ABSTRACT: Mosses are the pioneer and the first green land plants developed during the evolutionary process, they play an important role in the development of soil, biogeochemical cycling and facilitating plant colonization. Although species richness, composition, diversity and cover of moss communities vary, they grow well almost in all forests. Why mosses can grow in different conditions? What are the adaptive strategies of mosses in different forests along primary succession sequences? It is not still completely clear. In order to answer these questions, nutrient and carbohydrate accumulation in mosses were tested along the primary succession following deglaciation of Hailuogou glacier, Gongga Mountain, China. Nitrogen (N), phosphorus (P), potassium (K) content, total organic carbon (TOC), soluble sugar and starch accumulated in the dominant moss species were determined and compared. TOC increased insignificantly with forest age. N, P, K contents in mosses were significantly higher in forests with dense shrubs, where N content was separately 1.69% in *A. hookeri* and 1.35% in *P. schreberi* in 30 yr aged forest, P content in 30 yr and 52 yr aged forest was separately 0.022% and 0.020% in *A. hookeri* and 0.020% and 0.017% in *P. schreberi*, and K content in 30 yr and 52 yr aged forest was separately 0.570% and 0.553% in *A. hookeri* and 0.490% and 0.493% in *P. schreberi*. Soluble sugar was higher in the early stage of succession, but the opposite was observed for starch and non-structure carbohydrate content, which was lower in early successional stage. Mosses adopted different adaptive strategies in different aged forests along receding glacier, in which starch and N, P, K contents were key for adaptation. That is, mosses accumulated much more starch in the severe environment of early succession stage. In more favourable environment, N, P, K was found to be accumulated for plant growth.

KEY WORDS: glacier foreland, mosses, nutrient, primary succession, nonstructural carbohydrate

1. INTRODUCTION

As the pioneer and the first green land plants developed during the evolutionary process, mosses play an important role in the development of soil, element biogeochemical cycling, and facilitating plant colonization (Uchida *et al.* 2002). They also play an important role in seed germination, seedling growth and forest regeneration. Delach and Kimmerer (2002) found that the moss *Polytrichum piliferum* C. Mull. had a positive effect on germination of *Melilotus officinalis* Desr. Czarnecka (2004) and Turetsky (2003) also found that a dense moss cover may create a more humid microclimate with smaller temperature amplitudes and thereby
benefits the survival of seedlings. Although species richness, composition, diversity and cover of moss communities varied (Gustafsson and Hallingbäck 1988, Boudreault et al. 2000), they grow well almost in all kinds of forests, irrespective of forest age and forest continuity. Why could mosses grow in various forest conditions?

It is widely accepted that higher plants can adapt to different environment conditions by changes in morphology and physiology. In order to survive the nutrient deficient environment, plants might decrease growth rate, aboveground biomass, nutrient concentration and photosynthetic capacity of plant (Vance et al. 2003, Hill et al. 2006). They also can reprogram their metabolism and/or restructure root system architecture to maintain the growth rate as high as possible (Vance et al. 2003, Jain et al. 2007, Gang et al. 2012). Plants can even change their net photosynthetic production allocation to growth, defence, and storage (Chapin et al. 1990), for example, allocating more carbon to storage to enhance plant survival from severe environment (Myers and Kitajima 2007, Poorter and Kitajima 2007). However, much of literature on adaptive mechanism of plant were focused on vascular plants, particularly in juvenile plants (Kurokawa et al. 2004, Myers and Kitajima 2007). For mosses, the nonvascular poikilohydric plants with no root system and with totally different morphological and physiological characters of higher plants, what kind of growth strategies they adopt in different aged forests? It is not still completely clear.

The forefield of a receding glacier represents a pristine environment and offers an excellent opportunity to study vegetation succession (Noll and Wellinger 2008, Schmalenberger and Noll 2010). On a glacier foreland there are very heterogeneous conditions regarding microclimate, soil conditions, and dominant vegetation types, which makes it possible to study the successive and adaptive mechanisms of microorganisms and some vegetation, such as mosses. With an area of 80.5 km² and a length of 15 km, Hailuogou Glacier is in the east slope of Gongga Mountain in Sichuan, China, the highest mountain (7,556 m) in the eastern fringe of the Tibetan Plateau and the Hengduan Mountain region, and is the longest maritime glacier in the Hengduan Mountain region. With climate change, the retreat of glaciers in Gongga Mountain area has been fast (Wang and Zhang 1992). Various data indicate that the glaciers retreated by >1.88 km during the 20th century, and mass balance records show that it suffered a sustained mass loss of snow and ice in the period 1959/60–2003/04, with an accumulated mass balance of 10.83 m water equivalent (Li et al. 2010). On the other hand, retreat of the glacier also left a long glacier foreland, which provides an ideal place to study the adaptive mechanisms of mosses in different forest types.

