

GENETIC AND ENVIRONMENTAL EFFECTS ON ALLOMETRY OF THE MEDICINAL PLANT *DENDROBIUM OFFICINALE* (ORCHIDACEAE) FROM YUNNAN, SOUTHWEST CHINA

JI ZHANG¹, TAO LI², YIFAN CAI³ AND YUANZHONG WANG^{1*}

¹Medicinal Plants Research Institute, Yunnan Academy of Agricultural Sciences, Kunming 650200, China

²Scientific Research Department, Yuxi Normal University, Yuxi 653100, China

³Biology Department, Texas Technology University, Lubbock Texas 79409, USA

*Corresponding author's e-mail: yzwang1981@126.com

Abstract

Medicinal plant (MP) cultivation is taken into consideration for the sustainable use of MPs. The effort in developing effective management of MPs has focused on biomass allocation of to the medicinal parts. Two experiments were designed and carried out to explore genetic and environmental effects on the biomass partitioning patterns of *Dendrobium officinale* Kimura et Migo in southwest China. We found that there were significant differences in the average of stem biomass (SB), leaf biomass (LB), total biomass (TB), and stem length (SL), respectively, among nine provenances of *D. officinale* ($p < 0.01$). The allometric relationships differed among provenances, indicating different growth strategies in different provenances of *D. officinale*. Significant differences in the average of SB, LB, TB, and SL, respectively, were also found among the same provenance of *D. officinale* cultivated at five different sites ($p < 0.01$). It suggested that environmental factors influenced the biomass accumulation in the plants. These findings show that the biomass allocation of *D. officinale* was able to respond to both genetic and environmental effects. Therefore, the provenances with high-yield should be selected for commercial cultivation, and a suitable environment for *D. officinale* growth should be considered.

Key words: *Dendrobium officinale*; Allometry; Medicinal plant; Orchidaceae

Introduction

Medicinal plants (MPs) have a multi-billion-dollar industry for their therapeutic value worldwide. The usage of MPs rapidly increased along with market demand (Li *et al.*, 2015). Compared with wild non-MPs, wild MPs are more threatened because of over-harvesting (Chi *et al.*, 2017). Cultivation of MPs is widely viewed as a solution to relieve harvest pressure on natural plant populations (Astutik *et al.*, 2019). Therefore, cultivation practices and good agricultural practices can be taken into consideration for the sustainable use of MPs (Chen *et al.*, 2016). For example, the effort in developing effective management of MPs has focused on increasing biomass allocation to the medicinal parts (Zhang *et al.*, 2017).

Plant allometry is the quantitative relationship between the allocation of biomass to different structures and the plant size (Weiner, 2004). Plant biomass allocation may depend on environmental and genetic factors (Geng *et al.*, 2007; Pervaiz *et al.*, 2010; Poorter *et al.*, 2012). Plants will allocate relatively more biomass to their structures that can uptake of the most limiting environmental factors. Moreover, the allocation of biomass is also affected by many genes associated with abiotic stress response (Vasseur *et al.*, 2018). Therefore, it is important to explore the effects of environments and heritability on the allometry of plant biomass allocation (Niklas *et al.*, 2008; Xie *et al.*, 2012). Many previous studies have focused on intraspecific variability of tree allometry (Oleksyn *et al.*, 1999; Spinnler *et al.*, 2003); but in recent years, studies have added considerably to understanding the allometry of herbaceous plants. For example, in the study on *Malva parviflora*, the variations in the environmental factors between different bioclimatic regions affected the allometric relationships

of this species (Eideh & Elkarmi, 2005). Patty *et al.*, (2010) found that several perennial herbs in the high tropical Andes allocated more biomass on massive tap roots because of the substantial grazing pressure and low annual precipitation. In a previous study, changes in biomass allocation of *Coptis teeta*, a perennial herbaceous plant, might result from light availability change caused by the cultivation method (Zhang *et al.*, 2015). However, plant allometry may not always be altered by environmental changes. The variation in biomass allocation of *Laportea canadensis* in response to the environment was mediated by allometric realities (Menges, 1987). Müller *et al.*, (2000) found that the changes in biomass allocation of herbaceous plant species under different nutrient treatments were mainly a result of overall plant size, indicating these species had simple allometric trajectories.

Dendrobium officinale Kimura et Migo (Orchidaceae) is one perennial MP, and its stem is used in East and Southeast Asian countries like other *Dendrobium* plant species for maintaining gastric tonicity and promoting salivary secretion (Ng *et al.*, 2012). The market demand for several *Dendrobium* species has made the natural populations endangered (Liu *et al.*, 2014). In China, most *D. officinale* in markets are from tissue culture and have been planted in greenhouses (Chen *et al.*, 2012). The cultivated *D. officinale* is rich in genetic diversity, and the genetic relationships of *D. officinale* germplasms were correlated with their geography provenances (Yuan *et al.*, 2011). Although the important agronomic characteristics of this species, such as biomass and length of the stem, are correlated with the provenance (Gao *et al.*, 2012; Xu *et al.*, 2008; Zeng *et al.*, 2013), our knowledge on the allometry of different provenances *D. officinale* remains lacking. In addition, environmental

factors, such as humidity and temperature, were key factors for *D. officinale* growth in greenhouse cultivation (Yuan *et al.*, 2020). Therefore, the following questions have been addressed in this study: (1) Does the allometry of *D. officinale* differ among provenances in the same environment condition? (2) Does the allometry of the same provenance of *D. officinale* differ at different sites?

