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Climatic Factors for Limiting Northward Distribution of Eight Temperate Tree Species in Eastern North America

FANG Jing-Yun, LI Ying
(*Department of Urban and Environmental Sciences, and Center for Ecological Research and Education, Peking University*, Beijing 100871, China)

Abstract: Eight temperate deciduous tree species, *Acer rubrum* L., *A. saccharinum* L., *A. saccharum* Marsh., *Belluta alleghaniensis* Britton., *Fraxinus nigra* Marsh., *Quercus rubra* L., *Titia americana* L., and *Ulmus americana* L. in eastern North America, were selected to explore relationship between the northward distribution of temperate tree species and climatic factors. For each species, more than 30 sites at their north limits of distribution were obtained from their distribution maps, and 11 climatic indices at the north limits were computed. The standardized standard deviation (*SD*) method, which compares the magnitude of variance of climatic indices, was used to detect which climatic parameter was the most important for explaining northward distribution of these species. We presume that the climatic parameter that has the smallest variance at the north limit would be assigned as the dominant climatic factor for limiting the distribution of this species. The results derived from the standardized *SD* method indicated that the *SD* value of warmth index (*WI*) and/or annual biotemperature (*ABT*) were the smallest among the 11 climatic indices. Since both *WI* and *ABT* represent growing season temperature, it suggested that growing season temperature was the most important climatic factor for explaining the northward distribution of these temperate tree species. The relationships between several climatic indices, *WI*, coldness index (*CI*), annual precipitation (*AP*), annual range of temperature (*ART*) and humid/arid index were also analyzed. As a result, at the north limits of all these species, both *WI* and *CI* decreased with an increase of *AP*, and *CI* increased with an increase of *ART*. Besides growing season temperature, precipitation and climatic continentality also have influence on the northward distribution of the temperate trees in eastern North America.

Key words: eastern North America; northward limit of distribution; climatic index; growing season temperature; precipitation; standard deviation

Some studies have suggested that the winter low temperature is the dominant climatic factor for limiting northward distribution of temperate tree species[1, 2]. Fang and Lechowicz[3], however, in their study of beech (*Fagus* L.) species, which are widespread among the deciduous broadleaf forests in the north temperate zone, pointed out that the growing season temperature was of the most importance in explaining northward distribution of beech species. Considering the following two reasons, we suspect the reality of the viewpaint that the winter low temperature is the dominant climatic factor for limiting the northward distribution of temperate tree species:

(1) In eastern North America, the winter low temperature does not indicate an obvious change with an increase of latitudes in the south of 50° N, and is even higher in high latitudes than at middle latitudes in some cases. Compared to such a change in winter temperature, temperate tree species are not distributed more northward. Such a disagreement between temperature and distribution of trees does not support the hypothesis that the low temperature restricts the northward distributions of temperate tree species.

(2) Sakai and Weiser[2], based on freezing experiments, concluded that some temperate tree species were able to physiologically endure the lowest temperature of -80 ℃. Actually, however, temperate tree species do not occur under such a low temperature condition, suggesting that the distribution of temperate tree species can not be explained by a single low temperature factor.

This study aims at detecting the possible climatic factors for influencing horizontally northward distribution of temperate tree species from a large-scale and at discussing the relationships between their distributional north limits and climatic parameters. In eastern North America, plains and low hills are main landscape and Mt. Appalachian is the only mountain where the altitude is usually lower than 500 m. A small topographical relief in the eastern North American Continent provides a good region for examining the relationships between climatic factors and horizontal distributions of tree species.

1 Materials and Methods

1.1 Plant materials

According to Atlas of United States Trees[4], eight temperate deciduous trees in eastern North America were selected for this study. These species have clear natural boundary at their distributional north limits, and ranged from about 100° W in longitude to the coast of Atlantic Ocean and from 45° N in latitude to the most northern limit of the temperate zone. Because the north limits of

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these species run through regions with a small topographic relief, the influence of topographical factors on the relationship between species distribution and climate could be eliminated.

1.2 Data collection

(1) Data collection for north limits of species: The sites at the northern distribution limit were collected for the eight selected species from their distribution maps[4] by the following procedure:

We first plotted sites along the northern limit of distribution from west to east at an interval of about one degree in longitude, and then read their geographical location for the species. The sites that fall into the Great Lakes were excluded from the geographical site dataset and not used for the analysis.

