important for understanding not only the architectural development (Watson and Casper, 1984; Sprugel et al., 1991) but also the reproductive ecology of plants. Further research should reveal patterns of individual integration and branch behavior in different species and life forms.

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