Materials and Methods

Studying area and species: The study area was situated in five different places: Menghai (N21°58'43", E100°25'52", 1270 m.a.s.l.), Pu'er (N22°49'45", E100°59'27", 1350 m.a.s.l.), Puwen (N22°30'13", E101°04'32", 860 m.a.s.l.), Wenshan (N23°19'45", E104°15'41", 1250 m.a.s.l.), and Yuxi (N24°26'01", E102°31'53", 1660 m.a.s.l.) in Yunnan Province, China. The employees in each site received the same training of techniques for *D. officinale* cultivation. Seedlings of nine provenances (YT-01 – YT-09) of *D. officinale* from different places in Yunnan were obtained by tissue culture from Yuxi Xiangxin Agricultural Plantation on April 15, 2011. The plants were authenticated by Professor Hang Jin at the Medicinal Plants Research Institute, Yunnan Academy of Agricultural Sciences. Healthy tissue culture seedlings of *D. officinale* that were 4–5 cm in height were transplanted at a spacing of 15 cm × 10 cm to seedling beds with sterilized barks of *Pinus yunnanensis* as substrate (10 cm in depth). The seedling beds were elevated to avoid contacting the ground of the greenhouses. Plants were watered every three days. The concentration of 0.1% NPK 15-15-15 fertilizer was applied to plants every five days in spring and every seven days in summer.

Experimental design and sampling: Two experiments were designed and carried out in this study. In experiment 1, the seedlings of the nine provenances were transplanted on April 15, 2011, in a greenhouse in Yuxi. After 20 months the samples were harvested on December 15, 2012 (Fig. 1). In experiment 2, the seedlings of the provenance YT-08 were transplanted in greenhouses on April 15, 2011, at five different places, including Menghai, Pu'er, Puwen, Wenshan, and Yuxi. The samples were harvested on the same day as those in experiment 1.

When harvesting stems with leaves were cut from the whole plant. Fifty-three to fifty-five stems with leaves were randomly selected from each treatment. Only one stem was collected from each individual. The stem length (SL) was recorded after harvesting. Then, each specimen was divided into stem and leaves and then was oven-dried at 50°C to constant mass and then weighted to determine the biomass. Total biomass (TB) was calculated as stem biomass (SB) plus leaf biomass (LB).

Statistical analysis

One-way ANOVA test was used to compare the biomass or stem length among different provenances (or the same provenance cultivated at different places). Standardized Major Axis regression was employed for

estimating the allometric relationships, using 'smatr' R package (3.4) (Warton *et al.*, 2012). The 'sma' function in smatr was performed to compare the relationships among different provenances or the YT-08 provenance cultivated at different places (Warton *et al.*, 2006; Warton *et al.*, 2012). A test of heterogeneity in slopes among different provenances (or the same provenance cultivated at different places) was run, using likelihood ratio statistic. If the *p* value is above 0.01, which means the slopes are not significantly different, we then tested for differences in intercept or shift along the main axis of the allometric relationships with Wald statistics (Zhang *et al.*, 2015). The figures were generated using R 3.5.3 (R Development Core Team, 2019).



Fig. 1. Cultivated *Dendrobium officinale* plants in the greenhouse.

Results

In experiment 1, there were significant differences in the average of SB, LB, TB, and SL, respectively, among provenances (one-way ANOVA; $p < 0.01$; $df = 493$). Provenance YT-07 showed the greatest variation of SB, LB, TB, and SL, compared with other provenances (Fig. 2). There was an allometric relationship in each log-log relationship ($p < 0.001$, Table 1), but the slope of regressions differed significantly among provenances for the relationships of SB to TB, LB to TB, LB to SB, and SL to SB ($p < 0.001$, Table 2, Fig. 3).

Table 1. Regression parameters of the log-log relationships among different provenances of *Dendrobium officinale*, estimated by the SMA regression.

Relationship	Provenance code	r ²	p	Slope	95% CI of slope	Intercept	95% CI of intercept
logSB vs. logTB	YT-01	0.979	<0.001	1.078	1.035, 1.122	-0.169	-0.177, -0.161
	YT-02	0.966	<0.001	1.078	1.025, 1.133	-0.218	-0.227, -0.210
	YT-03	0.944	<0.001	1.130	1.059, 1.207	-0.230	-0.243, -0.218
	YT-04	0.986	<0.001	1.115	1.079, 1.152	-0.228	-0.236, -0.219
	YT-05	0.924	<0.001	1.014	0.939, 1.094	-0.205	-0.213, -0.197
	YT-06	0.906	<0.001	1.303	1.196, 1.419	-0.272	-0.286, -0.258
	YT-07	0.958	<0.001	1.028	0.972, 1.087	-0.219	-0.245, -0.193
	YT-08	0.969	<0.001	1.067	1.016, 1.120	-0.215	-0.225, -0.205
	YT-09	0.952	<0.001	1.150	1.082, 1.222	-0.256	-0.270, -0.242
logLB vs. logTB	YT-01	0.884	<0.001	0.925	0.841, 1.015	-0.492	-0.508, -0.476
	YT-02	0.900	<0.001	0.959	0.879, 1.046	-0.406	-0.419, -0.393
	YT-03	0.819	<0.001	0.937	0.834, 1.053	-0.403	-0.421, -0.384
	YT-04	0.944	<0.001	0.849	0.795, 0.906	-0.397	-0.409, -0.384
	YT-05	0.835	<0.001	1.136	1.016, 1.270	-0.418	-0.431, -0.405
	YT-06	0.705	<0.001	0.861	0.741, 1.002	-0.344	-0.360, -0.327
	YT-07	0.893	<0.001	1.052	0.961, 1.151	-0.447	-0.490, -0.405
	YT-08	0.889	<0.001	0.972	0.887, 1.065	-0.423	-0.440, -0.405
	YT-09	0.854	<0.001	0.899	0.810, 0.999	-0.371	-0.391, -0.352
logLB vs. logSB	YT-01	0.777	<0.001	0.858	0.754, 0.977	-0.347	-0.380, -0.313
	YT-02	0.766	<0.001	0.890	0.779, 1.016	-0.212	-0.248, -0.176
	YT-03	0.608	<0.001	0.829	0.698, 0.984	-0.212	-0.244, -0.179
	YT-04	0.879	<0.001	0.761	0.692, 0.838	-0.223	-0.237, -0.209
	YT-05	0.587	<0.001	1.120	0.939, 1.336	-0.188	-0.244, -0.133
	YT-06	0.403	<0.001	0.661	0.534, 0.819	-0.164	-0.209, -0.119
	YT-07	0.738	<0.001	1.023	0.889, 1.178	-0.223	-0.262, -0.185
	YT-08	0.756	<0.001	0.911	0.796, 1.044	-0.227	-0.250, -0.204
	YT-09	0.669	<0.001	0.782	0.668, 0.916	-0.171	-0.193, -0.150
logSL vs. logSB	YT-01	0.673	<0.001	0.791	0.676, 0.925	1.429	1.392, 1.467
	YT-02	0.692	<0.001	0.673	0.578, 0.784	1.278	1.246, 1.309
	YT-03	0.741	<0.001	0.675	0.587, 0.776	1.264	1.242, 1.285
	YT-04	0.590	<0.001	0.512	0.430, 0.611	1.381	1.363, 1.398
	YT-05	0.189	<0.001	0.680	0.532, 0.869	1.336	1.288, 1.384
	YT-06	0.552	<0.001	0.595	0.494, 0.716	1.204	1.170, 1.239
	YT-07	0.719	<0.001	0.622	0.538, 0.719	1.435	1.410, 1.459
	YT-08	0.666	<0.001	0.803	0.685, 0.940	1.343	1.319, 1.367
	YT-09	0.443	<0.001	0.637	0.519, 0.781	1.354	1.330, 1.378