(2) Collection of paired climatic data with sites of the north limits: Climatic data for a site obtained from the distribution map were estimated using climatic records at the nearest meteorological station that is close to and has similar altitude to the site. In general, the meteorological station should not be far from the site by 0.5 degree of latitude and 1.0 degree of longitude (about 50 – 60 km). For the sites without such closed meteorological stations nearby, the climatic data were obtained by averaging climatic variables of two meteorological stations that are not far from the site by less than 1.0 degree of latitude and 2.0 degree of longitude, otherwise the sites were eliminated from the dataset. As a result, at least 30 sites were available for each species.

Climatic data used in this study were from the "Canadian Climate Normals 1951 – 1980"[5] and the "Climate Normals for the U.S. 1951 – 1980"[6]. Climatic variables used included monthly mean temperatures (℃) from January to December, annual mean temperature (℃), mean temperature for the coldest month (℃), lowest winter temperature (℃), monthly precipitations (mm) from January to December and annual precipitation (mm).

1.3 Climatic parameters

Eleven climatic parameters were used in our study, including mean temperature for the warmest month (*MTWM*, ℃), mean temperature for the coldest month (*MTCM*, ℃), annual range of temperature (*ART*, ℃), annual mean temperature (*AMT*, ℃), annual precipitation (*AP*, mm) and the following six indices.

(1) Annual biotemperature (*ABT*, ℃, Holdridge[7]).

$$ABT = \frac{1}{12}\sum t_i$$

t_i is mean temperature for months in which $t > 0$ ℃; $t_i = 30$ ℃ if $t_i > 30$ ℃.

(2) Warmth index (*WI*, ℃·month, Kira[8]). *WI* is a simple index to calculate the growing season warmth from monthly mean temperature.

$$WI = \sum(t_i - 5)$$

t_i is mean temperatures for months in which $t > 5$ ℃.

In this study, we used both *ABT* and *WI* as the indices showing growing season warmth.

(3) Coldness index (*CI*, ℃.month, Kira[9]). We used *CI* to express degree of winter coldness.

$$CI = -\sum(5 - t_i)$$

t_i is mean temperatures for months in which $t < 5$ ℃.

(4) Annual potential evapotranspiration (*APE*, mm, Thornthwaite[10]). Evapotranspiration is the sum of surface evaporation and plant transpiration. Potential evapotranspiration is a measure of, in the ideal conditions, the maximum evapotranspiration transferred from the surface (vegetation, soil and water) to the air.

$$APE = \sum_{i=1}^{12} k_i e_i$$

where, *APE* is annual potential evapotranspiration (mm); e_i is monthly potential evapotranspiration, $e_i = 16(10t/I)^a$; t is monthly mean temperature (℃); I is an annual heat index, $I = \sum i = \sum_{n=1}^{12}(t/5)^{1.514}$;

$a = 6.75 \times 10^{-7} I^3 - 7.71 \times 10^{-5} I^2 + 1.79 \times 10^{-2} I + 0.4924$

k_i is correction factor of day-length. Fang[11] gave the following equation to calculate the values of k_i for each month, $k_i^n = aL + b$

where L is latitude (degree), and n, a and b are coefficients. For details of the coefficients for each month, see Fang[11].

(5) Moisture index (*Im*, Thornthwaite[10]). *Im* is a parameter of the relative humid/arid climate.

$$Im = \frac{100s - 60d}{APE}$$

s is annual water surplus (AWS); d is annual water deficit (AWD); *APE* is annual potential evapotranspiration. For calculation of these indices, see Thornthwaite[10].

(6) Humid/arid index (Bailey[12]). It is an index derived from monthly mean temperatures and monthly precipitation.

$$S = \sum_{i=1}^{12} S_i$$

S_i is monthly humid/arid index, $S_t = 0.18r/1.045^t$; r is monthly precipitation (mm); t is monthly mean temperature (℃).

