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Size-dependent gender modification in a hermaphroditic perennial herb

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The size-advantage model predicts that hermaphroditic organisms adjust sex allocation depending on their resource status. We investigated the relationship between size and sex allocation in the co-sexual perennial herbs *Trillium erectum* and *Trillium grandiflorum* at two sites in southern Ontario, Canada, by measuring pollen and ovule production and biomass allocation at flowering and fruiting. In both species, there was a strong relationship between size and gender; larger plants allocated proportionately more biomass to female reproduction and produced fewer pollen grains relative to ovules than smaller plants. Variation in gender was better explained by size than age, although age and size were correlated. While the relationship between size and gender was similar between species, *T. erectum* allocated proportionately more to female reproduction than *T. grandiflorum*, independent of size. In the absence of pollen limitation, there was no evidence of secondary adjustment of gender at fruiting. The results are discussed in the context of models predicting size-dependent gender modification in animal-pollinated plants. Evidence about the pollination and seed dispersal biology of *Trillium* spp. suggests that the relative effects of local mate and resource competition may be important in driving size-dependent sex allocation in these species.

Keywords: plant gender; simultaneous hermaphroditism; size-dependent sex allocation; local mate and resource competition; *Trillium*

1. INTRODUCTION

Studies of sex allocation in hermaphrodites have attempted to quantify and explain the patterns of variation between organisms in their relative investment in female and male reproductive components (Charnov 1982). While much of this research has focused on between-species comparisons, extensive within-population variation in sex allocation has also been observed (Ghiselin 1969; Warner 1975; Freeman *et al.* 1980; Policansky 1982; Lloyd & Bawa 1984; Klinkhamer *et al.* 1997). A central explanation for this has been that, within a population, sex allocation might depend on an organism's condition or resource status. If female and male components of fitness are differentially affected by changes in size or condition, then organisms are expected to modify their sex allocation according to their size (Ghiselin 1969; Charnov 1982; Lloyd & Bawa 1984; Iwasa 1991).

The size-dependence hypothesis has often been applied to the extreme case of sequential hermaphroditism, where male and female reproduction comprise discrete ontogenetic phases in the life cycle (e.g. Warner 1975; Policansky 1981; Charnov 1982; Lovett Doust & Cavers 1982; Iwasa 1991). However, continuous modification of sex allocation is also possible in simultaneous hermaphrodites (Lloyd & Bawa 1984; Petersen & Fischer 1996). In this case, all organisms in a population may be hermaphroditic, but the relative investment in male and female function changes with resource status. Evidence of such behaviour has been documented in both hermaphroditic animals (e.g. Petersen & Fischer 1996; St Mary 1997) and plants (reviewed in Lloyd & Bawa 1984; Klinkhamer *et al.* 1997).

Various sex-differential effects have been proposed as selective mechanisms driving gender adjustments in flowering plants. Hypotheses have incorporated a role for local mate competition (LMC) and local resource competition (LRC) (Lloyd & Bawa 1984), pollination syndrome (Burd & Allen 1988; Bickel & Freeman 1993), geitonogamous pollination (Klinkhamer & de Jong 1997) and sex-differential resource costs (Lloyd & Bawa 1984; Bickel & Freeman 1993; Day & Aarssen 1997) in determining the strength and direction of size-dependent sex allocation. These models are developed from the size-advantage model (Ghiselin 1969), which implies that size-dependent sex allocation is adaptive if fitness-gain curves differ between female and male reproductive components. The dynamics of resource allocation are also likely to depend on life history and growth form. Plants which are highly branched and modular, for example, are not likely to have uniform resource conditions, precluding an integrated response to resource levels or environmental effects (Watson & Casper 1984; Harper 1985). In addition, it has been hypothesized that co-sexual species with hermaphrodite flowers might be more constrained in their sex allocation than monoecious populations, since, in the latter, gender may be modified via the relative production of female versus male flowers (Fox 1993).

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Finally, for perennial organisms, trade-offs between survival and reproduction might also be important in driving dynamic allocation strategies (Iwasa 1991).

