Growth Performance, Sexual Reproduction and Clonal Propagation of *Iris japonica* Thunb. Natural Populations in Contrast Reciprocal Habitats on Jinyun Mountain, China

(Prestasi Pertumbuhan, Pembiakan Seks dan Propagasi Klon bagi Populasi Semula Jadi *Iris japonica* Thunb. dalam Habitat Perambatan Bertentangan di Gunung Jinyun, China)

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ABSTRACT

Growth performance, sexual reproduction and clonal propagation of I. japonica *population in contrast reciprocal habitats; Open Area of Forest Edge (OAFE) and Bamboo Forest (BF) on Jinyun Mountain were studied to understand the adaptability of growth and reproductive of* I. japonica *in different habitats. The results were as follows: quantitative characteristics of growth and clonal propagation of* I. japonica *at genet (a group of genetically identical individuals, consists of whole ramets) level and at ramet (a unit composed of a shoot and root, with independent morphological and physiological traits in the same genet) level were higher in BF. However, quantitative characteristics of sexual reproduction at genet and ramet level were higher in OAFE. Biomass and allocation also showed the same trend as quantitative characteristics. Reproductive components (at ramet level) were significantly different and had trade-off in contrast reciprocal habitats. Allocation to clonal propagation and sexual reproduction of mother ramet was significantly negative correlation with allocation to daughter ramet (especially in BF). There was a trade-off between reproduction components (allocation to sexual reproduction and clonal propagation of mother ramet) in OAFE. Therefore, it showed predominantly sexual reproduction in OAFE and clonal propagation in BF. The results indicated that the contrast environmental stress shaping growth performance and reproduction variation of* I. japonica *in genet and ramet level in contrasting habitats might pronounce adaptive population differentiation among forest habitats.*

Keywords: Contrast reciprocal habitat; genet; reproductive allocation; trade-off

ABSTRAK

Prestasi pertumbuhan, pembiakan seks dan perambatan klon bagi populasi I. japonica *dalam habitat resiprokal bertentangan; Kawasan Pinggiran Hutan Terdedah (OAFE) dan Hutan Buluh (BF) di Gunung Jinyun telah dikaji untuk memahami keupayaan beradaptasi pertumbuhan dan pembiakan* I. japonica *dalam habitat yang berbeza. Keputusan adalah seperti berikut: ciri kuantitatif pertumbuhan dan perambatan klon bagi* I. japonica *pada peringkat genet (sekumpulan individu mempunyai genetik seiras yang terdiri daripada keseluruhan ramet) dan ramet (satu unit terdiri daripada pucuk dan akar dengan ciri morfologi dan fisiologi yang bebas dalam genet yang sama) adalah lebih tinggi dalam BF. Biojisim dan peruntukan juga menunjukkan corak yang sama seperti ciri kuantitatif. Komponen pembiakan (pada peringkat ramet) berbeza secara signifikan dan menunjukkan pampasan dalam habitat resiprokal bertentangan. Peruntukan kepada perambatan klon dan pembiakan seks bagi ramet induk betina menunjukkan korelasi negatif secara signifikan dengan peruntukan terhadap ramet anak (terutamanya dalam BF). Pampasan diperhatikan antara komponen pembiakan (peruntukan terhadap pembiakan seks dan perambatan klon bagi ramet induk betina) dalam OAFE. Oleh itu, pembiakan seks ditunjukkan secara dominan dalam OAFE dan perambatan klon dalam BF. Keputusan kami menunjukkan tekanan persekitaran bertentangan yang membentuk pretasi pertumbuhan dan variasi pembiakan* I. japonica *pada peringkat genet dan ramet dalam habitat bertentangan mungkin membawa kepada pembezaan populasi adaptif antara habitat hutan.*

Kata kunci: Genet; habitat resiprokal bertentangan; pampasan; peruntukan pembiakan

INTRODUCTION

Many plants can maintain populations simultaneously by sexual reproduction and clonal propagation and the relative importance of the two reproduction modes varies among different habitats (Pan & Price 2002; Shimizu et al. 1998). Clonal propagation could adapt to severe habitats with limited resources (e.g. light, water and nutrients) by physiological integration (Kanno & Seiwa 2004; Wang et al. 2009). On the other hand, sexual reproduction can create new genetic combination and lead to acceleration of adaptation to new habitat (Wilk et al. 2009). Therefore, these two modes could influence further growth performance and reproduction.

