Postprint: Comparison of Floral Characteristics of Three Rhododendron Species from Different Habitats

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Date: 2021-04-02T00:00:00+00:00

Abstract

Habitat influences the differentiation of floral traits in plants. To investigate whether habitats with different intensities of anthropogenic disturbance affect rhododendron trait differentiation and resource allocation, as well as the distribution of different colored rhododendrons, this study utilized *Rhododendron delavayi*, *Rhododendron agastum*, and *Rhododendron irroratum* from habitats with high, medium, and low anthropogenic disturbance intensities in the Baili Rhododendron Nature Reserve as experimental materials, employing the five-point sampling method to count rhododendron individuals in different habitats, vernier calipers to measure floral traits, an optical microscope to count pollen grains, an Ocean Optics spectrometer to measure floral color reflectance spectra, and Gephi software to construct network diagrams of plant individual numbers. The results demonstrated that: (1) The number of *R. agastum* individuals was significantly greater than that of *R. delavayi* and *R. irroratum*. (2) In low-disturbance habitats, the characteristic indices of vegetative and reproductive organs of *R. delavayi* exceeded those in high- and medium-disturbance habitats; the effects of different disturbance intensities on floral traits of *R. agastum* were not significant; the characteristic indices of vegetative and reproductive organs of *R. irroratum* in medium- and low-disturbance habitats were significantly higher than those in high-disturbance habitats. (3) The floral colors of *R. delavayi* and *R. agastum* exhibited higher reflectance in the 400–500 nm wavelength range, whereas the floral color of *R. irroratum* exhibited higher reflectance in the 400–700 nm wavelength range. (4) In high- and medium-disturbance habitats, *R. agastum* was distributed in close proximity to the other two rhododendron species, while in low-disturbance habitats, *R. delavayi* and *R. agastum* were more closely distributed. This study provides an important theoretical foundation for rhododendron population management and biodiversity conservation.

Full Text

Preamble

Comparison of Floral Traits of Three Rhododendron Species in Different Habitats

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Abstract

Habitat influences the divergence of floral traits in plants. To investigate whether habitats with varying levels of anthropogenic disturbance affect floral trait differentiation and resource allocation in rhododendrons, as well as the distribution patterns of different colored species, we examined *Rhododendron delavayi*, *R. agastum*, and *R. irroratum* across high-, medium-, and low-intensity disturbance habitats in the Baili Rhododendron Nature Reserve. Using five-point sampling, we quantified plant abundance, measured floral traits with vernier calipers, counted pollen grains under an optical microscope, assessed flower color reflectance spectra with an ocean spectrometer, and constructed network diagrams of plant abundance using Gephi software. The results revealed: (1) *R. agastum* abundance was significantly higher than that of *R. delavayi* and *R. irroratum.* (2) *R. delavayi* exhibited larger vegetative and reproductive organ trait indices in low-intensity disturbance habitats compared to high- and medium-intensity habitats. Disturbance intensity had no significant effect on floral traits of *R. agastum.* For *R. irroratum*, vegetative and reproductive organ trait indices in medium- and low-intensity habitats were significantly higher than in high-intensity habitats. (3) Flower colors of *R. delavayi* and *R. agastum* showed higher reflectance in the 400–500 nm wavelength range, whereas *R. irroratum* exhibited higher reflectance across 400–700 nm. (4) In high- and medium-intensity habitats, *R. agastum* was closely distributed with the other two species, while in low-intensity habitats, *R. delavayi* and *R. agastum* showed closer distribution patterns. These findings provide a crucial theoretical foundation for rhododendron population management and biodiversity conservation.

Keywords: *Rhododendron*, habitats, floral traits, flower color, community net-

work structure

Introduction

The environment encompasses both biotic and abiotic factors in a habitat (climate, resources, etc.) as well as interactions with other species (competition, predation, mutualism) (Schluter, 2000, 2001). Increasing uncertainty in global environmental change and intensifying anthropogenic disturbances pose significant challenges to plant evolutionary development, making plant responses to environmental change a central focus of evolutionary ecology research (Dai, 2017).