While most flowering plants are simultaneous hermaphrodites, the majority of studies have examined taxa with unisexual flowers, presumably because of the ease with which gender can be assessed. In species with hermaphrodite flowers, relative investment into female and male reproduction has often been estimated indirectly, using such measures as the ratios of fruit to flower production (reviewed in Klinkhamer *et al.* 1997). To our knowledge, no study has yet compared size-dependent pollen and ovule production with investment in male and female components of reproduction. Here we investigate the effects of size and age on gender and reproduction in the hermaphrodite-flowered herbaceous perennials *Trillium erectum* and *Trillium grandiflorum* (Trilliaceae) by measuring both relative gamete production and patterns of biomass allocation. Several aspects of the reproductive ecology of *Trillium* spp., as discussed below, suggested that they may be particularly likely to exhibit size-dependent gender adjustment.

Lloyd & Bawa (1984) emphasized the importance of local mate and resource competition in determining size-dependent effects on gender. They predicted that larger plants should favour the gender function subject to the most intense competition for reproductive success among unrelated individuals. For example, if the number of pollen parents competing for ovules is low, then increased male investment may not lead to a corresponding increase in mating success, since increased pollen production leads to more competition for ovules by pollen grains from the same parent. Recent studies of pollination and mating in *T. erectum* and *T. grandiflorum* indicating low pollinator visitation rates, frequent pollinator limitation and high levels of correlated paternity (Broyles *et al.* 1997; Smith 1998; Kalisz *et al.* 1999; T. M. Laverty, unpublished data; S. I. Wright and S. C. H. Barrett, unpublished data) suggested that between-plant competition for ovules may be low and, hence, male fitness may rapidly saturate with increased investment in these species. Provided that there is not a similar saturation of the female gain curve due to competition among related seedlings (see § 4), these effects are likely to favour increased female allocation with size.

2. METHODS

(a) *Natural history of* Trillium *spp.*

Trillium erectum and *T. grandiflorum* are long-lived herbaceous perennials which are common as understorey species in woodlands of eastern North America (Case & Case 1997). When reproductive, they produce a single stem with a terminal hermaphroditic flower subtended by a single leaf each year. This simple determinate growth form indicates that resource conditions each season are probably uniform across the whole plant; evidence for trade-offs between reproduction and storage support this notion (Lubbers & Lechowicz 1989). *Trillium* plants exhibit striking variation in both plant and flower size. Age can be estimated by counting the number of annual rhizome growth rings (see Hanzawa & Kalisz 1993). While the two species have similar growth forms and life history, they differ in mode of pollination and population structure; *T. erectum* is fly pollinated and occurs at lower densities, while *T. grandiflorum* is bee pollinated and frequently occurs in high-density patches. While the mating systems of both species have long been contentious (see Broyles *et al.* 1997), recent compatibility and marker gene studies indicate that *T. grandiflorum* is self-incompatible and outcrossing (Broyles *et al.* 1997; Smith 1998; Kalisz *et al.* 1999) whereas *T. erectum* possesses a mixed-mating system (Broyles *et al.* 1997).

(b) *Flowering-stage allocation*

(i) *Sampling and data collection*

We sampled reproductive plants from both species at two sites in southern Ontario, Canada, separated by *ca.* 250 km: Joker's Hill (York, RM) and Kaladar (Lennox and Addington Co.). In early May 1997, we sampled plants across the full range of sizes at anthesis and separated them into their component parts: rhizomes, stems, leaves, petals, anthers, sepals and pistils. We estimated the age of each plant by counting the number of growth rings on the rhizome. Older plants were more likely to have the terminal end of the rhizome rotted away, so estimates should be considered a measure of minimum age (Hanzawa & Kalisz 1993). Pistils and three out of the six anthers per plant were preserved in 70% ethanol for ovule and pollen counts. We collected anthers at early dehiscence to prevent any pollen loss.

(ii) *Measurements of gamete production and biomass allocation*

We counted ovules under a dissecting microscope and used a Particle Data Elzone 282PC particle counter (Particle Data Inc., Elmhurst, IL, USA) to estimate pollen production per flower (see Harder (1990) for method). To determine whether pollen production per plant could be accurately estimated using a single anther, we compared the between-plant variation in pollen production to the within-plant variation for a subset of plants using ANOVA. The results indicated relatively low within-plant variation (plant effect, $p < 0.001$ for each population; minimum $r^2 = 0.83$) and total pollen production was subsequently estimated using one anther per plant. After dissection and ovule counts, the gynoecium and other plant tissues, including the remaining three anthers, were oven dried at 70 °C to constant weight and weighed.

