

1 **Thinning operations increase the demographic performance of the rare**
2 **subtree species *Magnolia stellata* in a suburban forest landscape**

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25 **Abstract**

26 To ensure the persistence of populations and species that maintain unique biodiversity in
27 suburban landscapes, it is necessary to establish an efficient management system for
28 abandoned suburban secondary forests. To inhibit the progress of forest succession, which
29 could lower the level of species diversity, thinning operations seem to be an effective
30 management approach. To evaluate the management efficiency of thinning operations on the
31 demographic performance (growth, survival and sexual reproduction) of the rare subtree
32 species *Magnolia stellata*, we set up a field experiment and monitored the population
33 dynamics over nine years. The results revealed that stem survival and flower production per
34 genet showed a decreasing trend in the non-thinned site. However, thinning operations
35 increased the demographic performance, in particular the stem growth and survival rates and
36 flower and seed production. The findings suggested that thinning operations may decrease not
37 only the extinction probability of the targeted local population but also the extinction
38 probability of the meta-population because the thinned population serves as a better seed
39 source. Thus, the creation of well-lit sites by thinning operations would be a useful
40 conservation strategy for the persistence of *M. stellata*.

41

42 **Keywords:** Conservation, Forest management, Rare species, Seed production

43

44

45 **Introduction**

46 Forest succession after stopping human land use could affect the abundance and richness of
47 understory plants (Pierce et al. 2009). Declining abundance of understory plants is often likely
48 resulted from changing environments via forest succession (Pierce et al. 2009; Andrieu et al.
49 2013). For example, populations of *Cornus florida* L. (an understory subtree commonly found
50 in mesic forests of North America) have recently been threatened (Pierce et al. 2009). About
51 36% of its decline over 10 years was attributed to canopy closure (McEwan et al. 2000).

52 Recent The National Biodiversity Strategy has highlighted the degradation of ecosystems
53 in suburban and rural landscapes, and vegetative succession in abandoned suburban
54 secondary forests is recognized as a key biodiversity crisis (Ministry of the Environment 2007).
55 Suburban secondary forests in Japan, called ‘Satoyama’, have been re-evaluated from the
56 perspective of conservation of indigenous biodiversity (Fukamachi et al. 2011; Werner 2011).
57 Satoyama has traditionally been managed by local people to obtain firewood and manure
58 (Hada et al. 1999; Yokohari and Bolthouse 2011). Since various environments with different
59 succession stages are created by human land use, Satoyama could maintain a unique
60 biodiversity (Washitani 2003). However, since the 1960s, the traditional land use pattern has
61 changed because of an energy revolution marked by a shift from firewood to fossil fuel
62 (Takeuchi 2003; Morimoto 2011). Recently, many Satoyama forests have been abandoned
63 and their species composition has gradually shifted from deciduous to evergreen trees
64 (Morimoto and Morimoto 2003).

65 *Magnolia stellata* (Sieb. et Zucc.) Maxim., a deciduous clonal subtree, is endemic to the
66 region around the Ise Bay in central Japan (Ueda 1988). The wetland plant community in this
67 region is unique, and 15 species, including *Acer pycnanthum* K. Koch, have been identified as

THINNING ENHANCES THE PERFORMANCE OF RARE *MAGNOLIA*.

68 endemic or semi-endemic (Tokai hilly land elements; Ueda 1989, 2002). Because of the
69 recent urban development and vegetative succession, *M. stellata* has declined and is classed as
70 near threatened (Ministry of the Environment 2007). The species blooms beautiful flowers
71 with pink petals in early spring (Setsuko et al. 2008) and is popular as a cultivated tree
72 (Callaway 1994). Many local organizations perform protection activities (Japan Association
73 for Shidekobushi Conservation 1996) and recognize *M. stellata* as a flagship species
74 (attracting attention and funding for the preservation of Satoyama). The local populations are
75 small and occur intermittently in swampy places (watersheds and bogs) but can contribute to a
76 meta-population (Setsuko et al. 2004; 2007). The flower/fruit production is affected by light
77 intensity (Setsuko et al. 2008), thus its regeneration seems to be limited to well-lit sites.

