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Implications of mass elevation effect for the altitudinal patterns of global ecology

ZHANG Baiping[1,2], *YAO Yonghui[1]

1. State Key Laboratory of Resources and Environment Information System, Institute of Geographic Sciences and Natural Resources Research, CAS, Beijing 100101, China;
2. Jiangsu Center for Collaborative Innovation in Geographical Information Resource Development and Application, Nanjing 210023, China

Abstract: The varied altitudinal gradient of climate and vegetation is further complicated by mass elevation effect (MEE), especially in high and extensive mountain regions. However, this effect and its implications for mountain altitudinal belts have not been well studied until recently. This paper provides an overview of the research carried out in the past 5 years. MEE is virtually the heating effect of mountain massifs and can be defined as the temperature difference on a given elevation between inside and outside of a mountain mass. It can be digitally modelled with three factors of intra-mountain base elevation (MBE), latitude and hygrometric continentality; MBE usually acts as the primary factor for the magnitude of MEE and, to a great extent, could represent MEE. MEE leads to higher treelines in the interior than in the outside of mountain masses. It makes montane forests to grow at 4800–4900 m and snowlines to develop at about 6000 m in the southern Tibetan Plateau and the central Andes, and large areas of forests to live above 3500 m in a lot of high mountains of the world. The altitudinal distribution of global treelines can be modelled with high precision when taking into account MEE and the result shows that MEE contributes the most to treeline distribution pattern. Without MEE, forests could only develop upmost to about 3500 m above sea level and the world ecological pattern would be much simpler. The quantification of MEE should be further improved with higher resolution data and its global implications are to be further revealed.

Keywords: mass elevation effect; intra-mountain base elevation; treeline; altitudinal belt; Tibetan Plateau

Our ecological world is extremely rich and varied. Complexity in ecology is of at least six distinct types: spatial, temporal, structural, process, behavioral, and geometric (Loehle, 2004), and any of these types has only been partially understood and, thus, deserves wide and thorough studies. Studies of classification and mapping of global climate and vegetation have provided us a relatively full but broad-brush view of the world ecology, and basic relationship between climate and vegetation has been explored (Köppon, 1920; Holdridge, 1947; Walter, 1979; Bailey and Hogg, 1986; Barry, 2008). Latitudinal patterns of montane altitud-

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Author: Zhang Baiping, Professor, specialized in physical geography and applied GIS. E-mail: zhangbp@lreis.ac.cn
***Corresponding author:** Yao Yonghui, Associate Professor, E-mail: yaoyh@lreis.ac.cn

inal (vegetation) belts have also been outlined (Hermes, 1955; Troll, 1973; Miehe *et al*., 2007; Körner, 2012), and one of the most striking ecological phenomena is the occurrence of extremely high treelines (4800 m or so above sea level) and snowlines (6000 m above sea level) at about northern latitude 30° and southern latitude 20°. In comparison, treelines are at only about 3500 m even in equatorial mountains, e.g., 3400–3700 m at Mount Kinabalu of Malaysia (Kitayama, 1992) and about 3400–3500 m in the Kilimanjaro in Tanzania (Malyshev, 1993; Bussmann, 2006). Although there exists indeed a trend for the treeline and snowline to rise from polar to equatorial areas and from continental rims to inland areas (Zhang and Zhao, 2014), these extremely high treelines and snowlines completely disrupt the overall global ecological pattern. This is truly a significant event in the altitudinal distribution of world ecosystems. Ecologically, treelines were often correlated with some isotherms, e.g., warmest month temperature of 10℃ (Brockmann, 1919; Daubenmire, 1954; Grace, 1977; Ohsawa, 1990), annual biotemperature of 3℃(Holdridge, 1947, 1967), warmth index of 15℃ • month (Kira, 1945; Ohsawa, 1990; Fang *et al*., 1996), seasonal mean ground temperature of 6.7℃±0.8℃ or 6.4℃±0.7℃ (Körner and Riedl, 2012; Paulsen and Körner, 2014), etc. But, what factors push the treelines or related isotherms upwards to so high elevations? The heating effect of immense mountains may easily come to mind. There was a German term "Massenerhebungseffekt" (in English, mass elevation effect) used to denote the heating effect and the resulting higher treelines in the interior of large mountains. This paper tries to quantify this effect and show its significances for the altitudinal patterns of global ecology.

