INTRODUCTION

*Lycoris radiata* (L’Hér.) Herb. (Amaryllidaceae) is a perennial, bulbous plant distributed from southwestern China eastward to Japan and South Korea, and is one of the most widely distributed species in genus *Lycoris* (Hsu, Kurita, Yu, & Lin, 1994). Since 1920s when the chromosome number of this taxon was first counted (Nishiyama, 1928), much work has been done on the chromosome number and karyotype of this species, particularly on the Japanese islands and East China (Bose, 1963; Kurita, 1987; Liu, Zheng, Xia, & Zhou, 2016; Qin, Zhou, & Wang, 2004; Shao, Yang, Zhang, & Nie, 1994; Zhou et al., 2004; Zhou, Yu, Luo, Hu, & Bi, 2007). For a long time, this species had been thought to harbor only two ploidy levels, diploid (2n = 22) and triploid (2n = 33), until about a decade ago the tetraploid was

### Abstract

Information on the spatial distribution of cytotypes and karyotype variation in plants is critical for studies of the origin and evolution of polyploid complexes. Here, the spatial distribution of cytological races and intraspecific variation in the karyotype of *Lycoris radiata*, an endemic species to East Asia, is investigated. Conventional karyotype analysis methods were used to determine ploidy level and karyotypical characteristics in 2,420 individuals from 114 populations of *L. radiata* nearly covering the whole distribution areas in China. Of 114 populations studied, 52 (45.61%), 58 (50.88%), and 4 (3.51%) are diploid, triploid, and mixoploid populations, respectively, with 1,224, 1,195, and 1 individuals being diploid, triploid, and tetraploid, respectively. The triploid possesses a much wider distribution range than the diploid, with the former almost occupying the entire range of this complex species in East Asia and the latter distributing in the middle and east regions of China. Triploids tend to occur at high altitudes, and the relationship between the ploidy and altitude is significantly positive but low ($r^2 = 0.103, p < 0.01$). About 98.6% of examined bulbs have a common karyotype consisting of 22 or 33 acrocentric (A) chromosomes. Some aberrant chromosomes which should be generated from A-type chromosome have been found including metacentrics (m), small metacentrics (m'), and B-type chromosome. The results can provide a fundamental cytogeographic data for further studies on the evolutionary origins and adaptive divergences of polyploids, especially the triploid, within *L. radiata* using molecular and/or ecological methods in the future.

**KEYWORDS**
diploid, geographic distribution, intraspecific variation, karyotype, *Lycoris radiata*, polyploidy

### 1 | INTRODUCTION

*Lycoris radiata* (L’Hér.) Herb. (Amaryllidaceae) is a perennial, bulbous plant distributed from southwestern China eastward to Japan and South Korea, and is one of the most widely distributed species in genus *Lycoris* (Hsu, Kurita, Yu, & Lin, 1994). Since 1920s when the chromosome number of this taxon was first counted (Nishiyama, 1928), much work has been done on the chromosome number and karyotype of this species, particularly on the Japanese islands and East China (Bose, 1963; Kurita, 1987; Liu, Zheng, Xia, & Zhou, 2016; Qin, Zhou, & Wang, 2004; Shao, Yang, Zhang, & Nie, 1994; Zhou et al., 2004; Zhou, Yu, Luo, Hu, & Bi, 2007). For a long time, this species had been thought to harbor only two ploidy levels, diploid (2n = 22) and triploid (2n = 33), until about a decade ago the tetraploid was
firstly found (Zhou et al., 2007). This species exhibits great variation in karyotypes and chromosome number throughout its geographical range. The main chromosome numbers observed in this species complex are as follows: 2n = 21, 22, 32, 33, and 44 corresponding to the abnormal diploid, diploid, abnormal triploid, triploid, and tetraploid levels, respectively (Liu et al., 2016; Shi, Qiu, Li, Wu, & Fu, 2006). Cytogeographic patterns on the Japanese islands and South Korea have been depicted clearly, based on 58 and 11 populations of L. radiata, respectively, and only triploids were discovered in Japan and South Korea (Chung, 1999; Kurita, 1987). In China, diploid, triploid, and tetraploid plants have been found (Liu et al., 2016; Zhou et al., 2007). However, compared with researches on the populations in Japan, cytological investigations of the Chinese populations, especially those populations in southwest and southeast of China, are cursory to some extent.

As part of a broader investigation into the chromosomal variation and evolution of Lycoris species, our objective in this study was to examine the diversity and distribution of L. radiata cytotypes in China. Particularly, we addressed the following questions: (a) what are the frequencies of diploid, triploid, and tetraploid plants? (b) what are the geographical patterns of cytotype variation? (c) do polyploids have a wider distribution range than diploid?

2 | MATERIALS AND METHODS

2.1 | Plant materials

Lycoris radiata is mainly distributed in middle east, southwest, and southeast regions of China, preferring such place as riversides and the edges of farmlands, or growing under evergreen or deciduous broad-leaved forests. Two thousand four hundred and twenty individuals of L. radiata were collected from 114 populations during the past decade (from 2007 to 2017) nearly throughout its distribution range (Table 1). Bulbs collected were more than 3 m apart to avoid biasing sampling of the same clone due to extensive vegetative propagation in this species. All bulbs collected from the wild were cultivated in experiment garden. The corresponding voucher specimens were deposited in Anhui Normal University.

The growth form and seasonality of L. radiata are very characteristic, that is, the productive and reproductive phases are separate (Figure 1a,b). The diploids can produce seeds and have sexual and asexual reproduction, while the triploids can only propagate by clone, producing no seed.

