ΦYTON
REVISTA INTERNACIONAL DE BOTÁNICA EXPERIMENTAL
INTERNATIONAL JOURNAL OF EXPERIMENTAL BOTANY
FUNDACION ROMULO RAGGIO
Gaspar Campos 861, 1638 Vicente López (BA), Argentina
www.revistaphyton.fund-romuloraggio.org.ar

Potential spatial expansion of *Ulmus macrocarpa* population in Keerqin sandy lands, China

Expansión espacial potencial de una población de *Ulmus macrocarpa* en áreas arenosas en Keerqin, China

Jianar A, JH Yuan, YF Yang

Abstract. *Ulmus macrocarpa* Hance can form monodominant woodlands in the semiarid Keerqin sandy lands, China. Methods of sampling at meter intervals from the bases of trees at the woodland edges and isolated trees, respectively, were employed along vertical sections in different directions. Using statistical methods based on the density function of the Weibull distribution, the patterns of seed dispersal and the spatial expansion response of *U. macrocarpa*, which is a typical anemochorous plant, were analyzed. Although as an effect of the wind direction varying owing to the monsoon, there were differences in the degree of dispersal of seeds in terms of distance, and cumulative seed number for the woodland edges and isolated trees, the seed dispersal patterns were all the same. That is, the seed dispersal patterns can be described by density functions of the Weibull distribution ($P<0.01$) for the frequencies of the number of seeds per unit area away from the tree bases. The shape parameter (α) of the Weibull distribution associated with the mechanism of seed dispersal always had values of $\alpha>1$ in different directions. Therefore, it is proposed that *U. macrocarpa* always displays a "long-distance" seed dispersal pattern, whether from isolated trees or those at woodland edges, or whether with or against the wind direction under natural conditions in the Keerqin sandy lands. This could be understood as the potential spatial expansion of *U. macrocarpa* populations in different directions always following the same pattern.

Keywords: Plant ecology; *Ulmus macrocarpa*; Woodland edge; Isolated tree; Seed dispersal; Weibull distribution.

Resumen. *Ulmus macrocarpa* Hance puede formar bosques monodominantes en las áreas arenosas de Keerquin, China. Métodos de muestreo a intervalos de un metro desde las bases de los árboles ubicados en la periferia del bosque y los árboles aislados se emplearon a lo largo de secciones verticales en diferentes direcciones. Usando métodos estadísticos basados en la función de densidad de la distribución Weibull, se analizaron los modelos de dispersión de semillas y la respuesta de expansión en el espacio de *U. macrocarpa*, que es una planta que dispersa sus semillas por el viento. Aunque por el efecto de la dirección del viento que varía de acuerdo a los monsones, hubo diferencias en el grado de dispersión de semillas en términos de distancia, y número acumulativo de semillas en los bordes de bosque y árboles aislados, los modelos de dispersión de semillas fueron los mismos. Es decir, los modelos de dispersión de semillas se pueden describir por funciones de densidad de la distribución de Weibull ($P<0,01$) para las frecuencias del número de semillas por unidad de superficie alejadas desde las bases de los árboles. El parámetro forma (α) de la distribución de Weibull asociado con el mecanismo de dispersión de semillas siempre tuvo valores de $\alpha>1$ en diferentes direcciones. Luego se propone que *U. macrocarpa* siempre exhibe un modelo de dispersión de semillas de grandes distancias, ya sea desde árboles aislados o aquellos en los bordes de bosques, o ya sea a favor o en contra la dirección del viento bajo condiciones naturales en las zonas arenosas de Keerqin. Esto se podría entender como la expansión en el espacio potencial de las poblaciones de *U. macrocarpa* en diferentes direcciones siempre siguiendo el mismo modelo.

Palabras clave: Ecología vegetal; *Ulmus macrocarpa*; Borde de bosque; Árbol aislado; Dispersión de semillas; Distribución Weibull.

Key Laboratory of Vegetation Ecology, Ministry of Education, Institute of Grassland Science, Northeast Normal University, Changchun, China 130024.
This work was funded by the National Key Research and Development Program of China (2016 YFC0500602), Natural Science Foundation of China (31472134, www.nsfc.gov.cn, YFY), and the Program of Introducing Talents of Discipline to Universities (B16011).
Address correspondence to: Prof. Yunfei Yang, Fax 086-431-85695065; Phone 086-431-85098994; *e-mail:* yangyf@nenu.edu.cn ; yuanjh040@nenu.edu.cn ; jiana0999@126.com
Received 19.X.2016. Accepted 14.XI.2017.