SB, Stem biomass; TB, total biomass; LB, leaf biomass; SL, Stem length

Table 2. Tests for heterogeneity of slope and shift in intercept or location along the common slope for log-log relationships among different provenances of *Dendrobium officinale*.

Relationship	A shift in slope?	p	A shift in intercept?	p	Shift the location along the common slope?	p
SB vs. TB	Y	<0.001	-	-	-	-
LB vs. TB	Y	<0.001	-	-	-	-
LB vs. SB	Y	<0.001	-	-	-	-
SL vs. SB	Y	<0.001	-	-	-	-

SB, Stem biomass; TB, total biomass; LB, leaf biomass; SL, Stem length

In experiment 2, there were significant differences in the average of SB, LB, TB, and SL, respectively, among the samples collected from different sites (one-way ANOVA; p<0.01; df=270). YT-08 samples from Yuxi showed the greatest medians of SB, LB, and TB, whereas the samples from Puwen showed the greatest median of SL (Fig. 4). An allometric relationship has been found in

every log-log relationship. In the relationships of SB to TB, LB to TB, and LB to SB, YT-08 samples from different sites had the same slope but the intercepts were different significantly (p<0.001, Table 3, Fig. 5). However, the slopes differed significantly among the samples from different sites for the regression of stem length versus stem biomass (p=0.009, Table 4).

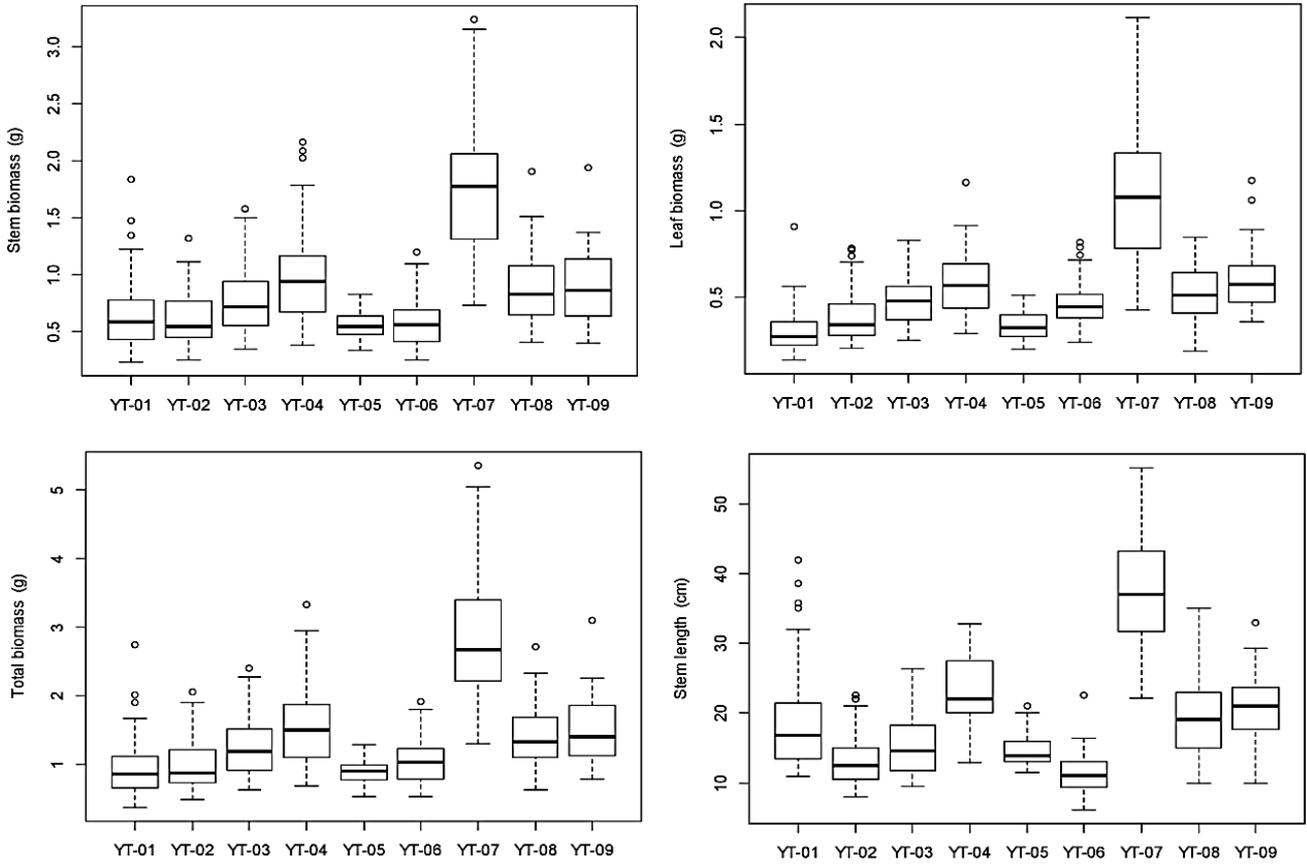


Fig. 2. Stem biomass, leaf biomass, total biomass, and stem length of different provenances of *Dendrobium officinale*.