(c) *Fruiting-stage allocation*

To distinguish between the effects of pollen limitation and resource status on reproductive investment at fruiting, we cross-pollinated individuals of both species by hand at the Joker's Hill site. We also selected nearby individuals of similar size to serve as open-pollinated controls. Both open- and hand-pollinated plants were collected in late July, when fruits were ripe. Plants were harvested, oven dried and weighed. Seed production and numbers of unfertilized ovules were also counted. Evidence for pollen limitation was obtained by comparing the seed:ovule ratio (S:O) between hand- and open-pollinated plants.

(d) *Statistical analysis*

(i) *Relationships between size, age and reproduction*

The measures of reproductive investment included those at flowering (pollen and ovule production, biomass of androecium and gynoecium and total flower biomass) and fruiting (fruit production, seed number and S:O ratio). We used an allometric model (see Klinkhamer & de Jong 1997) to measure relationships between size (x) and reproductive components (y): $y = ax^b$. Least-squares regression of the natural log of the various reproductive components on the natural log of size was performed.

Table 1. *Allometric analysis of reproduction in* T. erectum *and* T. grandiflorum *at two southern Ontario sites*

(Values are from least-squares regression of the natural log of each flowering-stage reproductive component on size. $^{***}p < 0.001$, $^{**}p < 0.01$, n.s., not significant.)

species	site	reproductive component	*n*	r^2	*b* (s.e.)
T. erectum	Joker's Hill	gynoecium	51	0.77^{***}	1.08 (0.08)
		ovule number	50	0.65^{***}	0.99 (0.11)
		androecium	51	0.63^{***}	0.61 (0.07)
		pollen number	47	0.50^{***}	0.48 (0.07)
		flower biomass	51	0.79^{***}	0.74 (0.05)
	Kaladar	gynoecium	8	0.96^{***}	1.29 (0.11)
		ovule number	8	0.77^{**}	1.42 (0.32)
		androecium	8	0.75^{**}	0.55 (0.13)
		pollen number	8	$0.27^{\text{n.s.}}$	0.52 (0.35)
		flower biomass	8	0.93^{***}	0.88 (0.10)
T. grandiflorum	Joker's Hill	gynoecium	51	0.84^{***}	1.30 (0.08)
		ovule number	51	0.60^{***}	0.74 (0.09)
		androecium	51	0.74^{***}	0.59 (0.05)
		pollen number	51	0.27^{***}	0.40 (0.09)
		flower biomass	51	0.87^{***}	0.83 (0.05)
	Kaladar	gynoecium	32	0.88^{***}	1.20 (0.08)
		ovule number	32	0.83^{***}	0.99 (0.08)
		androecium	32	0.79^{***}	0.79 (0.67)
		pollen number	28	0.47^{***}	0.52 (0.11)
		flower biomass	32	0.90^{***}	0.88 (0.10)

The regression coefficient estimates *b*, the exponent for the untransformed relationship and, thus, measures the rate of exponential increase of investment with size. For female and male reproductive components at flowering, we used total above-ground biomass as the measure of plant size. To avoid effects of autocorrelation, vegetative biomass was used to measure size for estimating relationships with total flower and fruit biomass, since flower and fruit biomass constituted a significant component of the above-ground biomass.

We used two measures of relative reproductive investment: proportional female allocation (pistil biomass:pistil + anther) and the pollen:ovule ratio (P:O). Least-squares regression analysis was performed to detect relationships between size and sex allocation, and size and P:O ratio. Stepwise regression was also performed to determine the relative importance of age and size effects on gender. ANCOVA was used to compare sex allocation between species, using size as the covariate. Site and species–site interaction were included in the model. All tests used the JMP statistical package (v. 3.0.2, SAS Institute, 1994).

