A Three-dimensional Analysis of Summer Dormancy in the Red Spider Lily (*Lycoris radiata*)

Junhuo Cai¹

College of Landscape and Art, Jiangxi Agricultural University, Nanchang 330045, China

Junjun Fan¹

College of Horticulture, Jinling Institute of Technology, Nanjing 210038, China

Xuying Wei

College of Art, Jiangxi Finance and Economics University, Nanchang 330032, China

Lu Zhang²

College of Landscape and Art, Jiangxi Agricultural University, Nanchang 330045, China; and 2011 Collaboration Innovation Center of Jiangxi Typical Trees Cultivation and Utilization, Jiangxi Agricultural University, Nanchang 330045, China

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Abstract. *Lycoris radiata* has beautiful bright-red flowers with both medicinal and ornamental value. However, the mechanisms underlying an unusual characteristic of *Lycoris radiata*, flowering without leaves, remain unclear. In this study, climatic influences, biomass composition, and yearly variations in bulb contents across eight developmental stages of *L. radiata* were analyzed. Thus, *L. radiata* summer dormancy was investigated in three dimensions: climate-associated phenology, biomass distribution characteristics, and physiologic bulb changes. The results showed that dormancy was most strongly affected by high ambient temperature, followed by scape development, flowering, leafing out, vigorous leaf growth, flower bud differentiation, flower bud predifferentiation, and leaf maturation. Biomass allocation, bulb contents, oxidoreductase activity, and root activity fluctuated significantly in *L. radiata* among developmental stages. Relative bulb dry weight was greatest during the dormant period (95.95% of total dry weight) and lowest during vigorous leaf growth (November–December). Root biomass was also significantly greater during dormancy than during flowering, leaf maturation, and flower bud differentiation. Only root biomass during vigorous leaf growth was greater than root biomass during dormancy. However, in dormant bulbs, soluble sugar content, soluble protein content, root activity, superoxide dismutase (SOD) activity, and peroxidase (POD) activity decreased. Thus, summer dormancy in *L. radiata* only constitutes a morphologic dormancy of the aboveground plant; the bulb and root remain physiologically active. The results suggest that *L. radiata* is sensitive to both ambient temperature and light, and that summer dormancy is triggered by the synergistic stimulation of these two factors. Although temperature controls dormancy, it plays only a limited regulatory role during the *L. radiata* flowering period. Thus, it is difficult to induce flowering or regulate annual flowering in this species through temperature control alone.

The genus *Lycoris* (Amaryllidaceae) is comprised of ≈20 species of herbaceous

bulbs native to East Asia (Iqbal et al., 2006; Ren et al., 2017). Of these, 15 species of are distributed in China, including 10 endemics (Tsi and Meerow, 2000; Yuan, 2010). *Lycoris* species have great commercial potential because this flower has medicinal as well as ornamental value (Jin, 2002). Indeed, *Lycoris* species are grown as cut flowers, potted flowers, and garden cover throughout Europe, the United States, and Japan. The Netherlands, in particular, cultivates *Lycoris* species over an area of more than 600,000 m² (Song et al., 2014).

Plants in the genus *Lycoris* have a period of summer dormancy and, uniquely, flower without leaves (Cui et al., 2004). This suggests that the summer growth rhythms of these plants are incompatible with the humid subtropical climate of their Chinese habitats (Wang, 1990). Based on sprouting time, leaves can be divided into autumn leaves and early spring leaves (Zhang and Cao, 2001). *Lycoris* species flower from July to September. However, the mechanisms underlying summer dormancy and flowering in this genus have not been fully characterized.

Lycoris radiata is a typical *Lycoris* species with autumn leaves (i.e., the leaves remain green throughout the winter) and beautiful bright-red flowers. Commonly known as the “Chinese tulip,” *L. radiata* is one of the two most widely cultivated *Lycoris* species (along with *L. aurea*) as a result of its beautiful color and flower morphology (Song et al., 2014). However, because it is difficult to regulate the flowering time of *L. radiata* effectively, this plant has been largely ignored by the global cut-flower industry (Cai et al., 2012; Meng et al., 2008). To address this knowledge gap, we therefore used *L. radiata* as a model *Lycoris*, and investigated summer dormancy comprehensively in three dimensions: phenologically, ecologically, and physiologically. Specifically, we studied the annual dynamics of biomass distribution, climate-associated phenology, and physiologic bulb characteristics. Our results give insights into the mechanisms underlying summer dormancy, and provide a framework for both future ecologic research on *Lycoris* and the industrial exploitation of other bulbous plants.