1.4 Standard deviation (*SD*) method for analyzing climatic indexes

Some studies have showed that the climatic parameter with the smallest variance at a specific distributional limit was regarded as the dominant climatic factor for limiting the distribution of tree species[13 – 15]. Kira[13] suggested that standard deviation (*SD*) could be used to express magnitude of variance of climatic parameters at the distributional north limits. In this paper, *SD* values of the climatic parameters at north limits of each tree species were used to determine the dominant climatic factor. Since *WI*, *CI* and *ABT* are the summation of monthly mean temperature for several months in a year, their *SD* values are not directly comparable with those of other variables that represent a simple temperature reading. For these three parameters, therefore, *SD* should be standardized by dividing them by the number of months summed (*n*) for *WI* and *CI*, and by multiplying 12/n for *ABT* for comparison on an equivalent basis[16]. Here we call it as standardization of *SD*. The index, which shows the smallest standardized *SD* value, could be considered as the dominant climatic factor for the species distribution[16].

2 Results and discussion

2.1 Climatic indexes at the north distributional limits

Mean and *SD* values of the eleven indexes were calculated for all eight species (Table 1). *WI* values at the north limits ranged from 38 to 56 ℃/month for the eight species. This was coincident with the critical climatic value at the north limit of cool-temperature zone which was defined as a *WI* value of 45 ℃·month by Kira[5]. *ABT* showed a narrow range from 5.7 to 7.6 ℃ and was basically coincident with the critical climatic value at the north limit of cool-temperature zone which was defined as an *ABT* value of 6.0 ℃ by Holdridge[7]. These indexes, therefore, suggested that the eight species were typical temperate tree species. Annual precipitation at the north limits for these eight species fluctuated from 850 to 900 mm, and another two indexes, *Im* and humid/arid index (*S*) varied from 55 to 83 and from 125 to 156, respectively. These corresponded to that of the humid climatic zone by Thornthwaite[10] who defined humid climate as *Im* values of 20 – 100, and of humid climatic region by Bailey[12] who defined humid climate as *S* values of 87 – 162. These suggest that the north limits of these eight tree species are under a humid climate.

2.2 Climatic factors for limiting the northward distribution

In eastern North America, annual precipitation decreases from east to west (Fig.1). Figure 1 demonstrates such a precipitation pattern for a case of the north limit of *A. rubrum*. Minimum annual precipitation was 500 mm for the distribution of *A. rubrum*; this could be regarded as the threshold of precipitation. According to the threshold, *A. rubrum* could be distributed, but actually have not occurred more northward in eastern coastal region where precipitation is rich. The same cases appear in the other tree species. This suggests that moisture condition is not the primary limiting factor for the northward distribution of these tree species. This also is evident as shown from the *SD* values of moisture parameters in Table 1. The *SD* value is a measure indicating the magnitude of variance of climatic indexes at the north limits. The *SD* values of two moisture parameters (*AP* and *Im*) and humid/arid index are relatively large, suggesting that they have a large variance. In this study, therefore, thermal variables were primarily used to detect which climatic factors are the most important for delimiting their northward distribution. Among the eight thermal parameters used, *WI* and *ABT* showed the least *SD* values for all the eight species, whereas *CI* and other thermal parameters had relatively large *SD* values (Table 1). It indicates that *WI* and/or *ABT* that are measures of the growing season warmth have the smallest variance at the north limits of these tree species. This is to say, that the effective growing season temperature is the most important climatic factor for explaining the northward distribution of these temperate tree species.

Table 1 Average and standard deviation (*SD*) of 11 climatic indices at the north limits of the eight tree species in eastern North America