2.2 | Karyotype analysis

All bulbs with the old roots cut were maintained in wet soil/tap water culture, and conventional karyotype analysis methods (Zhou et al., 2007) were used. The karyotype formula was based on the measurements of mitosis metaphase chromosomes taken from two or three well-spread metaphase cells. For the karyotype description and comparison, the simplified symbols were adapted according to Levan, Fredga, and Sandberg (1964), Kurita (1986), and Liu et al. (2012): m for large metacentric chromosome with arm ratio of 1.00–1.70; m’ for small metacentrics; st for subtelocentric chromosome with arm ratio of 3.01–7.00; t for acrocentric chromosome with arm ratio of 7.01–20.0; T for telocentric chromosome having mostly terminal centromere with dot-like short arm whose length is very short and with the arm ratio being more than 20.0; A-type chromosome includes both st- and t-type chromosome; SAT for A-type satellite chromosome; B for very small chromosome; r means arm ratio.

2.3 | Analysis of cytotype distribution

The relationship between altitude and ploidy of the sampled populations was tested using Pearson correlation analysis by SPSS v22.0. In order to exactly reveal the geographical distribution patterns of each cytotype of L. radiata complex in East Asia, we choose 43 previously published populations with precise chromosome number data and geographical location or longitude and latitude information, of which 7 populations (Liu et al., 2016), 29 populations (Kurita, 1987), and 7 populations (Chung, 1999) were from China, Japan, and South Korea, respectively. In total, 157 populations with exact ploidy data were mapped using ArcMap 10.0.

3 | RESULTS

3.1 | The ploidy and chromosome number of Lycoris radiata

A total of 2,447 individuals, from 114 populations of Lycoris radiata (Table 1), were examined to determine the chromosome number and karyotype. Of 114 populations investigated, 52 (45.61%), 58 (50.88%), and 4 (3.51%) were diploid, triploid, and mixoploid populations, respectively. A total of 1,224 bulbs and 1,195 bulbs are diploid and triploid, respectively, with a few bulbs possessing abnormal chromosomes and B chromosomes, and only one bulb from population 114 is tetraploid having 2n = 4x = 44 (Table 1).

