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Growth rate of mosses and their environmental determinants in subalpine coniferous forests and clear-cuts at the eastern edge of the Qinghai-Tibetan Plateau, China

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Abstract Mosses cover most of the forest floor of subalpine forests at the eastern edge of the Qinghai-Tibetan Plateau, the origin of many important rivers in China. They play a crucial role in preventing soil erosion and conserving large amounts of water thereby regulating the water budget of local ecosystems. This area has a harsh climate due to low temperatures and low air pressure at high elevations. But the temperature varies considerably during the growing season, which does not favor the regeneration of spruce seedlings on clear-cuts after logging. Leaves of mosses have a single layer of cells and are thus sensitive to environmental changes. This attribute may be useful for monitoring environmental conditions and guide artificial regeneration. The growth of mosses has never been studied in this area and the variables indicating their growth in the subalpine forest ecosystems still needs investigation.

Growth rates of mosses have been rarely studied worldwide because the methods are time consuming and often inaccurate. A more simple and accurate method for measuring moss growth would help and encourage relevant research. We have found a method that will promote the efficiency in field measurements. Because of the special growth properties of mosses, the apical cell of branches initiates growth and the preceding leaves will stay where they were as the tips grow. Once mosses are marked with red oil at the tip of branches surrounded by young leaves, that portion of the branch above the marked leaves represents growth after labeling.

Two plots, one in an old-growth spruce forest and another in a nearby clear-cut, were selected to label mosses in a subalpine area of western Sichuan Province

during the growing season in 2001. The labeling was done on May 7 and measurements were made on August 7. Microclimate measurements on both sites were simultaneously carried out.

Of the six mosses, five species were present in both the forest and on the clear-cut. One species, *Entodon concinnus*, was found only on the clear-cut. The growth rates of mosses varied among species and habitats. *Hylocomium splendens* grew the fastest while *Dicranum assamicum* had the slowest growth rate. Habitat conditions have a distinct effect on the growth of *Hylocomium splendens*, *Dicranum assamicum* and *Thuidium lepidoziaeum* and their growth rates were higher in forests than on clear-cuts. The growth rates of these mosses increased as their habitat approached the forest. *Actinothuidium hookeri* and *Rhytidadelphus triquetrus* have moderate growth rates and is almost entirely independent of the type of habitat. The mosses can therefore be classified into habitat-sensitive and habitat-insensitive types. Analysis of microclimate characteristics shows that from May to July, the solar radiation level is lower and the environment is drier in the forest than those on the clear-cut. But a vapor pressure deficit (*VPD*) regime shows that the *VPD* in the morning is almost always lower in the forest than that on the clear-cut. With lower radiation and *VPD*, forests are more favorable to moss growth. For habitat-insensitive species, favorable micro-topographic factors might have offset the effect of habitat type.

VPD is strongly correlated with the growth of mosses. Eco-physiological characteristics, such as poikilohydry, play an important role in the survival and growth of mosses under harsh climatic conditions. Temperature and humidity are two factors critical for seedling establishment in artificial regeneration processes in the subalpine areas of western Sichuan. Since the growth of mosses is a function of the two factors, moss growth rates can be used to indicate the more favorable habitats. Therefore, the status of moss growth can be used to indicate habitats potentially favorable to the growth of tree seedlings.

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1 Introduction

The eastern edge of the Qinghai-Tibetan Plateau in China is a transitional area from the low Sichuan basin to the high plateau. The landscape is characterized by a combination of deep valleys and high mountains. The large differences in elevation and a complex terrain provide this area with a rich variety of vegetation types, given the effect of high precipitation brought by monsoons from the Pacific and Indian oceans. The subalpine coniferous forest is the dominant vegetation in this area. A thick layer of feathermoss consisting of *Hylocomium splendens*, *Pleurozium schreberi*, *Actinotuidium hookeri* and *Rhytidiadelphus triquetrus* generally covers the ground in this kind of forest. As one of the five most important forest regions in China, large scale logging during 1950s and 1990s considerably changed the pattern of vegetation, leaving large areas of clear-cuts. This changed forest habitat also shifted the distribution of mosses. In this process, a remarkable moss carpet was replaced by a pattern of patches of mosses. Acrocarpous moss has become dominant and pleurocarpous moss disappeared on the clear-cuts.