However, the relative variation between the two reproduction modes is usually modified by abiotic and

biotic conditions in different habitats (Honnay & Bossuyt 2005; Mandujano et al. 1998), especially in forest environments, climatic conditions change with exposure and canopy density, resulting in patchy microhabitats and resources heterogeneity (Pluess & Stöcklin 2005; Wang et al. 2012b). Habitats with reciprocal patchiness (i.e. under forest and at forest edge) have low light-high soil water content and high light-low water content, respectively, which has been tough to typical heterogeneity (He et al. 2011). However, few studies have quantified intraspecific growth performance and reproductive variation along small-scale ecological gradients, although environmental conditions strongly affect the reproductive modes of perennial plants, such as spatial and temporal heterogeneity of light and water environments in forests.

Many studies have shown the variation in two reproductive modes within a species. Clonal propagation can increase in habitat (forest understory and nopaleras) of low light-high soil water content (Jacquemyn et al. 2006; Mandujano et al. 1998; Wang et al. 2013) and stressful conditions (forest gap) with high light may increase sexual reproduction (Kanno & Seiwa 2004). Hence, empirical study might be focus on exploring the relative contribution of the two reproductive modes (sexual reproduction and clonal propagation) to the maintenance of populations of understory herb in reciprocal patchiness of habitats (low light-high soil water content and high light-low water content) in natural forest environments.

Iris japonica Thunb. is a perennial, rhizomatous herb with two typical reproductive modes (by both seeds and vegetative rhizomes). The population is used for pharmacy and construction of understory horticultural landscape. The natural population has been widely distributed in the forest understory and forest edge that could affect herb distribution and diversity of communities by patterns of the clonal growth (Wang et al. 2012a). Therefore, it is significant in discussing clonal growth and reproduction of *I. japonica* population in natural habitats and for further understory vegetation construction.

In this study, we examine the effect of reciprocal patchiness of habitats on quantitative characteristics, biomass and allocation of growth and reproduction in populations of rhizomatous herb, *Iris japonica* Thunb. in Jinyun Mountain, southwest China. In details, we discussed: The variation of growth performance and reproduction in contrast reciprocal patchiness of habitats; and habitat adaptation of sexual reproduction and clonal propagation and their components.

Materials and Methods

Study species and area

Iris japonica Thunb. (Iridaceae) is a perennial, rhizomatous herb reproducing by both seeds and vegetative rhizomes. The natural population has been widely distributed in the forest understory, forest gap, forest edge and moist grassland, forming mono-dominant groups. The clonal

rhizome system includes vertical coarse rhizome and horizontal fine branched rhizome. New ramets are mainly produced by clonal propagation via fine branched rhizomes at the end of coarse rhizome. Plants are flowering from March to April and fruiting from May to June (Wang et al. 2012a).

The study area was located in Jinyun Mountain Nature Reserve (approximately 630–900 m a.s.l.) of Chongqing city, Southwest China. It belongs to subtropics climate with moist monsoon. The annual mean temperature is 13.6ºC and the annual precipitation capacity is approximately 1143 mm. The major soil type is of acidic yellow soil (Wang et al. 2012a).