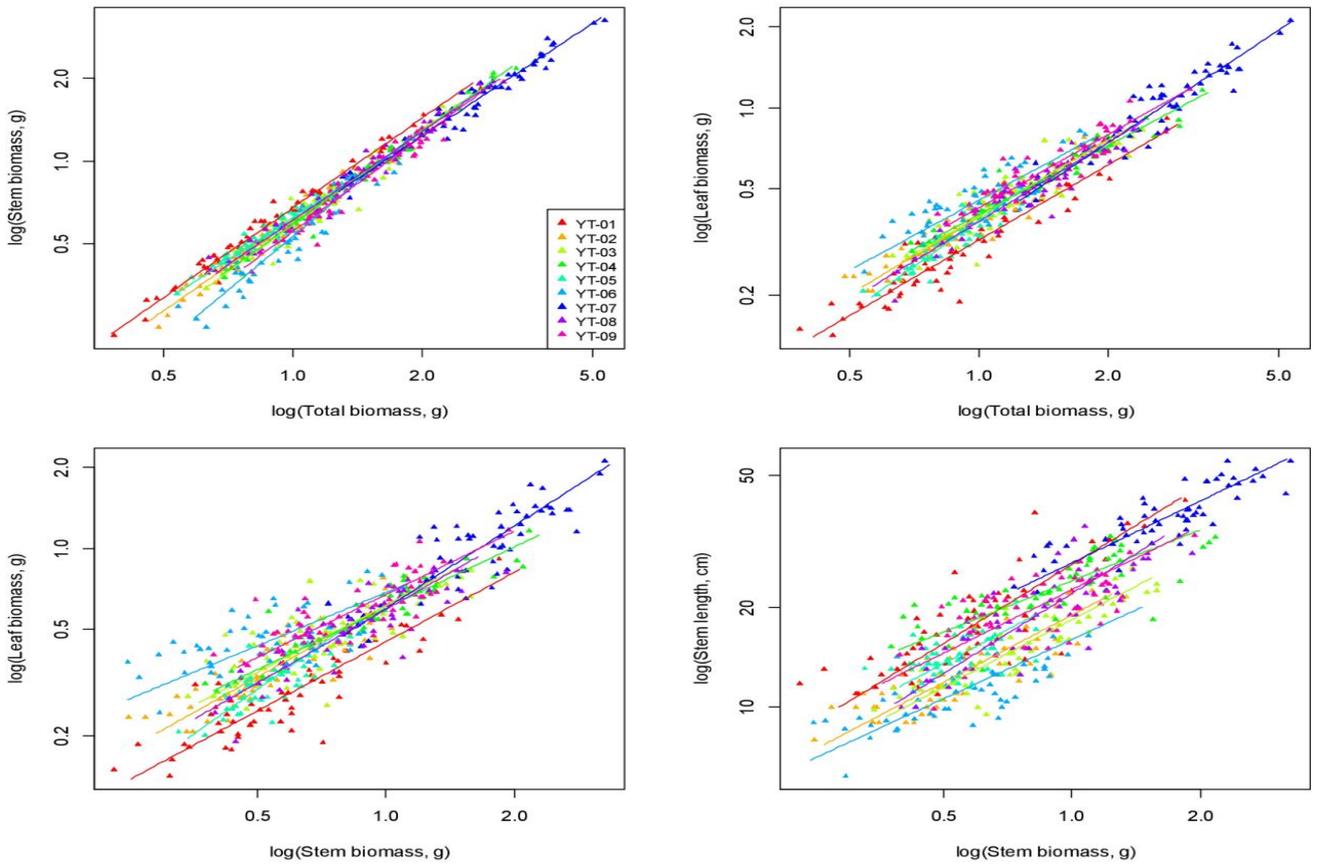


Fig. 3. Relationships of stem biomass and leaf biomass to total biomass, as well as leaf biomass and stem length to stem biomass of different provenances of *Dendrobium officinale*.

Table 3. Regression parameters of the log-log relationships in YT-08 provenance of *Dendrobium officinale* cultivated at different sites, estimated by the SMA regression.

Relationship	Site	r^2	p	Slope	95% CI of slope	Intercept	95% CI of intercept
logSB vs. logTB	Yuxi	0.969	<0.001	1.067	1.016, 1.120	-0.215	-0.225, -0.205
	Wenshan	0.862	<0.001	1.174	1.060, 1.300	-0.233	-0.250, -0.217
	Pu'er	0.965	<0.001	1.094	1.040, 1.152	-0.147	-0.156, -0.139
	Menghai	0.958	<0.001	1.150	1.086, 1.218	-0.243	-0.258, -0.228
	Puwen	0.954	<0.001	1.077	1.014, 1.144	-0.212	-0.224, -0.200
logLB vs. logTB	Yuxi	0.889	<0.001	0.972	0.887, 1.065	-0.423	-0.440, -0.405
	Wenshan	0.752	<0.001	1.033	0.901, 1.184	-0.370	-0.390, -0.350
	Pu'er	0.741	<0.001	0.978	0.850, 1.124	-0.539	-0.560, -0.518
	Menghai	0.867	<0.001	0.892	0.805, 0.988	-0.385	-0.406, -0.364
	Puwen	0.866	<0.001	1.002	0.904, 1.111	-0.419	-0.438, -0.399
logLB vs. logSB	Yuxi	0.756	<0.001	0.911	0.796, 1.044	-0.227	-0.250, -0.204
	Wenshan	0.391	<0.001	0.880	0.711, 1.089	-0.165	-0.232, -0.098
	Pu'er	0.566	<0.001	0.893	0.746, 1.070	-0.407	-0.449, -0.366
	Menghai	0.704	<0.001	0.776	0.666, 0.904	-0.196	-0.236, -0.156
	Puwen	0.692	<0.001	0.930	0.797, 1.087	-0.221	-0.267, -0.176
logSL vs. logSB	Yuxi	0.666	<0.001	0.803	0.685, 0.940	1.343	1.319, 1.367
	Wenshan	0.488	<0.001	0.665	0.547, 0.809	1.387	1.341, 1.433
	Pu'er	0.688	<0.001	0.608	0.522, 0.709	1.314	1.290, 1.338
	Menghai	0.490	<0.001	0.534	0.437, 0.652	1.404	1.368, 1.441
	Puwen	0.658	<0.001	0.754	0.640, 0.888	1.459	1.420, 1.498