Floral traits include not only flower structure, color, scent, and secretory substance types and yields, but also flower size, number of open flowers, and spatial arrangement patterns on inflorescences at a given time (Huang & Guo, 2000). Different habitats influence floral trait differentiation (Juan et al., 1995; Warren et al., 2001; Thomas et al., 2004; Li et al., 2007), thereby affecting reproductive success. For example, *Iris japonica* in bamboo forest habitats exhibits greater corolla length and width but smaller ovaries, floral parts (except pedicels), and total biomass per flower compared to forest edge habitats (Wang et al., 2010). In regions with high rainfall, flowers tend to face downward to protect reproductive structures (Chen, 2012). Floral traits determine not only sexual reproductive success, offspring genetic composition, and fitness (Lai et al., 2007; Fang et al., 2007; Wang et al., 2008), but also represent responses to external environments. According to resource allocation theory, plants invest limited resources in sexual reproduction and growth. Differential allocation among floral components in different habitats reflects distinct reproductive strategies (Wang et al., 2010).

Rhododendrons are world-renowned ornamental flowers, ranking among the top ten famous flowers globally and widely cultivated for ornamental purposes. *Rhododendron* species exhibit substantial differentiation in morphology, size, and color. Flower shapes range from open funnel-shaped, bell-shaped, or tubular forms depending on petal fusion (Stevens, 1976), with diameters varying from 20–50 cm and colors including white, yellow, pink, deep red, and even purple-red (Ma et al., 2016; Huang et al., 2017).

Southwest China represents the distribution and diversification center for *Rhododendron* (Zhuang, 2012; Wang, 2020), with Guizhou' s Baili Rhododendron area harboring particularly rich and unique germplasm resources. Early surveys identified 18 species across 4 subgenera in the reserve (Liu, 1987), while recent investigations have documented 33 species (including subspecies and varieties) across 6 subgenera and 4 sections (Zhang et al., 2015). Wu et al. (2017) analyzed niche characteristics of dominant populations, finding *R. delavayi*, *R. agastum*, *R. irroratum*, and *R. simsii* as community dominants, with reduced niche overlap between *R. delavayi* and *R. irroratum* reflecting long-term adaptive resource utilization. However, few studies have examined how different habitats affect rhododendron floral traits and resource allocation, and research on distribution patterns of different colored rhododendrons remains scarce.

Field observations revealed distinct disturbance intensity zones in the Baili Rhododendron Nature Reserve: (1) core scenic areas with maximum anthropogenic disturbance (key management zones and tourist areas), termed high-intensity interference habitats (HIIH); (2) peripheral areas with moderate management and tourist impact, termed medium-intensity interference habitats (MIIH); and (3) remote areas free from management and tourist interference, termed low-intensity interference habitats (LIIH). To compare floral traits of the same species across these habitats and explore distribution patterns of different colored rhododendrons, we selected the dominant species *R. delavayi*, *R. agastum*, and *R. irroratum* to address: (1) Do plant abundances differ among the three species across disturbance intensities? (2) Do floral traits vary within species across different disturbance intensities? (3) Do reflectance spectra differ among the three species? (4) Can we quantitatively analyze distribution relationships among the three species across habitats?

1.1 Experimental Site and Materials

The Baili Rhododendron Nature Reserve is located in northwestern Guizhou, central Bijie City (105°45 30 -106°04 45 E, 27°08 30 -27°20 00 N), characterized by a transitional plateau-mountain landscape at 1,400–1,900 m elevation (Tao et al., 2013; Zhang et al., 2015). The region has a subtropical humid monsoon climate with an annual mean temperature of 12.0°C and annual precipitation of 1,120.1 mm (Luo et al., 2012). The reserve hosts 35 *Rhododendron* species (including subspecies and varieties) across 6 subgenera, 4 sections, and 9 subsections, with a flowering period of March–April (40–50 days) (Huang, 2006; Chen et al., 2010). Dominant species include *R. delavayi*, *R. irroratum*, and *R. agastum* [Figure 1: see original paper].