3.2 | Karyomorphology

The karyotypes of 1,221 bulbs are all composed of 22 A-type chromosomes, of which 0–4 are satellite chromosomes. One example of representative chromosome constitution of diploid bulb from population 114 at Tangxi Zhen of Chizhou city is shown in Figure 2a,i. The representative karyotype consists of twenty-two A-type chromosomes of which two are SAT chromosomes. The measured and calculated values of each chromosome of the representative karyotype of diploid are summarized in Table 2. The short-arm length of both SAT chromosomes is much the same, and their r value is 10.73 and 9.27, respectively. Different types of SAT chromosome combination are observed in the inter- and intra-population. One SAT chromosome is observed in one bulb from population 4 in Bagongshan of Huainan city (Figure 2b,j). As shown in Figure 2c,k four SAT chromosomes are found in one bulb.
| Pop. | Locality (voucher) | Coordinates | Altitude (m) | Number of bulbs examined | Chromosome formula | Ploidy |
|------|-------------------|-------------|--------------|--------------------------|--------------------|--------|
| 1    | Laojiahe Village, Lu'an, Anhui; LR16001 | 31°29'N/115°24'E | 455 | 22 | 2n = 22A | 2x |
| 2    | Maotanchang Town, Lu'an, Anhui; LR16021 | 31°19'N/116°32'E | 164 | 20 | 2n = 22A | 2x |
| 3    | Hengdu Town, Chizhou, Anhui; LR16035 | 30°11'N/117°33'E | 78 | 40 | 2n = 22A | 2x |
| 4    | Bagongsan, Huaining, Anhui; LR0409 | 32°37'N/116°47'E | 103 | 20 | 2n = 22A | 2x |
| 5    | Marenshan, Wuhe, Anhui; LR15002 | 30°58'N/118°09'E | 150 | 18 | 2n = 22A | 2x |
| 6    | Fenghuangshan, Tongling, Anhui; LR15001 | 30°51'N/118°01'E | 180 | 30 | 2n = 22A | 2x |
| 7    | Dashan Village, Chizhou, Anhui; LR14002 | 30°01'N/117°21'E | 340 | 25 | 2n = 22A | 2x |
| 8    | Qinyunshan, Huangshan, Anhui; LR13016 | 29°48'N/118°02'E | 265 | 24 | 2n = 22A | 2x |
| 9    | Wenhuan Town, Anqing, Anhui; LR15003 | 30°56'N/116°17'E | 628 | 6 | 2n = 22A | 2x |
| 10   | Eshan Town, Wuhu, Anhui; LR16002 | 31°06'N/118°17'E | 95 | 14 | 2n = 22A | 2x |
| 11   | Yangxi Town, Ji'an, Jiangxi; LR15035 | 31°19'N/116°32'E | 164 | 20 | 2n = 22A | 2x |
| 12   | Zhuangkou Town, Ganzhou, Jiangxi; LR15033 | 28°05'N/116°38'E | 120 | 28 | 2n = 22A | 2x |
| 13   | Lujiawan Village, Huaihua, Hunan; LR16021 | 30°25'N/117°16'E | 38 | 30 | 2n = 22A | 2x |
| 14   | Xiaotian Town, Lu'an, Anhui; LR13009 | 31°11'N/116°35'E | 138 | 13 | 2n = 22A | 2x |
| 15   | Daguiling, Yi County, Huangshan, Anhui; LR11002 | 30°04'N/117°48'E | 281 | 10 | 2n = 22A | 2x |
| 16   | Xian'anjiang, Huangshan, Anhui; LR11003 | 29°39'N/118°11'E | 132 | 5 | 2n = 22A | 2x |
| 17   | Shitan Town, Qingyuan, Guangdong; LR16046 | 24°11'N/112°40'E | 130 | 26 | 2n = 22A | 2x |
| 18   | Fanjingshan Village, Tongren, Guizhou; LR15010 | 27°50'N/108°48'E | 642 | 22 | 2n = 22A | 2x |
| 19   | Wuchenhe Town, Xinyang, Henan; LR16034 | 31°45'N/114°47'E | 66 | 41 | 2n = 22A | 2x |
| 20   | Wufeng Town, Yichang, Hubei; LR16002 | 30°11'N/110°41'E | 760 | 11 | 2n = 22A | 2x |
| 21   | Rongmei Town, Enshi, Hubei; LR16028 | 29°49'N/109°54'E | 929 | 15 | 2n = 22A | 2x |
| 22   | Shadaogou Town, Enshi, Hubei; LR16030 | 29°41'N/109°36'E | 628 | 22 | 2n = 22A | 2x |
| 23   | Jiangyangping Town, Yichang, Hubei; LR16032 | 31°06'N/110°50'E | 543 | 20 | 2n = 22A | 2x |
| 24   | Beifeng Village, Yichang, Hubei; LR16007 | 31°06'N/110°49'E | 544 | 40 | 2n = 22A | 2x |
| 25   | Shaping Town, Xianning, Hubei; LR15005 | 29°22'N/113°50'E | 128 | 26 | 2n = 22A | 2x |
| 26   | Wudangshan, Shiyan, Hubei; LR16040 | 32°26'N/111°03'E | 353 | 11 | 2n = 22A | 2x |
| 27   | Maogou Town, Xiangxi, Hunan; LR15030 | 28°35'N/109°22'E | 273 | 30 | 2n = 22A | 2x |
| 28   | Miaoshi Town, Changde, Hunan; LR16018 | 29°28'N/111°12'E | 145 | 10 | 2n = 22A | 2x |
| 29   | Wulingyuan, Zhangjiajie, Hunan; LR15016 | 29°21'N/110°29'E | 423 | 28 | 2n = 22A | 2x |
| 30   | Biyunfeng, Yiyang, Hunan; LR15017 | 28°26'N/112°22'E | 488 | 23 | 2n = 22A | 2x |
| 31   | Houguashan, Chenzhou, Hunan; LR15020 | 25°52'N/113°17'E | 150 | 26 | 2n = 22A | 2x |
| 32   | Lujiaowan Village, Huaihua, Hunan; LR16022 | 28°35'N/110°27'E | 123 | 20 | 2n = 22A | 2x |
| 33   | Jiemuxi Town, Huaihua, Hunan; LR16024 | 28°47'N/110°25'E | 236 | 20 | 2n = 22A | 2x |
| 34   | Daping Town, Zhongjiajie, Hunan; LR16026 | 29°33'N/110°04'E | 502 | 40 | 2n = 22A | 2x |
| 35   | Liangshuikou Town, Zhongjiajie, Hunan; LR16027 | 29°00'N/110°30'E | 349 | 43 | 2n = 22A | 2x |
| 36   | Yixing forest park, Wuxi, Jiangsu; LR13001 | 31°17'N/119°45'E | 70 | 23 | 2n = 22A | 2x |
| 37   | Shipai Town, Suzhou, Jiangsu; LR11004 | 31°33'N/121°01'E | 9 | 16 | 2n = 22A | 2x |
| 38   | Zhangkou Town, Ganzhou, Jiangxi; LR15033 | 25°40'N/115°39'E | 160 | 23 | 2n = 22A | 2x |
| 39   | Yangxi Town, Ji'an, Jiangxi; LR15035 | 27°18'N/114°12'E | 196 | 8 | 2n = 22A | 2x |
| 40   | Tongtianyan, Ganzhou, Jiangxi; LR15022 | 25°55'N/114°54'E | 134 | 28 | 2n = 22A; 2n = 20A+1m | 2x |
| 41   | Nashan Village, Jinggangshan, Jiangxi; LR15023 | 26°43'N/114°16'E | 238 | 30 | 2n = 22A | 2x |
| 42   | Longhushan, Yingtan, Jiangxi; LR15025 | 28°05'N/116°38'E | 120 | 28 | 2n = 22A | 2x |
| 43   | Sishiba Town, Shangrao, Jiangxi; LR15026 | 28°12'N/118°02'E | 169 | 25 | 2n = 22A | 2x |

