



Effects of soil properties and clonal growth on the apparent sex ratio of the flowering stems of the dioecious clonal shrub *Aucuba japonica* var. *borealis* growing in an evergreen coniferous secondary forest

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ABSTRACT

In dioecious plants, the frequencies of flowering stems in each sex produced through clonal growth provide important information on the potential for reproductive success in the populations. However, apart from the light environment in their habitat, the factors affecting the flowering of each sex have not been well documented in shrub species that can maintain their populations in shady environments. In this research, we investigated seven soil variables and the flowering of stems of *Aucuba japonica* var. *borealis* in patches of this dioecious clonal shrub with different apparent stem sex ratios in an evergreen coniferous secondary forest with a shady forest floor. Of the 53 patches examined, 52 contained stems with flowers. Flowering stem ratios exhibited a positive relationship with available soil phosphate but a marginal negative relationship with exchangeable magnesium, whereas soil water content was associated with a female-biased flowering sex ratio. Stem density tended to be negatively related to flowering stem ratios in patches containing stems with female flowers but not males. While the results demonstrate that abundant amounts of certain nutrients and moisture in soils promote the production of flowers and/or a bias toward femaleness in patches, it is suggested that antagonistic effects of cations in the soil can inhibit the flowering of both sexes. In addition, the trade-off between sexual reproduction and clonal propagation in the females may amplify the variations in flowering in the population.

1. Introduction

Flowering states (i.e., flowering or not flowering) indicate the potential for sexual reproduction (Abe et al., 2016; Sakai, 2002). Dioecious plant species, in particular, are expected to be vulnerable to fluctuation in flowering states, for example caused by climatic changes, given that they often exhibit spatial segregation of sexes (hereafter SSS) and biased sex ratios (Hultine et al., 2016). The SSS and biased sex ratios originate from the sexually different resource requirements for sexual reproduction and/or survival, in which fruit maturation as well as flowering impose much higher energy demand upon females than males (reviewed by Obeso, 2002). As a result, female flowering tends to be biased towards sites with resource-rich soils, for example with abundant phosphorus (Eppley et al., 2009), nitrogen (Bertiller et al., 2002) or moisture (Chaurasia and Shukla, 2016; Hughes et al., 2010). These studies also report that males are able to flower even at sites with

poor soil. While studies have often reported single environmental factors that govern the general patterns of the SSS and/or biased sex ratios across populations (Bertiller et al., 2002; Eppley et al., 2009; Mizuki et al., 2012), it has also been shown that such environmental factors vary among populations depending on the types of forest communities (Zhang et al., 2010). Therefore, examining different populations growing where the environmental conditions differ from those in habitats typical for the species may provide further insights into the mechanisms underlying the SSS and variations in sex ratio.

Clonal growth also amplifies the SSS and biased sex ratios represented by flowering stems, since growth forms such as sprouting and layering commonly lead to a clumped distribution of the stems of each sex (Matsushita et al., 2010; Torimaru and Tomaru, 2005). Those growth forms usually result in physiological integration among stems within genets, and the connected smaller stems exhibit increased growth and/or survival due to the translocation of resources from the

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parental stems (Isogimi et al., 2011, 2014). Such positive growth and survival can shorten the time a stem takes to reach sexual maturity and increase the numbers of sexually mature stems within genets, indirectly increasing the frequencies of flowering stems (Matsushita et al., 2011). Furthermore, males exhibit higher proportions of flowering stems within genets than females (Matsushita et al., 2011; Torimaru and Tomaru, 2006). Thus, clonal growth also introduces variation in flowering states within populations in dioecious woody species (Barrett, 2015).

In the study presented here, we investigated the ecological (flowering states of stems, stem density, and area) and environmental properties (soil moisture and soil chemical properties) associated with a population of a dioecious understory shrub, *Acuba japonica* var. *borealis*. A previous study demonstrated that the species produces stems through layering when weighed down by heavy snow and forms distinct patches (Fig. A.1A); in well-lit environments the sex ratios are male-biased and there is SSS in deciduous broadleaved forest (Matsushita et al., 2016). The species is also found in evergreen coniferous secondary forests (Kume and Ino, 1993) where there is usually less light all year round than in the species' typical habitat of old-growth deciduous forests (Gonzales and Nakashizuka, 2010). Such populations are suitable for studies solely focusing on the heterogeneity of the soil environment in order to examine other factors responsible for variations in flowering states and flowering sex ratio. The specific aims of our study were: (i) to examine whether SSS could be found in the population examined, (ii) to examine whether the flowering stem and sex ratios are associated with traits representing the species' clonal growth, such as area and stem density of the patches, and (iii) to examine which soil environmental variables affect the flowering stem or sex ratios of patches. In addition, we discuss the ecological and physiological processes that may be responsible for shaping the SSS as well as variation in the ratio of flowering stems.