By comparing the nutrient and carbohydrate accumulation of mosses along primary succession following deglaciation of Hailuogou glacier, Gongga Mountain, China, the present study tested two hypotheses: (1) The reasons for which mosses could grow in various forest conditions are that mosses have adopted different adaptive strategies in different forest types. (2) Nutrient and nonstructure carbohydrate are the key materials for mosses adapting to different environments. This investigation will contribute to a better understanding of the adaptive mechanisms adopted...
Adaption mechanism of moss to environment

by mosses in different succession stages or in different vegetation types.

2. STUDY AREA

The study was conducted in the foreland of Hailuogou Glacier, Mt. Gongga (29°20′–30°20′N, 101°30′–102°15′E), China, where a well established chronological sequence of vegetation succession was observed (Li and Xiong 1995, He and Tang 2008). The succession stages (Fig. 1) with increasing ages are: (1) glacier stage 1998 – herbaceous community dominated by pioneers such as Astragalus mahoschanicus Hand.-Mazz., Anaphalis aureo-punctata Lingelsh Et Borza, Epilobium hirsutum Linn., Chamaenerion angustifolium (Linn.) Scop. and a few leguminous plant species and Hippophae rhamnoides Linn. Seedlings (12 yr), (2) glacier stage 1980 – midium shrubs dominated by Hippophae rhamnoides Linn., Salix rehderiana Schneid. and Populus purdomii Rehder saplings (30 yr), (3) glacier stage 1970 – Populus-Betula community dominated by medium P. purdomii, Betula utilis D. Don and Betula insignis Franch. (40 yr), (4) glacier stage 1958 – Populus-Betula community dominated by tall P. purdomii, B. utilis, B. insignis, and shrubs (52 yr), (5) glacier stage 1934 – mixed forest dominated by tall P. purdomii and Pinus brachytyla (79 yr), (6) glacier stage 1888 – conifer forest dominated by P. brachytyla (122 yr).

The local climate is typical of monsoon temperate regions with distinct rainy and dry seasons. The mean annual precipitation is 1949 mm, as most of which (over 70%) falling between June and October, and annual potential evaporation averages 264 mm. The mean monthly temperature ranges from −4.5°C to 12.7°C.

3. MATERIAL AND METHODS

Six sites with increasing ages (site 1 – site 6) were selected along the chronological sequence in the glacier foreland, representing the late 6 succession stages (Fig. 1). At each site, each dominant moss species was collected from 5–6 plots sized 50 × 50 cm area and combined to one collective sample. In the laboratory, moss samples were first cleaned of extraneous detritus and epiphytes, and the apices of the shoots (2–3 cm) were cut from the moss plants. The apices were then washed with tap water and then with distilled water to remove all the dusts and epiphytic organisms. After air dried, the moss samples were dried at 40°C for 48 h, and then ground to pass through a 2 mm mesh prior to analysis.

Organic carbon content in the mosses was determined by using the dichromate oxidation-sulphateferrous titration method (Bao 1999). The methods used for the analysis of universal nutrients were the semi-micro Kjeldahl procedure for N, vanadium molybdate colorimetric method for P, and flame photometry for K (Bao 1999). Concentration of the macronutrients was expressed as percent dry weight.

Tissue concentrations of soluble sugars and starch were analyzed following Teng et al. (2006) and Tan et al. (2010) with minor modifications. 0.1 g of the oven-dried powder of each sample was extracted with 80% ethanol (v/v) at 85°C for 1 h. The solutions were then centrifuged at 12,000 g for 10 min. The

Table 1. Moss species along the foreland of Hailuogou glacier.