(Continues)
| Pop. | Localities (voucher) | Coordinates | Altitude (m) | Number of bulbs examined | Chromosome formula | Ploidy |
|------|----------------------|-------------|--------------|--------------------------|--------------------|--------|
| 44   | Yantou Town, Wenzhou, Zhejiang; LR15028 | 28°20′N/120°43′E | 53 | 31 | 2n = 22A | 2x |
| 45   | Chichengshan, Taizhou, Zhejiang; LR15029 | 29°10′N/121°01′E | 240 | 33 | 2n = 22A | 2x |
| 46   | Jiufengshan, Zhejiang; LR13012 | 29°00′N/119°22′E | 601 | 16 | 2n = 22A | 2x |
| 47   | Jingling Town, Xiangxi, Zhejiang; LR13014 | 29°22′N/120°47′E | 238 | 18 | 2n = 22A | 2x |
| 48   | Yangduan Village, Jiuxiang, Jiangxi; LR15004 | 29°32′N/115°22′E | 510 | 24 | 2n = 22A | 2x |
| 49   | Longpan Town, Nanchong, Sichuan; LR17001 | 30°49′N/105°53′E | 386 | 10 | 2n = 22A | 2x |
| 50   | Dayang Town, Lishui, Zhejiang; LR15032 | 28°31′N/120°11′E | 900 | 18 | 2n = 22A | 2x |
| 51   | Xidian Town, Ningbo, Zhejiang; LR15037 | 29°26′N/121°25′E | 35 | 6 | 2n = 22A | 2x |
| 52   | Qingliangfeng Town, Hangzhou, Zhejiang; LR13013 | 30°06′N/118°54′E | 222 | 19 | 2n = 22A | 2x |
| 53   | Jingtangshan, Xuanchong, Anhui; LR11001 | 30°59′N/118°43′E | 161 | 25 | 2n = 33A | 3x |
| 54   | Langyashan, Chuzhou, Anhui; LR08002 | 32°16′N/118°16′E | 211 | 36 | 2n = 33A | 3x |
| 55   | Huangpushan, Chuzhou, Anhui; 803271 | 32°20′N/118°00′E | 151 | 30 | 2n = 33A | 3x |
| 56   | Sanqi Town, Lu’an, Anhui; LR13010 | 31°14′N/116°41′E | 176 | 8 | 2n = 33A | 3x |
| 57   | Meijie Town, Chizhou, Anhui; LR12003 | 30°27′N/117°34′E | 120 | 18 | 2n = 33A | 3x |
| 58   | Longshe Town, Pengshui, Chongqing; LR16005 | 27°07′N/108°11′E | 932 | 6 | 2n = 33A | 3x |
| 59   | Xianwushan Town, Wulong, Chongqing; LR16006 | 29°24′N/107°47′E | 812 | 36 | 2n = 33A | 3x |
| 60   | Wenfeng Town, Wuxi, Chongqing; LR16031 | 31°25′N/109°10′E | 1,061 | 1 | 2n = 33A | 3x |
| 61   | Jinhan Town, Ningde, Fujian; LR16042 | 26°41′N/119°28′E | 148 | 26 | 2n = 33A | 3x |
| 62   | Maixieyan Village, Putian, Fujian; LR16043 | 25°32′N/118°48′E | 654 | 15 | 2n = 31A + 1m + 1B | 3x |
| 63   | Heping Town, Zhangzhou, Fujian; LR16044 | 23°56′N/117°10′E | 665 | 26 | 2n = 33A | 3x |
| 64   | Laizhou Town, Nanping, Fujian; LR08006 | 26°37′N/117°58′E | 450 | 10 | 2n = 33A | 3x |
| 65   | Tianbaoyuan Reserve, Yong’an, Fujian; LR08004 | 25°58′N/117°22′E | 715 | 15 | 2n = 33A | 3x |
| 66   | Heshui Village, Shaoguan, Guangdong; LR16019 | 24°53′N/113°56′E | 240 | 30 | 2n = 33A | 3x |
| 67   | Wangbian Village, Shaoguan, Guangdong; LR15021 | 25°04′N/113°19′E | 130 | 21 | 2n = 33A | 3x |
| 68   | Lytian Town, Conghua, Guangdong; LR16045 | 23°48′N/113°55′E | 224 | 30 | 2n = 33A | 3x |
| 69   | Licheng Town, Guilin, Guangxi; LR15006 | 24°29′N/110°24′E | 148 | 24 | 2n = 33A | 3x |
| 70   | Rongjiang Town, Guilin, Guangxi; LR15007 | 25°41′N/110°19′E | 293 | 39 | 2n = 33A | 3x |
| 71   | Tangjia Village, Guilin, Guangxi; LR15008 | 25°19′N/110°19′E | 156 | 5 | 2n = 31A + 1m + 1B | 3x |
| 72   | Pingxi Village, Qindongnan, Guizhou; LR16014 | 27°07′N/107°46′E | 716 | 30 | 2n = 33A | 3x |
| 73   | Zhaibao Village, Tongren, Guizhou; LR15011 | 27°46′N/108°45′E | 436 | 11 | 2n = 33A | 3x |
| 74   | Dongfeng Town, Guiyang, Guizhou; LR15012 | 26°38′N/106°49′E | 1,015 | 5 | 2n = 33A | 3x |
| 75   | Ali Village, Guiyang, Guizhou; LR15013 | 26°34′N/106°48′E | 1,052 | 25 | 2n = 33A | 3x |
| 76   | Chengguan Town, Pan County, Liupanshui, Guizhou; LR15014 | 25°47′N/104°40′E | 1,625 | 8 | 2n = 31A + 1m + 1m′ | 3x |
| 77   | Yaojiaotun Village, Anshun, Guizhou; LR15015 | 26°12′N/105°54′E | 1,399 | 27 | 2n = 33A | 3x |
| 78   | Hongshan Town, Suizhou, Hubei; LR15034 | 31°36′N/112°55′E | 210 | 21 | 2n = 33A | 3x |
| 79   | Cibe Town, Xiangyang, Hubei; LR15036 | 32°01′N/111°48′E | 166 | 24 | 2n = 33A | 3x |
| 80   | Bajiaodongzu Town, Enshi, Hubei; LR16004 | 30°07′N/109°23′E | 590 | 24 | 2n = 33A | 3x |
| 81   | Moudao Town, Lichuan, Hubei; LR16020 | 30°29′N/108°39′E | 1,032 | 25 | 2n = 33A | 3x |
| 82   | Zhonglu Town, Enshi, Hubei; LR16041 | 30°08′N/108°45′E | 1,088 | 31 | 2n = 33A | 3x |
| 83   | Majiawan, Hefeng County, Enshi, Hubei; LR16029 | 29°52′N/110°00′E | 583 | 1 | 2n = 33A | 3x |
| 84   | Xiaojiacun Town, Yongzhou, Hunan; LR16015 | 26°21′N/112°00′E | 103 | 20 | 2n = 33A | 3x |
| 85   | Dankou Town, Shaoyang, Hunan; LR16013 | 26°25′N/110°13′E | 400 | 25 | 2n = 33A | 3x |