3. RESULTS

(a) *Flowering-stage biomass allocation*

In all four populations, investment in both female and male reproductive components, as well as total floral biomass, increased with plant size (table 1). Biomass allocation into the gynoecium increased at a faster rate than the androecium and, hence, there was a strong relationship between proportional female allocation and plant size (figure 1). Larger plants were more female biased in their sex allocation in all four populations. The same relationship was observed when attractive structures are included as male components (in all populations, $b > 0$; $p < 0.001$). *Trillium erectum* had a more female-biased sex allocation, independent of the effects of size (species effect, $F = 264.25$; $p < 0.001$, non-significant interaction with size removed from model). Proportional female allocation also increased significantly with age ($p < 0.05$, in three out of the four populations), but age explained much less of the variation in sex allocation than size (range of r^2 0.11–0.24). Comparisons of complete and reduced models indicated that the effects of age and size were correlated and age did not significantly affect allocation independent of the size effect ($p = 0.35$, comparing reduced to complete model). Total floral biomass also increased with size, although relative to total above-ground biomass showed a proportional decrease with increased size ($b < 1$, table 1).

(b) *Gamete production*

The relationship between plant size and gamete production revealed a similar pattern to biomass investment. Both pollen and ovule production increased with plant size, but ovule production increased more rapidly. Allometric relationships were similar for gamete production and the corresponding biomass investment, although size explained somewhat less of the variation in gamete production (table 1). In all four populations, there was a significant negative relationship between the P:O ratio and size (figure 2). ANCOVA revealed a significant species effect on the P:O ratio; *T. erectum* has a lower P:O ratio, independent of the effects of size (main effect of species, $F = 20.32$, $p < 0.0001$).

(c) *Fruiting-stage allocation*

The S:O ratio did not differ significantly between hand- and open-pollinated treatments for *T. erectum* (Wilcoxon rank-sum test, $p > 0.05$). In contrast, the S:O ratio was significantly greater in hand-pollinated plants for *T. grandiflorum* (Wilcoxon rank-sum test, $z = 3.27$; $p < 0.01$). There was a strong relationship between size