SB, Stem biomass; TB, total biomass; LB, leaf biomass; SL, Stem length

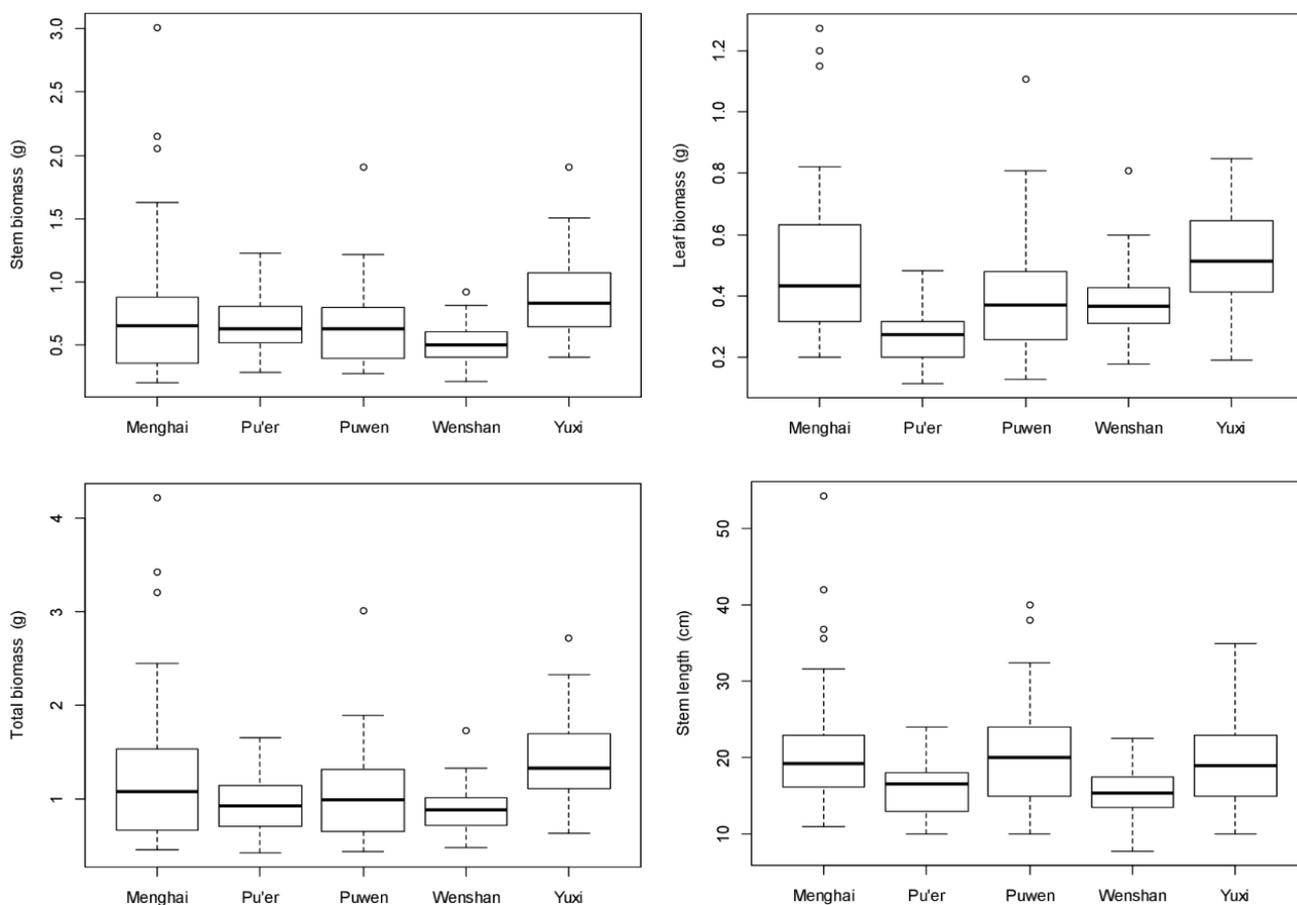


Fig. 4. Stem biomass, leaf biomass, total biomass, and stem length of YT-08 *Dendrobium officinale* at different sites.

Table 4. Tests for heterogeneity of slope and shift in intercept or location along the common slope for log-log relationships in YT-08 provenance of *Dendrobium officinale* cultivated at different sites.

Relationship	A shift in slope?	P	A shift in intercept?	P	Shift the location along the common slope?	P
SB vs.TB	N	0.201	Y	<0.001	-	-
LB vs. TB	N	0.427	Y	<0.001	-	-
LB vs. SB	N	0.488	Y	<0.001	-	-
SL vs. SB	Y	0.009	-	-	-	-