(Continues)
from population 114. The four SATs, reported for the first time here, are the maximum number of SAT chromosome in this species known so far. Of 1,195 triploid bulbs, 1,166 bulbs are typical triploid consisting of 33 A-type chromosomes with 0–3 SAT chromosomes. A representative karyotype of triploid is shown in Figure 2d.

Some aberrant chromosomes which should be generated from A-type chromosome are found including metacentrics (m), small metacentrics (m′), and B-type chromosome (Table 3). The occurrence of Robertsonian fusion of A-type chromosomes is confirmed in some bulbs from five populations, for example, population 39, 62, 71, 76, and 113 32, 36, 40, 60, and 72. The karyotype of one bulb from population 39 in Tongtianyan mountain of Ganzhou city comprises two types of chromosome (A- and m-type chromosome), formulated as 2n = 21 = 20A + 1m (Figure 2e,m). Eight bulbs from population 76 in Pan County and one bulb from population 113 at Caishiji park are abnormal triploids and have 33 chromosomes with 31 A-type chromosomes, one metacentric chromosome (m-type chromosome) and a small metacentric chromosome (m′-type chromosome). The karyotype of them is formulated as 2n = 33 = 31A + 1m + 1m′ (Figure 2f,n). In addition, five bulbs from population 71 at Tangjia village of Guilin city and fifteen bulbs from population 62 at Maixie village of Putian

**TABLE 1** (Continued)

| Pop. | Localities (voucher) | Coordinates | Altitude (m) | Number of bulbs examined | Chromosome formula | Ploidy |
|------|----------------------|-------------|--------------|--------------------------|--------------------|--------|
| 86   | Bozhou Town, Huaihua, Hunan; LR16017 | 27°23′N/109°17′E | 325 | 24 | 2n = 33A | 3x |
| 87   | Yidushi Village, Shaoyang, Hunan; LR15009 | 26°34′N/111°12′E | 349 | 29 | 2n = 33A | 3x |
| 88   | Qingwei Village, Loudi, Hunan; LR15018 | 27°51′N/110°58′E | 626 | 12 | 2n = 33A | 3x |
| 89   | Liuxin Village, Loundi, Hunan; LR15019 | 27°51′N/110°59′E | 693 | 31 | 2n = 33A | 3x |
| 90   | Longtan Village, Zhuzhou, Hunan; LR16008 | 26°09′N/113°45′E | 480 | 20 | 2n = 33A | 3x |
| 91   | Huaguoshan, Lianyangang, Jiangsu; LR13002 | 34°39′N/119°16′E | 131 | 15 | 2n = 33A | 3x |
| 92   | Laoshan, Nanjing, Jiangsu; LR14001 | 32°06′N/118°36′E | 104 | 3 | 2n = 33A | 3x |
| 93   | Yushan, Lianyangang, Jiangsu; LR13004 | 34°38′N/119°15′E | 30.9 | 13 | 2n = 33A | 3x |
| 94   | Wutong Town, Guilin, Guangxi; LR16016 | 25°22′N/110°03′E | 180 | 28 | 2n = 33A | 3x |
| 95   | Wanger Town, Shangrao, Jiangxi; LR15031 | 28°17′N/117°30′E | 66 | 22 | 2n = 33A | 3x |
| 96   | Chenshan, Shanghai; LR16010 | 31°04′N/121°10′E | 25 | 38 | 2n = 33A | 3x |
| 97   | Sheshan, Shanghai; LR16011 | 31°05′N/121°11′E | 57 | 37 | 2n = 33A | 3x |
| 98   | Longwangou, Lueyang County, Shannxi; LR13015 | 33°22′N/106°09′E | 692 | 6 | 2n = 33A | 3x |
| 99   | Liyushan, Ankang, Shannxi; LR16036 | 32°41′N/108°55′E | 300 | 6 | 2n = 33A | 3x |
| 100  | Taibai Village, Hanzhong, Shannxi; LR16039 | 33°00′N/106°47′E | 554 | 36 | 2n = 33A | 3x |
| 101  | Dahanshan, Hanzhong, Shannxi; LR16038 | 32°57′N/106°56′E | 950 | 6 | 2n = 33A | 3x |
| 102  | Taibaishan, Baoji, Shannxi; LR16039 | 34°05′N/107°42′E | 1,136 | 6 | 2n = 33A | 3x |
| 103  | Motan Town, Guangyuan, Sichuan; LR16003 | 32°10′N/106°03′E | 868 | 24 | 2n = 33A | 3x |
| 104  | Dafo Town, Leshan, Sichuan; LR10001 | 29°46′N/104°03′E | 436 | 27 | 2n = 33A | 3x |
| 105  | Changyuanguo Village, Nanchong, Sichuan; LR16009 | 30°51′N/105°59′E | 310 | 15 | 2n = 33A | 3x |
| 106  | Dayun Village, Yibin, Sichuan; LR13005 | 28°22′N/104°46′E | 597 | 30 | 2n = 33A | 3x |
| 107  | Futou Village, Yibin, Sichuan; LR13006 | 28°20′N/104°53′E | 447 | 31 | 2n = 33A | 3x |
| 108  | Gaojian Village, Yibin, Sichuan; LR13007 | 28°17′N/104°59′E | 604 | 30 | 2n = 33A | 3x |
| 109  | Emeishan, Leshan, Sichuan; LR16033 | 29°36′N/103°23′E | 880 | 6 | 2n = 33A | 3x |
| 110  | Baishanzu Town, Lishui, Zhejiang; LR08005 | 27°43′N/119°12′E | 1,074 | 5 | 2n = 33A | 3x |
| 111  | Huilongchang Village, Nanchong, Sichuan; LR16012 | 30°53′N/105°59′E | 387 | 6 | 2n = 22A; 2n = 33A | 2x(1) + 3x(5) |
| 112  | Lianhua Village, Wuhu, Anhui; LR13011 | 31°03′N/117°32′E | 223 | 13 | 2n = 22A; 2n = 33A | 2x(11) + 3x(2) |
| 113  | Caishiji park, Ma’anshan, Anhui; LR08003 | 31°39′N/118°27′E | 101 | 26 | 2n = 22A; 2n = 22A + 1B; 2n = 33A; 2n = 31A + 1m + 1m′ | 2x(16) + 3x(10) |
| 114  | Tangxi Town, Chizhou, Anhui; LR12002 | 30°20′N/117°36′E | 112 | 36 | 2n = 22A; 2n = 44A | 2x(35) + 4x(1) |
city also have the m-type chromosome, and the karyotype of them is formulated as \(2n = 33 = 31A + 1m + 1B\) (Figure 2g,h,o,p). Two and one SAT chromosomes are observed in the population 71 and 62, respectively. The arm ratio of m-type chromosome in the bulbs from population 71 and population 62 is 1.0 and 1.1, respectively. Small B-type chromosome is also observed in two bulbs from population 113, with the karyotype formulated as \(2n = 22 = 22A + 1B\). Both m'-type chromosome and B-type chromosome should originate from A-type chromosomes, but the former has at least twofold length than the latter.