78 To ensure the persistence of species that maintain unique biodiversity in suburban forests,
79 it is necessary to establish an efficient management system (Morimoto et al. 2011). To inhibit
80 the progress of forest succession that may decrease species diversity, thinning dominant trees
81 seems to be a useful management approach (Saeki 2007; Lindh 2008; Morimoto et al. 2011;
82 Andrieu et al. 2013). In this context, the effect of thinning on the performance (survival, growth
83 and sexual reproduction) of declining plants has attracted interest (Kisanuki et al. 2008;
84 Setsuko et al. 2008, 2013). However, there is relatively little information about management
85 effects on the demographic performance of declining plants (Saeki 2007; Andrieu et al. 2013).

86 Here, we hypothesized that the reproduction and regeneration of the rare subtree species *M.*
87 *stellata* may be prevented by limited light intensity because of an increase in the density of
88 evergreen broad-leaved trees via forest succession. To address this issue, we evaluate the
89 management efficiency of thinning operations on the demographic performance of *M. stellata*
90 in a suburban secondary forest by conducting a field experiment in which the population

91 dynamics were monitored over nine years. Specifically, we addressed the following questions:

92 1) What was the change in the population structure (i.e. plant size and number) after thinning

93 operations? 2) What was the change in the survivorship and growth after thinning operations?

94 3) What was the long term trend in sexual reproduction (production of flowers, fruits and

95 seeds) of *M. stellata* and how was it affected by thinning?

96

97 **Materials and Methods**

98

99 Study sites

100

101 The study was carried out in a wetland forest area located along the upper stream of the

102 Terayama River watershed within the Kaisho Forest landscape, near Nagoya City, Aichi

103 Prefecture, Japan (35°11'N, 137°6'E; 960 ha; 90-150 m a.s.l.). The mean annual temperature

104 and precipitation for this region were 15.4°C and 1560 mm, respectively (Japan Metrological

105 Agency). In the landscape, the soil is mainly covered with weathering products of granite, but

106 some areas are composed of gravel deposits and are thus nutrient poor (Hada et al. 1999).

107 Like many other suburban secondary forests in Japan, the Kaisho Forest was utilized by

108 local people up until the 1960s, when most of the area was bald due to heavy cutting of trees

109 for firewood and manure (Hada et al.1999). Following cessation of the forest's exploitation in

110 the 1960s, alders and pines were planted for greening. Those planted trees have recently been

111 replaced by deciduous oak (*Quercus serrata* Murray and *Q. variabilis* Blume), and most of

112 forest is now dominated by *Q. serrata* and some broadleaved trees, e.g. *Clethra barbinervis*

113 Sieb. et Zucc. (Clethraceae) (Tamaki et al. 2005). Over the last decade, evergreen tree species

THINNING ENHANCES THE PERFORMANCE OF RARE *MAGNOLIA*.

114 like *Q. glauca* Thunb., *Ilex pedunculosa* Miq. (Aquifoliaceae) and *Camellia japonica* L.
115 (Theaceae) have increased via the process of secondary succession, causing the forest
116 understory to get darker (Kimura unpubl. data).

117

118 Experimental plots and thinning treatments

119

120 To test whether the increased light conditions via thinning could improve the performance
121 (growth, survival and reproduction) of *M. stellata*, we established four experimental plots
122 within the watershed. The four plots were adjacently located c. 10~80 m apart from each other.
123 Two plots (30×20 and 20×20 m) were set in 2007, and thinning on the other woody stems
124 (mainly of evergreen trees in canopy/subcanopy layer) except *M. stellata* was conducted in
125 2008 (hereafter referred to as “Early thinning sites”). The other two plots (both 20×20 m)
126 were set in 2009, and thinning was conducted in 2010 (referred to as “Late thinning sites”).
127 The residuals of stand BA were about 52.4% and 64.0% for the early and late thinning sites,
128 respectively (Table 1). To contrast with the thinned sites, the remaining habitat of *M. stellata*
129 within the watershed was left intact (referred to as “background sites”). We did not conduct
130 additional silvicultural treatments, because although some tree species resprouted from the
131 stump, most of the sprouted shoots kept small size (Nishimura 2009). Details of these sites
132 and thinning treatments were summarized elsewhere (Nishimura 2009; Tomaru 2007, 2010).

133

134 Light intensity

135

136 We checked whether thinning increased light levels, by measuring the photosynthetic photon

THINNING ENHANCES THE PERFORMANCE OF RARE *MAGNOLIA*.