I. japonica populations were mainly distributed in two contrast reciprocal patchiness of habitats, at the edge of evergreen broad-leaved forest (high light-low water content) and sparse forest (low light-high soil water content). The first habitat type that open area of forest edge (OAFE) included two study sites (OAFE1 and OAFE2) (29°50′15″N, 106°23′22″E) was located within Reserve at the edge (with a distance of 10 m) of a *Cinnamomum camphora* evergreen broad-leaved forest. The second type is bamboo forest (BF) which also had two sites (BF1 and BF2) (29°49′38″N, 106°23′4″E), was located 5 km away. At these sites, overstory wood species *Phyllostachys pubescens*, a giant bamboo with sparse canopy can be found. Two study sites of each habitat type had a distance of 800 m.

Field investigation

Quantitative characteristics In each site of two habitat type, an area of 20×30 m was chosen and twelve 3×3 m plot was randomly placed. Thus there were 24 plots in each habitat and total 48 plots. We marked four whole genets (means a group of genetically identical individuals, consists of whole ramets (means clonal ramet, a unit composed of a shoot and root, with independent morphological and physiological traits in the same genet) from the same origin, total 96 genets in each habitat) in each plot in August 2007 and 96 random flowering genets were marked in each habitat only for reproductive analysis. At the end of May 2008, number of daughter ramets (a unit composed of a shoot and root, with independent morphological and physiological traits in the same genet), number of inflorescences and fruits of each genet above were counted in each plot. Number of flowers (data from the number of tracks of flower stalk), number and angle of branches (first, second and total) and number of fruits per inflorescence were recorded from data of flowering genets above. Length, surface area and volume of coarse and fine rhizome, root was analyzed by WinRHIZO Pro v.2004c Root Analysis System (Regent, Canada) by using one randomly chosen genet of *I. japonica* in each plot.

Biomass and allocation Twelve whole genets of *I. japonica* growing well (from 48 genets above) were collected in each site to analyze the reproduction allocation. One genet including mother ramet and daughter ramet can

be divided into growth, sexual reproduction and clonal propagation. Growth part included leaves of non-flowering ramets. Sexual reproduction included inflorescences and seeds and clonal propagation included coarse rhizome, fine rhizome, root and non-flowering daughter ramets. All plant material was dried at 80°C for 48 h and weighed.

DATA ANALYSIS

The figures were drawn by Origin Pro 7.0 (software) and the analyses that *t*-test of independent samples, one-Way ANOVA were carried out using SPSS statistical package (SPSS Inc., Chicago, USA).

RESULTS

QUANTITATIVE CHARACTERISTICS OF GROWTH AND REPRODUCTIONS

Growth performance that plant height and specific leaf area (SLA) of *I. japonica* was significantly higher in BF (low light-high soil water content) than in OAFE (high light-low water content) sites, whereas sexual reproduction traits that fruit percentage per inflorescence, fruit percentage per flower, multi-inflorescences ratio per genet were higher in OAFE sites (Table 1). Similarly, number of flowers per inflorescence, fruits per fruiting inflorescence, second branch per inflorescence and angle of first branch of inflorescence were significantly higher in OAFE sites than in BF sites. In contrast, number of daughter ramets

(clonal genet) was significantly higher in BF sites (Table 1). Furthermore, clonal trait that length, surface area and volume of coarse and fine rhizome, root (per genet and per mother or daughter ramet) were significantly higher in BF sites (Table 2).

Therefore, the absolute growth performance was better in BF and the absolute reproductive performance showed predominantly sexual reproduction in OAFE and clonal propagation in BF.

BIOMASS AND ALLOCATION OF GROWTH AND REPRODUCTIONS

At genet level, biomass of total, reproduction, growth, aboveground and underground of *I. japonica* were significantly higher in BF than in OAFE. Similarly, biomass and allocation of clonal propagation, fine rhizome and root, coarse rhizome, leaves of CP and undergrowth were significantly higher in BF except for allocation to coarse rhizome. However, biomass and allocation of sexual reproduction flower and fruit were significantly higher in OAFE. In addition, allocation to aboveground and underground was significantly higher in OAFE and in BF, respectively, which showed a higher root-shoot ratio in BF via in OAFE (Table 3).