The changes in species composition and structure in the moss habitat could be used to indicate habitat conditions. In subalpine areas of western Sichuan, the regeneration of forests is quite difficult after logging due to high solar radiation and low water availability. The rate of survival of spruce seedlings in the mountain plateaus of northwestern Sichuan is less than 40%. The main reasons for the survival of seedling are temperature and water conditions.

As dwarf cryptogamous plants, mosses take water mainly through absorption of moisture in the air or from interception of precipitation. Due to the single cell layered leaves, except for the midrib, mosses are quite sensitive to environmental changes. The growth of mosses is a process of integrating proper light, temperature and humidity. Under dry and hot conditions, mosses can survive via dormancy and revive in a more favorable environment (Vitt et al., 1988; Vitt, 1990). The shape of mosses barely changes during dormancy. Therefore the size of moss could be expressed as a function of growth over time. Growth rates of the same moss species under different habitats can be explained as a measure of fitness to the environment, which is similar to the expression of degree days as the length of the growing period.

Due to their dwarf stature and the difficulty for marking growth, studies on their growth are quite few. Available marking methods include thread tying, clip fastening, inner growing mesh, standing poles and morphological markers (Vitt et al., 1988; Økland, 1995; Gower

et al., 1997; Vogel and Gower, 1998; Rydgren et al., 2001). But all these methods are time-consuming and/or inaccurate. The growth of mosses is initiated from a single apical cell surrounded by young leaves. The part beneath the tip of the branch is irrelevant to the growth in elongation. Based on this fact, we use a new marking method in mosses. We applied a red oil-based paint to the tip of mosses. The basic idea is that this paint does not affect the apical growing cell since it is only applied on the surrounding leaves which enwrap the apical cell. With the growth of apical cells, the surrounding young leaves become mature and stay in a fixed position of the branch. So, the markers on the leaves become the initial position for growth. The length from top to the marked initial position on the branch of mosses is the actual length of growth during a particular period.

For our investigation, we studied growth rates of mosses in different habitats and will discuss the reasons for differences in combination with the results of our simultaneous recording of ground surface microclimates in the interior forests and clear-cuts. We hope that this method can be useful for the monitoring of habitats.

2 Materials and methods

2.1 Study area

The study areas are located in an old-growth spruce forest and a nearby clear-cut of 1986 in the tenth hills along the Yuke valley in the upper reaches of the Dadu River of northwestern Sichuan Province, China. The geographic location is at 32°21'N and 100°48' E and the elevation ranges from 3670 to 3750 m for plots. The aspect is 350° and slope angle is between 30° to 40°. The terrain of this region is a type of mountain plateau with differences in elevation of less than 1000 m from peaks to the bottom of valleys. Its distance to Rangtang (Zamtang) County (32°16'N, 100°59'E), as the crow flies, is about 26 km. The growing season in this area is from the end of April to the end of September. The soil, at a depth of 20 cm, in the forest begins to thaw after the middle of June. During the 2001 growing season in the clear-cut areas, the mean air temperature 50 cm above the ground was 11.3°C and the mean surface temperature was 13.6°C. The mean relative humidity was about 70% at the same site.

The clear-cut had been planted with spruce seedlings in 1988. The current vegetation are dominated by shrubs and herbs. Dominant species in the shrub layer are from the genera of *Ribes*, *Rosa*, *Spiraea* and *Lonicera* and *Elymus*, *Potentilla* and *Rhodiola* in the herb layer. *Picea balfouriana* and *Abies squamata* constitute the tree layer of the forest. The under storey vegetation is rather sparse in the forest.

The distribution of mosses in the two plots is quite different. The large sized pleurocarpous mosses are widely

distributed in the forest and usually form a thick ground cover. The small sized acrocarpous mosses usually clump under shaded areas, such as behind of rocks or stumps, in the clear-cut areas.