137 flux density (PPFD) at the crown of each stem of *M. stellata* on a cloudy day in July, using
138 LI-250A light meters (LI-COR Biosciences). The mean relative PPFD [rPPFD = (PPFD
139 above the crown of each stem) / (PPFD above forest canopy) × 100] was compared among the
140 sites. We confirmed that the mean rPPFD measured in 2011 was significantly higher in both
141 thinning sites than in the background sites (Table 1, $P < 0.01$ by Tukey-HSD post-hoc tests).

142

143 Stem survival and growth

144

145 All living stems (>1.3 m long) of *M. stellata* within the watershed were tagged in 2003 and
146 the spatial coordinates were mapped. The status (alive/dead) of each tagged stem and the
147 recruitment of stems were repeatedly checked in 2005, 2007, 2009 and 2011 (Appendix). As
148 an indicator of individual stem size, we measured the diameter at breast height (DBH) in 2003,
149 2007 and 2011(Appendix). The diameter growth rate ($\text{cm } 4 \text{ years}^{-1}$) was then calculated from
150 the change in DBH between censuses (2003-2007, 2007-2011). We defined the largest-sized
151 stem in terms of DBH within each genet as a 'main stem' of the genet.

152

153 Reproductive status

154

155 To investigate the time-series trends in flowering of *M. stellata* populations, the numbers of
156 flowers produced per genet were counted in 2003, 2005, 2007, 2009 and 2011(Appendix). In
157 the early thinning sites, the flowering censuses were conducted every year. However, some
158 years were unfortunately missed in the background and late thinning sites.

THINNING ENHANCES THE PERFORMANCE OF RARE *MAGNOLIA*.

159 To test whether seed production increased after thinning, we randomly selected 6, 7, 14
160 and 6 genets within the early thinning sites in 2007, 2009, 2011 and 2013, respectively. The
161 numbers of floral buds were marked, and the numbers of carpels and sound seeds within the
162 mature fruits (sampled in August) were counted. The fruit set, seed set per fruit and surviving
163 ovules (ovules that developed into filled seeds) were calculated for each genet according to
164 the method presented by Setsuko et al. (2008). The percentage of surviving ovules was
165 calculated as fruit set \times seed set /100. Next, the total seed production per genet was estimated
166 by multiplying the flower number, average ovule number per flower and ovule survival rate.

167 The census evaluating the annual trend in seed productive ability after thinning began in
168 2007 in the early thinning sites, but there were missing census years for flowering and seed
169 production as mentioned above. To compare the seed productive ability of genets among sites,
170 we conducted an additional census in 2013. We randomly selected 6 and 5 genets for the
171 background and late thinning sites, respectively. Fruit sets, seed sets, ovule survival rates and
172 seed production per genet were examined according to the method described above.

173

174 Genet identification using microsatellite analysis

175

176 Genets were identified by examining the connections between stems above the ground in
177 conjunction with microsatellite analysis from a previous study (Setsuko et al. 2007) and the
178 present study. Leaf samples were collected from one stem within each clump (a cluster of
179 connected stems) and from stand-alone stems (without confirmed connections to each other).
180 Genomic DNA was extracted from leaves using the cetyltrimethylammonium bromide
181 (CTAB) method (Murray and Thompson 1980) with minor modifications. Polymerase chain

182 reaction (PCR) amplification was performed using seven nuclear microsatellite markers
 183 (*stm0062*, *stm0163*, *stm0214*, *stm0223*, *stm0353*, *stm0415* and *stm0423*) for *M. stellata*
 184 (Setsuko et al. 2005) and a Multiplex PCR Kit (Qiagen). PCR fragments were separated using
 185 a 3100 Avant Genetic analyzer in conjunction with GeneScan software (Applied Biosystems),
 186 and the genotypes were determined at the seven loci of the nuclear microsatellites.

187

188 Data analysis

189

190 To test whether thinning operations could increase the performance (growth, survival and
 191 sexual reproduction) of *M. stellata*, we analyzed the data using mixed effect models (Bolker et
 192 al. 2009). We treated a ‘genet’ as a random effect to account for pseudo-replication (i.e.
 193 demographic data of stems were repeatedly collected from the same genets over multiple
 194 years). All the analyses were performed using R 2.8.1 (R Development Core Team 2008).