SB, Stem biomass; TB, total biomass; LB, leaf biomass; SL, Stem length

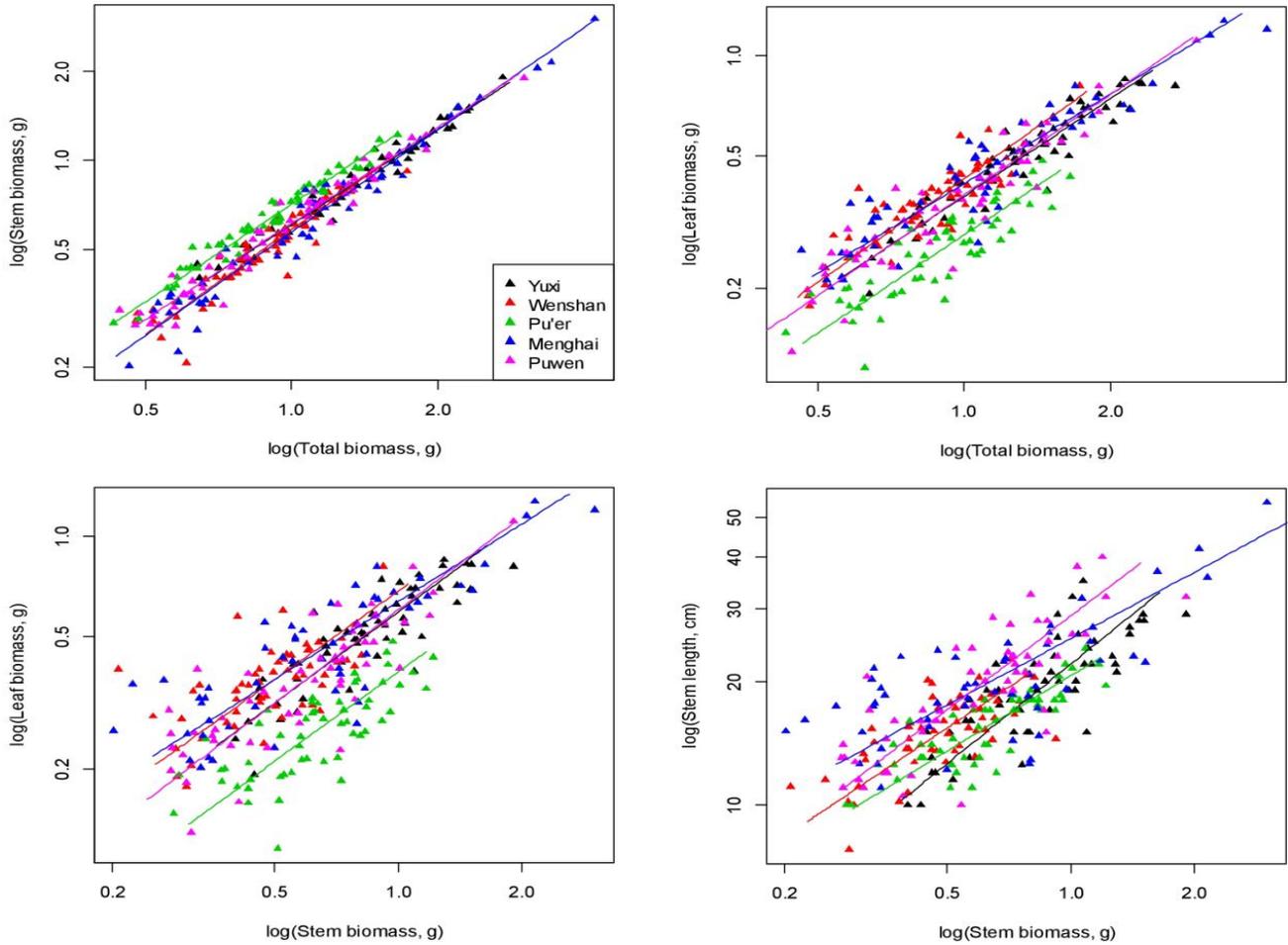


Fig. 5. Relationships of stem biomass and leaf biomass to total biomass, as well as leaf biomass and stem length to stem biomass of YT-08 *Dendrobium officinale* at different sites.

Discussion

Genetic effects on biomass allocation: Provenance often results in different changes in the characteristics of the same plant species collected from different places (Osterc *et al.*, 2017). Prock & Körner (1996) have discovered that the herbaceous plant *Ranunculus glacialis* transplanted from northern Sweden to Austria showed significantly lower leaf weight ratio when compared with the local Austria transplants. Our data indicate that the different provenances of *D. officinale* grown under the uniform environmental conditions showed differences in biomass allocation and stem length. Similar results have been achieved for *D. denneanum* (He *et al.*, 2010). Previous studies on wild *D. officinale* plants suggested that there was low genetic diversity of the species at the population level but high at the species level, which was most likely resulting from

population distribution and limited gene flow mainly due to habitat fragmentation and loss (Ding *et al.*, 2008; Li *et al.*, 2008; Hou *et al.*, 2012). This could be the reason for the observed differences among the provenances in our study. The allometric relationships differed among provenances *D. officinale*, indicating different growth strategies in different provenances. Therefore, the provenances with high-yield should be selected for commercial cultivation to meet the market demand.

Environmental effects on biomass allocation: Site-specific variation in plant biomass allocation is widely known in response to numerous selection pressures for adaptations to environmental changes (Bonser & Aarssen, 2003; Enquist & Niklas, 2002; Kamal *et al.*, 2021; Weiner, 2004). Small vascular epiphytes could adjust their relative growth rate in response to optimal environmental

conditions (Laube & Zotz, 2003). For example, the epiphytic orchids can adjust to light availability by morphophysiological changes, (Pires *et al.*, 2012). In the case of *Dendrobium* species, plant growth could be affected by temperature (Ai *et al.*, 2010), light (Zheng *et al.*, 2012), and substrate (Xie *et al.*, 2017).

In our study, the environmental effects on the growth of YT-08 of *D. officinale* existed. Considering that the same substrate and fertilizer were used for the cultivation of YT-08 of *D. officinale* at different sites in this study, environmental factors such as light, temperature, or moisture could be the key factors that influence the biomass accumulation in the plants. In a previous study, significant differences of the contents of two phenolic components, quercetin and erianin, have also been detected in the stems of YT-08 *D. officinale* from Menghai, Pu'er, and Puwen (Wang *et al.*, 2018). Many plants have developed the mechanisms to produce large amounts of phenolic compounds which are very important for their interaction with the environment (Malik *et al.*, 2012; Cheynier *et al.*, 2013). The differences in the allocation of biomass and the contents of the phenolic compounds in YT-08 *D. officinale* reflected the environmental differences of the cultivation places.

Conclusion

Our data show that the allometry of *D. officinale* differed among provenances in the same environmental condition and the allometry of the same provenance of *D. officinale* differed at different sites. Overall, the results indicated that the allometry of *D. officinale* can be the response to the comprehensive effects of genetic and environmental factors.