At ramet level, each part of growth, clonal propagation and sexual reproduction were consistent with those in genet level for both mother and daughter ramet. Biomass and allocation to growth and clonal propagation (fine and coarse rhizome) were significantly higher in BF and sexual reproduction (flower and fruit) was higher

TABLE 1. Quantitative characteristics of growth performance, sexual reproduction and clonal propagation in *Iris japonica* populations in reciprocal patchiness of habitats

Parameters	BF	OAFE	*P*
	(2 sites, *n*=96)	(2 sites, *n*=96)	
Growth performance			
Plant height (cm)	49.90±1.19	43.36±1.21	<0.05
Basal diameter (cm)	0.81±0.02	0.78±0.02	0.19
Specific leaf area (cm²/g)	166.01±3.40	129.34±5.64	<0.001
Sexual reproduction			
Fruit percentage per inflorescence (%)	33.33	81.08	–
Fruit percentage per flower (%)	1.88	5.75	–
+Multi-inflorescences ratio (per genet) (%)	0	20.46	–
Number of flowers per inflorescence	24.42±0.63	31.52±0.66	<0.001
Number of fruits per fruiting inflorescence	1.30±0.21	2.13±0.18	<0.05
Total branches per inflorescence	11.63±0.33	12.58±0.37	0.18
Number of first branch per inflorescence	9.21±0.20	9.23±0.16	0.43
Number of second branch per inflorescence	2.40±0.21	3.37±0.25	<0.01
Angle of first branch of inflorescence (°)	50.44±1.39	34.57±1.69	<0.001
Clonal propagation			
Number of daughter ramets per clonal genet	3.92±0.32	1.37±0.19	<0.001

+Multi-inflorescences indicate that number of inflorescences per genet was more than one

TABLE 2. Rhizome characteristics of clonal propagation in genet and ramet level of *Iris japonica* (mean±s.e.) in reciprocal patchiness of habitats

Parameter	Coarse rhizome			Fine rhizome			Root		
	BF	OAFE	P	BF	OAFE	P	BF	OAFE	P
Genet									
Length (cm)*	28.2±3.1	10.6±1.3	<0.01	1200.6±125.5	153.0±14.7	<0.01	1734.5±197.1	212.2±18.2	<0.01
Surface area (cm²)	–	–	–	472.0±52.6	84.8±8.6	<0.01	152.7±17.1	18.6±1.5	<0.01
Volume(cm³)	–	–	–	24.01±3.22	2.24±0.27	<0.01	1.23±0.14	0.15±0.01	<0.01
Mother ramet									
Length (cm)	19.2±1.5	8.9±0.6	<0.01	567.2±73.0	121.1±14.8	<0.01	724.1±92.6	168.1±16.7	<0.01
Surface area (cm²)	–	–	–	241.9±35.5	68.7±9.1	<0.01	64.5±8.2	14.7±1.4	<0.01
Volume (cm³)	–	–	–	14.36±2.70	1.85±0.29	<0.01	0.53±0.07	0.12±0.01	<0.01
Daughter ramet									
Length (cm)	10.2±0.7	3.8±0.9	<0.01	662.5±99.0	31.9±10.1	<0.01	1054.6±173.9	44.2±15.5	<0.01
Surface area (cm²)	–	–	–	240.4±36.1	16.1±5.5	<0.01	92.3±15.1	3.9±1.3	<0.01
Volume (cm³)	–	–	–	10.05±1.56	0.39±0.13	<0.01	0.74±0.12	0.03±0.01	<0.01

Different letters mean significant differences (A, B: $p<0.01$) between two micro-habitats. the same below
* references to Wang et al. 2013

TABLE 3. Biomass and allocation (mean ± SE) of *Iris japonica* in reciprocal patchiness of habitats (genet level)