Climatic variables	*Acer rubrum* Mean/*SD*	*Acer saccharinum* Mean/*SD*	*Acer saccharum* Mean/*SD*	*Betula alleghaniensis* Mean/*SD*	*Fraxinus nigra* Mean/*SD*	*Quercus rubra* Mean/*SD*	*Tilia americana* Mean/*SD*	*Ulmus americana* Mean/*SD*
Thermal variables								
AMT (℃)	2.3/1.21	4.7/1.29	2.2/0.95	2.4/1.34	1.2/1.82	2.6/1.39	2.5/1.57	1.2/1.32
WI (℃·month^{1})	43.4/0.76	56.1/0.65	43.7/0.76	41.6/0.93	37.9/1.10	45.2/0.77	47.0/0.84	39.7/0.78
CI (℃·month^{1})	75.3/2.25	59.5/1.37	77.4/1.29	72.9/2.41	83.9/2.44	73.9/2.53	74.6/1.68	85/1.61
ABT (℃)	6.3/0.96	7.6/0.69	6.3/0.95	6.1/1.07	5.7/1.01	6.5/1.00	6.6/1.04	5.8/0.70
MTWM (℃)	17.3/1.02	19.2/0.99	17.4/1.05	16.9/1.17	16.5/1.38	17.6/1.01	17.9/1.26	16.8/0.72
MTCM (℃)	– 14.9/3.99	– 11.7/2.58	– 15.3/2.56	– 14.1/4.33	– 16.1/4.75	– 14.5/3.61	– 14.9/2.75	– 16.6/3.64
ART (℃)	32.1/4.57	30.9/2.40	32.7/2.95	31.0/4.98	32.6/5.19	32.1/3.75	32.7/3.06	33.4/3.77
APE (mm)	370.9/27.77	446.3/40.19	370.4/30.49	361.2/33.05	334/42.52	380.3/34.70	390.4/38.97	343.8/20.35
Moisture variables								
AP (mm)	880.7/196.00	862.0/147.08	855.1/155.27	904.1/210.74	884.5/140.59	903.2/190.21	896.5/263.09	891.0/129.04
Im	73.3/42.46	54.7/31.15	68.2/34.16	80.3/45.16	82.8/32.75	75.9/39.53	72.9/55.22	81.4/27.63
Humid/arid index	145.9/38.14	125.4/34.59	143.1/32.53	150.1/37.81	153.6/25.69	148.8/36.41	147.6/50.34	156.2/24.84

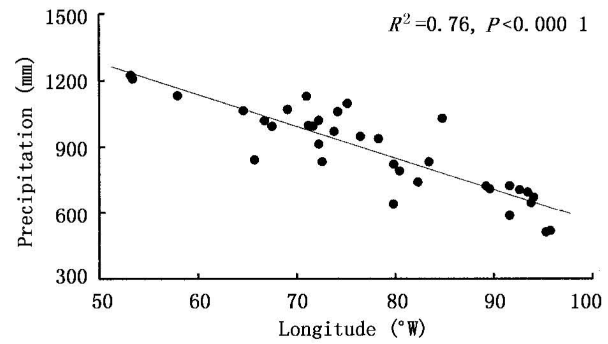

Fig.1. Change in annual precipitation with longitude at the north limit for *Acer rubrum*.

2.3 Relationships between *WI*, *CI* and precipitation

Annual precipitation at the north limits of the eight species increased significantly from west to east. Although *WI* showed a small SD value for most tree species, indicating a small variance, it still had a clear pattern along a longitudinal direction that increased from east to west due probably to a change in precipitation. This implies that the northward distribution of the temperate deciduous tree species could not be explained only by a single growing season temperature, but by a combination of temperature and other climatic factors, such as precipitation and climatic continentality. Figure 2 exhibits the relationship between *WI* and precipitation at the north limits for all the species. *WI* declined with an increase of precipitation, demonstrating that the growing season temperature was higher under a precipitation-rich climate than under a precipitation-poor climate. Similar results have been obtained from previous studies[14, 16, 17]. Such a pattern between *WI* and precipitation showed in Fig. 2 was also found between *WI* and humid/arid index. Thus, although the growing season temperature delimitted dominantly the northward distribution of temperate tree species, the influence of precipitation also could not be neglected.