Acknowledgments

We thank Mr. Ji-Xiang Li for providing the plant material. This research was supported in part by the National Natural Science Foundation of China (no. 81760684 and 82060690) and the Key Project of Yunnan Provincial Natural Science Foundation (no. 2017FA049).

References

- Ai, J., N. Yan, H. Hu and S. Li. 2010. Effects of temperature on the growth and physiological characteristics of *Dendrobium officinale* (Orchidaceae). *Acta Botanica Yunnanica*, 32: 420-426.
- Astutik, S., J. Pretzsch and J. Ndzifon Kimengsi. 2019. Asian medicinal plants' production and utilization potentials: A review. *Sustainability*, 11: 5483.
- Bonser, S.P. and L.W. Aarssen. 2003. Allometry and development in herbaceous plants: functional responses of meristem allocation to light and nutrient availability. *Amer. J. Bot.*, 90: 404-412.
- Chen, S.L., H. Yu, H.M. Luo, Q. Wu, C.F. Li and A. Steinmetz. 2016. Conservation and sustainable use of medicinal plants: problems, progress, and prospects. *Chin. Med.*, 11: 37.
- Chen, X.M., F.F. Wang, Y.Q. Wang, X.L. Li, A.R. Wang, C.L. Wang and S.X. Guo. 2012. Discrimination of the rare medicinal plant *Dendrobium officinale* based on naringenin, bibenzyl, and polysaccharides. *Sci. China Life Sci.*, 55: 1092-1099.
- Cheynier, V., G. Comte, K.M., Davies, V. Lattanzio and S. Martens. 2013. Plant phenolics: recent advances on their biosynthesis, genetics, and ecophysiology. *Plant Physiol. Biochem.*, 72: 1-20.
- Chi, X., Z. Zhang, X. Xu, X. Zhang, Z. Zhao, Y. Liu, Q. Wang, H. Wang, Y. Li, G. Yang and L. Guo. 2017. Threatened medicinal plants in China: Distributions and conservation priorities. *Biol. Conserv.*, 210: 89-95.
- Ding, G., D. Zhang, X. Ding, Q. Zhou, W. Zhang and X. Li. 2008. Genetic variation and conservation of the endangered Chinese endemic herb *Dendrobium officinale* based on SRAP analysis. *Plant Syst. Evol.*, 276: 149-156.
- Eideh, R.A. and A. Elkarmi. 2005. Allometric relationships of *Malva parviflora* growing in two different bioclimatic regions. *J. Plant Biol.*, 48: 319-325.
- Enquist, B.J. and K.J. Niklas. 2002. Global allocation rules for patterns of biomass partitioning in seed plants. *Science*, 295: 1517-1520.
- Gao, T.T., J.P. Si, Y.Q. Zhu and H. Huang. 2012. Effects of light quality and germplasm on growth and effective ingredients of *Dendrobium officinale* germchit. *China J. Chinese Mat. Med.*, 37: 198-201.
- Geng, Y.P., X.Y. Pan, C.Y. Xu, W.J. Zhang, B. Li and J.K. Chen. 2007. Plasticity and ontogenetic drift of biomass allocation in response to above- and below-ground resource availabilities in perennial herbs: a case study of *Alternanthera philoxeroides*. *Ecol. Res.*, 22: 255-260.
- He, T., L. Deng, Y. Lin, B. Li, X. Yang, F. Wang and Z. Chun. 2010. Comparative analysis of agronomic and qualitative characters in different lines of *Dendrobium denneanum*. *China J. Chinese Mat. Med.*, 35: 2124-2128.
- Hou, B., M. Tian, J. Luo, Y. Ji, Q. Xue and X. Ding. 2012. Genetic diversity assessment and *ex situ* conservation strategy of the endangered *Dendrobium officinale* (Orchidaceae) using new trinucleotide microsatellite markers. *Plant Syst. Evol.*, 298: 1483-1491.
- Kamal, A., M.S.A. Ahmad, M. Hussain and R. Ahmad. 2021. Role of physiological plasticity in adaptability of some native grasses to hyper-saline environments. *Pak. J. Bot.*, 53: 791-804.
- Laube, S. and G. Zotz. 2003. Which abiotic factors limit vegetative growth in a vascular epiphyte? *Fun. Ecol.*, 17: 598-604.
- Li, X., X. Ding, B. Chu, Q. Zhou, G. Ding and S. Gu. 2008. Genetic diversity analysis and conservation of the endangered Chinese endemic herb *Dendrobium officinale* Kimura et Migo (Orchidaceae) based on AFLP. *Genetica*, 133: 159-166.
- Li, X., Y. Chen, Y. Lai, Q. Yang, H. Hu and Y. Wang. 2015. Sustainable utilization of traditional Chinese medicine resources: systematic evaluation on different production modes. *Evid.-based Compl. Altern. Med.*, 2015: 218901.
- Liu, H., Y.B. Luo, J. Heinen, M. Bhat and Z.J. Liu. 2014. Eat your orchid and have it too: a potentially new conservation formula for Chinese epiphytic medicinal orchids. *Biodive. Conserv.*, 23: 1215-1228.
- Malik, R.N., Z.K. Shinwari and H. Waheed. 2012. Linkages between spatial variations in riparian vegetation and floristic quality to the environmental heterogeneity: A case study of River Soan and its associated streams, Pakistan. *Pak. J. Bot.*, 44: 187-197.
- Menges, E.S. 1987. Biomass allocation and geometry of the clonal forest herb *Laportea canadensis*: adaptive responses to the environment or allometric constraints? *Amer. J. Bot.*, 74: 551-563.
- Müller, I., B. Schmid and J. Weiner. 2000. The effect of nutrient availability on biomass allocation patterns in 27 species of herbaceous plants. *Perspect. Plant Ecol. Evol. Syst.*, 3: 115-127.