195 The diameter growth (log-transformed) was analyzed by an ANCOVA-like linear mixed
 196 model. The main stem DBH was treated as a covariate, whereas the sites (background, early
 197 and late thinning sites) and census period (2003-2007 vs. 2007-2011) were fixed factors,
 198 including up to second-order interactions among these variables. The time-series trends in
 199 stem survival and flower production per genet were analyzed by generalized linear mixed
 200 models (GLMMs), using binomial and Poisson distributions for the survival and flower
 201 production, respectively. In the analyses for the survival and flower production, the explanatory
 202 variables were the main stems’ DBH, year and thinning. The DBH of the main stem was set
 203 as a covariate. The year effect was set as a time-series covariate. The thinning treatment effect
 204 was a main factor and included as dummy variables, i.e., 0 and 1 for pre- and post-treatment,

205 respectively. The levels of fruit sets, seed sets, ovule survival rates and seed production were
 206 analyzed, using binomial and Poisson distributions for binomial and count data, respectively.

207

208 **Results**

209

210 Characteristics of *M. stellata* population

211

212 Within the study population along the Terayama River watershed, a total of 124 genets were
 213 identified. In the background sites, the six genets had been lost during 2003-2011, while there
 214 was no loss of genets in both thinning sites (Table 1). There were 369 and 262 living stems in
 215 2003 and 2011, respectively. The mean (\pm SD) DBH of the main stem and number of stems
 216 within a genet in 2003 were 3.7 ± 2.7 cm and 2.1 ± 1.9 , respectively, compared to 4.0 ± 2.5
 217 cm and 1.7 ± 1.6 , respectively, in 2011.

218

219 Survival and growth

220

221 Over the nine year study period, the cumulative survivorship of stems showed a decreasing
 222 trend (Fig. 1; $P < 0.01$, ‘Year effect’ in Table 2). The stem survivorship in the background sites
 223 was lower than in the thinning sites, and the decreasing trend was most apparent during 2007 -
 224 2011 (Fig. 1). Thinning marginally positively affected the survivorship (Table 2, $P = 0.07$).

225 The changes in diameter growth between the two census periods differed significantly
 226 among the sites (Table 3, Period: Sites, $P = 0.032$). Stem growth in the early thinning sites
 227 increased significantly from 2003-2007 to 2007-2011 (Fig. 2; $P = 0.003$, Tukey-HSD test).

228 Although there was no significant difference between the three sites in 2003-2007 (i.e. before
229 thinning), stem growth in the early thinning sites was slightly higher than in the background
230 sites in 2007-2011 ($P = 0.058$).

231

232 Flower, fruit and seed production

233

234 Over the nine years, flower production in the study sites showed a decreasing trend (Fig. 3; P
235 < 0.01 , 'Year effect' in Table 4). However, the number of genets in the early thinning sites did
236 not decrease (Fig. 3), owing to the significant positive effect of thinning (Table 4).

237 When annual trends in the reproductive success of some genets in the early thinning sites
238 were analyzed, reproductive success parameters (fruit and seed sets, ovule survival rates and
239 seed production) were found to vary significantly among the years (Fig. 4). Overall, the fruit
240 set and number of seeds produced in the post-treatment years (2009, 2011 and 2013) were
241 higher than in the pre-treatment year 2007. The estimated seed production per genet was
242 2.7-3.6 times greater in the post-treatment years (2011 and 2013) than in 2007.

243 When we compared differences in the levels of reproductive success among the sites for
244 individual years, the number of seed sets, ovule survival rates and seed production per genet
245 in 2013 were higher in the early thinning sites than in the background sites (Table 5).

246

247 **Discussion**

248

249 Our field study showed that the local population of the rare subtree, *M. stellata* has decreased
250 over the last decade in areas where forest managers have not conducted any conservation

THINNING ENHANCES THE PERFORMANCE OF RARE *MAGNOLIA*.

251 management for their habitats. However, the field experiment also demonstrated that thinning
252 operations increased the demographic performance of the species, in terms of the growth and
253 survival rates and flower and seed production. Therefore, the present results supported our
254 hypothesis that the reproduction and regeneration of *M. stellata* were prevented by limited
255 light intensity because of an increase in the density of evergreen broad-leaved trees via forest
256 succession.