<table>
<thead>
<tr>
<th>Sites</th>
<th>Age (yr)</th>
<th>Dominant moss species</th>
<th>Grow status</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site 1</td>
<td>12</td>
<td>Racomitrium ericoides</td>
<td>erect</td>
</tr>
<tr>
<td>Site 2</td>
<td>30</td>
<td>Racomitrium ericoides, Pleurojium schreberi, Thuidium cymbifolium, Actinothuidium hoereri</td>
<td>erect, creeping</td>
</tr>
<tr>
<td>Site 3</td>
<td>40</td>
<td>Pleurojium schreberi, Actinothuidium hoereri, Brachythecium homocladum</td>
<td>creeping</td>
</tr>
<tr>
<td>Site 4</td>
<td>52</td>
<td>Pleurojium schreberi, Actinothuidium hoereri, Brachythecium homocladum</td>
<td>creeping</td>
</tr>
<tr>
<td>Site 5</td>
<td>76</td>
<td>Pleurojium schreberi, Actinothuidium hoereri, Hylcomiastrum pyrenacium</td>
<td>creeping</td>
</tr>
<tr>
<td>Site 6</td>
<td>122</td>
<td>Pleurojium schreberi, Actinothuidium hoereri, Hylcomiastrum pyrenacium</td>
<td>creeping</td>
</tr>
</tbody>
</table>
ethanol extraction step was repeated three times. The three resulting supernatants were combined and made up to a known volume and then subjected to soluble sugar analysis using the anthrone-sulfuric acid method (Tan et al. 2010). The residues after soluble sugar extraction were oven-dried overnight at 60°C and retained for starch analysis according to the procedures described by Tan et al. (2010). Total nonstructural carbohydrate (NSC) was calculated as the sum of soluble sugar and starch.

All samples were analyzed in triplicate and data were expressed as means ± standard deviation (SD). The significant difference among different succession stages was tested by one-way ANOVA at P <0.05 or P <0.01 level. All the above mentioned statistical analyses were performed with the SPSS 11.0 program.

4. RESULTS

Dominant moss species differed in forest stands with different ages (Table 1). Along the six succession stages, the mosses are separately dominated by: site 1, Racomitrium ericoi-
des (Hedw.) Brid. (12 yr); site 2, R. ericoi
des, Pleurozium schreberi (Brid.) Mitt., Thuidium cymbifolium (Doz. et molk.) doz. et molk. and Actinothuidium hookeri (Mitt.) Broth (30 yr); site 3, P. schreberi, A. hookeri and Brachythe-
cium homocladium C. Muell. (40 yr); site 4, P. schreberi, A. hookeri and B. homocladium (52 yr); site 5, P. schreberi, A. hookeri and Hylo-
comiastrum pyrenacium (Spruce) Lindb. Ex Broth (76 yr); site 6, P. schreberi, A. hookeri and H. pyrenacium (122 yr). Table 1 also shows that growth status of mosses in the early stage of deglation was erect, with time going, moss layer was dominated by species with creeping status.

Organic carbon content increased insignificantly with successional stage (Fig. 2). However, the impact of successional stage on N, P, K concentrations in mosses was significant (P <0.01). N concentration was highest in the stand aged 30 yr, which was separately 1.69% in A. hookeri and 1.35% in P. schreberi, then it decreased with increasing stand age (Fig. 2). For P and K, there was a tendency of higher concentrations in stage with many shrubs, i.e., the forests aged 30 yr and 52 yr, when P content was separately 0.022% and 0.020% in A. hookeri and 0.020% and 0.017% in P. schreberi, and K content was separately 0.570% and 0.553% in A. hookeri and 0.490% and 0.493% in P. schreberi. Contrarily, P and K concentrations were significantly lower in mixed broadleaf-conifer forest (76 yr and 122 yr) and herbaceous community (12 yr) (P <0.01). Fig. 2 also indicates that nutrient accumulation in R. ericoi
des was significantly lower than in P. schreberi and A. hookeri.

Fig. 2. TOC (total organic carbon), total N, total P, and total K contents (mean ± SE) in mosses along the 6 succession stages.
Soluble sugar concentrations increased significantly in mosses from 30 yr of stand and then kept stable with time. However, concentration of starch and nonstructural carbohydrate (NSC) decreased in mosses from 30 yr of stand (Fig. 3). Fig. 3 also indicates that the stand aged 30 yr, which was dominated by *H. rhamnoides-P. purdomii*, was one key stage and was also the key point for moss growth and succession, in which the nutrient element contents and carbon and nitrogen metabolizing products reached the maximum or minimum, after this site, the values of the parameters changed in the reverse direction.

5. DISCUSSION

Mosses are the pioneer and the first green land plants developed during the evolutionary processes, they play an important role in vegetation succession (Uchida *et al.* 2002). Many studies showed that the composition of bryophyte communities varies with forest age and that community diversity increases with forest continuity (Selva 1994, Boudreau *et al.* 2000). In this study, moss species also changed with the succession processes. The dominant moss species changed from erect form to creeping form. The covers of moss in the six succession processes were 5%, 25%, 55%, 65%, 70% and 60%, respectively (He and Tang 2008). Although Nicole and Yves (2006) deemed that succession of bryophyte community in an boreal forest after fire was driven by changes in available moisture and light, we thought differences in moss community compositions, diversities, and covers were related to both the microclimate and the adaptive mechanisms of mosses.