1 Mass elevation effect (MEE): conceptual model

The concept of MEE was first introduced by A. de Quervain in 1904 to account for the observed tendency for temperature-related parameters such as treeline and snowline to occur at higher elevations in the central Alps than on their outer margins (Quervain, 1904). The occurrence of physiognomically and sometimes floristically similar vegetation types at higher altitudes on large mountain masses than on small isolated peaks and even islands are also regarded as MEE (Grub,1971; Barry, 2008; Leuschner, 1996; Flenley, 2007). Steenis (1961) even considered as "MEE" the difference between the lowest distribution height of a species and the necessary height for the species to occur at. The much higher elevation of the same type of altitudinal belts in the interior than in the outsides of the Tibetan Plateau was attributed to MEE (Zheng, 2000).

MEE is essentially the results of the thermodynamic effect of mountain masses (Schroeter, 1908). It leads to higher temperature in the interior than in the outside of mountain masses on the same elevations and at similar latitudes. The most prominent example is the lofty Tibetan Plateau (averagely 4500 m), which acts as a "hot source", especially in warm seasons of the year. For example, at an elevation of the mean elevation of the plateau, the monthly mean temperature differences between the plateau and the Sichuan Basin range from 3.58℃ for April to 6.63℃ for June (Yao and Zhang, 2015). Temperature difference between inside and outside of a mountain mass is essential for MEE and has been defined as the real value of MEE (Zhang and Yao, 2015). Higher limits of the same type of altitudinal belts in the inside than in the outside are the result of MEE, and the vertical difference is proportional to

MEE. To a great extent, the intra-mountain base elevation (MBE) could represent MEE, for it is closely related with MEE (Han *et al.*, 2011; Zhang and Yao, 2015). In other words, MEE, height difference in altitudinal belts between inside and outside, and the intra-mountain base elevation are all closely related. They all can indicate the magnitude of MEE, to varied degrees (Figure 1).

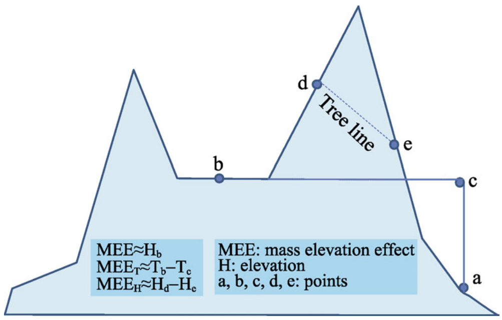

Figure 1 A conceptual model of mass elevation effect

2 The digital model of mass elevation effect

As defined above, MEE is virtually the temperature difference on a given elevation between inside and outside of a lofty mountain mass. We have calculated MEE for the main mountain ranges or plateaus of the world, namely, the Tibetan Plateau, the Alps, Scandinavia, the Rocky Mountains, the Andes, and the New Zealand Mountains (Zhang and Yao, 2015; Yao and Zhang, 2015), and the results for three giant mountain masses are shown in Figures 2-4. For the high-elevation weather stations, air temperature of the hottest month is usually 2–4 ℃ higher than in the outside for the Alps, about 4–8℃ for the Andes, and 4–12℃ for the Tibetan Plateau. The MEE of the Tibetan Plateau is the highest and most varied thanks to its extremely high, extensive and complex mass. It was ever considered that the magnitude of MEE depends on the average height and the area of a mountain mass (Holtmeier, 2003; Körner, 2012). This really seems quite rational. But we found that the magnitude of MEE is closely related with the inner base elevation rather than with the absolute height and the average height. In other words, intra-mountain base elevation, namely, the average elevation of the intra-mountain basin or the great river basin (Zhang *et al.*, 2012), is the most important factor for the formation of MEE. Other factors must also contribute to MEE. Through trial and error, we had such a hypothesis that latitude and moisture conditions (hygrometric continentality) are also significant to MEE. Then, we developed a linear model for MEE, with MEE as the dependent variable and the three factors just mentioned as independent variables. The mode is like this:

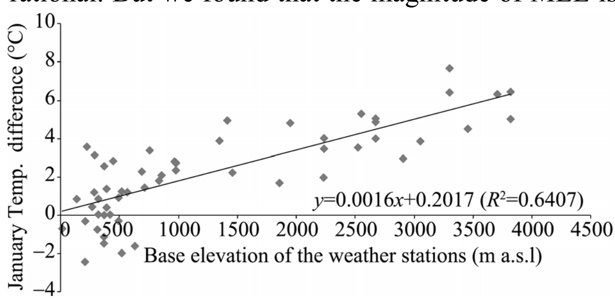

Figure 2 MEE and intra-mountain base elevation in the Andes

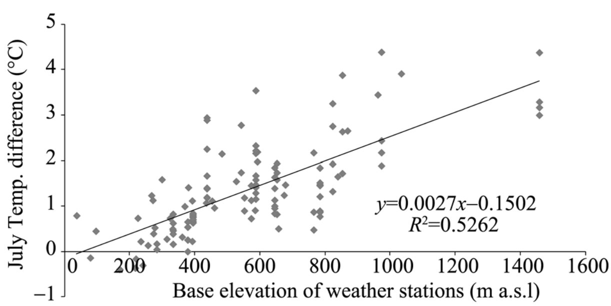

Figure 3 MEE and intra-mountain base elevation in the Alps

$$MEE = aLAT + bMBE + cHCONT + d \quad (1)$$

where LAT is latitude, MBE intra-mountain base elevation, HCONT hygrometric continentality, and a, b, c and d are coefficients or constant.

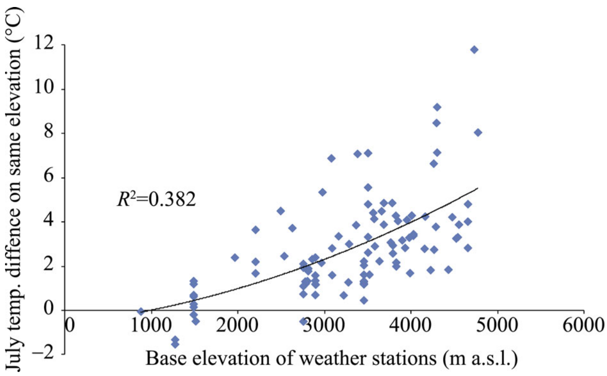

Figure 4 MEE and intra-mountain base elevation in the Tibetan Plateau

The result was shown in Table 1. It was clearly shown that MEE could be well explained by the three factors and that intra-mountain base elevation contributes the most to MEE and acts, therefore, as the primary MEE-forming factor. A slight exception occurs for the New Zealand mountains where hygrometric continentally contributes the most. This is understandable that marine climate prevails in New Zealand and the mountains are not very high.

Table 1 Contribution of MEE-influencing factors to MEE and the model coefficient of determination

MEE factors	Tibetan Plateau	Alps	Scandinavia	Rocky Mts.	Andes	New Zealand
Latitude	38.41	6.19	17.67	38.52	4.36	28.30
Intra-mountain base elevation	42.66	56.67	56.10	61.01	82.80	32.84
Hygrometric continentality	18.93	37.14	26.23	0.47	12.84	38.86
Model R^2	0.515	0.563	0.476	0.501	0.646	0.544

3 Extremely high treelines and snowlines as the results of MEE

The most significant contribution of MEE to the global ecological pattern is pushing montane plants and communities upwards to high elevations, especially in the extensive and massive mountain regions. Extremely high forests, defined as those above 4500 m in this paper, are distributed only in two highlands of the world, the southeastern Tibetan Plateau (29°N and 30°N) and central Andes, with a few treeline sites at about 4000 m in southern Rocky Mountains (Table 2).

Table 2 Distribution of the extremely high treelines in the world

Treeline site	Longi (°)	Lati (°)	Elev (m)	MBE (m)	Location	References
Nevado Sajama	–68.9	–18.1	4800	4200	Central Andes	Troll, 1973
Baxoi county	96.74	29.75	4900	4200	S.E. Tibetan Plateau	Miehe, 2007
Nyemo River (E)	90.03	29.31	4800	3850	S.E. Tibetan Plateau	Schickhoff, 2005
Kyi Chu catchment	91.60	30.29	4850	3800	S.E. Tibetan Plateau	Miehe, 2007
Porong Ka Monastery	91.16	29.77	4600	3700	S.E. Tibetan Plateau	Schickhoff, 2005
Pamtschü	91.96	29.30	4600	3650	S.E. Tibetan Plateau	Schickhoff, 2005
Nevado de Toluca	–99.7	19.1	4010	2800	Southern Rocky Mts.	Körner & Paulsen, 2004
Pico de Orizaba	–97.3	19.1	4020	2600	Southern Rocky Mts.	Körner & Paulsen, 2004
Pico de Valley	–97.3	19.1	4000	2600	Southern Rocky Mts.	Hoch & Körner, 2005