1.2 Methods

1.2.1 Quantifying Plant Abundance To investigate distribution patterns and abundance relationships among the three rhododendron species across habitat types, we established five 50 m × 50 m quadrats per habitat using five-point sampling (Fang et al., 2009). We recorded the number of *R. delavayi*, *R. agastum*, and *R. irroratum* individuals in each quadrat and calculated the percentage of each species relative to the total.

1.2.2 Measuring Floral Traits To compare floral traits within species across disturbance intensities, we randomly selected six individuals per species per quadrat and measured ground diameter with a tape measure (precision 0.1 cm). On each plant, we selected one inflorescence to count flower number and one anthetic flower to measure 17 traits with vernier calipers (precision 0.01 mm): leaf length, leaf width, flower length, flower width, opening diameter, tube depth, petal length, petal width, pistil length, stigma length, stigma width, stigma depth, longest stamen length, shortest stamen length, anther length, anther width, and anther thickness [Figure 2: see original paper].

To visualize stigma and anther sizes, we approximated stigmas as ellipses using the area formula $S = \pi ab$, where S is stigma area, a is half the stigma length, and b is half the stigma width. Anthers were approximated as rectangular prisms using the volume formula $V = abc$, where V is anther volume, a is anther length, b is anther width, and c is anther thickness.

To compare pollen quantity within species across habitats, we randomly collected one bud from six individuals per species per quadrat, preserving them in 2 mL tubes with 75% ethanol. In the laboratory, buds were transferred to 4 mL tubes, softened in 8 $\mathrm{mol \cdot L^{-1}}$ NaOH for 4 h, then anthers were ground to create pollen suspensions and diluted to 4 mL. After thorough mixing, 20 µL aliquots were placed on slides (three drops per sample) and pollen grains were counted under an optical microscope (denoted as a_1, a_2, a_3). Total pollen per bud was calculated as $(a_1 + a_2 + a_3)/3 \times 200$ (Wang et al., 2019).

1.2.3 Measuring Flower Color Reflectance Spectra To compare petal color reflectance among species, we randomly selected 10 anthetic flowers per species per quadrat. Reflectance was measured using an Ocean Optics RPH-1 spectrometer with a QR400-7-UV-BX fiber optic probe held at a 45° angle to the petal surface (Johnson & Andersson, 2002). Reflectance values were averaged every 5 nm across 300–700 nm wavelengths (Liu et al., 2018) and plotted in Excel 2010.

1.2.4 Constructing Network Diagrams To quantitatively analyze distribution patterns, we used Gephi software to construct quantitative network diagrams based on plant abundance data. Each rhododendron species represented a node, with connections weighted by abundance-based interaction strength (Fang & Huang, 2012).

1.2.5 Data Analysis We used generalized linear models (GLM) with normal distribution and identity link to compare floral traits across habitats (traits as dependent variables, habitat as independent variable). Poisson distribution with log-linear function was used to analyze plant abundance and pollen counts. All analyses were conducted in SPSS 20.0 (IBM Inc., New York, NY).

2 Results

2.1 Plant Abundance Across Habitats

Analysis revealed that *R. agastum* abundance (91.00 ± 10.22, mean ± SE) was significantly higher than *R. delavayi* (50.00 ± 9.66) and *R. irroratum* (46.87 ± 9.86) (Wald ^{2} = 12.435, $P = 0.002$, df = 2) when combining data across habitats. Detailed abundance comparisons for each habitat are presented in Table 1 .