INTRODUCTION

The regeneration of plant populations and the expansion of their niche space depend on the spread of propagules, which have different forms, including seeds for sexual reproduction and the organs of vegetative reproduction (Howe & Smallwood, 1982). Although the method of vegetative reproduction is more favorable for the regeneration of populations, its mobility and spatial expansion are limited, so the spatial expansion of populations over longer distances is still dependent on seed dispersal (Harper, 1977; Xiao et al., 2005).

Darwin, the founder of the theory of evolution, proposed the importance of seed dispersal in his book "On the Origin of Species" published in 1859; however, the analysis and investigation of seed dispersal from experiment to theory has only become the focus of research within the last 30 years (Silvertown, 1982).

Plants have developed many types of seed dispersal with the aid of various dispersal media during the long process of convergent adaptation and evolution (Howe & Smallwood, 1982). Among these, dispersal by wind is one of the most important types of long-distance distribution, although the process of seed dispersal by wind is complicated because of differences in site conditions, and wind direction and speed (Howe & Smallwood, 1982). However, seed dispersal by wind will generate a continuously distributed pattern over a certain distance compared with movement and storage, feeding and excretion, and adhesion to and dispersal by animals. Therefore a model that fit the function needs to be built to analyze the pattern on the basis of quantitative analysis, as well as a model of a mechanism to predict the pattern of seed dispersal based on the characteristics of the seed morphology and propagation media (Okubo & Levin, 1989; Nathan & Muller-Landau, 2002; Schupp et al., 2010). Furthermore, the species diversity of the communities will be increased and community succession could be promoted when seeds are spread to other communities (Peart, 1989; Moles & Drake, 1999; Godoy & Jordano, 2001; Silva & Tabarelli, 2001). At the same time, successfully established populations may adapt to, and differentiate in, their new habitat when seeds are spread across the region (Dow & Ashley, 1996; He et al., 2004; Nathan, 2006; Schnabel et al., 1998). Therefore, the study of seed dispersal is the basis of the further study of population and community dynamics (Michael, 1985; Levine & Murrell, 2003). There have been many studies of the spatial pattern of seed dispersal (He et al., 1999; Murell, 2003; Xing et al., 2004) and the laws governing seed dispersal (Yang & Zhu, 1994, 1995; Zhang et al., 2005; Yang et al., 2010), but such studies are still in urgent need of further development (Yu et al., 2007).

Any biological response has its own biological significance, so that if seed dispersal is regarded as the expansion of a population into another space, the laws governing seed dispersal will imply a mechanism of population development in the study of plant population ecology.

The Weibull distribution is a statistical distribution of a continuous random variable, which was originally used for the analysis of the reliability and longevity testing of engineering materials. Subsequently, it has been widely used in various fields because of its multi-parameter estimation procedure and multifunctional analysis. The Weibull distribution is also used for the temporal and spatial distribution of insect populations (Huang et al., 1989; Chen et al., 1992), the species abundance of communities (Wu et al., 1997), and population structure (Fang & Kan, 1987; Hong et al., 1995) in biological research. However, for the study of the dispersal of large amounts of seeds (Hong et al., 1995; Dow & Ashley, 1996; He et al., 1999; Hang & Wang, 2002; Nathan, 2006; Zhang et al., 2007; Zou et al., 2007; Yang et al., 2010) the Weibull distribution has seldom been used (Yang, 1990; Yang & Zhu, 1994; 1995).

Ulmus macrocarpa Hance is one of the constituent species of native forest in the Keerqin sandy lands, China. It has fruits with broad wings, and is a typical anemochorous plant. *U. macrocarpa* can usually form monodominant woodland over large areas. Although the local area is preserved well at present, and some regions are set aside for nature reserves by the government, it plays an important role in maintaining the ecological balance of the site and the sandy region and in protecting biological diversity. However, there have been few basic studies about the biology and ecology of *U. macrocarpa* (Han et al., 2008).

The methods of sampling at meter intervals from the bases of trees at the woodland edges and from isolated trees were used in different directions in the *U. macrocarpa* woodland reserve. The density function of the Weibull distribution was used to analyze the laws governing seed dispersal far away from the seed source of *U. macrocarpa*. Our objectives were: (i) to reveal differences in distance and cumulative seed numbers from seed dispersal in different directions from the woodland edges and isolated trees of the *U. macrocarpa* woodland; (ii) to determine whether the pattern of seed dispersal in different directions from woodland edges is the same as that for isolated trees; and (iii) to discover the biological and ecological significance of the parameters after fitting the Weibull distribution, and (iv) to define and put forward the response mechanism of the potential spatial expansion of the *U. macrocarpa* population. The aim of this study was to provide a scientific body of evidence for the further study of the spatial expansion of the anemochorous plant populations, and a reference for similar research into the application of the Weibull distribution and its statistical analysis method.