Materials and Methods

Plant materials and growth conditions. All pot experiments were performed outdoors in the flower gardens of Jiangxi Agricultural University, Nanchang, Jiangxi, China (lat. 28.76°N, long. 115.83°E). We planted 4-year-old *L. radiata* bulbs (diameter, 3.5 ± 0.1 cm), obtained via vegetative propagation, in red soil (derived from quaternary red clay). The red soil layer was up to 40 cm thick and was comprised of several different sizes of particles: <0.002 mm (12.12%), 0.002 to 0.05 mm (51.63%), 0.05 to 2.00 mm (35.87%), and >2.00 mm (0.38%). The concentrations of organic matter, nitrogen, phosphorus, and potassium in the soil were 13.5, 0.84, 0.24, and 24.9 g·kg⁻¹, respectively. The soil pH was 6.43. The climate of Nanchang is a subtropical monsoon climate, with sufficient sunshine, an average temperature of 17 to 18 °C, an annual precipitation of 1600 to 1700 mm, and an annual average relative humidity of 78.5%. The average minimum temperature in Nanchang is 3.9 °C in January; the average maximum temperature is 38.7 °C in July.

Methods. An outdoor pot experiment, using potted *L. radiata*, ran from 15 Oct. 2016 to 15 May 2017. For this experiment, we dug up *L. radiata* bulbs in mid May 2016, after the leaves had died. We selected 720

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¹These authors contributed equally to this article.

²Corresponding author. E-mail: zhlu856@163.com.

bulbs of about the same size and planted them in individual pots (10 × 15 cm) in 3 parts perlite:4 parts peat:3 parts laterite (v/v). We subjected groups of 240 potted *L. radiata* plants to one of three different treatments; each treatment group was replicated twice. Every 15 d, we measured the dry weight of three randomly selected *L. radiata* plants. To measure dry weight, each whole plant was first excavated and rinsed in tap water, with special care taken to keep the root system intact, then allowed to dry naturally. When dry, each plant was separated into its root system, bulb, and leaves plus flowers (including scapes). Each component was dried separately at 85 °C until weight was constant.

In addition, we selected at random three *L. radiata* plants per plot every 30 d, extracted the bulbs, and measured soluble sugar content, soluble protein content, root activity, SOD activity, and POD activity in each bulb. Root activity was determined using the triphenyltetrazolium chloride method (Cai et al., 2018a), and concentrations of other substances in the bulb were determined as described previously (Cai, 2012). In brief, soluble sugar content, soluble protein content, SOD activity, and POD activity were measured using anthrone colorimetry, Coomassie brilliant blue staining (g-250), nitrotriazolium blue chloride photochemical reduction (for which the inhibition of 50% of the photochemical reduction was considered one enzyme activity unit), and guaiacol colorimetry, respectively.

Phenologic indices. To observe the phenologic characteristics of *L. radiata* throughout its entire lifecycle (i.e., from leafing out to flower wilting), several phenologic indices were recorded every 10 d between 1 Sept. 2013 and 20 Oct. 2016. The indices were associated primarily with the leaves (the number of new leaves, the length and width of the leaves, and the degree of leaf yellowing and withering) and the flowers (the sprouting of scapes, the number of flower buds, and the degree of flowering and withering).

Data analysis. The mean and SD of each index were calculated using Microsoft Excel 2013. We compared the different levels of any given factor using one-way analyses of variance, followed by Duncan's multiple range tests, in SPSS version 19.0 (IBM Corporation, Armonk, NY).

Results

***L. radiata* morphology.** To adapt to local environments effectively, plants allocate their limited biomass resources to different organs and functional structures (Ren et al., 2009). Therefore, plants with different types of life cycles usually display distinct biomass distribution patterns across various organs (Tao and Zhang, 2014). In particular, most perennial herbaceous plants typically have large root-to-shoot biomass ratios (Li et al., 2009). Based on the annual growth rhythms and phenologic characteristics of *L. radiata*, the development of this species can be divided into eight distinct stages (Fig. 1): 1) leafing out (i.e., the leaf extends to the soil

surface), 2) vigorous leaf growth (i.e., rapid leaf extension), 3) leaf maturity (i.e., the leaf stops growing), 4) flower bud predifferentiation (i.e., the leaf tip begins to turn yellow), 5) flower bud differentiation (i.e., the leaf withers), 6) dormancy (i.e., leafless), 7) scape development, and 8) flowering (Fig. 1).