In this study, mosses from different stages differed in N, P, K, soluble sugar and starch content, indicating different nutrient utilization patterns of mosses during succession processes. N, P and K content was higher in mosses from forest with dense shrubs, indicating that mosses accumulated more nutrients for plant growth in suitable environment. As consequent products of plant photosynthesis, soluble sugar concentrations of mosses were higher in the late stages of succession, indicating the higher photosynthetic activities of mosses in stands older than 12 yr.

Contrarily, starch contents were substantially higher in the early stage of succession. As mosses are poikilohydric plants, the growth of mosses was heavily influenced by their water content and the relative humidity in the environment (Stark 1983). In the present study, mosses grown in the early stage would endure heavier water stress, because stand 1 was rarely dominated by pioneer herbaceous communities such as *Astragalus mahoschanicus*, *Anaphalis aureo-punctata* Anaphalis sp, *Epilobium hirsutum* Linn., *Chamaenerion angustifolium*, etc., the canopy could not maintain a high humid environment for moss growth. Kitajima (1996) indicated that there are a trade-off between plant growth and survival caused by a trade-off between carbon allocation to growth and allocation to storage and defense. Carbon allocation to storage enhances plant survival, as it allows plants to overcome periods of stress.
and disturbance (Poorter and Kitajima 2007, Myers and Kitajima 2007). Therefore, the higher starch contents in site 1 in the present study was one of the adaptive strategies of mosses to survive environmental water stress. But site 2 to site 6 were covered by thick forest, which could provide appropriate shade and temperature for moss growth, due to the shade-loving property of mosses. Additionally, the litterfall and infiltrated water from upper vegetation could provide sufficient nutrients for mosses, therefore it was not necessary for mosses to accumulate much starch for survival.

Compared with starch, soluble sugar represented the smaller part of nonstructure carbohydrate content, inducing a similar trend of NSC with starch in different succession stages, in which a higher value of NSC (nonstructural carbohydrates) content at site 1 was observed. It was indicated that NSC storage in plants generally allow plants to overcome periods of stress and should enhance survival (Poorter and Kitajima 2007). Soluble carbohydrates might function as cryoprotectants, antioxidants and osmotic regulators in drought–stressed plants (Popp and Smirnoff 1995), acquisition of desiccation tolerance in some plant is also associated with the accumulation of carbohydrates (Norwood et al. 2000). Therefore, higher NSC content in site 1 was also benefit for the survival of mosses from the water–stressed environmental conditions in site 1. However, from the perspective of light requirement of plant, our result was in contrast to previous studies conducted on vascular plants, which demonstrated that shade-tolerant species tend to have greater carbohydrate reserves (Veneklaas and den Ouden 2005). For example, Gaucher et al. (2005) found that saplings of the shade-tolerant Acer saccharum had higher NSC concentrations than the intermediate light-demanding Betula alleghaniensis. Poorter and Kitajima (2007) found higher carbohydrate contents and pools in shade-tolerant species than in shade-intolerant species in the moist forest. And, this phenomenon was also observed between other shade–tolerant and shade–in-tolerant plants, for example Quercus and Castanea (Imaji and Seiwa 2010). Our results were different to others due to mosses were not only shade-tolerant but shade-loving plants. Different trends of soluble sugar and starch in mosses were observed along the succession stages, which disclosing the different contribution of them to the moss metabolism. We deemed that starch was more responsible for moss survival from environmental stress.

ACKNOWLEDGMENTS: The present work was supported by the “National Natural Science Foundation of China” (Grant No. 30900201) and the “Knowledge Innovation Project of the Chinese Academy of Sciences” (Grant No. KZCX2–EW–QN310, KZCX2–YW–BR–20).

6. REFERENCES


Boudreault C., Gauthier S., Bergeron Y. 2000 – Epiphytic lichens and bryophytes on Populus tremuloides along a chronosequence in the southwestern boreal forest of Québec, Canada – Bryologist, 103: 725–738.


Gaucher C., Gougeon S., Mauffette Y., Messier C. 2005 – Seasonal variation in biomass and carbohydrate partitioning of understory sugar maple (Acer saccharum) and yellow birch (Betula alleghaniensis) seedlings – Tree Physiol. 25: 93–100.


Hill J.O., Simpson R.J., Moore A.D., Chapman D.F. 2006 – Morphology and re-
Adaption mechanism of moss to environment

Sponse of roots of pasture species to phosphorus and nitrogen nutrition – Plant Soil, 286: 7–19.


Received after revision July 2012