257 We found that thinning can counteract the decreasing trend in stem survivorship of *M.*
258 *stellata* and also increase the growth of the surviving stems for 4 years after thinning. Similar
259 results showing increases in growth and survivorship after thinning have been reported for
260 other deciduous broad-leaved trees, including sugar maple, yellow birch (Gasser et al. 2010)
261 and yellow poplar (Keyser and Brown 2014). Therefore, the positive effects on stem growth
262 and survival of *M. stellata* due to increased light conditions after thinning operations can, to
263 some extent, contribute to maintaining the size of the remaining local populations.

264 We studied the demographic response within the first two- to four-year periods after
265 thinning. However, the long-term effect of thinning on *M. stellata* was unclear. Some studies
266 reported that the effect of thinning lasted in relatively short term. In *Quercus velutina* Lamb.,
267 *Q. coccinea* Muenchh. (Cutter et al. 1991) and *Q. ilex* L. (Mayor and Rodà 1993), stem
268 growth increased only for the ten-year period after thinning. The remaining trees adjacent to
269 canopy gaps can elongate branches and will fill the gaps immediately after thinning (Gasser et
270 al. 2010). There was a possibility that the change in demographic performances might be
271 related to other environmental changes (e.g. water or nutrient) after thinning (Vild et al. 2013).
272 Further work is needed to explore long-term responses to thinning in relation to the
273 environmental changes and its implications for management procedure.

THINNING ENHANCES THE PERFORMANCE OF RARE *MAGNOLIA*.

274 We found that thinning operations can counteract the ongoing decrease in flowering of *M.*
275 *stellata* and increase seed production by 2.7-3.6 times for up to six years after thinning. A
276 previous study testing the effect of thinning on reproduction found that low intensity thinning
277 could lead to increased flowering of several herb species (Lindh 2008); forest-understory herb
278 species that have evolved to respond to canopy gaps showed a clear response in flowering (4-
279 to 25-fold increase), while forest generalist herb species showed an equivocal response. This
280 indicates that the response of flowering to thinning varies among species. Clear responses in
281 reproduction to thinning have also been found in other forest plants (Verkaik and Espelta
282 2006; Peters and Sala 2008; Morimoto et al. 2011; Andrieu et al. 2013). For *M. stellata*,
283 Setsuko et al. (2008) found that genets that have large stems and located in well-lit sites tend
284 to have many flowers and the reproductive success is positively correlated with flowering
285 amplitude. Moreover, the authors argued that genets with a greater number of flowers are
286 more attractive to pollinators (i.e. synergetic pollination success). Taken together, these results
287 indicate that the sexual reproduction of *M. stellata*, a flagship plant of wetland communities in
288 suburban secondary forests, seems to be limited by light resources. Therefore, increasing the
289 light conditions can enhance sexual reproduction of this species via both direct (i.e. direct
290 effect of increased light on flowering) and indirect pathways (i.e. larger-sized stems resulting
291 from increased growth response under well-lit conditions can produce more flowers).

292 Although the seed production of *M. stellata* showed a positive response to increased light
293 conditions via thinning, we did not observe the recruitment of new sprouting stems (>1.3 m
294 long). This lack of enhancement of clonal reproduction indicates that although *M. stellata* can
295 reproduce clonally via sprouting or layering, much resource might be allocated to sexual
296 reproduction rather than to clonal reproduction (Lindh 2008). Sprouting abilities after thinning

297 management have been shown to vary greatly among woody species in temperate forests
298 (Kawashima et al. 2002; Imanishi et al. 2010; Tamaki et al. 2014), reflecting different species-
299 specific strategies in clonal growth (Bond and Midgley 2001; DelTredici 2001; Matsushita
300 and Tomaru 2012; Isogimi et al. 2014). Tamaki et al. (2014) studied the relationship between
301 the basal diameter of *M. stellata* and the number of first-year sprout production just after clear
302 cutting management; *M. stellata* with 12-20 cm basal diameter produced the greatest number
303 of small sprouts (the height of initiated sprouts was smaller than 1.3m). However, Kawashima
304 et al. (2002) found no clear relationship between the basal diameter and sprout production of
305 *M. stellata* after clear cutting. Further studies assessing the complex relationship between the
306 sexual and clonal reproduction, plant size and changing environmental conditions via thinning
307 would provide useful information for future conservation management procedure.