The annual dynamics of biomass distribution in *L. radiata*. Similar to other *Lycoris* species, *L. radiata* is a bulbous perennial with an unusual biomass distribution pattern (Kawano, 2009). The *Lycoris* bulb, which is critical for energy storage and regulation, plays an important role in the growth of *Lycoris* species throughout their entire life cycle (Yang and Nie, 2007). In our study, *L. radiata* plants typically had four to six leaves and an average of 0.5 scape per bulb. The average relative amounts of annual dry matter accumulated in the bulbs, roots, leaves, and flowers were 82.81%, 7.54%, 7.11%, and 2.55%, respectively, whereas the ratio of aboveground dry matter to belowground dry matter was ≈1:9. In *L. radiata*, relatively more biomass was allocated to the leaves and roots than to the floral organs, increasing the photosynthetic area and improving organic matter synthesis. A similarly high percentage of biomass is allocated to the roots in the Xinjiang tulip (Abdusalam et al., 2012).

Belowground and total biomass remained relatively stable in *L. radiata* throughout the growing season; belowground biomass correlated positively and significantly with total biomass ($R = 0.99$). In contrast, aboveground biomass fluctuated with phenologic changes (i.e., during the development of leaves, flowers, or fruit). In winter (January–February) and autumn (October–December), below- and aboveground biomass increased; below- and aboveground biomass decreased in the spring and early summer (March–July). The dry matter content of the aboveground biomass decreased in the spring (February–May; as the leaves yellowed and withered), but increased continuously during the late summer and fall as a result of scape development (August), flowering (September), leafing out (October), and leaf development (November–December). The dry matter content of the belowground biomass increased continuously from January to August (most dramatically between January and May), decreased sharply in September, and remained stable during the autumn and early winter (October–December).

Root biomass correlated weakly and negatively with flower biomass ($R = -0.287$, $P = 0.174$), bulb biomass correlated moderately negatively with flower biomass ($R = -0.566$, $P = 0.004$), and leaf biomass correlated moderately positively with flower biomass ($R = -0.612$, $P = 0.001$). Bulb biomass correlated weakly with leaf biomass ($R = 0.074$, $P = 0.732$) and root biomass ($R = -0.126$, $P < 0.558$), whereas root biomass correlated very weakly and positively with leaf biomass ($R = 0.385$, $P = 0.063$). These results suggest that different organs might compete for biomass, resulting in incom-

pletely synchronized growth rhythms with shifting biomass allocation priorities.

We observed a clear growth rhythm in the *L. radiata* root system. Root biomass decreased significantly during leaf yellowing ($P < 0.0001$; March–April), and increased continuously during vigorous leaf growth (September–December). The replacement of old roots with new roots occurred during leaf yellowing (March–May), whereas the development of new primary roots (rough roots) was most rapid in the spring (April–June). The development of new secondary roots (fine roots) was most rapid during the autumn (November–December) (Cai et al., 2018a). This was consistent with a previous observation that old *L. radiata* roots were replaced with new roots in April (Nishitani et al., 2013).

Biomass content at different developmental stages. Biomass accumulation across various *L. radiata* organs differed significantly at different developmental stages ($P < 0.0001$; Fig. 2). Biomass accumulation peaked in the roots during vigorous leaf growth, in the leaves during leaf maturation, in the bulbs during dormancy, and in the scapes (including flowers) during flowering.

During vigorous leaf growth, the dry weight of the *L. radiata* plant roots was greatest, and the relative root biomass peaked (14.07% of the total biomass). The relative root biomass during this period was significantly greater than during any other developmental stage ($P < 0.0001$). The dry matter weight of the bulbs was greatest during dormancy. During dormancy, relative biomass allocation also peaked (96.73% of the total biomass), and was significantly greater than during any other stage ($P < 0.0001$). Relative bulb biomass was lowest during vigorous leaf growth (November–December). Interestingly, relative root biomass was also high in *L. radiata* plants during dormancy, and significantly greater than relative root biomass during flowering, leaf maturity, and flower bud differentiation ($P < 0.0001$ for all comparisons). These results highlight the pattern of asynchronous growth between the roots and leaves of *L. radiata*.

Meteorologic characterization of summer dormancy in *L. radiata*. Ambient temperatures may affect the growth rhythms of *L. radiata* significantly (Cai, 2012; Cai et al., 2018b). Ambient temperatures had the greatest effect on *L. radiata* during dormancy, followed by scape development, flowering, leafing out, vigorous leaf growth, flower bud differentiation, flower bud predifferentiation, and leaf maturation (Fig. 2). Before flower bud differentiation, a short period of low temperatures (6 to 12 °C) was necessary. Plants required high temperatures (26 to 30 °C) before flowering initiation, but only required temperatures around 25 °C during flowering. In contrast, the ambient temperatures required for leafing out and vigorous leaf growth were relatively low (≈20 °C and ≈14 °C, respectively).

