云 南 植 物 研 究 2009, 31 (3): 219～226
Acta Botanica Yunnanica DOI: 10.3724 SP.J.1143.2009.08074

尖叶拟船叶藓营养元素生殖配置格局

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摘要: 为了揭示尖叶拟船叶藓营养元素生殖配置规律, 本文对其 12 种营养元素的生殖配置格局和季节动态进行了研究。其结果如下: 成熟孢子体的生物量配置为 6.67%; 在成熟孢子体中 12 种营养元素的含量顺序是: C (452 mg g) > N (35 mg g) > K (8439.9 μg g) > Ca (7012.9 μg g) > P (2129.2 μg g) > Mg (1482.9 μg g) > Na (432.9 μg g) > Mn (196.3 μg g) > Fe (177.7 μg g) > Al (174.8 μg g) > Zn (68.1 μg g) > Cu (19.4 μg g); 成熟孢子体中营养元素生殖配置顺序是: K (17.7%) > P (15.1%) > Cu (13.3%) > N (11.6%) > Na (10.5%) > Mn (7.8%) > Zn (7.5%) > C (6.9%) > Mg (6.8%) > Ca (5.4%) > Fe (1.3%) > Al (1.2%)。

关键词: 苔藓植物; 营养元素; 生殖配置格局
中图分类号: Q 948.1 **文献标识码**: A **文章编号**: 0253-2700 (2009) 03-219-08

Study on the Reproductive Allocation Pattern of Nutrients in *Dolichomitriopsis diversiformis* (Bryopsida: Lembophyllaceae)

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Abstract: In order to reveal the reproductive patterns of *Dolichomitriopsis diversiformis*, twelve nutrients allocation patterns and seasonal dynamics were studied. The results were as follows: mature sporophyte biomass allocation was 6.67%; 12 nutrient contents in mature sporophyte followed the order: C (452 mg g) > N (35 mg g) > K (8439.9 μg g) > Ca (7012.9 μg g) > P (2129.2 μg g) > Mg (1482.9 μg g) > Na (432.9 μg g) > Mn (196.3 μg g) > Fe (177.7 μg g) > Al (174.8 μg g) > Zn (68.1 μg g) > Cu (19.4 μg g); nutrient allocation patterns in mature sporophyte followed the order: K (17.7%) > P (15.1%) > Cu (13.3%) > N (11.6%) > Na (10.5%) > Mn (7.8%) > Zn (7.5%) > C (6.9%) > Mg (6.8%) > Ca (5.4%) > Fe (1.3%) > Al (1.2%).

Key words: Bryophyte; Nutrients; Reproductive allocation pattern

Reproductive allocation of resources is defined as the proportion of resources allocated to the reproductive parts relative to the total nutrients in the reproductive process of a plant (Jiang, 1992). Plants act in such a way that shortage or excess of a resource will influence the way in which other resources are acquired and allocated, and that the resulting adjustment optimizes plant performance. Keeping a balance between resources entails homeostatic adjustment of resource concentrations by alteration of resource allocation patterns (Chapin *et al*., 1987).

In bryophytes, it appears that spore production (i.e., sexual reproduction) comes at a great energy cost including assumption or reallocation of nutrients.

Foundation item: The National Natural Science Foundation of China (Grant No. 30470181)
Received date: 2008-12-13, Accepted date: 2009-03-04
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Bisang and Ehrlén (2002) proved that the gametophyte and sporophyte must compete for limited resources (like nutrients) within the plant, which may, to some extent, contribute to the rarity of perigonium and sporophyte in some bryophyte species because of the high reproductive costs (Stark *et al*., 2000).

Dolichomitriopsis diversiformis (Mitt.) Nog., which belongs to Lembophyllaceae, is one dioecious moss species. The morphology is remarkably different between its perigonium and perichaetium, the number of perichaetia is much more than that of perigonia, and the perigonia are very rare and difficult to find (Liu *et al*., 2006a). It was found that the frequency of sporophyte abortion in this moss was 7.3% (Li *et al*., 2007). For a better understanding of the mechanisms underlying the sporophyte development and the life cycle of this moss, it is essential that we examine the reproductive allocation and seasonal dynamics of nutrients in reproductive process of this plant. However, to our knowledge, very few studies have addressed the reproductive allocation and seasonal dynamics of nutrients in bryophyte species with respect to the sexual reproduction, which may due partly to the difficulties in determining gametophyte biomass and in identifying parts serving reproduction (Bisang and Ehrlén, 2002).