Parameters	Biomass (g)			Allocation (%)*		
	BF	OAFE	P	BF	OAFE	P
Total	11.79±0.69	6.22±0.40	<0.001	–	–	–
Growth	4.54±0.32	2.14±0.17	<0.001	38.97±2.30	34.58±1.92	0.10
Reproduction	7.25±0.55	4.08±0.31	<0.001	61.03±2.30	65.42±1.92	0.13
Sexual reproduction	0.38±0.16	1.91±0.23	<0.001	3.33±1.44	31.09±3.22	<0.001
Flower	0.37±0.15	1.51±0.18	<0.001	3.19±1.34	24.32±2.43	<0.001
Fruit	0.01±0.01	0.41±0.08	<0.001	0.15±0.15	6.77±1.27	<0.001
Clonal propagation	6.87±0.53	2.16±0.24	<0.001	57.69±2.38	34.33±2.37	<0.001
Fine rhizome (with root)	1.36±0.12	0.41±0.04	<0.001	11.69±1.05	7.02±0.67	<0.001
Coarse rhizome	2.38±0.27	1.15±0.09	<0.001	19.78±1.74	18.75±0.82	0.36
Leaf of CP	3.13±0.36	0.60±0.18	<0.001	26.22±2.47	8.52±2.06	<0.001
Aboveground	8.06±0.47	4.67±0.33	<0.001	68.52±1.08	74.23±1.07	<0.01
Underground	3.74±0.28	1.56±0.10	<0.001	31.48±1.06	25.77±1.01	<0.01

Clonal percentage per genet: number of genets with daughter ramets / total number of genets
* references to Wang et al. 2013

in OAFE for mother ramet, except for allocation to fine rhizome and root (Table 4). Biomass and allocation to clonal propagation were significantly higher in BF for daughter ramet, except for allocation to coarse rhizome and underground (Table 4).

REGRESSION BETWEEN REPRODUCTIVE COMPONENTS

At genet level, linear regression analyses indicated that the number of flowers per inflorescence was significantly positively related to the total branches per inflorescence ($p<0.001$). However, the increase in number of flowers with increasing branches per inflorescence was more remarkable in OAFE than in BF (Figure 1(a)).

At ramet level, biomass of mother ramet allocated to sexual reproduction was significantly negatively correlated with that to clonal propagation in OAFE, whereas there was no significant relation in BF (Figure 1(b)). Biomass of the whole genet allocated to the whole daughter ramet was significantly negative correlated with that to clonal propagation and sexual reproduction of mother ramet. However, the decrease in allocation to daughter ramet with increasing allocation to clonal propagation and sexual reproduction of mother ramet was more remarkable in BF than in OAFE (Figure 1(c), 1(d)).

DISCUSSION

GROWTH PERFORMANCE AND REPRODUCTIVE MODES IN RECIPROCAL PATCHINESS OF HABITATS

Our results suggested that growth performance, sexual reproduction and clonal propagation of wild rhizomatous

TABLE 4. Biomass and allocation to each part of mother and daughter ramet of *Iris japonica* (mean±s.e.) in reciprocal patchiness of habitats (ramet level)

Components	Mother ramet				Daughter ramet			
	Biomass (g)		Allocation (%)		Biomass (g)		Allocation (%)	
	BF	OAFE	BF	OAFE	BF	OAFE	BF	OAFE
Total	7.23±0.47A	5.35±0.34B	–	–	4.56±0.51A	0.87±0.25B	–	–
Sexual reproduction	0.38±0.16B	1.92±0.23A	4.70±1.94B	34.53±3.44A	–	–	–	–
Flower	0.37±0.15B	1.51±0.18A	4.55±1.86B	26.87±2.52A	–	–	–	–
Fruit	0.01±0.01B	0.41±0.08A	0.15±0.15B	7.65±1.40A	–	–	–	–
Clonal propagation	2.31±0.18A	1.29±0.08B	31.76±1.45A	24.91±1.22B	4.56±0.51A	0.87±0.25B	100	100
Fine rhizome with root	0.71±0.12A	0.34±0.03B	9.54±1.31	6.88±0.84	0.65±0.09A	0.07±0.02B	13.67±1.13A	5.54±1.43B
Coarse rhizome	1.67±0.18A	0.95±0.08B	23.28±1.97a	18.02±0.84b	0.78±0.13A	0.20±0.06B	16.95±1.74	18.85±3.37
Leaf	4.54±0.33A	2.14±0.18B	63.55±2.59A	40.57±2.94B	3.13±0.36A	0.60±0.18B	69.39±1.71A	49.07±6.80B
Aboveground	4.92±0.32ns	4.06±0.28ns	68.24±1.45B	75.09±1.22A	3.13±0.36A	0.60±0.18B	69.39±1.71A	49.07±6.80B
Underground	2.31±0.18A	1.29±0.08B	31.76±1.45A	24.91±1.22B	1.43±0.19A	0.27±0.08B	30.61±1.71	24.39±4.18