2.2 Floral Trait Variation Across Habitats

GLM analyses revealed species-specific responses to disturbance intensity. For *R. delavayi* vegetative organs, ground diameter in low-intensity habitats was significantly larger than in high- and medium-intensity habitats (Wald $^2 = 15.172$, $P = 0.001$, df = 2). Leaf length and width did not differ between high- and low-intensity habitats but were significantly greater than in medium-intensity habitats. For reproductive organs, flower length, width, and stigma area in low-intensity habitats were significantly larger than in high- and medium-intensity habitats (all $P < 0.05$). Tube depth, petal width, and pistil length in medium- and low-intensity habitats exceeded those in high-intensity habitats (all $P < 0.05$). Petal length and longest stamen length in low-intensity habitats were significantly greater than in high-intensity habitats but did not differ from medium-intensity habitats (all $P > 0.05$). Flower number per inflorescence was significantly higher in high-intensity habitats (Wald $^2 = 8.588$, $P = 0.014$, df = 2), while anther volume was significantly larger in high-intensity habitats compared to medium- and low-intensity habitats (Wald $^2 = 22.482$, $P < 0.001$, df = 2). Opening diameter and shortest stamen length showed no significant differences across habitats (all $P > 0.05$) . Overall, *R. delavayi* vegetative and reproductive traits were most suppressed in high-intensity habitats.

For *R. agastum*, vegetative traits (ground diameter, leaf length, leaf width) showed no significant differences across habitats (all $P > 0.05$). Among reproductive traits, flower width, petal length, petal width, longest stamen, and shortest stamen also showed no significant differences (all $P > 0.05$). Opening diameter and tube depth were significantly larger in low-intensity habitats than in medium- and high-intensity habitats (all $P < 0.05$). Flower number per inflorescence was greatest in medium-intensity habitats (Wald $^2 = 19.811$, $P < 0.001$, df = 2). Anther volume was significantly larger in medium-intensity habitats than in high-intensity habitats but did not differ from low-intensity habitats (Wald $^2 = 11.48$, $P = 0.003$, df = 2). Stigma area was significantly larger in high-intensity habitats than in medium-intensity habitats (Wald $^2 = 4.499$, $P = 0.034$, df = 1) but did not differ from low-intensity habitats (Wald $^2 = 3.054$, $P = 0.081$, df = 1). Pistil length showed no significant differences across habitats (Wald $^2 = 3.977$, $P = 0.137$, df = 2) . In summary, disturbance intensity had minimal impact on *R. agastum* floral traits.

For *R. irroratum*, vegetative traits showed no significant differences in ground diameter and leaf length across habitats (all $P > 0.05$), while leaf width in high- and low-intensity habitats was significantly greater than in medium-intensity habitats (Wald $^2 = 7.641$, $P = 0.022$, df = 2). Among reproductive traits, shortest stamen length showed no significant differences (Wald $^2 = 3.584$, $P = 0.167$, df = 2). Floral display traits (flowers per inflorescence, flower length, flower width, petal width) were significantly larger in medium- and low-intensity habitats than in high-intensity habitats (all $P > 0.05$). Opening diameter, tube depth, and pistil length were significantly greater in medium-intensity habitats than in high- and low-intensity habitats (all $P > 0.05$). Petal length and longest stamen length in medium-intensity habitats exceeded those in high-intensity habitats but did not differ from low-intensity habitats (all $P > 0.05$). Stigma area was significantly larger in low-intensity habitats than in medium-intensity habitats (Wald ^{2} = 8.933, $P = 0.003$, df = 1) but did not differ from high-intensity habitats (Wald ^{2} = 0.623, $P = 0.430$, df = 1). Anther volume was significantly larger in high-intensity habitats than in low-intensity habitats (Wald ^{2} = 4.658, $P = 0.031$, df = 1) . Overall, *R. irroratum* vegetative and reproductive traits were significantly enhanced in medium- and low-intensity habitats compared to high-intensity habitats.