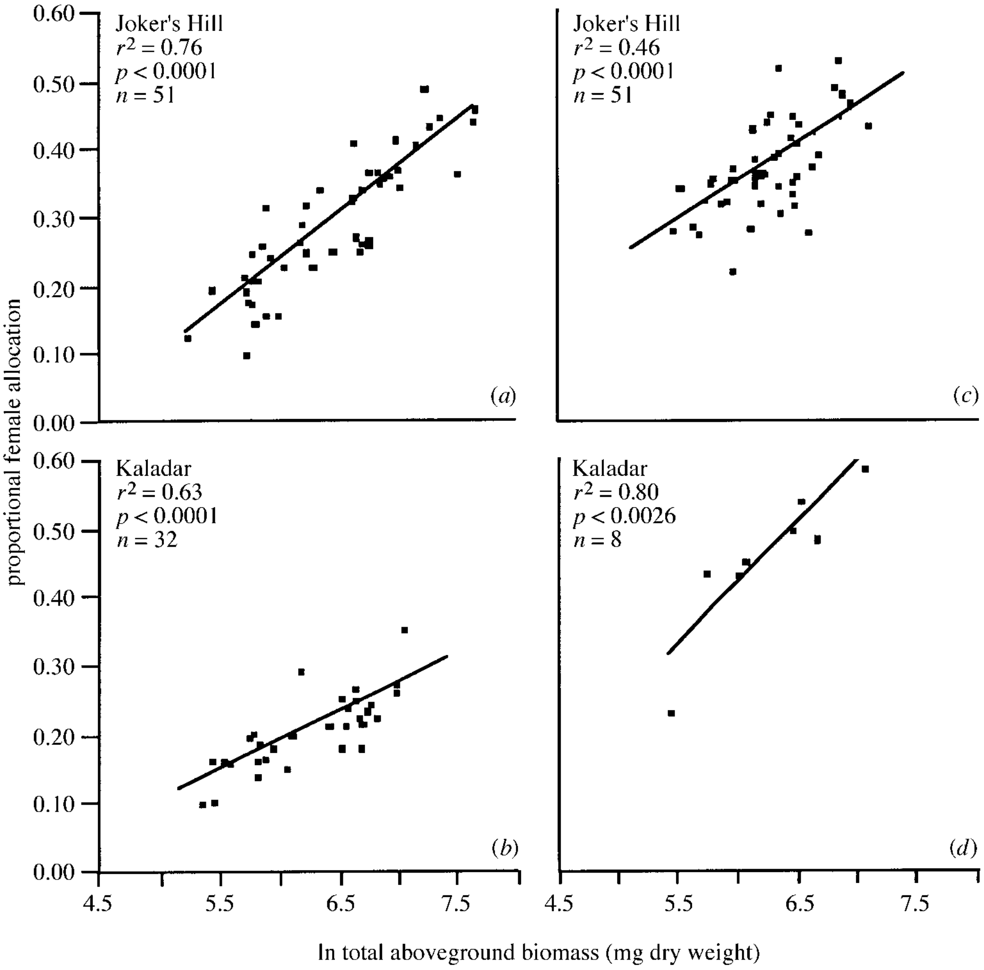

Figure 1. Relationships between sex allocation (pistil biomass:pistil biomass+anther biomass) and size (natural log of total above-ground biomass) in *T. grandiflorum* (*a*,*b*) and *T. erectum* (*c*,*d*) from two sites in southern Ontario, Canada.

and fruit biomass and size and seed production in hand-pollinated plants in both species (table 2). In *T. grandiflorum*, there was no significant relationship between vegetative and fruit biomass or between vegetative biomass and seed set in open-pollinated plants (table 2). There was no effect of plant size on the S:O ratio in either hand- or open-pollinated treatments for both species (all least-squares regressions, $p > 0.05$).

4. DISCUSSION

Our results provide strong evidence for size-dependent sex allocation in a co-sexual plant species. Within *Trillium* populations, larger plants allocated more resources to reproduction than smaller plants and investment into female reproduction increased more rapidly with size relative to male investment, both in terms of biomass and gamete production. Our results indicate that plants respond directly to the effects of resource status, since there was no evidence of an effect of age independent of size. This result is in accordance with an earlier study of *T. grandiflorum* demonstrating that onset of reproduction was better explained by size than age (Hanzawa & Kalisz 1993). Figure 3 shows a diagrammatic summary of size-dependent effects on sex allocation and reproductive effort in *Trillium*, based on the observed allometric relationships.

Lloyd & Bawa (1984) suggested that gender modification might occur at various stages, including floral development and fruit production. However, while *Trillium* populations show evidence of flowering-stage gender modification, our study provided no evidence to suggest a secondary adjustment at fruiting. In the absence of pollen limitation, the relationship between size and female investment was very similar at flowering and fruiting. The similarity in allometric relationships for female reproductive components at both stages suggests that allocation is set at flowering and, given sufficient pollination, this translates into a corresponding increase in resource investment at fruiting. When plants were pollen limited, as in *T. grandiflorum* at Joker's Hill, the relationship between size and seed production was not significant, presumably because of the greater variation in pollination success in open-pollinated plants. Thus, floral sex allocation may set the upper limits for offspring production, but ecological factors such as pollinator availability strongly influence effective reproductive investment and success. In perennial plants with pre-formed flowers such as *Trillium*, secondary resource adjustments during fruiting may be constrained and allocation 'decisions'