- Ng, T.B., J. Liu, J.H. Wong, X. Ye, S.C.W. Sze, Y. Tong and K.Y. Zhang. 2012. Review of research on *Dendrobium*, a prized folk medicine. *Appl. Microbiol. Biotechnol.*, 93: 1795-1803.
- Niklas, K.J., D.A. DeMason and E.D. Cobb. 2008. Genetic effects on the biomass partitioning and growth of *Pisum* and *Lycopersicon*. *Amer. J. Bot.*, 95: 424-433.
- Oleksyn, J., P.B. Reich, W. Chalupka and M.G. Tjoelker. 1999. Differential above- and below-ground biomass accumulation of European *Pinus sylvestris* populations in a 12-year-old provenance experiment. *Scand. J. Forest Res.*, 14: 7-17.
- Osterc, G., M.M. Petkovsek, F. Stampar, B. Ravnjak and J. Bavcon. 2017. Impact of specific environmental characteristics of the site of origin (shady, sunny) on anthocyanin and flavonol contents of replanted plants at common cyclamen (*Cyclamen purpurascens* Mill.). *Acta Physiol. Plant*, 39: 64.
- Patty, L., S.R. Halloy, E. Hiltbrunner and C. Körner. 2010. Biomass allocation in herbaceous plants under grazing impact in the high semi-arid Andes. *Flora*, 205: 695-703.
- Pervaiz, Z.H., M. A. Rabbani, Z. K. Shinwari, M. S. Masood and S. A. Malik. 2010. Assessment of genetic variability in rice (*Oryza sativa* L.) germplasm from Pakistan using RAPD markers. *Pak. J. Bot.*, 42: 3369-3376.
- Pires, M.V., A.A.F. de Almeida, P.P. Abreu and D. da Costa Silva. 2012. Does shading explain variation in morphophysiological traits of tropical epiphytic orchids grown in artificial conditions? *Acta Physiol. Plant.*, 34: 2155-2164.
- Poorter, H., K.J. Niklas, P.B. Reich, J. Oleksyn, P. Poot and L. Mommer. 2012. Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytol.*, 193: 30-50.
- Prock, S. and C. Körner. 1996. A cross-continental comparison of phenology, leaf dynamics and dry matter allocation in arctic and temperate zone herbaceous plants from contrasting altitudes. *Ecol. Bull.*, 45: 93-103.
- R Development Core Team. 2019. R: a language and environment for statistical computing v. 3.00. Vienna, Austria: R Foundation for Statistical Computing.
- Spinnler, D., P. Egli and C. Körner. 2003. Provenance effects and allometry in beech and spruce under elevated CO₂ and nitrogen on two different forest soils. *Basic Appl. Ecol.*, 4: 467-478.
- Vasseur, F., M. Exposito-Alonso, O.J. Ayala-Garay, G. Wang, B.J. Enquist, D. Vile, C. Violle and D. Weigel. 2018. Adaptive diversification of growth allometry in the plant *Arabidopsis thaliana*. *Proc. Natl. Acad. Sci. USA.*, 115: 3416-3421.
- Wang, Y., H.Y. Huang, Z.T. Zuo and Y.Z. Wang. 2018. Comprehensive quality assessment of *Dendrobium officinale* using ATR-FTIR spectroscopy combined with random forest and support vector machine regression. *Spectrochim. Acta A.*, 205: 637-648.
- Warton, D.I., I.J. Wright, D.S. Falster and M. Westoby. 2006. Bivariate line-fitting methods for allometry. *Biol. Rev.*, 81: 259-291.
- Warton, D.I., R.A. Duursma, D.S. Falster and S Taskinen. 2012. smatr 3- an R package for estimation and inference about allometric lines. *Methods Ecol. Evol.*, 3: 257-259.
- Weiner, J. 2004. Allocation, plasticity and allometry in plants. *Perspect. Plant Ecol. Evol. Syst.*, 6: 207-215.
- Xie, J., H. Xu, J. Wu, Y. Qiu, Q. Wang, Y. Jin, H. Hu, J. Yang and J. Tan. 2017. Effects of culture substrates on the growth of *Dendrobium officinale*. *Chinese J. Trop. Crops*, 38: 28-32.
- Xie, J., L. Tang, Z. Wang, G. Xu and Y. Li. 2012. Distinguishing the biomass allocation variance resulting from ontogenetic drift or acclimation to soil texture. *Plos One*, 7: e41502.
- Xu, C., Z.G. Zhan and S.M. Liao. 2008. Studies on agronomic characteristics, polysaccharide and cellulose contents of 8 kinds *Dendrobium officinale* from different distribution areas. *J. Zhejiang Uni. (Science Edition)*, 35: 576-585.
- Yuan, H., E.P. Lin, B. Zhu, Q.X. Yu and J.P. Si. 2011. Genetic diversity in cultivated populations of *Dendrobium officinale*. *Chinese Trad. & Herbal Drugs*, 42: 566-569. (in Chinese with English abstract)
- Yuan, Y., X. Tang, Z. Jia, C. Li, J. Ma, and J. Zhang. 2020. The effects of ecological factors on the main medicinal components of *Dendrobium officinale* under different cultivation modes. *Forests*, 11: 94.
- Zeng, S.H., G.S. Wen, S.Z. Xu, Y.H. Zha, S.C. Yang and C.L. Duan. 2013. Study on growth process and polysaccharide accumulation of *Dendrobium officinale*. *Hubei Agri. Sci.*, 52: 2352-2360.
- Zhang, J., T. Shen, Y.L. Zhao, H. Jin, L.H. Wu, H.G. Liu and Y.Z. Wang. 2015. The impact of human activity on the biomass allocation of a medicinal herbaceous species in an agroforestry system of Southwest China. *Agroforest. Syst.*, 89: 469-476.
- Zhang, J., Y.L. Zhao, H. Jin, J.Y. Zhang and Y.Z. Wang. 2017. Morphological variability and allometric relationships of the herb *Panax notoginseng* in Yunnan, China. *Acta Ecologica Sinica*, 37: 65-69.
- Zheng, Y., W. Jiang, E.N. Silva, L. Mao, D.B. Hannaway and H. Lu. 2012. Optimization of shade condition and harvest time for *Dendrobium candidum* plants based on leaf gas exchange, alkaloids and polysaccharides contents. *Plant Omics*, 5: 253-260.

(Received for publication 11 August 2019)