Different letters mean significant differences (a, b: $p<0.05$; A, B: $p<0.01$) between two reciprocal patchiness of habitats
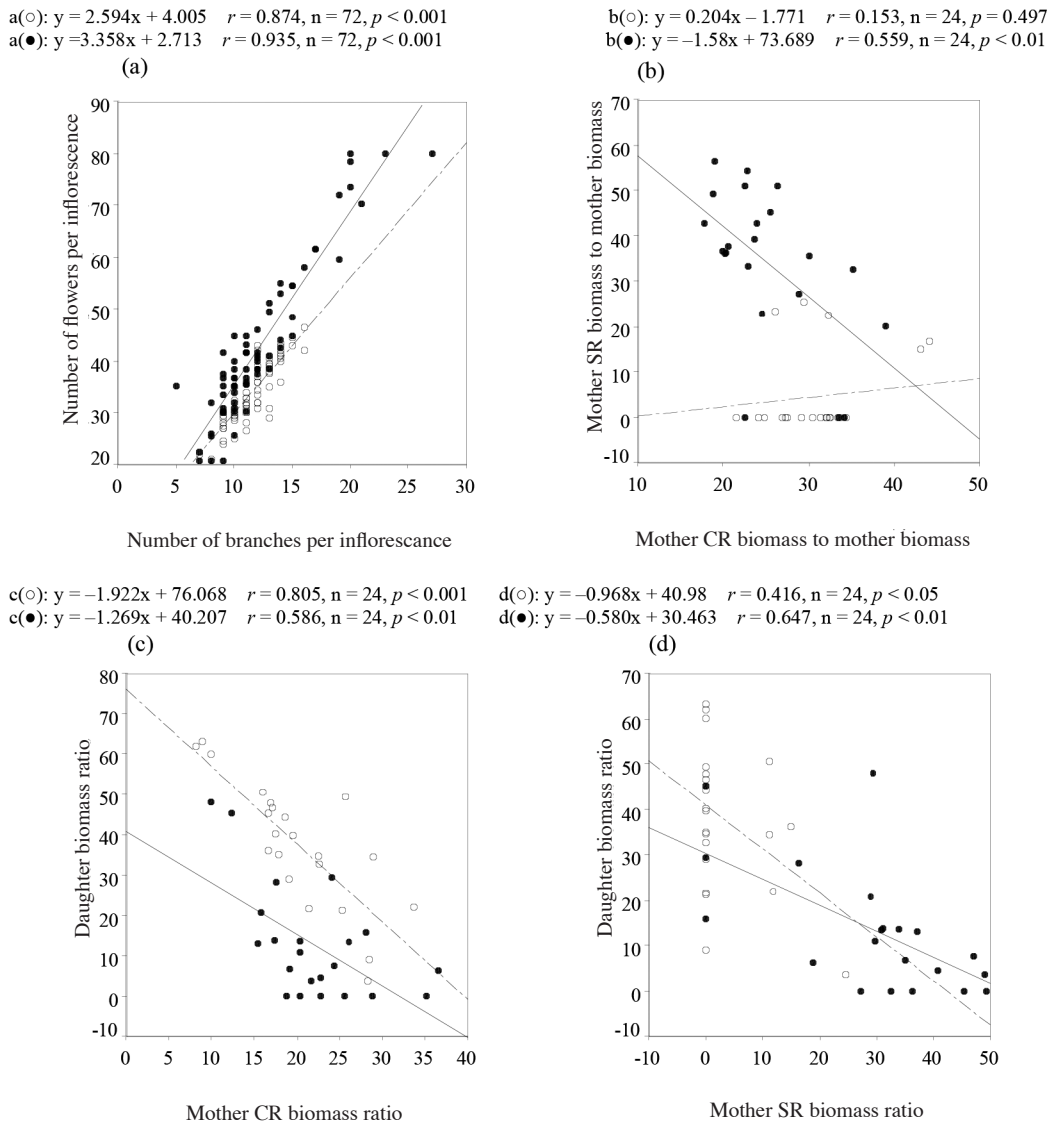
a(○): y = 2.594x + 4.005   r = 0.874, n = 72, p < 0.001
a(●): y =3.358x + 2.713   r = 0.935, n = 72, p < 0.001