2.2 Plot selection and moss marking

We selected different habitats in the two plots, including rocks, stumps, bare soil, shrubs and the northern edge of the forest as well as its interior. Our moss samples included *Hylocomium splendens*, *Actinothuidium hookeri*, *Entodon concinns*, *Thuidium lepidoziaeum*, *Dicranum assamicum* and *Rhytidiadelphus triquetrus*. The tips of moss branches were dotted with red oil paint with a writing brush to indicate the initial position of moss growth. The mosses were collected in order to measure their growth in length after three months. We marked the mosses on May 7, 2001 and the harvest took place on August 7 of that year.

2.3 Microclimate data collection

Microclimate data on the clear-cut were collected by a set of automatic microclimate data logging systems (NZY-2, Changchun Meteorological Institute, China). Two automatic tape loggers for humidity and temperature (ZJ1-2A/B, Shanghai Meteorological Instrument Company) were installed at a position 10 cm above the ground in the clear-cut and in the spruce forest. These loggers recorded air temperature, humidity, global radiation, photosynthetically active radiation (PAR), precipitation, soil temperature and ground surface temperature.

2.4 Data processing

2.4.1 Calculation of VPD

VPD (vapor pressure deficit) is calculated after the method of Jensen et al. (1990).

$$VPD = \left(1 - \frac{R_H}{100}\right) e^{\frac{16.78T_{db} - 116.9}{T_{db} + 273.3}} \quad (1)$$

where T_{db} is dry bulb temperature and R_H relative humidity.

2.4.2 Analysis of variance

One way analysis of variance (ANOVA) is used for inner group variance analysis.

3 Results

3.1 Microclimate characteristics in clear-cut and forest

3.1.1 Temperature and relative humidity

There is an obvious difference in the microclimate between the clear-cut and the interior of the forest. In

May, the temperature in the interior of the forest was a bit lower than that in the clear-cut, while the relative humidity did not show much difference. However, the relationship of the two variables was reversed in July. The relative humidity was clearly lower than that in the clear-cut (Fig. 1).

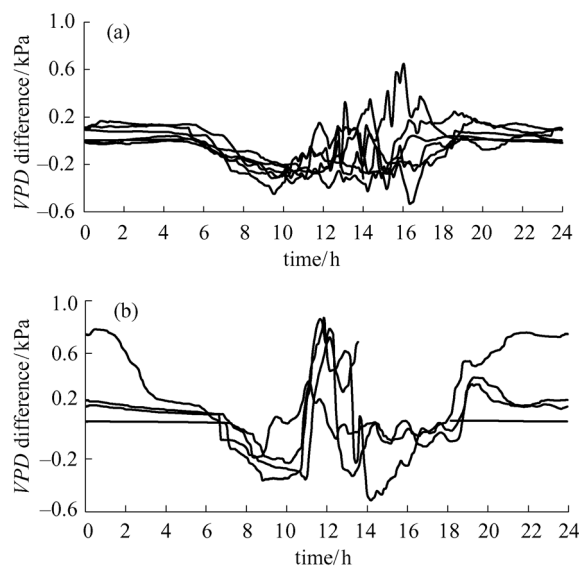


Fig. 1 Calculated diurnal course of VPD differences at consecutive days between forest interior and clear-cut in May (a) and July (b)

3.1.2 VPD

The VPD of the clear-cut was higher in May and then dropped to a level lower than that of the forest interior in July. The VPD of the clear-cut did not change much during May and July, but changed considerably in the forest during the same period. In the mornings, from 6:00 to 11:00, the VPD on the clear-cut was higher than the VPD means in May and July. However, for the VPD in the forest, the direct opposite occurred. In the mornings, VPD in the forest was generally lower than that of the clear-cut (Fig. 1 and Table 1).

3.2 Mean growth rate of mosses in different habitats

All the marked mosses grew more or less in all plots, showing that this method of marking is effective. But to what extent this method hinders the growth of moss still needs further study.