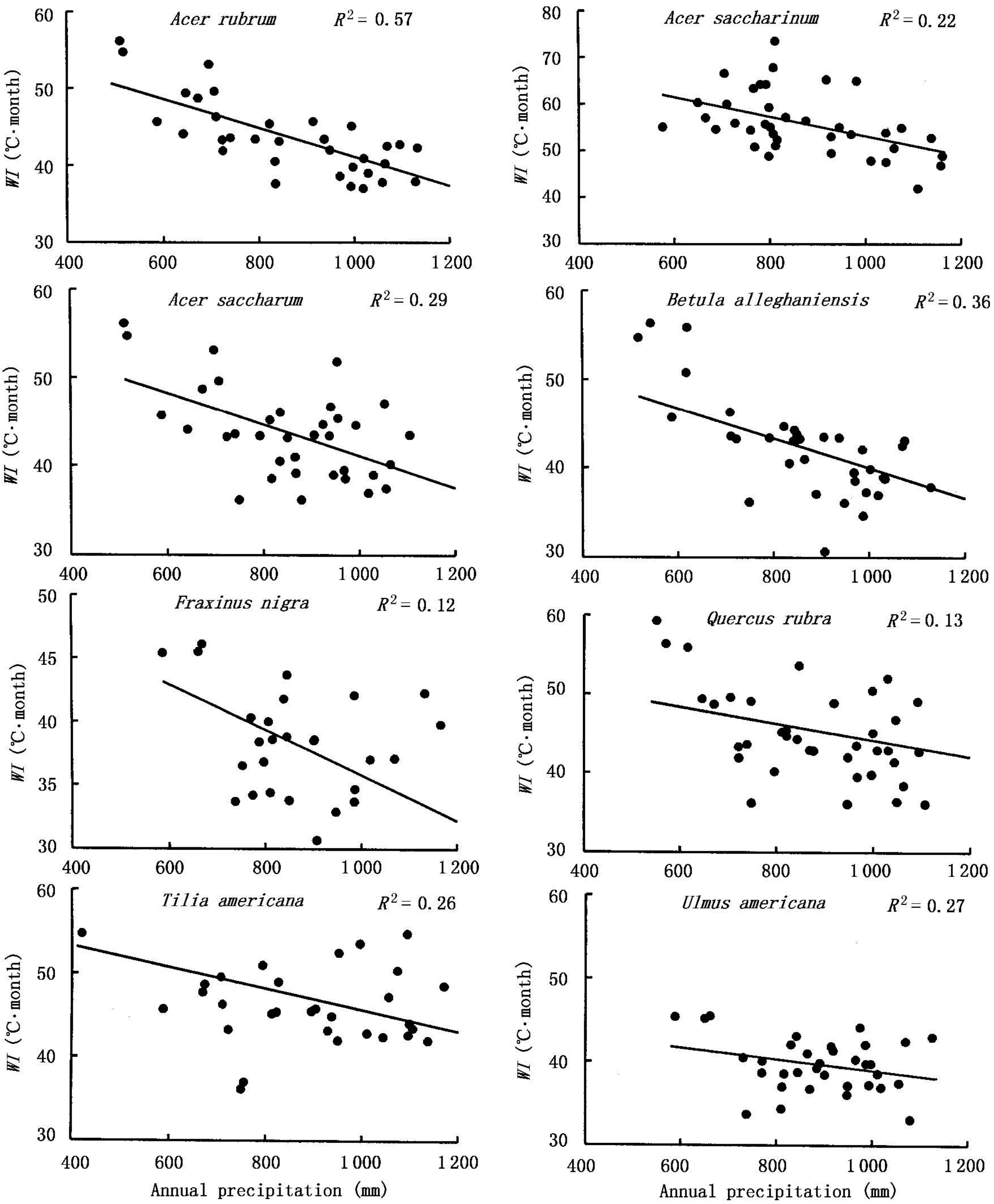

Fig.2. Relationship between warmth index (*WI*) and annual precipitation.

Analyzing the relationship between *CI* and precipitation, it was indicated that *CI* decreased as precipitation increased for five of the eight species, and no clear relationship was exhibited for the remainders (*A. saccharinum*, *A. saccharum* and *F. nigra*).

2.4 Relationships between *WI*, *CI* and annual range of temperature

Annual range of temperature (*ART*) can be an index expressing climatic continentality. In the present study, *ART* increased from east to west at the north limits of the eight species, indicating an increasing trend from the coast inland. On the other hand, *CI* increased significantly with an increase of *ART* ($R^2 > 0.9$ for some species). This is to say, at their north limits, *CI* was larger at a smaller *ART*, and vice versa. No clear correlation was showed between *WI* and *ART*.