Fig. 1. Annual growth rhythms and phenologic characteristics of *L. radiata*. (I) Leafing out (October). (II) Vigorous leaf growth (November). (III) Leaf maturity (December–February). (IV) flower bud predifferentiation (March). (V) Flower bud differentiation (April–May). (VI) Dormancy (June–July). (VII) Scape development (August). (VIII) Flowering (September).

The length of the light/dark cycle is closely related to plant growth and development (Burns, 1946; Cai, 2012). In *Lycoris* plants, short days promote vegetative growth whereas long days increase reproductive growth (Cai, 2012). In our study, the average daylength during vigorous leaf growth was 10.7 to 11.5 h, whereas the average daylength during flower bud differentiation, dormancy, and scape development was 12.9 to 13.9 h. The effective amount of solar radiation also affected the growth and development of *L. radiata*. Scape development required the greatest monthly average effective solar radiation, followed by flowering, dormancy, leafing out, vigorous leaf growth, flower bud differentiation, leaf maturity, and flower bud predifferentiation.

Ambient humidity, as well as the amount and frequency of rainfall, also affected the growth and development of *L. radiata*. During flowering, leafing out, and vigorous leaf growth, humidity was relatively low (68% to 74%), with lower than average monthly rainfall (54.5–86.9 mm), and fewer rainy days (≈ 6.8 –8.8). In contrast, relative humidity was significantly greater (78% to 82%) during flower bud differentiation and scape development ($P < 0.0001$). *L. radiata* transitioned from the vegetative phase to the reproductive phase during April and

May. As this period coincides with the rainy season in eastern China (substantial increases in both rainfall frequency and rainfall amount), this transition may be related to increased levels of humidity.

Physiologic characterization of summer dormancy in *L. radiata*. During the summer, the aboveground parts of the *L. radiata* plant are withered and the belowground bulbs are dormant (Cai, 2012). To investigate summer dormancy in this species, we characterized the annual dynamic changes in bulb physiology and root activity. We identified significant differences in bulb contents (i.e., soluble sugars and proteins), bulb oxidoreductase activity, and root activity across the different developmental stages ($P < 0.0001$; Fig. 3).

During vigorous leaf growth (October–February), soluble sugar content and the activity levels of the enzymes SOD and POD in the bulbs decreased continuously, whereas bulb soluble protein content and root activity increased. In contrast, soluble sugar content increased rapidly and soluble protein content decreased significantly ($P < 0.0001$) from leaf maturity to flower bud differentiation (March–May). This indicated that, before flower bud differentiation, the formation of the mature leaves used much of the soluble sugar as energy. However, during flower bud

differentiation, soluble protein was consumed to support the morphologic differentiation of the bulb terminal bud, consistent with previous morphologic and anatomic studies of bulb flower differentiation (Cai, 2012).

During the dormant period, soluble sugar content decreased significantly ($P < 0.0001$), whereas soluble protein content and root activity increased significantly. This indicates that active physiologic changes continued in the bulb terminal bud during dormancy, and that the development and morphogenesis of the floral organs occurred simultaneously (Cai, 2012).

Bulb soluble protein content and root activity continued to decrease during scape development, whereas bulb soluble sugar content, SOD activity, and POD activity increased. This increase then decrease in SOD and POD activity might be associated with scape development after dormancy, and might allow *L. radiata* to tolerate higher ambient temperatures. Bulb soluble sugar content, bulb soluble protein content, root activity, and SOD activity decreased between flowering and leafing out, whereas POD activity increased. This might have been a result of the increases in cell wall synthesis and energy consumption associated with flowering and leafing out.

Fig. 2. Biomass of *Lycoris radiata* organs and climatic data corresponding to different development stages. (A) Biomass of *Lycoris radiata* organs at different development stages. (B) Temperature data at different development stages. (C) Solar radiation data at different development stages. (D) Rainfall data at different development stages. I, leafing out (October); II, vigorous leaf growth (November); III, leaf maturity (December–February); IV, flower bud predifferentiation (March); V, flower bud differentiation (April–May); VI, dormancy (June–July); VII, scape development (August); VIII, flowering (September). Climatic data for Nanchang, Jiangxi province, China, from 1986 to 2015 was obtained from the Jiangxi meteorologic bureau.