The highest mean growth rate of moss was exhibited by *Hylocomium splendens* in the forest. It reached 0.14 mm/day. The lowest growth rate, below 0.01 mm/day, was shown by *Dicranum assamicum* in the clear-cut. There were profound differences in growth rates between forest and clear-cut for mosses such as *Hylocomium splendens*, *Dicranum assamicum* and *Thuidium lepidoziaeum*.

Table 1 One-way ANOVA of data from May and July

variable	mean		SD		P	
	May	July	May	July	May	July
CAT/°C	6.18	9.05	4.54	5.09	<0.001	0.009
FAT/°C	2.15	8.49	3.74	4.32		
CRH/%	71.44	74.49	23.9	23.5	0.026	<0.001
FRH/%	69.51	59.36	24.5	23.8		
CVPD/kPa	0.344	0.371	0.369	0.389	<0.001	<0.001
FVPD/kPa	0.276	0.513	0.302	0.417		
CVPD (6:00–11:00)/kPa	0.431	0.417	0.266	0.295	<0.001	<0.001
FVPD (6:00–11:00)/kPa	0.241	0.331	0.232	0.228		

Note: CAT: air temperature on clear-cut; FAT: air temperature in forest interior; CRH: relative humidity on clear-cut; FRH: relative humidity in forest interior; CVPD: VPD on clear-cut; FVPD: VPD in forest interior.

However, these differences are not clear for *Actinothuidium hookeri* and *Rhytidiadelphus triquetrus*. *Entodon conncinus* was only found on the clear-cut and has a growth rate of 0.03 mm/day (Fig. 2 and Table 2). Given the effect of habitat on growth rates, we can divide mosses into two groups: habitat sensitive and insensitive types. *Hylocomium splendens*, *Dicranum assamicum* and *Thuidium lepidoziaaceum* belong to the sensitive group and *Actinothuidium hookeri* and *Rhytidiadelphus triquetrus* are insensitive mosses.

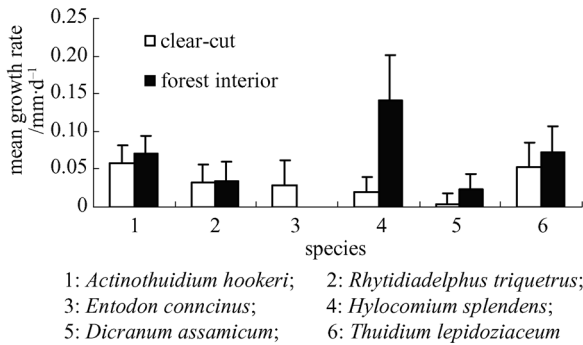


Fig. 2 Mean growth rate of mosses in clear-cut and forest interior during growing season (mean growth rate+standard deviation)

Mosses have different growth rates in different habitats (Fig. 2). *Hylocomium splendens* grows much better in the forest, with a mean growth in length of 13 mm, which is about a layer of stair segment. However, its growth in length on the clear-cut is only about 1/7 of that in the forest. This fact demonstrates that most of the growth occurred during the growing season and some individuals even grew two layers of stair segments. *Actinothuidium hookeri* grows less well in the forest, but its growth is statistically not significantly different from that in the clear-cut. Its mean growth in length is about 6 mm. The mean growth in length of *Rhytidiadelphus triquetrus* is about 3 mm. It grows best on bare soils and worst on rock

surfaces. The growth rate of mosses near the northern edge of the forest also increases when approaching the forest. The growth in length of *Thuidium lepidoziaaceum* increases from 4.9 mm on the clear-cut to 6.6 mm in the forest along that gradient. Growth of *Dicranum assamicum* in the forest is about five times of that under shrubs of the clear-cut. Its growth in length is about 2 mm in the forest. *Entodon conncinus* grows better on soils than on rock with a growth in length of 5 and 2 mm, respectively.