2. Materials and methods

2.1. Study site and the species

The stand studied was situated in a *Cryptomeria japonica* secondary forest in the Shirakami Mountains, located close to the isolated natural beech forest named Shirakami-Promenade (40°40'40"N, 140°12'4" E; ca. 290 m above sea level [a.s.l.]) in Aomori Prefecture, Japan (Fig. 1A). The dominant soil types are Brown Forest Soil (Sasaki et al., 2009). The mean annual precipitation is 1306 mm, monthly mean precipitation ranges from 65 mm (March) to 150 mm (November), and the mean monthly maximum temperature is the highest in August (22.6 °C) and the lowest in January (−0.7 °C), maximum snow depth in winter is reported to reach ca. 52 cm, according to records from the Ajigasawa local meteorological observatory (ca. 40 m a.s.l.) located ca. 11 km from the study stand (Japan Meteorological Agency, 2011).

Acuba japonica var. *borealis* (Aucubaceae) is an evergreen broadleaved dioecious shrub, and is a variety of *Aucuba japonica* found in snowy regions adjacent to the Sea of Japan, mainly in Honshu and the southern part of Hokkaido, Japan. This species is a common shrub of deciduous broadleaved forests in the cool temperate zone along the Sea of Japan, which are dominated by Japanese beech, *Fagus crenata* (Ishizuka, 1974). *A. japonica* var. *borealis* reaches up to 1 m in height and has decumbent shoots. The plants bloom in April and May, and small brown flowers are produced at the axil of current-year shoots (Fig. A.1B and C). A female flower has single ovule and produces one seed per fruit. Fruit starts to mature in mid-March and is ripe by mid-April. Insect-mediated pollination and avian seed dispersal have been reported for Aucubaceae, including *A. japonica* var. *borealis* (Abe, 2001; Yamaguchi and Hayashida, 2009).

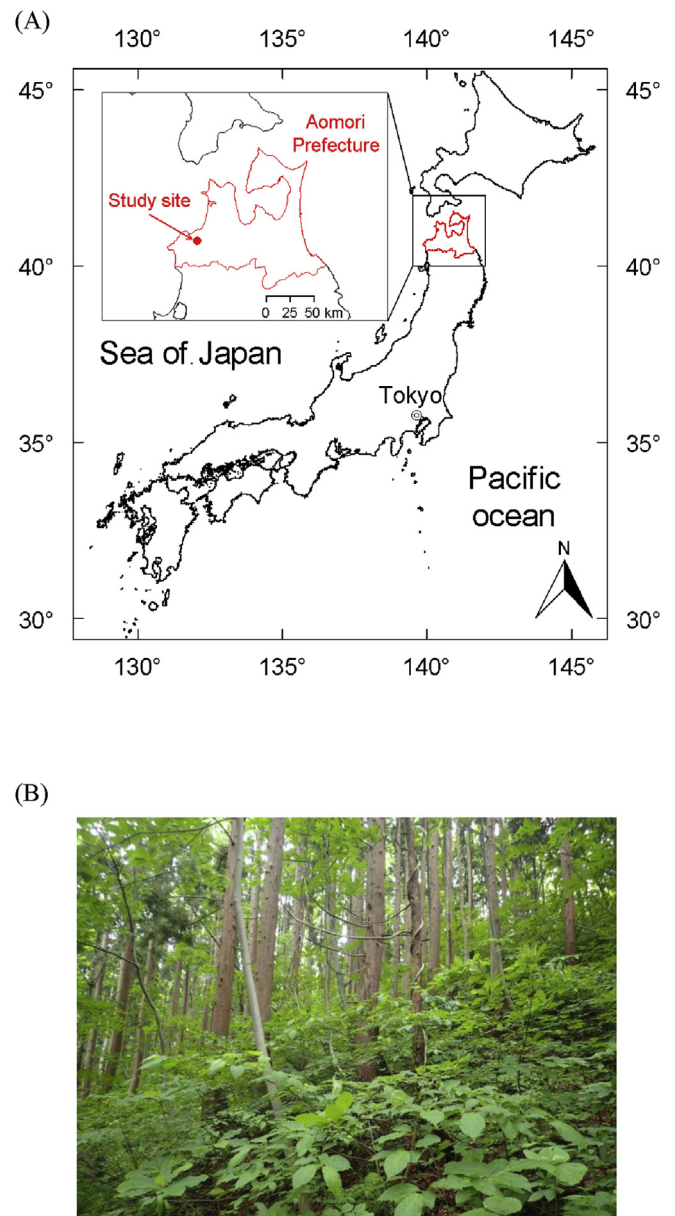


Fig. 1. (A) The location of the study site and (B) a photograph of *Cryptomeria japonica* secondary forest in the study plot.

2.2. Field method

A field survey was performed to identify the patches of *A. japonica* over an area of 0.3ha (30 m × 100 m) in the secondary forest (Fig. 1B) during the flowering season in 2013. In the present study, a patch is defined as a cluster of *A. japonica* stems, and the spatial coordinates of the center of each patch and the stems of *C. japonica* and deciduous broadleaved species with girth at breast height > 50 cm were recorded. The shape and size of each patch were determined by measuring the width and length of each (Fig. A.2) and by sketching the patches during the field survey. A 1 m² (1 m × 1 m) quadrat was set in the center of each patch, and all the stems it enclosed were counted to estimate stem density. Furthermore, we randomly selected 10–30 stems in each patch and classified them into one of the following three states: stems with male flowers; stems with female flowers; and stems with no flowers.

We collected single soil cores from the 0–15 cm depth after removing forest floor debris at the center of each patch. Each sample was put into a zip-lock plastic bag and taken to the laboratory, where each

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