### 3.3 Distribution of different cytotypes in China

Diploid cytotypes are located primarily in the middle and east regions of China. Isolated diploid populations are found in southeast areas of China. The triploid cytotypes have a wider distribution, occupying nearly the whole distribution range of this species in China. Six provinces located on the periphery of the distribution area have no more than one diploid population (Figure 3).

In Figure 4, it is indicated that the triploids have a broader altitudinal range than the diploids. The triploids grow over a broad range of altitudes, from 25 to 1,625 m, with the average being 513.39 ± 382.53 m, while the diploids have a narrower altitudinal range of 9–929 m, with an average of 299.06 ± 226.76 m. The difference in mean altitude of localities between diploid and triploid is highly significant (\(p < 0.01\); Figure 4a), Moreover, a significantly positive but low correlation was found between the ploidy and altitude (\(r^2 = 0.103, p < 0.01\); Figure 4b).

### 4 DISCUSSION

#### 4.1 The chromosome number and karyotype of *Lycoris radiata*

Several cytological studies on *L. radiata* have been made by various authors (Bose, 1963; Kurita, 1987; Nishiyama, 1928; Qin et al., 2004; Shao et al., 1994; Zhou et al., 2007). Recently, Liu et al. (2016) reported the somatic chromosome numbers of four hundred and sixty-six individuals from 25 populations of *L. radiata* in China, of which 10 were diploid (\(2n = 22\)) and 15 were triploid (\(2n = 33\)), and no tetraploid cytotype was found. In this study, 1,224 diploid individuals, 1,195 triploid individuals, and one tetraploid individual were detected. Despite the small proportion for the tetraploid, these new counts, together with data from the previous reports (Kurita, 1987; Liu et al., 2016; Zhou et al., 2007), further confirm that *L. radiata* is a species complex concluding diploid with \(2n = 22\), triploid with \(2n = 33\), and tetraploid with \(2n = 44\).

The common karyotype of *L. radiata* only consists of typical acrocentric chromosomes (A-type chromosome) with different types of SATs combination. To date, many abnormal karyotypes of this complex have been reported, such as \(2n = 22 = 1m + 20A + 1B\) (Shao et al., 1994); \(2n = 33 = 1m + 31A + 1B\), \(2n = 32 = 1m + 31A\) (Bose, 1963; Kurita, 1987); \(2n = 21 = 1m + 10st + 9T + 1B\) (Zhou et al., 2004); \(2n = 21 = 1m + 20st, 2n = 25 = 1m + 20st + 2t + 2T\) (Zhou et al., 2007), due to the various rearrangements of A-type chromosome. Through careful examination on the karyotype of 519 bulbs of *L. radiata* in Japan, Kurita (1987) observed 14 bulbs with aberrant chromosomes.
whereas no bulb with aberrant chromosomes was found by Liu et al. (2016) based on the cytological study of 466 bulbs of this species in China. As reported in the previous studies, some rearranged chromosomes from A-type chromosome which are aberrant have been also found in this paper. The number of bulbs with aberrant chromosomes is small, only accounting for 1.32% of total examined bulbs (32/2,420), and the aberrants could be classified into three types and include metacentric chromosome (m), small metacentric chromosome (m‘), and B-type chromosome. The diploid populations have less abnormal individuals with aberrant chromosomes than the triploid populations. Because the diploids have both sexual and asexual reproduction, and the individual with aberrant chromosomes producing no seeds might be gradually excluded from the population due to intraspecific competition, so less individuals with aberrant chromosomes were found from the diploid population than from the triploid population.