3.3 Growth pattern analysis

From an analysis of kurtosis and skewness of length growth in mosses (Table 2), we can see that all the mosses, except *Actinothuidium hookeri*, have some plants that do not grow and their percentages are quite high on the clear-cut. The growth of *Entodon conncinus* shows a type of negative exponential distribution while others have a slightly skewed or normal distribution. All indices of skewness are above zero. Measures of kurtosis and skewness of mosses growing in favorable habitats are larger than of those growing in a less favorable habitat. Mosses grow well in the forest.

4 Discussion

4.1 Difference in growth rate between species

Differences in growth rate between species are obvious. *Hylocomium splendens* is the leading species in growth in the forest and *Dicranum assamicum* is the slowest growing. It is also the only acrocarpous moss in our study area. *Hylocomium splendens* will grow a stair segment during the growing season. Because of its sympodial branching pattern, its ability of spatial expansion is much stronger than that of other mosses. *Actinothuidium hookeri* and *Rhytidiadelphus triquetrus* grow well in both clear-cut and forest areas. They have stocky branches and may have a good ability to resist unfavorable conditions.

4.2 Effect of habitat on growth rate

Habitat type also affects the growth rates of mosses. The growth rates of mosses near the edge of the forest increase when they are approaching the forest. What kind of factors in the habitat leads to differences in the growth rate of mosses? We will discuss these factors below.

4.2.1 Vegetation type and micro-topography

The habitat diversity of the clear-cut is much richer than that of the forest. The vigorous growth of herbs and shrubs and the undulating terrain provide many suitable environments for the settlement of mosses. In contrast, the habitat in the forest is monotonous. A thick layer of mosses on the ground diminishes the undulation of the

Table 2 One-way ANOVA of mean growth rates of mosses in two habitats

species	habitat	mean	SD	sample size	skewness	kurtosis	F	P
<i>Actinothuidium hookeri</i>	C*	0.058	0.023	23	0.103	2.20	3.90	0.052
	F*	0.070	0.024	50	0.802	4.47		
<i>Rhytidiadelphus triquetrus</i>	C	0.032	0.025	94	0.535	2.61	1.19	0.280
	F	0.035	0.024	215	0.961	6.20		
<i>Entodon concinicus</i>	C	0.029	0.033	166	1.646	6.33	–	–
	F	–	–	–	–	–		
<i>Hylocomium splendens</i>	C	0.020	0.020	25	0.048	1.42	21.02	<0.001
	F	0.142	0.059	215	0.398	3.78		
<i>Dicranum assamicum</i>	C	0.004	0.014	141	3.366	13.57	49.52	<0.001
	F	0.023	0.021	55	0.125	1.64		
<i>Thuidium lepidoziaecum</i>	C	0.053	0.032	82	0.367	3.20	14.94	<0.001
	F	0.072	0.035	100	1.109	4.79		

Note: *: C is clear-cut, F is forest interior

terrain. Herbs and shrubs are also sparse in the forest. Fluctuation of the microclimate in the forest is also less intense due to the presence of the spruce canopy. The habitat on the clear-cut can be roughly divided into three types: rock, soil and shrubs. The microclimate around rocks is severe because of its low specific heat capacity and low coverage of vegetation. Changes of solar radiation, temperature and humidity are therefore severe around rocks. The microclimate above the soil surface is quite like that of shrubs in the summer when herbs grow tall. Its fluctuation is not quite as high as that at rocks. The transitional habitat between the northern edge of the forest and the clear-cut enable mosses to increase their growth along the gradient. Mosses in shady areas on the clear-cut grow better than in habitats with direct sunshine. Site selection may be a reason for the small differences in growth rates of insensitive mosses for they may offset the effect of an overall harshness of the habitat.

4.2.2 Light

The growth of mosses is also controlled by photosynthesis which depends on a suitable photosynthetic photon flux density (PPFD), on temperature and humidity. Feathermosses are usually present on sites with direct light and low evaporation (Busby et al., 1978; Vogel and Gower, 1998; Bisbee et al., 2001). The photosynthetic rate of the feathermoss reaches its maximum when PPFD increases to 50 $\mu\text{mol}/(\text{m}^2\cdot\text{s})$ (Busby and Whitfield, 1978). Simply increasing light intensity over that level will not increase the photosynthetic rate. However high intensity of light will increase leaf temperature and the drying rate of feathermoss (Rydgren et al., 2001) and eventually induce dormancy. Therefore the growth of moss will decrease under high light intensity.

