



Original article

Sex-different response in growth traits to resource heterogeneity explains male-biased sex ratio

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ABSTRACT

In dioecious plants, differences in growth traits between sexes in a response to micro-environmental heterogeneity may affect sex ratio bias and spatial distributions. Here, we examined sex ratios, stem growth traits and spatial distribution patterns in the dioecious clonal shrub *Aucuba japonica* var. *borealis*, in stands with varying light intensities. We found that male stems were significantly more decumbent (lower height/length ratio) but female stems were upright (higher height/length ratio). Moreover, we found sex-different response in stem density (no. of stems per unit area) along a light intensity gradient; in males the stem density increased with increases in canopy openness, but not in females. The higher sensitivity of males in increasing stem density to light intensity correlated with male-biased sex ratio; fine-scale sex ratio was strongly male-biased as canopy openness increased. There were also differences between sexes in spatial distributions of stems. Spatial segregation of sexes and male patches occupying larger areas than female patches might result from vigorous growth of males under well-lit environments. In summary, females and males showed different growth responses to environmental variation, and this seemed to be one of possible causes for the sex-differential spatial distributions and locally biased sex ratios.

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1. Introduction

In dioecious plants, resource allocation to sexual reproduction is often greater for females than males, and females invest usually less for growth and maintenance (Obeso, 2002; Barrett and Hough, 2013; but see Harris and Pannell, 2008). The difference in resource allocation between sexes may account for sex-different sensitivities to environmental factors; this can be a part of a micro evolutionary process in which females and males show sex-specific resource utilization (Delph, 1999, 2005).

Sex-different resource utilization often associates with sex-different life history (Obeso, 2002; Barrett and Hough, 2013). For example, males and females differ in architectural traits (Nakagawa et al., 2015) and physiological integration (Isogimi et al., 2011, 2014; Matsushita et al., 2011). Males tend to have larger sizes than females (Zhang et al., 2010) and show higher rates of growth (Ortiz et al., 2002; Nanami et al., 2005), survival (Allen and Antos, 1993) clonal growth (Mizuki et al., 2005; Matsushita and Tomaru, 2012).

These sex-different life histories can bias the sex ratio of populations (West et al., 2002; Field et al., 2013).

Biased sex ratios can also result from spatial segregation of sexes (SSS) if sexes prefer different habitats (Bierzychudek and Eckhart, 1988; Nicotra, 1998; Eppley, 2005; Nuñez et al., 2008). In dioecious plants, SSS has been found along several environmental gradients, e.g. light (Barrett and Thomson, 1982; Nicotra, 1998), water (Dawson and Ehleringer, 1993), nutrients (Eppley, 2005) and soil pH (Cox, 1981). Differences in resource utilization between sexes are thought to be one of the causes for SSS and biased sex ratios (Nicotra, 1998; Queenborough et al., 2007).

In forest understories, environmental conditions are highly heterogeneous, and light is often the most limited resource for understory plants (Nicotra, 1998; Queenborough et al., 2007). Clonality can be the adaptive strategy of understory plants in harsh environments (Jeník, 1994; Del Tredici, 2001; Bond and Midgley, 2001). For example, layering (i.e. the production of new stems from the terminal parts such as branches of a parent plant) is one of the clonal growth forms spreading into favourable (i.e. well-lit) sites, while basal sprouting (i.e. the production of new stems from the base of the clump center of a plant) allows individual plants (genets) to stay at favourable sites for a long time. It could be expected that the females and males of understory clonal plants

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might show different sensitivity to light resources, in terms of stem growth and forms, and clonal growth.

In this study, we investigated the flowering sex ratio, stem sizes and spatial distributions in a dioecious understory shrub, *Aucuba japonica* var. *borealis*. We addressed the following questions. 1) Is the sex ratio biased towards male stems and, if so does the strength of the bias vary among stem size classes? 2) Do the height, length and decumbency (height to length ratio) of stems differ between sexes, and if so do the responses to light gradients differ between sexes? 3) Do the fine-scale sex ratio and stem density (number of stems per unit area) change along light gradients? 4) Do spatial patterns differ between sexes?

2. Materials and methods

2.1. Study species

In Japan, there are two varieties of *Aucuba japonica* (Aucubaceae): var. *japonica* and var. *borealis*, which are distributed along the Pacific Ocean side and Japan Sea side, respectively (Kurosawa, 1971). *Aucuba japonica* var. *borealis* has shorter (up to 1 m tall) decumbent stems (Kume and Ino, 2000). The branches of their stems that are pushed to the ground by heavy snow can develop adventitious roots and propagate clonally via layering. In *A. japonica* var. *borealis*, the sex ratio bias and between-sex differences in stem size and growth have not been investigated. A previous study found that no trade-off between sexual reproduction and growth, and no between-sex differences in basal sprouting ability in *A. japonica* var. *japonica* (Abe, 2002). The stems of *A. japonica* produce inflorescences at the top of their shoots in previous autumn, and then bloom during next May–June. The flowering phenologies of both sexes largely overlap (Abe, 2001). The flowers have four dark-purple petals and are 8–10 mm in diameter. A female flower has one ovule and produces a one-seeded fruit, which matures over winter and is ripe by the following spring (Abe, 2002). At the inflorescence level, fruits comprised about 90% of total female reproductive biomass, and the reproductive investment of males was 0.20–0.57 times that of females.