The phenomenon of Robertsonian fusion of A-type chromosome was found in some bulbs from five different populations. As confirmed in some previously published researches, the m-type chromosome in one diploid bulb from population 40 may be produced by the fusion of two A-type chromosomes. Concerning the origin of the triploid individuals carrying aberrant m-type chromosome, there are two alternative explanations. The one is that the m-type chromosome was generated from a diploid population including the bulb with m-type chromosome by hybridization between a normal haploid gamete and an unreduced diploid gamete; the other is that it started from a somatic cell of a bulb having only A-type chromosomes, in which m-type chromosome was formed by Robertsonian change, as it was observed in the diploid bulb of population 40. Which explanation is reasonable, hybridization or somatic cell mutation? Eleven abnormal triploid bulbs with m-type chromosome had been also found by Kurita (1987). He considered that the latter, somatic cell mutation, might be the actual occurrence, because only a very small proportion of examined bulbs carried the aberrant m-type chromosome. The authors agreed with Kurita’ opinion, considering that the m-type chromosome in aberrant diploid and triploid bulbs should be produced by Robertsonian fusion.

Although the karyotypes of L. radiata have some variability among inter-populations and even within intra-population to some extent, it was convinced that L. radiata have a relatively stable karyotype composed of 22/33/44 A-type chromosomes on the basis of large-scale sampling from China and Japan.

**TABLE 2** Measurements of somatic chromosomes in a representative karyotype of diploid

| No. | SL  | LL  | TL  | Arm ratio | Type |
|-----|-----|-----|-----|-----------|------|
| 1   | 0.83| 4.61| 5.44| 5.57      | A    |
| 2   | 0.75| 4.41| 5.16| 5.89      | A    |
| 3   | 0.59| 4.57| 5.16| 7.73      | A    |
| 4   | 0.71| 4.41| 5.12| 6.22      | A    |
| 5   | 0.43| 4.65| 5.08| 10.73     | A*   |
| 6   | 0.47| 4.41| 4.89| 9.33      | A    |
| 7   | 0.55| 4.33| 4.89| 7.86      | A    |
| 8   | 0.67| 4.14| 4.81| 6.18      | A    |
| 9   | 0.51| 4.06| 4.57| 7.92      | A    |
| 10  | 0.59| 3.98| 4.57| 6.73      | A    |
| 11  | 0.75| 3.78| 4.53| 5.05      | A    |
| 12  | 0.63| 3.86| 4.49| 6.13      | A    |
| 13  | 0.51| 3.94| 4.45| 7.69      | A    |
| 14  | 0.43| 4.02| 4.45| 9.27      | A*   |
| 15  | 0.51| 3.90| 4.41| 7.62      | A    |
| 16  | 0.63| 3.74| 4.37| 5.94      | A    |
| 17  | 0.67| 3.55| 4.22| 5.29      | A    |
| 18  | 0.32| 3.66| 3.98| 11.63     | A    |
| 19  | 0.59| 3.27| 3.86| 5.53      | A    |
| 20  | 0.55| 3.31| 3.86| 6.00      | A    |
| 21  | 0.32| 3.55| 3.86| 11.25     | A    |
| 22  | 0.63| 3.19| 3.82| 5.06      | A    |

Note: Asterisk indicates SAT chromosome.
Abbreviations: LL, relative length of long arm; SL, relative length of short arm; TL, total relative length; SL + LL=TL.

**4.2 | The distribution patterns of cytotypes and origin of polyploids**

Information on the geographical variation of cytotypes is critical for studies of origin and evolution of polyploids (Wu et al., 2016). A detailed investigation of the distribution of diploids and derivative polyploids can provide critical insights into the origins and establishment of new polyploids and cryptic speciation within a morphological species (Baack, 2004; Odee, Wilson, Omondi, Perry, & Cavers, 2015; Segraves, Tompson, Soltis, & Soltis, 1999; Steussy, Weiss-Schneeweiss, & Keil, 2004). In this study, we conducted an exhaustive survey of the chromosomal races in most populations within the natural range of L. radiata across the entire distribution regions in China.

Although whether or not polyploids have a broader niche breadth than diploids remains controversial (te Beest et al., 2012; Glennon, Ritchie, & Segraves, 2014; Martin & Husband, 2009), in numerous complex species documented by many authors (Lowry & Lester, 2006; McIntyre, 2012; Treieret al., 2009), the polyploids show wider