4.2.3 Temperature

Temperature changes in May and July were larger on the clear-cut than in the forest. The main reason for this

difference is the light regime. There is no tree canopy on clear-cuts. Solar radiation can directly reach the ground and increase its temperature. However, direct solar radiation can only reach the forest floor around noon through the gap between the tree crowns. Mosses on clear-cuts experience daily radiation for several hours before this occurs in the forest. They have to cope with long time periods and high intensity radiation on clear-cuts. Except for habitat selection, physiological strategies, such as dormancy, can be used for mosses to survive the extremes of temperature and water deficiency. Such dormancy can be recovered very soon in a favorable environment (Vitt et al., 1988). For example, *Pleurozium schreberi* can revive in one hour after exposure of 10–15 hours to -30°C . Its active temperature for photosynthesis can be dropped to -10°C (Kallio and Karenlampi, 1975). Therefore, the limiting factor for growth during growing season is not likely to be low temperature but dormancy induced by high temperature.

4.2.4 Relative humidity

Mosses generally live in a cool and moist environment. Air moisture controls the process of drying and rewetting on the surface of feathermosses (Busby and Whitefield, 1978; Skre et al., 1983). Tolerance of mosses to physiological drought is called poikilohydry. Mosses become dry and dormant in arid habitats and revive when rewetted (Vitt et al., 1988). A thick layer of mosses provides a moisture gradient for individual plants to grow under suitable water conditions along the vertical stratum of a moss carpet (Økland, 1995). Apocarpous mosses are able to absorb water from the soil and avoid moisture stress from the atmosphere as is usually experienced, to some extent, by pleurocarpous mosses. The low density of pleurocarpous mosses on clear-cuts prevents them from forming a thick moss layer. They are just spreading on the matrix of the ground, which helps to avoid water stress from the atmosphere. The windbreak and effect of diminished light of the forest also helps to decrease water loss from mosses (Granstrom and Schimmel, 1998).

4.2.5 VPD

VPD is a variable that integrates temperature and relative humidity. It reflects the condition of water vapor deficiency of the atmosphere. Evaporation in the forest is not directly related to light intensity (Baldocchi and Meyers, 1991; Schaap and Bouten, 1997), but it coincides closely with VPD. Therefore the VPD can be used to reflect the condition of habitat stress. The VPD in forests is always lower than that of clear-cuts in the morning. Mosses in the forest will have more time to grow under suitable light than on clear-cuts. Both in the forest and on clear-cuts, growth of mosses at other times will mostly be suppressed by high solar radiation and high temperatures. Mosses will grow under favorable condition and will stop under conditions of adversity. Because of the short revival time after dormancy, moss growth continues without the after-effects of interruption. The length of growth in a period reflects the suitability of an integrated temperature and water regime.

4.3 Significance of mosses on the indication of habitat

Plant growth in the subalpine belt is suppressed by the high intensity of solar radiation, low temperature, strong winds and stratified thawing of the soil. It is the last condition that usually causes physiological drought of plants. The sensitivity of mosses to light, temperature and water can be used to indicate the condition of clear-cuts. Good habitats usually feature well-grown mosses. The growth rate of mosses provides a quantitative indication of the suitability of habitats. Clear-cuts are the main plantation sites in subalpine areas of western Sichuan. But at such high elevations, the environment is harsh when the primary forest is cut. Seedling survival rates are quite low due to the disequilibrium of temperature and water. If we use mosses as indicators with the aim of regeneration, the survival of seedlings will be effectively enhanced in selected habitats. The integration of temperature and water is more appropriate at high elevations than degree days that only reflect temperature conditions. Therefore moss growth rates as habitat indicators are helpful for ecological monitoring of forest ecosystems.

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