Discussion

The relationship between summer dormancy and biomass distribution in L. radiata. Biomass distribution among plant organs may reflect the genetic and developmental characteristics of the plant (Ren et al., 2009). Across the entire growing season, the ratio of dry matter to bulbs, roots, leaves, and flowers in *L. radiata* was $\approx 11:1:1:0.36$, and the ratio of aboveground dry matter to belowground dry matter was $\approx 1:9$ (belowground dry matter was 90.35% of the total dry matter). The bulb represented most of the belowground biomass (82.81%); indeed, relatively large bulbs are a typical physiologic feature of *L. radiata* (Yang and Nie, 2007).

The weight of *L. radiata* dry matter changed significantly at different developmental stages ($P < 0.0001$). Biomass accu-

mulation peaked in the roots, leaves, bulbs, and scapes (including flowers) during vigorous leaf growth, leaf maturity, dormancy, and flowering, respectively. Of the developmental stages investigated in our study, bulb dry weight was greatest during dormancy (95.95% of total dry weight), which is significantly greater than bulb dry weight during other developmental stages ($P < 0.0001$). Bulb dry weight was lowest during vigorous leaf growth. In comparison, the dry weight of roots was greatest during vigorous leaf growth (13.84% of total dry weight), followed by dormancy; root dry weight then decreased significantly ($P < 0.0001$) during flowering, leaf maturity, and flower bud differentiation. Thus, the phenologic period of root growth in *L. radiata* (December) is slightly earlier than that of leaves (mid January), and leaf growth occurs before bulb growth (May–July).

Based on the yearly dynamic changes in biomass accumulation, the below- and aboveground biomasses of *L. radiata* increased synchronously from January to February and from October to December, and decreased synchronously from March to July, with an especially steep decrease between May and August. During the first half of the year, the leaves (aboveground) withered, whereas the biomass of the bulbs and roots (belowground) increased. This increase was probably associated with the development and maturation of the flower organs in the bulbs. Notably, belowground biomass accumulation decreased sharply in September, probably a result of the concomitant development of scapes—an energy-consuming process. Previous studies have shown that root senescence in *L. radiata* occurs primarily during leaf withering (mid to late April and May), whereas new primary and

Fig. 3. Enzyme and root activity levels of *Lycoris radiata* at different development stages. I, leafing out (October); II, vigorous leaf growth (November); III, leaf maturity (December–February); IV, flower bud predifferentiation (March); V, flower bud differentiation (April–May); VI, dormancy (June–July); VII, scape development (August); VIII, flowering (September). POD, peroxide; SOD, superoxide dismutase.

secondary roots sprout in the spring (April–June, after leaf withering) and fall (September–October), respectively (Cai et al., 2018a). This strongly suggests that, during summer dormancy, only the aboveground parts of *Lycoris* plants are morphologically dormant; the belowground parts remain physiologically active.

The relationship between *Lycoris* summer dormancy and environmental factors. The life cycles of *Lycoris* species are unique as a result of their irregular seasonal growth rhythm (Kawano, 2009). It is difficult to determine whether these plants flower after leafing out, or leaf out after flowering, because vegetative and reproductive growth (i.e., growth and reproduction) are asynchronous (Kawano, 2009). This growth pattern is similar to that of the Mediterranean geophyte *Narcissus serotinus* L. (Marques and Draper, 2012).

Ambient temperatures affect *Lycoris* growth rhythms significantly. Temperature is also the dominant meteorologic factor regulating summer dormancy (Mori et al., 1990). In *L. radiata*, scape development was most affected by ambient temperature, followed by dormancy, flowering, leafing out, vigorous leaf growth, flower bud differentiation, flower bud predifferentiation, and leaf maturation. During dormancy, the average daytime temperature was 26.0 to 29.6 °C, the average daytime high was 29.8 to 33.7 °C, and the average daytime low was 23.2 to 26.3 °C. During scape development, the average daytime temperature was 28.24 °C whereas the average daytime temperature during flowering was 24.42 to 26.97 °C. The average daytime temperature during flower bud differentiation was relatively

low: 13.92 to 22.83 °C. Thus, the initiation of flower bud differentiation in *L. radiata* required appropriately low temperatures, whereas higher temperatures were required for flower bud differentiation, flower organ development, scape development, and flowering. Temperature changes are probably important triggers of dormancy or flowering in *Lycoris*. Indeed, *L. radiata* begins to undergo flower bud differentiation at a wide range of temperatures (10 to 30 °C), but the optimal temperature for flowering is 20 to 25 °C (Cai, 2012). In addition, *L. radiata* flowering is not only affected by average temperature, but also by other temperature-related factors, including daytime low temperature, daytime high temperature, accumulated temperature, short-term high temperature, temperature difference between daytime and nighttime, and soil temperature (Cai et al., 2018b).