The objectives of this study were to investigate the nutrient allocation patterns, to compare the seasonal dynamics in 12 nutrient contents (C, N, P, K, Ca, Na, Mg, Fe, Zn, Mn, Al and Cu) in reproductive and vegetative parts, and to discuss whether the sporophyte development depend on the availability of certain nutrients in the moss *D. diversiformis*. Most studies on reproductive allocation patterns were performed on tracheophyte and only a few on bryophytes, hence, the study on nutrient allocation patterns in moss will assist further research on the reproductive allocation of bryophyte species.

1 Materials and methods

1.1 Site description

The study was conducted in Fanjing Mountain (27°49′50″-28°11′30″N, 108°45′55″-108°48′30″E) in the eastern part of Guizhou, China (Liu *et al*., 2006a). The annual precipitation ranges from 1100 to 2600 mm, the annual mean relative humidity is above 80%, and the annual temperature ranges from 5 to 17℃ (Li *et al*., 2002). The moss *D. diversiformis* is one of the endemic bryophytes in East Asia with limited distribution areas (Wu, 1992). In Fanjing Mountain, the species are mainly distributed in the forest community which is dominated by *Cyclobalanopsis stewardiana* and *Sinarundinaria nitidacommunit* ranges from 1650 m to 2080 m elevation (Liu *et al*., 2006b).

1.2 Species studied

D. diversiformis is a perennial dioecious species, which mainly grows on tree trunks (epiphytic), and are seldom found on rocks. The perigonium is rarely found, and the development of the plant population depends largely on vegetative propagation rather than sexual reproduction. Stark (2002) suggested 20 stages for scoring the developmental stages of bryophyte species, centering on the reproductive phases only. As for the rarity of sporophyte and the difficulties in finding perigonium, we scoring the developmental stages of this moss simply as five important stages based on a long period of field observations (from April, 2004 to January, 2006):

GG: gametophyte rapid growing stage;

PG: perichaetium growing stage, i.e., before fertilization;

SI: sporophyte developing initial stage. This corresponds with the development of the embryo following fertilization;

YS: young sporophyte growing stage (capsule is green with calyptra on it);

MS: mature sporophyte stage (capsule is brown and green with an intact calyptra).

1.3 Sampling and measurements

Plant materials from certain populations were collected on February, April, July, September, November and December, 2006 (Table 1), respectively. Specimens (B. Liu 05 - 102) were deposited at the Plant Herbarium of Jishou University (JIU). The sampling sites were in the elevation about 1900 m. The choice of the sites was subjective because most sporophyte plants were found near this elevation. All samples were collected within a short period without precipitation. In the reproductive period (from September to December, 2006), only plants bearing sporophytes were sampled. Plant materials collected (- 60 g) were rinsed several times with distilled water after removing of old brown parts.

The reproductive parts (only include perichaetium and sporophyte because the perigonium can hardly be found) were carefully separated from the vegetative parts (gametophyte) under stereo microscope, then they were oven-dried to a constant weight at 80℃ for 24 h and weighed to the nearest 0.0001 g, separately. After ground to fine powder with an electric grinder, the samples were placed in paper bags, and stored frozen up until nutrients analyses. Before analyses for nutrients the samples were oven-dried to a constant weight again (80℃ for 24h). After digesting, total C and N contents were determined on an elementary analyzer (Vario EL III, made in German). Total nutrient contents (P, K, Ca, Na, Mg, Fe, Zn, Mn, Al and Cu) were determined by the plasma atomic emission spectrometer (IRIS Intrepid II XSP, made in America). All the analyses were performed at the Center of Analysis and Test of Wuhan University. The laboratory included its own blank and standard samples. The nutrient allocation (NA) to a plant part was estimated as follows:

NA = nutrient mass of reproductive parts total nutrient mass of the plant

= nutrient content of reproductive parts × corresponding proportion of dry mass (nutrient content of reproductive parts × corresponding proportion of dry mass + nutrient content of vegetative parts × corresponding proportion of dry mass)

2 Results and analysis

2.1 Biomass allocation

As was shown in Table 1, biomass allocation to reproductive parts increased with the development of sporophyte, it was only 0.74% at PG stage, but increased more than three times at SI stage, and reached its peak of 6.67% at MS stage.