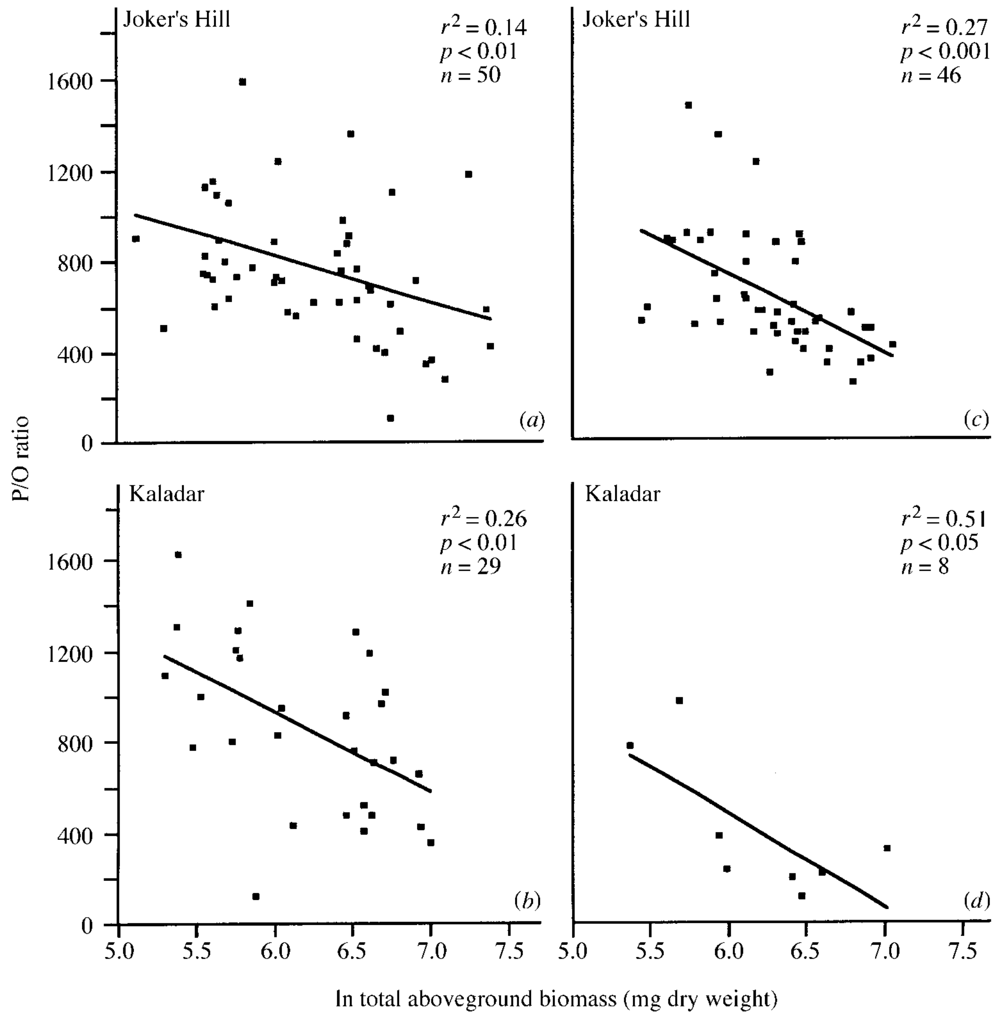

Figure 2. Relationships between pollen:ovule ratio (P:O) and size in *T. grandiflorum* (*a*,*b*) and *T. erectum* (*c*,*d*) from two sites in southern Ontario, Canada.

Table 2. *Least-squares regression of the natural log of each fruiting-stage reproductive component* (*fruit biomass and seed number*) *on the natural log of vegetative biomass for each species, in both open-pollinated and hand-pollinated treatments*

(All plants were sampled from Joker's Hill. $^{***}p < 0.001$, $^{**}p < 0.01$, n.s., not significant.)

species	treatment	reproductive component	*n*	r^2	*b* (s.e.)
T. erectum	control	fruit biomass	25	0.66^{***}	1.21 (0.18)
		seed number	24	0.75^{***}	1.09 (0.13)
	hand-pollinated	fruit biomass	26	0.44^{***}	0.89 (0.21)
		seed number	31	0.40^{***}	0.85 (0.19)
T. grandiflorum	control	fruit biomass	23	$0.13^{\text{n.s.}}$	0.88 (0.51)
		seed number	31	$0.13^{\text{n.s.}}$	1.05 (0.49)
	hand-pollinated	fruit biomass	23	0.51^{***}	1.10 (0.25)
		seed number	21	0.40^{**}	1.14 (0.30)

limited to the flowering stage. In *T. grandiflorum*, for example, defoliation during peak flowering had no effect on fruit production but reduced biomass investment in rhizomes (Lubbers & Lechowicz 1989).

(a) *Size-dependent sex allocation and reproductive effort: hypotheses*

Several selective mechanisms, not mutually exclusive, may be important in driving size-dependent gender modification in *Trillium* spp. We next consider the potential importance of local mate and resource competition, as well as briefly addressing the relevance of several additional hypotheses.

(i) *Effects of pollen and seed dispersal: LMC versus LRC*

Our results are consistent with several features of the predictions of Lloyd & Bawa's (1984) local mate and resource competition model for size-dependent sex allocation; all plants in the population are simultaneous hermaphrodites and there is a continuous, resource-based