Light also influences the growth and development of *L. radiata* (Cai, 2012). The unique seasonal separation of vegetative growth and reproductive growth in this species (i.e., summer dormancy) is largely associated with the shaded native habitat of this plant: inside temperate broad-leaved forests (Abdusalam et al., 2012; Kawano, 2009). Indeed, moderate shade (30%–65%) improves the yield and quality of cultivated *L. radiata* flowers (Cai et al., 2012; Nishitani et al., 2013). Net photosynthetic rate and flower quality are optimal in *L. radiata* under 45% shade (Cai et al., 2013, 2018b). The ratio of daytime to nighttime hours, and the daily duration of effective solar radiation, may also affect growth phase transitions strongly in *L. radiata*. In our study, we found that the minimum required daytime hours fluctuated

among developmental stages. From March to September, daytime duration exceeded nighttime duration. During this period, *L. radiata* underwent a transition from vegetative growth (leaf yellowing) to reproductive growth (scape development and flowering). During dormancy, the average daylength was 13:40 to 13:56 h. Different developmental stages required different levels of daily average effective solar radiation. Scape development required the longest period of average effective solar radiation, followed by flowering, dormancy, leafing out, vigorous leaf growth, flower bud differentiation, leaf maturity, and flower bud predifferentiation. The average daylength during dormancy was only 5.1 to 7.96 h, indicating that short days benefited vegetative growth in *L. radiata*, whereas long days and long periods of effective solar radiation increased reproductive growth and dormancy.

Water supply may also affect the development of *Lycoris* plants strongly (Cai et al., 2018b). Both high rainfall frequency and excessive precipitation affected flowering and leaf growth negatively in *L. radiata*, whereas relatively dry environments increased reproductive growth (Fig. 2). During flowering, leafing out, and vigorous leaf growth, ambient relative humidity was comparatively low ($\approx 70\%$), monthly precipitation was low (< 100 mm), and there were few rainy days (8.8). From flower bud differentiation to scape development, relative humidity was significantly higher ($\approx 78\%$; $P < 0.0001$). This indicates that the transition between the growth phase and the dormant phase occurred during April and May in *L. radiata*, which corresponds to the rainy season in eastern China. Therefore, in addition to temperature, high humidity might also trigger summer dormancy in *L. radiata*. Consequently, we concluded that dormancy in *Lycoris* plants might be triggered by a combination of environmental factors, including average temperature, temperature differential between day and night, length of day and night, and ambient humidity. In addition, the main factors affecting the life rhythm of *Lycoris* were initially determined in this study. In future studies, chlorophyll fluorescence, photosynthetic rate, and other indicators will be determined and verified for other *Lycoris* species.

Relationship between summer dormancy and physiologic bulb characteristics in *L. radiata*. Unlike the deep, simple epicotyl morphophysiologic dormancy of bulbous plants in Liliaceae, summer dormancy in *Lycoris* is temporary and physiologic (Rees, 1966; Savos'kin, 1960). Indeed, *Lycoris* dormancy is similar to that of *Narcissus*, involving complicated physiologic differentiation (of the flower buds) and morphologic changes (Marques and Draper, 2012; Rees, 1966). As a result of dormancy, *Lycoris* plants have almost no leaves during flower bud differentiation (Wang et al., 2012). The eight-stage development of mature bulbous flowers in *L. radiata* begins in mid March and ends in early July; from May to July, the

aboveground parts of the plant are morphologically dormant (Cai, 2012). The shift to the growth phase begins around mid to late April, which means that flower bud differentiation only occurs after the leaves begin to wither (Park et al., 1991).

Previous studies have shown that as *L. radiata* bulb-lets (young bulbs) mature, bulb weight, diameter, starch content, root system activity, and zeatin riboside concentration correlate positively with the activity levels of the enzyme soluble starch synthase and bound starch synthetase (GBSS) (She et al., 2014). As carbohydrate concentration increases, the activity levels of the beta enzyme increase significantly, but the activity levels of the alpha enzyme change only slightly (Chang et al., 2013). In addition, the soluble sugar content in the mature bulb correlates positively with the activity of the beta enzyme (Chang et al., 2013). The soluble sugar content, soluble protein content, oxidoreductase activity, and root activity of *L. radiata* differed significantly among various developmental stages across one growth season. During the vigorous leaf growth stage, soluble sugars accumulated in the bulb, whereas soluble protein content and root activity decreased continuously. During flower bud differentiation (before dormancy), soluble sugar and soluble protein accumulated rapidly, as did root and POD activity. As the plant entered dormancy, soluble sugar content, soluble protein content, root activity, SOD activity, and POD activity decreased. During scape development (after dormancy), soluble protein content and root activity continued to decrease, whereas the soluble sugar content, SOD activity, and POD activity increased. Our data thus indicate that *L. radiata* bulbs remain physiologically active during dormancy, undergoing floral organ morphogenesis (Cai, 2012). Our results are consistent with a previous study showing that, during dormancy, *L. radiata* had a physiologic flowering period of 10 to 14 d (Yang et al., 2010).