**TABLE 3** The percentage of bulbs having aberrant chromosomes

| Ploidy level | Number of bulbs examined | Number of bulbs with aberrant chromosomes |
|--------------|--------------------------|------------------------------------------|
|              | m            | m’         | B       |
| Diploid      | 1,224        | 1          | 0       | 2     |
| Triploid     | 1,195        | 20         | 9       | 20    |
| Tetraploid   | 1            | 0          | 0       | 0     |
| Total number | 2,420        | 21         | 9       | 22    |
geographic ranges and greater stress tolerances of extreme ecological conditions. In comparison with the diploids, the triploids have a significantly larger geographic range. The triploids distribute from the southwest of China eastward to the south of Korea and south of Japan, covering the whole geographic distribution ranges of the complex. In contrast, the diploids are primarily limited to the middle and east of China, with some diploid populations scattering in the southeast of China. Together with some previous reports (Kurita, 1987; Liu et al., 2016), it can be concluded that the triploid shows a significantly wider distribution range than the diploid, with the former occupying almost the whole distribution range of this complex in East Asia.
A positive correlated relationship between polyploidy and elevation is fairly well supported (Brochmann et al., 2004; Soltis, 1984; Stebbins, 1984). However, in several other cases, the polyploids occupy the lower latitude localities, and a negative correlation of polyploidy with elevation was found, for example, *Atriplex confertifolia* (Stutz & Sanderson, 1983), *Chamerion angustifolium* (Husband & Schemske, 1998), *Centaurea jacea* (Hardy, Vanderhoeven, Loose, & Meerts, 2000), and *Isoetes* spp. (Liu, Gituru, & Wang, 2004). In general, the triploids tend to prefer such place as roadsides, riversides, and the edges of rice paddies or farmlands, and occupy the high altitude regions. Diploids are specific to undisturbed or less-disturbed habitats, frequently growing under forests, in the lower latitude localities. Moreover, the triploids are expected to present a stronger tolerance to cold temperature, because the triploids show a higher relative distribution dominance than the diploids at higher latitudes. In regard to the north boundary of *L. radiata* distributed in East Asia, the latitude value of diploid and triploid is about 32.6° and 39.0°, respectively. However, this hypothesis needs to be empirically confirmed by further controlled experiments in common garden or greenhouse.

In addition, there is a complicated and perplexing question about the origin and distribution pattern of the polyploids, especially the triploid. The triploid was usually supposed to be an autotriploid (Hayashi, Saito, Mukai, Kurita, & Hori, 2005; Kurita, 1987; Nishiyama, 1928). About the origin of the triploid, there are two key hypotheses. The first is that they are generated from the hybridization of diploid with tetraploid. The second is that they are derived from a crossing between a normal haploid gamete and a nonreduced diploid gamete (Hsu et al., 1994; Kurita, 1987; Zhou et al., 2007). Because the tetraploid has only recently been discovered (Zhou et al., 2007; this paper), most researchers agree to the latter interpretation (Hayashi et al., 2005; Kurita, 1987). To date, only two mixploid populations with the tetraploid cytotype are found, and no independent tetraploid population is detected. In view of the very few tetraploid individuals in natural populations, the authors also agree with the latter explanation.

However, based on an extensive cytogenetical study on the Japanese triploid populations, Kurita (1987) thought that *L. radiata* var. *radiata* is not a simple autotriploid. Namely, the triploid is structurally heterozygous at least in regard to the SAT chromosomes (Kurita, 1987). By analyzing the nucleotide sequences of genomic DNA regions in 15 triploid strains and two diploid strains from Japan and China, Hayashi et al. (2005) found some genetic variations between the Japanese and Chinese triploid strains, indicating that *L. radiata* var. *radiata* is not a typical autotriploid, supporting Kurita’s notion. In our extensive field investigations, we found that the triploids in China also have different SAT chromosome combination, supporting their notion.

Another perplexing problem is why the triploids are distributed very commonly in Japan and South Korea where no diploid mother taxon can be found. The diploids are only distributed in China, and no diploid cytotype has been found so far in Japan and South Korea. Based on the genetic constancy of Japanese triploids in both the nuclear and chloroplast DNA sequences (Hayashi et al., 2005) and the monomorphism on all 24 allozyme loci in Korean *L. radiata* populations (Chung, 1999), they thought that the sterile triploids in Japan and South Korea were introduced from China, that is, one and more triploid bulb were brought to Japan and South Korea firstly, and then via extensive asexual reproduction by the rapid formation of new bulbs the triploid spread throughout Japan (except Hokkaido) and South Korea, accompanying human activities to some extent, such as rice cultivation and movement of monks in temples (Chung, 1999; Hayashi et al., 2005; Kurita, 1987). Because the peripheral regions of China, including Yunnan, Guangxi, and South Guizhou possess only triploid populations, as Japan and South Korea do, it is conceivable that it may be the same reason responsible for the formation of the current distribution pattern of *L. radiata* complex cytotypes and nonexistence of the diploid population on the periphery of the distribution range.

With regard to the geographical patterns of different cytotypes of *L. radiata* complex, especially the triploids, there are two possible interpretations. The one is that the triploids are generated from the diploids located in the middle and east of China, then they spread to the surrounding areas where the triploids generally prefer more local environment; the other is that the parental diploid taxon which once had been distributed relatively widely in China, Japan, and South Korea was extinct in Japan, South Korea and many peripheral distribution areas of China for some unknown reasons, only leaving the triploid bulbs. In order to find the key to the questions of the origin, migration routes and distribution patterns of polyploids of *L. radiata*, some molecular and cytogenetic methods are needed in the future study.

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**CONFLICT OF INTEREST**

None declared.

**AUTHORS’ CONTRIBUTIONS**

Liu, K. and Zhou, S.B. designed the research. Liu, K. and Meng, W.Q. collected the samples. Liu, K., Wang, L.D., Meng, W.Q., and Zheng, L. generated and analyzed the data. Liu, K. and Zhou, S.B. wrote the manuscript.

**DATA ACCESSIBILITY**

The data supporting the conclusions of this manuscript can be found in the manuscript.
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