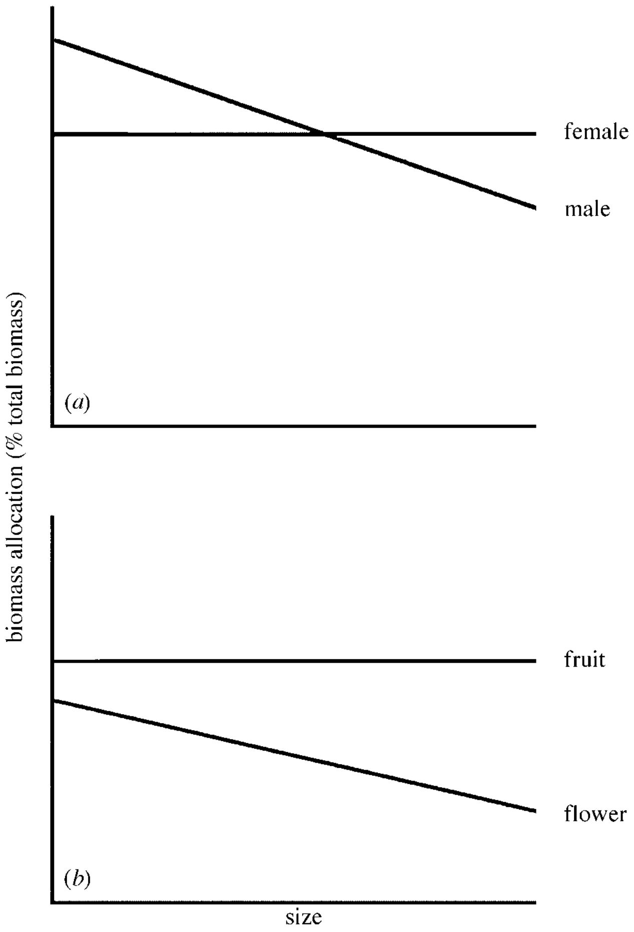

Figure 3. Diagrammatic representation of size-dependent changes in reproductive allocation as a percent of total biomass in *T. erectum* and *T. grandiflorum* based on the regression coefficients, *b*, of log–log relations with total size. For male and total floral biomass there was a proportional decrease in investment with size (both $p < 0.05$), while for female investment proportional allocation did not change with size. See tables 1 and 2 for values of *b*.

adjustment of gender. As discussed above, the reproductive biology of *Trillium* spp. indicates that the effects of between-plant competition may be important in driving size-dependent increases in female allocation; low pollinator visitation rates and high levels of correlated mating may reduce the fitness benefits of increasing male investment. Thus, an important selective pressure driving gender adjustment in these species may result from reduced competition for ovules between unrelated individuals. A key assumption of this hypothesis is that there is no similar reduction in female fertility with increased investment, due to enhanced competition between related offspring during seedling establishment. There is preliminary evidence that this assumption is met from a study of seed dispersal by ants in *T. grandiflorum* (Kalisz *et al.* 1999). The results of their work indicated that, while dispersal is variable, it can be effective in reducing the average relatedness of neighbours. In addition, the study found no evidence for an effect of seed density on chances for seed germination and survival. These factors indicate that the female gain curve may saturate less rapidly than the male gain curve, because of greater competition for resources among unrelated seedlings and weak density-dependent effects on mortality. This dichotomy provides the conditions favouring increased female allocation with size.

Due to difficulties in measuring reproductive success, the shapes of fitness-gain curves have rarely been empirically investigated (see Klinkhamer *et al.* 1997). These difficulties are compounded in perennial organisms, where lifetime reproductive output can rarely be accurately assessed. However, to test the assumptions of the local mate competition hypothesis for gender adjustment further, experiments which determined the relationship between fruit and pollen investment and components of offspring fitness would be useful. For example, larger *Trillium* plants are not expected to have significantly greater chances of pollen dispersal and male mating success. In contrast, plants which produce more seeds would be expected to have greater chances of seedling establishment. Fruits with greater seed production may also be more attractive to ants, leading to greater rates of dispersal. Finally, greater seed dispersal may incur other fitness benefits in addition to the effects of resource competition, such as higher chances of offspring mating success (Kalisz *et al.* 1999).

Significant differences between *T. erectum* and *T. grandiflorum* in patterns of sex allocation may also reflect the effects of local mate competition in the two species, particularly with respect to differences in mating system. *Trillium erectum* exhibited higher female bias in biomass allocation and a lower P:O ratio than *T. grandiflorum*. *Trillium erectum* has higher selfing rates (Broyles *et al.* 1997) and, hence, this difference is consistent with theoretical predictions which indicate that selfing selects for greater relative investment into female function (Charlesworth & Charlesworth 1981; Charnov 1982). Selfing is expected to reduce the levels of pollen competition between unrelated individuals, enhancing the effects of local mate competition (Charnov 1982; but see Lloyd 1987). There is also evidence that *T. erectum* may have higher rates of seed dispersal due to greater investment into elaiosomes (Gunther & Lanza 1989), causing further linearization of the female gain curve.