308 Previous studies have ascertained that the local populations within a meta-population in *M.*
309 *stellata* are linked via gene flow (pollen and seed movements) within the Satoyama landscape
310 (Setsuko et al. 2007, 2013). Gene flow among the local populations can compensate for the
311 loss of genetic variation (Tamaki et al. 2008) and is thus important for the persistence of
312 populations and the species conservation. These findings suggest that thinning operations may
313 decrease not only the extinction probability of the target local population but also that of the
314 meta-population because the thinned population serves as a better pollen and/or seed source.

315 In conclusion, we found that thinning operations increased the demographic performance
316 of the rare subtree *M. stellata* in terms of stem growth and survival rates and flower and seed
317 production. Seedlings of endemic wetland plants such as *M. stellata* and *Acer pycnanthum*
318 require high light intensity for rapid initial growth, and thus their regeneration is limited to
319 open, wet sites (Saeki 2005; Kisanuki et al. 2008; Setsuko et al. 2009). However, Tamaki et al.

320 (2015) found that clearcutting operations at the wetland where *M. stellata* grew not only
321 increased largely light environments but also caused seasonal changes in the role of soil water
322 conditions. Soil moisture conditions had positive and negative effects on seedling growth and
323 survival of *M. stellata* in the growing and winter seasons, respectively. We found that the
324 thinning by about 50% in stand BA could counteract the ongoing decrease in flowering of *M.*
325 *stellata* and increase its seed production by 2.7-3.6 times for up to six years after thinning.
326 Based on the present results and previous findings, the creation of well-lit sites by thinning
327 will be a useful conservation strategy for the persistence of *M. stellata*, particularly in terms of
328 increasing sexual reproduction. It is needed to evaluate the effect of thinning intensity on the
329 demographic performance at several life stages in *M. stellata*.

330

331

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THINNING ENHANCES THE PERFORMANCE OF RARE *MAGNOLIA*.

466 **Table 1** Summary of site characteristics.

467

	Background	Late thinning	Early thinning
Area surveyed (m ²)	1650	800	1000
Thinning operations			
Conducted year	-	2010	2008
Residual BA [§] (%)	100.0	64.0	52.4
Relative PPFD [¶] (%)			
2007	No data	No data	7.0 ± 10.1
2011	11.1 ± 4.6	31.8 ± 25.4	28.7 ± 25.7
Total no. of genets			
2003	57	23	44
2007	55	23	44
2011	51	23	44
Total no. of stems			
2003	176	65	128
2007	165	62	120
2011	102	51	109

468

469 [§] Residual basal areas of woody stems within sites after thinning operations.

470 [¶] Relative photosynthetic photon flux density.

471

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THINNING ENHANCES THE PERFORMANCE OF RARE *MAGNOLIA*.

474 Table 2 Summary of generalized linear mixed-effect model for stem survivorship.

475

Fixed effects [†]	Survival		
	Coef.	Z-value	P-value
Intercept	13.787	11.997	<0.001
DBH of main stem	0.215	0.320	0.749
Year effect	-5.517	-6.452	<0.001
Thinning effect	2.902	1.791	0.073

476

477 [†]DBH of main stem was set as a covariate. Year effect was set as a time-series covariate.

478 Thinning treatment effect was a main factor and included in the model as dummy variables, 0

479 and 1 for pre-cut and post-cut, respectively.

480

481

482

THINNING ENHANCES THE PERFORMANCE OF RARE *MAGNOLIA*.

483 Table 3 Summary of mixed-effect ANCOVA for the growth rate of stems within genets.

484

Fixed effects [†]	d.f.	DBH growth	
		<i>F</i> -value	<i>P</i> -value
DBH of main stem	1,71	0.443	0.508
Period	1,71	5.856	0.018
Sites	2,86	1.524	0.224
Period:Sites	2,71	3.607	0.032

485

486 [†]DBH of main stem was set as a covariate, whereas census period (2003-2007 vs. 2007-2011)

487 and sites (background, early thinning and late thinning sites) were set as main factors.

488

489

THINNING ENHANCES THE PERFORMANCE OF RARE *MAGNOLIA*.