MATERIALS AND METHODS

Natural condition of the study site. The experiment was carried out in a natural *U. macrocarpa* woodland reserve with its original appearance and characteristics, located 2 km southwest of Xinglongshan town, Tongyu county, in the west of Jilin province, China (44° 48' – 44° 49' N, 122° 22' – 122° 23' E). The area of the study site is 50 km^2. This area has a northern temperate continental monsoon climate. The average annual temperature, number of frost-free days, and rainfall are 6.6 °C (January min: -34.1 °C, July max: 38.7 °C), 162 days, and 332.4 mm, respectively. The dominant wind direction is from the southwest in spring, summer, and autumn, and the northwest in winter. The average wind speed was 5.4 m/s in May (http://www.weather.com.cn). The soil type of the study site is sandy. *U. macrocarpa* saplings are semi-intrazonal forest vegetation in this area, with two to six individuals growing in a cluster as shrubs. The species composition of the tree layer is simple, with the dominant *U. macrocarpa* only accompanied by some *Ulmus pumila* Linn, *Morus alba* L, *Euonymus bungeanus* Maxim, *Rhamnus davurica* Pall, and *Armeniaca sibirica* (Linn.) Lam. The main plant species in the intermediate layer is *Ampelopsis aconitifolia* Bunge. There are two kinds of plants in the herbaceous layer, including annual plants: *Setaria viridis* (Linn.) Beauv, *Digitaria sanguinalis*,(Linn.) Scop and *Chenopodium glaucum* Linn, and perennial species: *Cleistogenes squarrosa* (Trin.) Keng and *Achnatherum avenoides* (Honda) Y. L. Chang (Han et al., 2008). The difference in size of *U. macrocarpa* individuals is very large because of the anthropogenic influences of deforestation and grazing: the height of plants with fruits was between 3 and 8 m. The open area at the forest edge is usually pasture, whereas some large areas have been turned into farmland.

Sampling methods of seed dispersal. We carried out sampling at two types of sites (woodland edges and isolated trees) by using a GPS after all seeds of *U. macrocarpa* fell off in the middle of June 2011. Woodland edges: The environment of the study site was representative. The average height of the trees and the spacing between trees were 19.69–26.25 inch (6–8 m) and 4.59–10.50 inch (1.4-3.2 m), respectively. *U. macrocarpa* grew homogeneously and the canopy density was greater than 0.8. The distance of the open area at the woodland edges was greater than 262.47 inch (80 m) and the surface was flat. We sampled quadrats along four horizontal sections in different directions (northeast, north, south, and west), because some open areas at the woodland edges were claimed and each direction contained three repeated sections of the woodland edges. Isolated trees: Single trees of *U. macrocarpa* growing at a distance of more than 164.04 inch (50 m) from other trees were selected as study objects. We chose three isolated trees in our study and sampled quadrats in six directions (north, northeast, east, southeast, south, and northwest), because of undulations in the local terrain. We marked out a vertical line by using a tape and set quadrats at intervals of 3.28 inch (1 m) from the base of each tree. We obtained one sample per unit area away from woodland edges/isolated trees until samaras of *U. macrocarpa* disappeared along vertical sections in every direction. We counted the number of intact and non-fusty seeds, that is to say, the white/faint yellow seeds that had fallen off in the same year. The quadrat area in this study was 1.64 inch (50 cm) × 1.64 inch (50 cm).

Data analysis. The number of seeds in each quadrat was converted into the number per m^2. Firstly, we calculated the average number of seeds per m^2 at every distance from the woodland edges and isolated trees along vertical sections in every direction, and the sum of the number of seeds in each direction. Then we calculated the frequency of seeds at every distance:

$$F = [x_i/\Sigma x_i] \times 100\%$$

where F is the frequency of seeds per m^2 at distance i, x is the number of seeds per unit area, Σx is the sum of the number of seeds per unit area along the vertical section of each direction, and i = 1,2,3,…,n.

The density function of the Weibull distribution was used to fit the seed dispersal away from the seed source along the vertical sections in different directions (Fang & Xu, 1987):

$$f(x;\alpha,\beta,\mu)= \frac{\alpha}{\beta}(x - \mu)^{a-1}\, e^{-\left[\frac{(x-\mu)^{-a}}{\beta}\right]}, 0\leq x \leq +\infty$$

where $\alpha>0$ was the shape parameter, $\beta>0$ was the scale parameter, and $\mu\geq0$ was the location parameter, analyzing the seed dispersal mechanism based on the value of the shape parameter (α).