2.2 Nutrients allocation patterns

Reproductive allocation patterns and seasonal dynamics of nutrients in the moss *D. diversiformis* at different reproductive stages were shown in Table 2 and Fig. 1.

The highest content of carbon (C) was 452 mg g. No significant difference was found in C content between vegetative and reproductive parts, and the content of C was very stable at different stages.

Nitrogen (N) content showed a similar trend in both vegetative and reproductive parts during PG and YS stage, it ranged from 19 to 26 mg g in vegetative parts, while in mature sporophyte the content was 35 mg g which was 1.8 times as high as vegetative parts.

A constant trend was found in phosphor (P) accumulation in the reproductive parts, with the highest content of 2129.2 μg g which was about 2.5 times as high as that of the vegetative parts at MS stage. During SI and MS stages, P contents were always much higher in reproductive parts than in vegetative parts. In vegetative parts, P content dropped with the development of sporophyte (from 1114.2 to 855.8 μg g).

Kalium (K) accumulative pattern appeared to be similar to that of P. K also accumulated steadily in reproductive parts with the development of sporophyte, with the highest content of 8439.9 μg g which was 3 times as high as that of vegetative parts at MS stage. No significant difference of K content was found in vegetative parts at different stages.

Calcium (Ca) content was 9212.4 μg g in vegetative parts at PG stage coupled with the highest Ca content (12673.4 μg g) in perichaetium. It decreased by 44.7% in mature sporophyte (7012.9 μg g) while did not vary strongly in vegetative parts.

Natrium (Na) contents in reproductive parts were on average 29.2% higher than in vegetative parts after PG stage. Na contents did not vary strongly in vegetative parts.

When perichaetia began to develop, magnesium (Mg) content increased on average by 46.6% in vegetative parts. The highest Mg content (1662.4 μg g) in vegetative parts was coupled with the highest Mg content (2254.7 μg g) in perichaetium at PG stage. After a slightly decrease during SI and YS stage, Mg content increased again at MS stage.

Table 1 Biomass allocation to vegetative and reproductive parts in the moss *D. diversiformis*

Developmental stages	Sampling date	Biomass allocation (%)		
		Gametophyte	Perichaetium	Sporophyte
GG	17th, April	100.00	—	—
PG	27th, July	99.26	0.74	—
SI	30th, September	97.07	—	2.93
YS	1st, November	95.23	—	4.77
MS	10th, December	93.33	—	6.67

Notes: The "—" indicates that there is no reproductive parts exist.

Table 2 Reproductive allocation patterns and seasonal dynamics of nutrients in the moss *D. diversiformis* at different reproductive stages

Nutrient	Developmental stage	Structure content			NA (%)
		Gametophyte	Perichaetium	Sporophyte	
C	GG	439	—	—	0
	PG	435	429	—	0.7
	SI	434	—	422	2.9
	YS	437	—	429	4.7
	MS	433	—	452	6.9
N	GG	19	—	—	0
	PG	252	3	—	0.7
	SI	26	—	28	3.1
	YS	19	—	22	5.5
	MS	19	—	35	11.6
P	GG	800.7	—	—	0
	PG	1114.2	838.6	—	0.6
	SI	777.6	—	1512.9	5.5
	YS	1009.2	—	1862.5	8.5
	MS	855.8	—	2129.2	15.1
K	GG	2615.1	—	—	0
	PG	2735.8	2708.7	—	0.7
	SI	2125.7	—	4447.5	5.9
	YS	2524.7	—	6966.9	12.1
	MS	2799.4	—	8439.9	17.7
Ca	GG	7982.9	—	—	0
	PG	9212.4	12673.4	—	1
	SI	7409.6	—	7138.6	2.8
	YS	9064.2	—	6599.3	3.5
	MS	8746.1	—	7012.9	5.4
Na	GG	219.7	—	—	0
	PG	307.1	472.8	—	1.1
	SI	272.6	—	480.2	4
	YS	290.8	—	388.6	6.3
	MS	264.5	—	432.9	10.5
Mg	GG	1014.2	—	—	0
	PG	1662.4	2254.7	—	1
	SI	1461.1	—	1647.5	3.3
	YS	1363.3	—	1174.3	4.1
	MS	1461.2	—	1482.9	6.8
Fe	GG	865.1	—	—	0
	PG	1530.5	807.1	—	0.4
	SI	2023.1	—	160.4	0.2
	YS	1715.6	—	260.3	0.8
	MS	972.6	—	177.7	1.3
Zn	GG	80.0	—	—	0
	PG	62.8	170.2	—	2
	SI	93.5	—	125.7	3.9
	YS	79.3	—	81.9	4.9
	MS	60.3	—	68.1	7.5
Mn	GG	151.0	—	—	0
	PG	155.3	150.1	—	0.7
	SI	322.8	—	425.7	3.8
	YS	247.7	—	258.1	5
	MS	165.4	—	196.3	7.8
Al	GG	738.2	—	—	0
	PG	1438.1	843.6	—	0.4
	SI	1882.9	—	161.4	0.3
	YS	1904.1	—	285.3	0.7
	MS	1006.3	—	174.8	1.2
Cu	GG	12.3	—	—	0
	PG	13.2	21.4	—	1.2
	SI	14.9	—	11.8	2.3
	YS	11.9	—	17.6	6.9
	MS	9.0	—	19.4	13.3