Conclusions

L. radiata, a bulbous flower with medicinal value, has great exploitation potential. To understand the unusual biologic characteristics of this species, we investigated the relationships between climatic factors and annual dynamic changes in *L. radiata* biomass composition and bulb contents across different developmental stages. The “summer sleep” dormancy of *L. radiata* was analyzed with respect to three factors: environment, biomass allocation, and bulb physiology. Based on these analyses, two general conclusions were drawn. First, the growth rhythms of *L. radiata* are temperature sensitive, and the ambient temperature required differed by growth stage. The dormant period required the highest temperatures, followed by the reproductive growth period and the vegetative growth period. Growth rhythms were also affected by light. Dormancy initiation in *L. radiata* thus might

require simultaneous light and temperature stimulation. Therefore, it would be difficult to regulate the flowering period precisely in this species using temperature only. Second, during dormancy, *L. radiata* bulbs make up most of the dry weight and the roots have the strongest vitality (in addition to a high biomass). Thus, only the aboveground parts of the plant are dormant; the underground parts (the bulb and root) remain physiologically active.

Literature Cited

- Abdusalam, A., D.Y. Tan, and O. Tahan. 2012. Effects of vegetative growth, plant size and flowering order on sexual reproduction allocation of *Tulipa sinkiangensis*. *Biodiversity Sci.* 20:391–399.
- Burns, W. 1946. Corm and bulb formation in plants, with special reference to the Gramineae. *Trans. Botanical Soc. Edinb.* 34(3):316–347.
- Cai, J.H. 2012. Studies on the floral development physiology and key cultivation techniques of cut-flower of *Lycoris radiata*. Ph.D. Thesis. Jiangxi Agriculture University, Nanchang.
- Cai, J.H., Q.R. Huang, Y.H. Cheng, X.Y. Wei, and L. Zhang. 2012. Effects of shading level and fertilization on the yield and quality of *Lycoris radiata* cut flower. *Acta Pedologica Sinica* 49(4):780–787.
- Cai, J.H., J.F. Li, X.Y. Wei, and L. Zhang. 2018a. Dynamic change in biomass, root vigor and replacement rate during the green leaf period of *Lycoris radiata*. *J. Nanjing For. Univ. (Natural Sciences Edition)* 42(1):55–59.
- Cai, J.H., X.Y. Wei, J.F. Li, and L. Zhang. 2018b. The regulation and control of ambient temperature on growth rhythm of *Lycoris radiata*. *Acta Agriculturae Universitatis Jiangxiensis* 40(1):24–31.
- Cai, J.H., X.Y. Wei, and L. Zhang. 2013. Effects of shading on matter accumulation, bulb yield and cut flower morphologic quality of *Lycoris radiata*. *Pratacultural Sci.* 30(9):1401–1406.
- Chang, L., Y.M. Xiao, L.F. She, and Y.P. Xia. 2013. Analysis of gene expression and enzyme activities related to starch metabolism in *Lycoris sprengeri* bulbs of different sizes. *Scientia Hort.* 161:118–124.
- Cui, Y., X. Zhang, Y. Zhou, H. Yu, L. Tao, L. Zhang, and M. Huang. 2004. Identification and expression analysis of EST-based genes in the bud of *Lycoris longituba*. *Genomics Proteomics Bioinformatics* 2(1):43–46.
- Iqbal, Z., H. Nasir, S. Hiradate, and Y. Fujii. 2006. Plant growth inhibitory activity of *Lycoris radiata* Herb. and the possible involvement of lycorine as an allelochemical. *Weed Biol. Mgt.* 6(4):221–227.
- Jin, Y.Q. 2002. Studies on the blades growth rule and the variation of endogenous hormone of *Lycoris*. Nanjing Forestry University, Nanjing, China.
- Kawano, S. 2009. Life-history monographs of Japanese plants.13: *Lycoris sanguinea* Maxim. (Amaryllidaceae). *Plant Species Biol.* 24(2):139–144.