Pollen quantity analysis revealed that for *R. delavayi*, high- and low-intensity habitats did not differ significantly (Wald ^{2} = 0.086, $P = 0.769$, df = 1), but both exceeded medium-intensity habitats (Wald ^{2} = 14.274, $P = 0.001$, df = 2) [Figure 3: see original paper]A. For *R. agastum*, high- and medium-intensity habitats showed no significant difference (Wald ^{2} = 0.217, $P = 0.642$, df = 1), but both were significantly higher than low-intensity habitats (Wald ^{2} = 9.853, $P = 0.007$, df = 2) [Figure 3: see original paper]B. For *R. irroratum*, high- and medium-intensity habitats did not differ significantly (Wald ^{2} = 1.220, P = 0.269, df = 1), but both exceeded low-intensity habitats (Wald ^{2} = 14.037, P = 0.001, df = 2) [Figure 3: see original paper]C.

2.3 Flower Color Reflectance Spectra

R. delavayi and *R. agastum* showed similar reflectance patterns, distinct from *R. irroratum*. Specifically, *R. delavayi* (deep red) and *R. agastum* (pink) exhibited higher reflectance in the 400–500 nm range, with *R. agastum* showing greater reflectance than *R. delavayi*. In contrast, *R. irroratum* (yellow-white) displayed higher reflectance across 400–700 nm [Figure 4: see original paper].

2.4 Network Analysis of Plant Distribution

Network diagrams revealed that in high- and medium-intensity habitats, *R. agastum* abundance was significantly higher than *R. irroratum* and *R. delavayi* (all $P < 0.05$), resulting in close distribution between *R. agastum* and the other two species. In low-intensity habitats, *R. irroratum* abundance was significantly lower than *R. delavayi* and *R. agastum* (Wald ^{2} = 51.562, $P < 0.001$, df = 2), leading to closer distribution between *R. delavayi* and *R. agastum* [Figure 5: see original paper].

3 Discussion and Conclusion

This study compared floral trait differentiation and resource allocation in *R. delavayi*, *R. agastum*, and *R. irroratum* across disturbance intensity gradients and examined distribution patterns of different colored rhododendrons. Results showed that *R. agastum* was most abundant in the Baili Rhododendron Nature Reserve, while *R. delavayi* and *R. irroratum* were more sensitive to anthropogenic disturbance, exhibiting optimal growth in low-intensity habitats. *R.*

agastum floral traits remained relatively stable across disturbance levels. In high- and medium-intensity habitats, pink-flowered *R. agastum* was closely distributed with deep red *R. delavayi* and yellow-white *R. irroratum*, whereas in low-intensity habitats, *R. delavayi* and *R. agastum* showed tighter association.

Habitat heterogeneity drives intraspecific floral trait divergence. Different habitats profoundly affect sprout morphology and reproductive characteristics (fruit size, seed number, fruiting rate) in *Magnolia sinostellata* (Du et al., 2018). In *Lysimachia arvensis*, most populations have red flowers, but the frequency of blue-flowered morphs decreases with latitude and increases with temperature and photoperiod (Arista et al., 2013). Floral traits reflect adaptation to specific pollinator guilds (Fægri et al., 1966; Charles et al., 2004; Huang, 2007). Variation in rhododendron floral traits across habitats likely relates to shifts in pollinator communities and visitation frequencies. During peak flowering in high-intensity habitats, high tourist traffic coincides with peak pollinator activity, reducing visitation by birds and bees and potentially favoring selfing, which influences floral trait differentiation. Longer flower longevity, larger inflorescence displays, and increased pollen production represent adaptive responses to pollination environments consistent with mating system transitions (Dai, 2017). Greater flower numbers enhance floral display to attract pollinators: *R. delavayi* produced the most flowers per inflorescence in high-intensity habitats, *R. agastum* in medium-intensity habitats, and *R. irroratum* in medium- and low-intensity habitats. Opening diameter and tube depth critically affect pollinator access, with smaller openings restricting visitor size and tube depth indicating pollinator proboscis length. *R. delavayi* showed greatest tube depth in medium-intensity habitats, *R. agastum* exhibited larger opening diameter and tube depth in high-intensity habitats, and *R. irroratum* displayed these traits most prominently in medium-intensity habitats. Intra-individual pistil length variation correlates with reproductive success (Lloyd, 1980; Diggle, 1995, 1997; Granado-Yela et al., 2017), with longer styles potentially enhancing pollen deposition and tube growth (Campbell, 1989; Bernasconi et al., 2007). Wang et al. (2019) demonstrated that long-style plum flowers facilitate pollen germination and tube elongation, significantly improving fruit set. Our results showed longer pistils in medium- and low-intensity habitats for *R. delavayi*, in high-intensity habitats for *R. agastum*, and in medium-intensity habitats for *R. irroratum*. Future research on pollinator communities and visitation frequencies across these habitats is essential.