2.2. Study sites and field methods

The study was conducted in an old-growth beech forest near Lake Towada, northern Japan (40°24'N, 140°53'E, 670 m a.s.l.). The mean annual temperature and precipitation are 7.6 °C and 1786 mm, respectively. Snow cover on the forest floor can reach 3 m between November and April. The canopy is mainly dominated by beech (*Fagus crenata*) and some other deciduous trees (*Magnolia obovata* and *Acer mono*), while dwarf bamboo (*Sasa kurilensis*) dominates the understory (Abe et al., 2001).

In May 2012, we established three 20 × 20 m plots (relatively similar ground conditions but heterogeneous canopy closures). To avoid sampling from same genotypes, we carefully choose the locations (50 m away from each other), and confirmed that there were several patches of *A. japonica* var. *borealis* within each plot. In these plots, all of the stems (≥10 cm tall) were marked, and their spatial coordinates were mapped. The flowering status (flowered or not) and sex were checked when they bloomed. The height and length of each stem were measured, and the height/length ratio (H/L ratio) was calculated as an index of decumbency (ranging from 0 for stems sprawling on the ground to 1 for upright stems). To evaluate understory light conditions, each 20 × 20 m plot was divided into sixteen boxes (5 × 5 m), and hemispherical photographs were taken at 80 cm above the ground in the four places within each box (i.e. 64 photos per plot) in October 2012 (e.g. Oki et al., 2013). The canopy openness (%) in each box was then calculated using CanopOn 2.03 (Takenaka, 2009).

2.3. data analyses

All the analyses here were performed using R 2.12.0 (R development core team, 2010). In this study, “sex ratios” were expressed as numbers of flowering male stems/(flowering female stems + flowering male stems). Deviations of observed sex ratios from random expectations (female:male = 1:1) were tested by a binomial test. To test whether the degree of sex ratio bias might vary among the size classes of stem variables (height, length and H/L ratio), we analysed the relationships using generalized linear mixed effect models (GLMMs) with a binomial error, in which “plot” was set as a random effect (cf. Bolker et al., 2009).

To compare the averages of stem height, length, and H/L ratio between sexes, we tested the averages by ANOVA in which “sex” was set as a fixed factor. To test for between-sex differences in responses of the stem variables (height, length and height/length ratio) to light variation, we analysed the relationships by ANCOVA, in which “canopy openness” was a covariate and “sex” was a fixed factor. In these analyses, “box” was nested within “plot”, and both were treated as random effects. By setting “box” as the random effect, we thought “over-significance” caused by pseudo-replication of stems could be somewhat controlled, although we did not have the data of genet identity that was the random effect more appropriate to be set.

To test whether sexes differ in the responses of increasing stem density along light intensity, the observed number of stems per 5 × 5 m-box (response variable) was analysed by GLMM (negative binomial distribution). As the explanatory variables, “sex” and “canopy openness” were set as the fixed factor and covariate, respectively, while “plot” was set as a random effect. The relationship between fine-scale sex ratios at 5 × 5 m-box (response variable) and canopy openness (explanatory variable) was analysed by GLMM (binomial distribution), and “plot” was set as a random effect.

Ripley's $L(t)$ and $L_{12}(t)$ functions, those were modified $K(t)$ and $K_{12}(t)$ functions, were used to analyse spatial distribution patterns (univariate point patterns) and spatial interactions (bivariate point patterns) of sexes, respectively (Ripley, 1977; Diggle, 1983). Ripley's edge correction was used to account for edge effects. First, to examine whether the stems of each sex showed different clumping patterns, the univariate point pattern analysis was conducted along distance scale t (0–10 m) using the function $L(t) = [K(t)/\pi]^{1/2} - t$. All female and male stems within each plot were tested against the null hypothesis of complete spatial randomness. If the observed $L(t)$ values were greater than, similar to and less than 95% confidence intervals obtained from 1000 Monte Carlo simulations, the distribution patterns were assumed to be clumped, random or regular respectively.

Second, to examine spatial association/segregation of sexes, bivariate point pattern analysis was conducted using the function $L_{12}(t) = [K_{12}(t)/\pi]^{1/2} - t$. Random labelling approach was used to assess the significance of spatial segregation of sexes (e.g., Nanami et al., 2005). In this approach, if the observed $L_{12}(t)$ values were greater than or less than the confidence intervals obtained from 1000 Monte Carlo simulations, these indicate significant spatial association or segregation between sexes, respectively. The overlapping of the confidence intervals indicates spatial independency in the distribution pattern of the sexes.

3. Results

3.1. Sex ratio

Observed flowering sex ratios in all study plots significantly deviated from the expected 1:1 sex ratio and were strongly male-

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