(ii) *Additional hypotheses*

Several additional explanations have also been proposed which predict size-dependent female bias in animal-pollinated plants. One hypothesis, which suggests a role for geitonogamous pollination (Klinkhamer & de Jong 1997), is not relevant here since even large *Trillium* plants commonly produce only a single flower each season and the species lacks clonal propagation. However, a similar effect might occur if larger plants are more susceptible to self-pollen deposition than smaller plants, leading to greater pollen wastage by large-flowered individuals. This possibility could be tested by comparing self-pollen loads between small and large plants.

Another mechanism which may drive gender modification concerns the differential costs associated with female and male reproduction. Various researchers have emphasized the importance of greater resource costs of female reproduction, due to investment at both flowering and fruiting (Lloyd & Bawa 1984; Iwasa 1991; Bickel & Freeman 1993; Day & Aarssen 1997). For plants with sequential hermaphroditism, size-dependent sex allocation may result from direct resource limitation, if small plants do not have the resources to produce seeds (Schlessman 1987; Pickering & Ash 1993). However, this difference in cost alone is not expected to drive continuous gender modifications in simultaneous hermaphrodites unless limiting resources differ between the two sex functions (Lloyd & Bawa 1984). Thus, if size differences primarily affect the ability to mature fruit, differential costs may be a factor in driving gender adjustments. However, given that investment into male function also increases with size in *Trillium*, this explanation seems unlikely.

In the case of perennial organisms, sex-differential costs might also affect survivorship; smaller plants are likely to have a higher risk of mortality and so would be expected to favour male reproduction, if male function costs less in terms of energy and resources. Thus, the effects of future reproductive success may be a factor driving gender modification. The survival-advantage model has been studied theoretically for the case of sequential hermaphroditism (Iwasa 1991). For this model to apply for simultaneous hermaphrodites, one would expect that smaller plants should invest proportionately less overall into reproduction than larger plants, increasing vegetative allocation and, hence, survivorship. However, there is no evidence of such a relationship in *Trillium*; although there was an absolute increase in reproductive investment with size, the proportion of total biomass allocated to reproduction at flowering in fact decreased with size and there was no relationship between size and proportional reproductive effort at the fruiting stage (figure 3). Thus, small plants do not appear to be investing proportionately less into reproduction, suggesting that the survival-advantage model may not be relevant.

A fourth potential mechanism influencing gender dynamics is a direct effect of plant size on pollinator attraction. Larger plants allocate more resources to pollinator attraction and this effect may differentially increase female reproductive success (Klinkhamer & de Jong 1997). If so, larger plants should maximize reproductive success by investing proportionately more into female reproduction. While secondary floral characters have traditionally been assumed to affect male success primarily, the reverse might also be the case (Morgan & Schoen 1997). However, this hypothesis does not appear to apply since, even in pollen-limited *T. grandiflorum*, there was no relationship between the S:O ratio and size. Thus, larger plants did not appear to have a higher probability of pollination success, suggesting that direct effects of plant size on pollinator attraction are not driving gender modification.

Finally, it is important to note that the observed size–gender relationships may simply be associated with plant allometry. Pistils in *Trillium* spp. are near spherical in shape and, hence, greater size leads to an increase in volume. In contrast, anthers enlarge primarily in rectangular area. Therefore, the rate of increase in ovule versus pollen production may reflect geometric constraints associated with sex organ growth. Both species showed similar relationships between size and gender suggesting a possible role for common ancestry. If gender adjustment is determined by such patterns of growth, then sex organ shape may be a primary determinant of the relationship between size and gender across taxa.

The reproductive ecology, architecture and patterns of biomass allocation in *Trillium* suggest that the relative effects of local mate and resource competition are the most probable selective mechanisms driving gender adjustment in these species. However, further comparative studies of hermaphroditic species combined with data on the effects of size on fitness are necessary to help distinguish the effects of natural selection and developmental constraints on gender modification and understand dynamic allocation strategies in these and other perennial organisms.

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