490 Table 4 Summary of generalized linear mixed-effect model for flower production.

491

Fixed effects [†]	Flower production		
	Coef.	Z-value	P-value
Intercept	2.593	20.702	<0.001
DBH of main stem	0.643	9.721	<0.001
Year effect	-0.428	-26.704	<0.001
Thinning effect	0.217	6.074	<0.001

492

493 [†]DBH of main stem was set as a covariate. Year effect was set as a time-series covariate.

494 Thinning treatment effect was a main factor and included in the model as dummy variables, 0

495 and 1 for pre-cut and post-cut, respectively.

496

497

498

THINNING ENHANCES THE PERFORMANCE OF RARE *MAGNOLIA*.

499 Table 5 Differences in the parameters (mean and standard error) of reproductive success
 500 among treatment sites in 2013.

501

	Background		Late thinning		Early thinning		χ^2 -value	<i>P</i> -value
Fruit set (%)	46.9	(17.8)	52.2	(10.1)	58.7	(20.3)	3.9	0.141
Seed set (%)	8.9	(3.0) a	10.1	(3.2) a	16.1	(4.9) b	10.4	0.006
Ovule survival rate (%)	4.5	(2.9) a	5.1	(1.2) a	9.6	(4.9) b	241.3	<0.001
Seed production	91.1	(51.3) a	106.6	(39.2) b	194.9	(85.7) c	1485.5	<0.001

502

503 Different small letters indicate significant differences among sites at $P < 0.05$ (based on
 504 Tukey's method).

505

506

507 **Figure captions**

508

509 **Fig. 1.** Cumulative survivorship curves for *M. stellata* stems at each site.

510

511 **Fig. 2.** Changes in the mean stem diameter growth rates within genets at each site for
512 2003-2007 and 2007-2011. Thin bars indicate standard errors.

513

514 **Fig. 3.** Time-series trends in flower production per genet in the background (upper), late
515 thinning (middle) and early thinning sites (lower). Arrows indicate when selective thinning
516 operations were carried out. Thin bars indicate standard errors.

517

518 **Fig. 4.** Annual trends in the percentage of fruit and seed sets, ovule survival and seed
519 production per genet in early thinning sites. Thin bars indicate standard errors. Arrows
520 indicate when selective thinning operations were carried out. The seed production was
521 estimated by multiplying the flower number, average ovule number per flower and ovule
522 survival rate. Different lowercase letters indicate significant differences among years at $P <$
523 0.05 (based on Tukey's method).

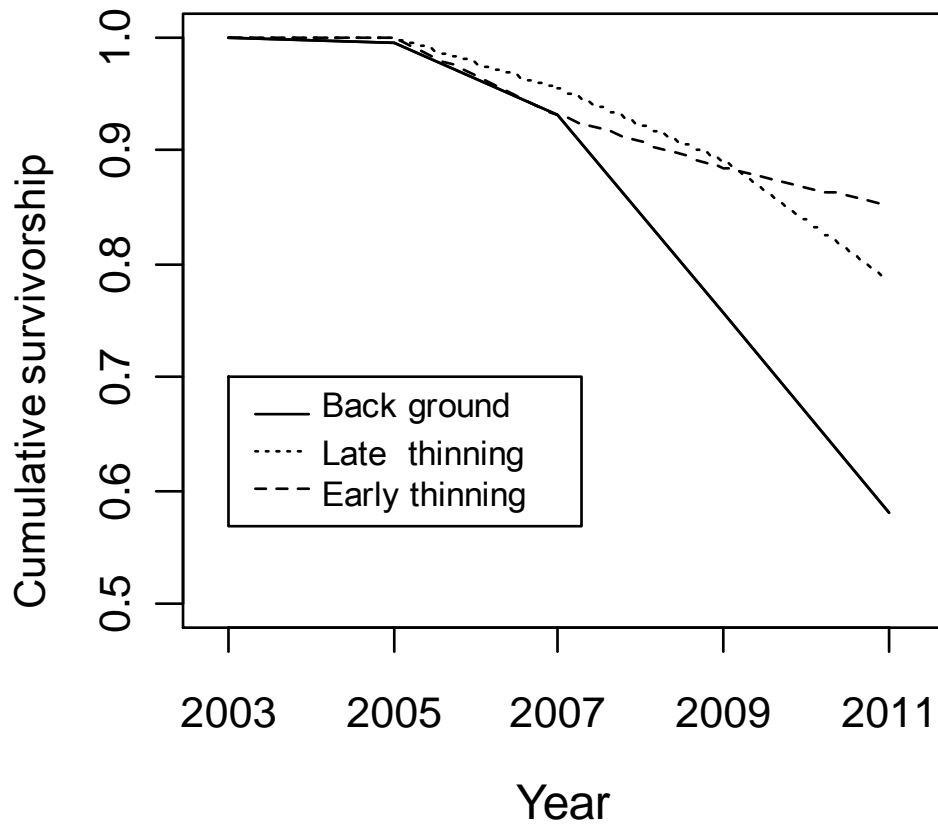
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527 **Fig. 1**