Note: The units of all the nutrient contents are μg g, except C and N (mg g); the"—" indicates that there are no reproductive parts exist

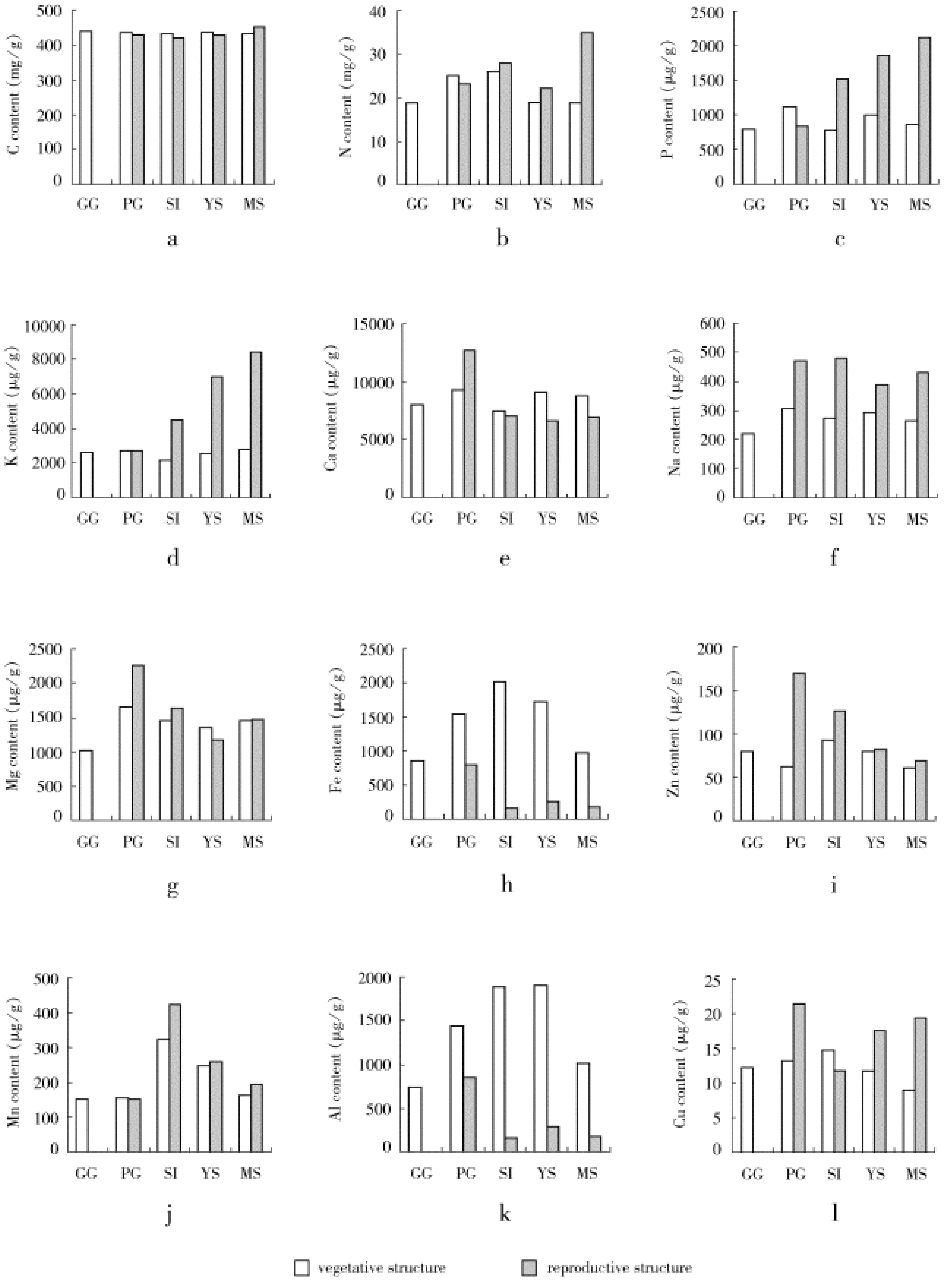

Fig. 1 a-l: Seasonal dynamics of 12 nutrients in vegetative (gametophyte) and reproductive parts (perichaetium or sporophyte) in the moss *D. diversiformis*. Here, GG, PG, SI, YS, and MS represent different developmental stages

Ferrum (Fe) contents were relatively higher in vegetative parts than in reproductive parts. In vegetative parts, Fe content increased gradually before SI stage, with the highest content of 2023.1 μg g, and then it decreased with the development of sporophyte. Fe content in reproductive parts decreased sharply after fertilization (i.e., after PG stage), from 807.1 to 160.4 μg g.

At PG stage, zinc (Zn) content was 2.7 times as high in reproductive parts as in vegetative parts. Zn content declined steadily with the development of sporophyte, with the lowest content (68.1 μg g) in mature sporophyte.

Surprisingly, manganese (Mn) content increased sharply in both vegetative and reproductive parts at SI stage, which were over 2 times as high as that of previous period, and then both decreased gradually with the development of sporophyte.

Aluminium (Al) contents were relatively higher in vegetative parts than in reproductive parts. In vegetative parts, Al increased rapidly before YS stage, with the highest content of 1904.1 μg g, and then decreased sharply when the sporophyte became mature (from 1904.1 to 1006.3 μg g). Al content in reproductive parts decreased sharply after fertilization (from 843.6 to 161.4 μg g).

The highest copper (Cu) content (21.4 μg g) was found in perichaetium at PG stage, after a decrease at SI stage it increased again with the development of sporophyte. Cu content in vegetative parts increased slightly before SI stage, and then decreased (from 14.9 to 9.0 μg g).