Habitat-specific species diversity, root microbiota, and species' life history characteristics contribute to floral trait variation. *R. irroratum* tolerates drought and poor soils (Wang et al., 2020), making intensively managed high-disturbance habitats suboptimal. Landscape management for tourism involves removing non-rhododendron species to create pure stands, severely damaging community structure, reducing species diversity, decreasing litter cover, accelerating soil evaporation, compromising water retention, and destabilizing communities while increasing soil fungal diversity and disease susceptibility (Chen et al., 2019; Chen et al., 2019; Ren et al., 2020).

Floral trait variation likely results from combined genetic and community-level processes. Flower color is a genetically regulated trait. *R. delavayi* and *R. irroratum* within the reserve show notable intraspecific color variation, from blood-red to pink in *R. delavayi* and from cream to pale pink in *R. irroratum* (Huang et al., 2016), influencing pollinator preferences (Gigord et al., 2001; Takahashi et al., 2015; Tang et al., 2019). *R. agastum* abundance significantly exceeded that of the other two species. Described as a new species by Balfour in 1917, *R. agastum* was later hypothesized to be of hybrid origin, potentially between *R. delavayi* and *R. decorum* (Huang et al., 2016). Molecular evidence confirmed its hybrid status (Zhang, 2007; Zha et al., 2008), and Zha et al. (2010) definitively identified it as an F_1 hybrid between *R. delavayi* and *R. irroratum*, representing a classic case of a hybrid misidentified as a distinct species. This suggests *R. agastum* inherited stable traits from both parents, conferring strong adaptability and disturbance resistance. Interspecific pollen transfer is common in natural communities (Fang & Huang, 2013, 2016) and generally detrimental to reproductive success through pollen interference. However, for *R. delavayi* and *R. irroratum*, heterospecific pollen transfer is advantageous, producing the stable hybrid *R. agastum*.

Floral traits are primarily shaped by environmental selection pressures (Wang, 2014; Babu et al., 2016). Anthropogenic disturbance severely impacts plant-pollinator relationships through habitat fragmentation, pollinator loss, introduced species competition, and climate warming-induced phenological mismatches, limiting pollination and directly affecting reproductive fitness (Aguilar et al., 2006; Memmott et al., 2007; Hegland et al., 2009). Huang et al. (2016) documented severe threats to rhododendron habitats, including weak natural regeneration, tourism infrastructure impacts, and habitat fragmentation from human disturbance. Conservation and management of *Rhododendron* resources in the Baili Rhododendron Nature Reserve require innovative approaches and sustainable development strategies from researchers and managers.

Acknowledgments

We thank Wang Lingjun and staff at the China Baili Rhododendron Nature Reserve Management Committee, master' s student Tang Hanqing from Guizhou Normal University for fieldwork support, and Associate Professor Fang Qiang and master' s student Zhang Tao from Henan University of Science and Technology for data analysis assistance.

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Note: Figure translations are in progress. See original paper for figures.