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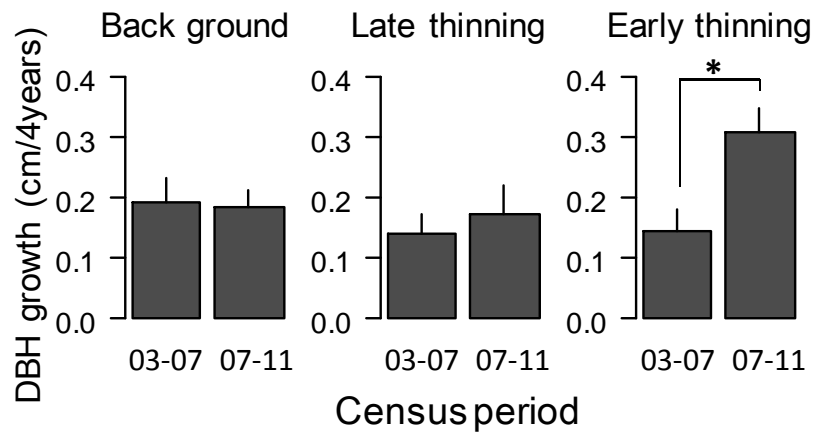
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532 **Fig. 2**

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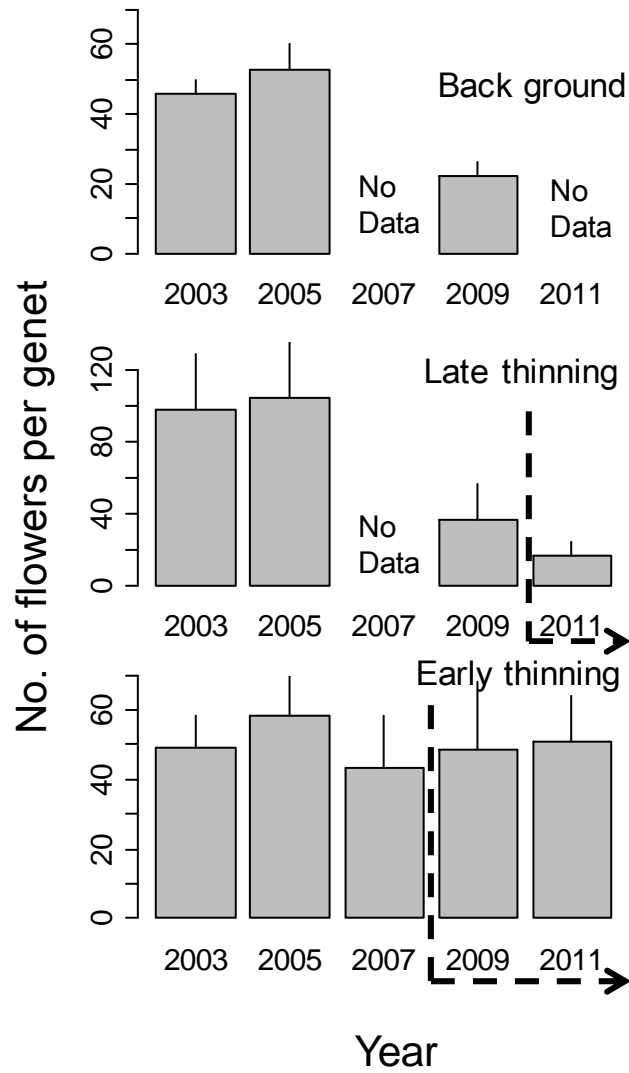
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538 **Fig. 3**

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542 **Fig. 4**

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