3 Discussion

In comparison with other bryophyte species, *D. diversiformis* had a relatively lower biomass allocation to mature sporophyte (6.67%). For example, the biomass allocation to mature sporophyte was 16% in *Dicranum polysetum* (Ehrlén *et al.*, 2000), and 30% in *Tetraphis pellucid* (Kimmerer, 1991). This indicates that *D. diversiformis*, as a perennial species, allocates much lower resources to reproductive parts than that of vegetative parts and is largely depends on vegetative propagation for population development.

Nutrient contents in mature sporophyte followed the order: C (452 mg g) > N (35 mg g) > K (8439.9 μg g) > Ca (7012.9 μg g) > P (2129.2 μg g) > Mg (1482.9 μg g) > Na (432.9 μg g) > Mn (196.3 μg g) > Fe (177.7 μg g) > Al (174.8 μg g) > Zn (68.1 μg g) > Cu (19.4 μg g).

C made up a very large proportion of plant dry mass which was high above the contents of other nutrients. N and P are essential in making proteins and DNA, and P is needed in ATP to maintain energy. K is mainly located in the most active parts of a plant which is a translocatable nutrient that can move easily to the young parts of a plant. High contents of N, P, and K coincided with the capacity for rapid growth in reproductive conditions of *D. diversiformis*. The rapid contents accumulation in developing sporophyte can be explained as: N, P and K are moved from vegetative to reproductive parts, or reproductive parts actively uptake these three nutrients (Gerdol *et al.*, 2005; Rydin and Clymo, 1989).

In this paper, as there was no significant difference in K contents in vegetative parts at different stages, the strong increase of K could be explained mainly as the active uptake of K by developing sporophyte. While the increase of N and P could be explained as both the translocation of N and P from gametophyte to sporophyte and the active uptake of N and P by developing sporophyte.