These extremely high treelines are not close to the equator. Rather, they occur in the highlands with high base elevation (Table 2). This is just what we want to show. Let's consider the elevation of treelines in the southern flank of the Himalaya and in Mt. Kilimanjaro. We have expected their treelines to be very high. But actually, their treelines are at elevations of 3500–3600 m or slightly higher, much lower than those (4600–4800 m) in the southeastern Tibetan Plateau and the central Andes where the base elevation is at about 3800–4300 m. Therefore, we must say that the high intra-mountain base elevation induces intense heating effect and pushes treelines to very high position. Calculation showed that the July isotherm of 10℃ is at about 4700–4900 m in the inner southeastern Tibetan Plateau, which almost perfectly coincides with the elevation of treelines (Yao and Zhang, 2013). In the same areas, the world highest snowlines are also identified, at about 5800–6000 m. Our analysis reveals that MBE contributes significantly to the extremely high distribution of snowlines (Han *et al*., 2011).

We have also shown that treelines could even occur above 5000 m in the western Tibetan Plateau and western central Andes if precipitation were enough there (Zhang and Yao, 2015). It is safe to say that high intra-mountain base elevation gives rise to intense MEE which, in turn, leads to extremely high distribution of montane forests. What can we call these forests? At so high elevation, could we still only call them montane forests? According to our traditional paradigm or classic mountain ecological classification, forests could not be matched with the term "alpine"! Then, the term "alpine forests" could not be coined and used. Out of frustration, the forests at elevations of about 4500 m above sea level could at least be called "high-elevation forests" before the term "Alpine forests" is accepted.

4 Global treeline distribution model with MEE as a variable

Treelines, as a prominent transitional ecotone between forested mountain slopes and alpine meadow/shrub, are highly complex in altitudinal distribution and sensitive to warming climate. Great efforts have been made to explore their distribution patterns and ecological mechanisms for more than 100 years, and quite a number of geographical and ecophysiological models were developed to correlate treeline altitude with latitude or a isotherm of given value. But these models are all mountain/region-specific or global-specific, having great difficulties in explaining cross-scale treeline patterns due to the extreme diversity and complexity of treeline site conditions. Jobbagy and Jackson (2000) developed a global treeline elevation distribution mode, with annual mean temperature and the annual arrange of temperature as independent variables. Their model could only explain 79% of the variation of forest lines (almost treelines). Their data for model development were extremely limited, almost without treeline data sites above 3500 m. So, their so-called "global control of forest line elevation" must be unreliable. Just like other researchers, they completely neglected the crucial "mass elevation effect." We collected and compiled a second-hand dataset for a total of 594 treeline sites all over the world, and explored how MEE affects global treeline elevation by developing a ternary linear regression model with intra-mountain base elevation (MBE, as a proxy of MEE), latitude and continentality as independent variables (Zhao *et al*., 2015). The results indicated that MBE, latitude and continentality together could explain 92% of global treeline elevation variability, and that MBE contributes the most (52.2%), latitude the second (40%) and continentality the least (7.8%) to the altitudinal distribution of global treelines. Comparatively, MEE is more significant in the Northern Hemisphere than in the Southern. This is understandable for more extensive and higher mountain masses exist in the Northern Hemisphere. It is clear that taking MEE into treeline model development greatly enhanced the ability of explanation of the model and effectively deepened our understanding of the global geographic control of treeline distribution.

5 Conclusions

(1) MEE is a powerful agent in shaping the altitudinal pattern of global ecology. The strong heating effect or MEE push forests upwards to about 4800–4900 m in southeastern Tibetan Plateau and the central Andes. But, this effect has been largely neglected in the past.

(2) Intra-mountain base elevation is the most important MEE-forming factor. The area, average elevation and absolute height of mountain masses only seem important.

(3) MEE, defined as the temperature difference on a given elevation between inside and outside of a mountain mass could be digitally modeled with intra-mountain base elevation, latitude and hygrometric continentality.

(4) When MEE is taken into account, the global treeline model would have much higher ability of explanation. This greatly deepens our understanding of geographic pattern and formation mechanism of global treelines.

(5) MEE makes the world full of variety. Without MEE, any trees grow at most up to the elevation of 3500 m; without MEE, temperature laps rate would be rather consistent; and without MEE, the world of climate and vegetation would be much plainer.

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