- Li, X.H., X.L. Li, D.M. Jian, Y.M. Luo, and H.M. Wang. 2009. A comparative study of the individual biomass and modular biomass of 70 herbaceous species found in the Horqin Sandy Land. *Arid Zone Research* 26(2):200–205.
- Marques, I. and D. Draper. 2012. Decoupling of reproduction and growth: An unusual pattern in the life cycle of the Mediterranean geophyte *Narcissus serotinus*. *Plant Species Biol.* 27(1):106–109.
- Meng, P., Y. Ge, Q. Cao, J. Chang, P. Pan, C. Liu, and S.X. Chang. 2008. Growth and photosynthetic responses of three *Lycoris* species to levels of irradiance. *HortScience* 43:134–137.
- Mori, G., H. Imanishi, and Y. Sakanishi. 1990. Effect of temperature on flowering on *Lycoris squamigera* Maxim. and *L. radiata* Herb. *J. Jpn. Soc. Hort. Sci.* 59(2):377–382.
- Nishitani, S., T. Nakamura, and N. Kachi. 2013. Nitrogen uptake during the leafless period in juvenile plants of a winter-green perennial herb, *Lycoris radiata* var. *radiata* (Amaryllidaceae). *Botany* 91(10):715–721.
- Park, Y.J., E.H. Park, and S.O. Yoo. 1991. Studies on the flower bud differentiation of the genus *Lycoris* native in Korean. *J. Korean Soc. Hort. Sci.* 32(4):545–550.
- Rees, A.R. 1966. The physiology of ornamental bulbous plants. *Bot. Rev.* 32(1):1–23.
- Ren, H.Y., S.X. Zheng, and Y.F. Bai. 2009. Effects of grazing on foliage biomass allocation of grassland communities in Xilin River basin, inner Mongolia. *Acta Phytocool. Sin.* 33(6):1065–1074.
- Ren, Z.M., Y.P. Xia, D. Zhang, Y. Li, and Y. Wu. 2017. Cytological analysis of the bulblet initiation and development in *Lycoris* species. *Scientia Hort.* 218:72–79.
- Savos'kin, I.P. 1960. Specific biological characteristics of bulbous geophytes as related to their past and present ecology. *Bot. Zhur* 45:1073–1078.
- She, L.F., Y.P. Xia, L. Chang, Y.M. Xiao, Z.M. Ren, and L. Zhang. 2014. Biochemical and physiological responses of bulblets of *Lycoris aurea* to exogenously applied N-(2-chloro-4-pyridyl)-N1-phenylurea. *J. Hort. Sci. Biotechnol.* 89(5):549–556.
- Song, H., W.D. Cui, M. Yu, and X.M. Sun. 2014. Study on progress of *Lycoris* herb. *Journal of Harbin University of Commerce (Natural Sciences Edition)* 30(6):649–653.
- Tao, Y. and Y.M. Zhang. 2014. Biomass allocation patterns and allometric relationships of six ephemeroïd species in Junggar Basin, China. *Acta Pratacultural Sinica* 23(2):38–48.
- Tsi, Z.H. and A.W. Meerow. 2000. Amaryllidaceae, p. 264. In: Z.Y. Wu, P.H. Raven, and D.Y. Hong (eds.). *Flora of China*, Vol. 24. Science Press, Beijing, and Missouri Botanical Garden Press, St Louis.
- Wang, R.S. 1990. The ecogeography concerning genus *Lycoris*. *J. Southwest For. College* 10(1):41–48.
- Wang, Z., Y. Li, Y.H. Zheng, S.L. He, F. Peng, and X.C. Shu. 2012. Anatomical observation on the process of flower bud differentiation in *Lycoris*. *Jiangsu Agr. Sci.* 40(7):155–157.
- Yang, L.P. and Q.J. Nie. 2007. Study on biomass reproduction allocation of *Lilium pumilum* in different habitats, p. 366–369. In: Q. Zhang (ed.). *Collected papers of the 2007 annual meeting of the Chinese ornamental horticulture committee*. China Forestry Publishing House, Beijing.
- Yang, Z.L., X. Yang, Z.F. Tan, H.H. Yu, X. Shu, R.N. Liu, and J. Wang. 2010. Variation in phenotypic characteristics and difference in phenological phases of different wild populations of *Lycoris radiata*. *Chin. J. Appl. Environ. Biol.* 16(3):369–375.
- Yuan, J.H. 2010. Numerical taxonomy and principal component analysis of *Lycoris* from China. *Subtropical Plant Science* 39(3):32–37.
- Zhang, L. and F.L. Cao. 2001. Advance on the cultural technology in genus *Lycoris*. *Acta Agriculturae Universitatis Jiangxiensis* 23(3):375–378.