(a)

b(○): y = 0.204x – 1.771   r = 0.153, n = 24, p = 0.497
b(●): y = –1.58x + 73.689   r = 0.559, n = 24, p < 0.01

(b)

c(○): y = –1.922x + 76.068   r = 0.805, n = 24, p < 0.001
c(●): y = –1.269x + 40.207   r = 0.586, n = 24, p < 0.01

(c)

d(○): y = –0.968x + 40.98   r = 0.416, n = 24, p < 0.05
d(●): y = –0.580x + 30.463   r = 0.647, n = 24, p < 0.01

(d)

FIGURE 1. Regression of reproduction components of *Iris japonica* in genet (a) and ramet (b, c and d) level in reciprocal patchiness of habitats. Open symbols (○) and broken lines refer to plants that grew in BF. Filled symbols (●) and solid lines refer to plants that grew in OAFE

herb *I. japonica* populations, were different in reciprocal patchiness of habitats, which showed predominantly sexual reproduction in OAFE and growth performance and clonal propagation in BF at our study sites in Jinyun Mountain. The relative variation of growth and reproduction was closely related to reciprocal patchiness of habitats in natural forest environments (Mandujano et al. 1998; Prati & Schmid 2000) especially for light level and substrate conditions of the forest floor that low light-high soil water content or high light-low water content. Clonal propagation can increase in habitat of low light-high soil water content, such as in forest understory and nopaleras microhabitats of *Hydrangea paniculata* (Kanno & Seiwa 2004), *Paris quadrifolia* (Jacquemyn et al. 2006) and *Opuntia rastrera* (Mandujano et al. 1998). For stressful conditions, in forest gap with high light may increase sexual reproduction in the *Hydrangea paniculata*

(Kanno & Seiwa 2004). As light availability decreases with canopy closure, understory species would shift their reproductive mode from seed reproduction to the more conservative vegetative propagation (Wang et al. 2013). Thus, the formation of forest edge or forest gaps played an important role in the sexual reproduction of clonal plants (Wang et al. 2012b). Similarly, reproductive components (at ramet level) were significantly different and had trade-off in two habitats resulted from micro-environmental differences (Fujitaka & Sakai 2007; Mizuki et al. 2005). Allocation to clonal propagation and sexual reproduction of mother ramet was significantly negative in correlation with allocation to daughter ramet (especially in BF), which indicated trade-off between two reproduction modes in ramet level and between clonal expand and establishing in components of reproduction. Similarly, there was a trade-off between reproduction components (allocation

to sexual reproduction and clonal propagation of mother ramet) in OAFE.