As is known Na is beneficial to the growth of C_3 plant (Pan, 2004), the high Na content was found in the rapid growing sporophyte in the moss *D. diversiformis*, indicating that Na might be beneficial to the growth of this moss. Raven et al. (1998) have reviewed the evidence for the C_3 pathway in bryophytes, and our result indirectly corresponds with such evidence.

The decrease of Ca and Zn contents in reproductive parts may partly due to the growth of sporophyte which "diluted" their contents, and the stability of Ca content in vegetative parts could be explained as the immobile feature of Ca.

Mg is one of the major constitutes of chlorophyll, hence the pattern of seasonal changes in Mg content in different parts of the moss suggest different photosynthetic activity. During reproductive stages, both the gametophyte and sporophyte seemed to have high photosynthetic activity. The highest content of Mg in perichaetium indicates that it had a high photosynthetic activity.

Fig.1h and Fig.1k showed obvious differences in Fe and Al contents between vegetative and reproductive parts. One of the factors contributing to high contents of Fe and Al in gametophyte is that as cells become old or other ions move to the sporophyte, new binding sites are exposed, permitting more of these ions to accumulate there, and may also partly due to the rapid growth of sporophyte.

Cu is one of constitutes of plastocyanin in chloroplast, and play a role in photosynthesis. Therefore, high Cu content in sporophyte suggestted a high capacity of photosynthesis and a high demand for Cu (Pan, 2004).

Mn is an activator of several enzymes, such as dehydrogenase, decarboxylase, kinase, oxidase and so on, and especially has an effect on Tricarboxylic Acid Cycle (Pan, 2004). So, the high Mn content in perichaetium suggested a high rate of biosynthesis in the developing sporophyte and also a high demand for Mn after fertilization.

In this study, the results that all contents of the 12 nutrients in mature sporophyte were greater than that of gametophyte at MS stage except Ca, Fe and Al partly supports the assumption that sporophyte development is the most expensive developmental stage in terms of demands for resources (Rydgren, 2003), indirectly indicating that the developing sporophyte of compete nutrients with gametophyte in the moss *D. diversiformis*.

Mosses mostly depend upon atmospheric deposition for their supplies of water and mineral nutrients (Schintu *et al*., 2005) which was especially the case for the epiphytic mosses. Research on substrate-related element uptake by epiphytic lichens has shown minimal accumulation due to what is probably an overall deficiency of elements in bark tissues (De Bruin and Hackenitz, 1986). Also, bryophytes seem to have uptake specificity for things they need over things they do not. For example, the thallose liverwort *Dumortiera hirsuta* preferentially took up Ca, Mg, and Zn over Cd (Mautsoe and Beckett, 1996).

In this paper, N, P, K, Na and Cu contents in mature sporophyte were much higher than in gametophyte, and the NA of 12 nutrients in mature sporophyte followed the order: K (17.7%) > P (15.1%) > Cu (13.3%) > N (11.6%) > Na (10.5%) > Mn (7.8%) > Zn (7.5%) > C (6.9%) > Mg (6.8%) > Ca (5.4%) > Fe (1.3%) > Al (1.2%), which indicates that there was a high demand for these 5 nutrients in the developing sporophyte of *D. diversiformis*. Mn was also essential to the developing sporophyte of *D. diversiformis*. However, Fe and Al contents were much lower in sporophyte than in gametophyte, suggesting there was a little demand for them. Therefore, we assumed that if the needs for N, P, K, Na, Cu and Mn can not be satisfied due to lack of precipitation during the reproductive seasons or due to failure of competition with gametophyte, then the failure of sexual reproduction in *D. diversiformis* may occur.

Acknowledgements: This study was supported by the Center of Analysis and Test of Wuhan University for nutrients analysis and the Nature Protection Bureau of Fanjing Mountain for field assistance. We thank Songquan SONG, Institute of Botany, Chinese Academy of Sciences, for reading an early draft and offered numerous suggestions, and Gongxi CHEN for offering constructive criticisms on the manuscript.

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4.4 为使作者的稿件顺利通过审稿和及时发表，请作者在撰写稿件时严格按我刊格式准备，写作时做到思路清晰、逻辑严密、句子通顺、衔接过渡、前后呼应、凸显创新、详简适度。对写作粗糙的稿件 (如格式不符、英文摘要不地道、输入文字错误较多、句子不通、写作思路不清晰、标点符号使用不规范或中英文标点混用等)，编辑部将直接退稿。

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