3 Conclusion

Northward distributions of temperate tree species are strongly related to climatic conditions. Among 11 climatic parameters used in the present study, *WI* and/or ABT showed the least standard deviation values, or the smallest magnitude of variance at the distributional north limits of the eight temperate deciduous tree species. Since both *WI* and *ABT* represent effective growing season temperature, it was considered that the growing season temperature was the most important climatic factor for explaining the northward distribution of these species. This implies the hypothesis that winter low temperature as the dominant climatic factor for limiting northward distribution of temperate tree species may not be true at least for the case of our study. On the other hand, at the north limits of the eight tree species, both *WI* and *CI* decreased with an increase of precipitation, *CI* increased with an increase of *ART*, and *WI* decreased with an increase of humid/arid index. These findings indicate that annual precipitation, humid/arid index and climatic continentality, as well as growing season temperature, also significantly influence northward distribution of temperate trees in eastern North America.

References:

[1] Woodward E I. Climate and Plant Distribution. Cambridge: Cambridge University Press, 1987. 1 – 174.

[2] Sakai A, Weiser C J. Freezing resistance of evergreen and deciduous trees in North America with reference to tree regions. *Ecology*, 1973, **54**:118 – 126.

[3] Fang J-Y, Lechowicz M J. Climate limitation to the present distribution of beech (*Fagus* L.) species in the world. (in press)

[4] USDA Forest Service. Atlas of United States Trees. Vols. 1 – 5. Washington D C. United States Government Printing Office, 1975 – 1986.

[5] Atmospheric Environment Service, Environment Canada. Canadian Climate Normals 1951 – 1980, Temperature and Precipitation (Quebec, Ontario, and Atlantic Provinces), 1985.

[6] National Oceanic and Atmospheric Administration. Climate Normals for the U.S. 1951 – 1980, 1st ed. Detroit: Gale Research Company Book Tower, 1985.

[7] Holdridge L R. Determination of world plant formations from simple climatic data. *Science*, 1947, **105**:367 – 368.

[8] Kira T. A New Classification of Climate in Eastern Asia as the Basis for Agricultural Geography. Kyoto: Horticultural Institute Kyoto University, 1945. 23.

[9] Kira T. On the altitudinal arrangement of climatic zone in Japan. *Kanti-Nougaku*, 1948, **2**:143 – 173.

[10] Thornthwaite C W. An approach toward a rational classification of climate. *Geography Rev*, 1948, **38**:57 – 94.

[11] Fang J-Y. Distribution of vegetation and climate in China. Osaka: Doctoral Dissertation of Osaka City University, 1989.

[12] Bailey H P. Semi-arid climates: their definition and distribution. *Ecol Study*, 1973, **34**:73 – 97.

[13] Kira T. A climatological interpretation of Japanese vegetation zones. Miyawaki A, Tuxen. Vegetation Science and Environmental Protection. Tokyo: Maruzen, 1977. 21 – 30.

[14] Fang J-Y, Yoda K. Climate and vegetation in China. V. Effect of climate factors on the upper limit of distribution of evergreen broadleaf forest. *Ecol Res*, 1991, **6**:113 – 125.

[15] Hattori T, Nakanishi S. On the distribution limit of the lucidophyllous forest in the Japanese Archipelago. *Bot Mag Tokyo*, 1985, **98**:317 – 333.

[16] Fang J-Y, Ohsawa M, Kira T. Vertical vegetation zones along 30° N latitude in humid East Asia. *Vegetatio*, 1996, **126**:135 – 149.

[17] Kure H, Yoda K. The effect of the Japan sea climate on the abnormal distribution of Japanese beech forests. *Jpn J Ecol*, 1984, **34**:63 – 73.

北美东部 8 种温带树种向北分布的限制气候因子

方精云　李　莹

（北京大学城市与环境学系，北京大学生态学研究与教育中心，北京 100871）

摘要：利用分布于北美东部的 8 种温带落叶树种为研究材料，应用反映热量和降水状况的 11 个变量为气候指标，用标准差分析方法分析了这 8 个树种的分布北界与气候因子之间的关系。结果表明，在所使用的气候指标中，同一树种不同地点的温暖指数或年生物温度的标准差最小，说明积温是限制这些树种向北分布的主要气候因子；温暖指数和寒冷指数随着年降水量的增大而减小，寒冷指数随着年较差的增加而增加，温暖指数随着水热综合指数的增加表现出减小的趋势。表明，除了生长季节的积温之外，降水和大陆性等气候条件对温带树种向北分布也起着重要作用。

关键词：北美东部；分布北界；气候指数；积温；降水；标准差

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