ADAPTATION OF GROWTH AND REPRODUCTIVE MODES IN RECIPROCAL PATCHINESS OF HABITATS

The light in contrast habitats has particularly significant effects on the number of flowers and other sexual components. Notably, fewer flowers were produced in BF. Light might have restricted accumulation of photosynthate for sexual reproduction and differentiation of flower bud. Many forest plants understory adapted to low light and hardly reproduced sexually (Kanno & Seiwa 2004). Water content in soil also influenced the growth of the whole plant and root. Reciprocal patchiness of habitats (low light-high soil water content in BF and high light-low water content in OAFE) might negatively affect flowering production more than clonal production, indicating that the fate of sexual reproduction was influenced directly by environmental conditions of forest (He et al. 2011). A shift towards greater sexual production from understory to forest edge is an advantage for a plant such as *I. japonica*, because inter-specific competition for space and nutrients resource at stressful forest edge, population persistence from sexual reproduction is more important (Chaloupecká & Lepš 2004; Wang et al. 2013).

Further, high accumulation of litters, are helpful to water content of soil, under canopy might inhibit seed germination and seedling emergence and be in favor of growth of clonal rhizome and root (Wang et al. 2009, 2012b). Establishment of *I. japonica* was strongly promoted in forest edge, because this could provide rich light, suitable substrates such as soil temperature and exposed mineral soil for germination (Kanno & Seiwa 2004). In our previous study, greater biomass investment in sexual components of *I. japonica* in OAFE could be resistant to strong wind-rain disturbance on flowers and fruits, which could promote their reproductive success (Wang et al. 2013).

Simultaneously, inter-specific competition for space and nutrients resource might be a key factor for sexual reproduction. Thus, most of the resources should be allocated to sexual reproduction in habitats with fluctuating environmental conditions and strong competition, while clonal propagation should be dominant in stable and without competition habitats (Chaloupecká & Lepš 2004; Pluess & Stöcklin 2005). In our previous study, strong inter-specific regeneration niche (above-ground spatial niche and below-ground root niche) and trophic niche (nutrient and water) competition between *I. japonica* and other herbs occurred in OAFE (Wang et al. 2013), which lead the predominance of sexual reproduction. Seeds could spread much longer than clonal offspring and easily spread favorable habitats for maintenance of populations (Rautiainen et al. 2004).

With low light availability for understory species, many new ramets were produced by clonal propagation. Such increase in plant sizes might lead to a greater proportion of photosynthetic organs (leaves) to non-photosynthetic ones/clonal components (fine and coarse rhizome) between mother ramet and daughter ramet (Pluess & Stöcklin 2005; Rautiainen et al. 2004). Ramet system could get more resources for survival and growth by clonal integration understory. These morphological changes could be an adaptation to maintain the carbon balance of the individuals under shaded conditions and to achieve clonal expansion by new ramets.

On the forest floor, weak inter-specific competition due to low coverage of herbs and adequate growth space was in favor of clonal propagation. Clonal offspring could easily live through seedling period and establish successfully. Therefore, clonal propagation strongly enhanced *I. japonica* population stability and adaptations to habitat with limited resources (e.g. light and temperature) by physiological integration, such as *Hydrangea paniculata* and *Opuntia rastrera* where clonal propagation increased in forest understory for the less nutrient-demanding (e.g. light, nutrients) than seed production (Kanno & Seiwa 2004; Mandujano et al. 1998).

CONCLUSION

The relative importance of two reproductive modes were different in reciprocal patchiness of habitats, it showed predominantly sexual reproduction in OAFE and clonal propagation in BF. Our results marginally indicated that the contrast environmental stress shaping growth performance and reproduction variation of *I. japonica* in genet and ramet level in contrasting habitats might pronounce adaptive population differentiation among forest habitats. Thus, *I. japonica* populations formed local adaptation of reproduction to local heterogeneous forest habitats. We suggest analysis on characteristics of two reproductive modes of *I. japonica* populations in field and simulated experiments are significant to further understand the effects of habitats and populations evolution.

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