In order to test whether the pattern analysis of the seed dispersal frequency was effective and feasible, we analyzed the relationship between the average value of the seed dispersal frequency per unit area away from the seed source along vertical sections in different directions and the expected value of the frequency simulated by the Weibull distribution theory.

We used SPSS statistical software (version 12.0, SPSS, Inc., Chicago, IL, USA) to process and analyze the data.

RESULTS AND DISCUSSION

Differences in the seed dispersal distance in different directions. The seed dispersal distance in the four directions from the woodland edges varied from 23 to 25 m, whereas those in the six directions from isolated trees varied from 22 to 26 m. The seed dispersal of *U. macrocarpa* was continuous, and the distance of seed dispersal was shortest to the north and longest to the northeast. In other words, the difference in the seed dispersal distance was 2–4 m.

The average value of the total number of seeds accumulated per unit area along the vertical sections in the different directions from the woodland edges and isolated trees was greatest to the northeast. For the woodland edges, the maximum value in the northeast was greater than that in the south and west, and was 2.34 times as large as the minimum value in the west. For isolated trees, the maximum value to the northeast was larger than that to the southwest and southeast, and was 3.23 times as large as the minimum value to the southwest. This was mainly due to differences in wind direction and speed when the seeds fell off: wind speed affects the distance of seed dispersal, whereas wind direction affects the number of seeds in different directions (Yang & Zhu, 1995). The seed dispersal of *U. macrocarpa* from the woodland edges and isolated trees displayed the largest quantities and longest distances to the northeast, and the smallest quantities and shortest distances to the west, southwest, and southeast. This is related to the fact that the dominant wind direction was from the southwest in summer in this study area (http://www.weather.com.cn). The northeast is downwind, whereas the southwest is against the wind direction. Furthermore, there were some differences in the repeated sampling sections of the same direction in the data for the range between the maximum and minimum and the coefficient of variation (11.9–46.6%), as shown in Table 1. This may be due to differences either in the microtopography or the coverage or degree of exposure of the surface, causing some seeds to be dispersed twice (Han & Wang, 2002; Shen et al., 2004; Nathan, 2006).

In the study of plant ecology, seeds are seen as potential populations, and only those seeds that can germinate and survive will contribute to the regeneration and expansion of the population (Bai & Romo, 1997; Drake, 1998). The greater the number of seeds, the greater is the probability of germination and survival. Therefore, the *U. macrocarpa* population will expand to the northeast and northern directions more easily than to the southwest and west directions.

Statistical analysis of the Weibull distribution for the seed dispersal frequencies. The outcome of the model fitting for the frequency of the seed number per unit area away from the seed source in different directions reached levels of extreme significance (P<0.01). This significance was valid for both woodland edges and isolated trees for fitting a parameter and as a fitting test of the density function of the Weibull distribution. The results for the frequencies of the observed average values of seed dispersal and the fitting curves of the Weibull distribution are shown in Figures 1 and 2. Although the extent of seed dispersal in distance and direction displayed some differences between woodland edges and isolated trees, they have similar patterns of seed dispersal, and the shape parameters of both curves were $\alpha>1$.

Validity test of the Weibull distribution for the seed dispersal frequencies. The observational data were directly used to fit and test the parameters due to small values in the study of seed dispersal based on the Weibull distribution in the past (Yang, 1990; Yang & Zhu, 1994; Yang et al., 2010). We used the frequency to analyze the seed dispersal pattern of *U. macrocarpa*, which is a relatively quantitative index that takes into consideration the entire situation; that is to say, this analysis is the analysis of the seed distribution spectrum. The results for the three parameters of the fitted curve used the direct observational data, which were the same as the frequency data based on the Weibull distribution. However, our observational data were generally large, which meant that the results of the χ^2 test were not applicable. Therefore, we used an indirect test method to analyze the linear relationship between the observed values of the seed densities

Table 1. The statistics on total cumulative seeds of *Ulmus macrocarpa* and the difference marks on significant tests in the sequential seed dispersal per unit area away from the seed source in woodland edges and isolated trees along vertical sections of different directions.
Tabla 1. Estadística del total de semillas acumuladas de *Ulmus macrocarpa* y las marcas de la diferencia en pruebas significativas en la dispersión secuencial de semillas por unidad de área desde la fuente de semillas en los márgenes del bosque y árboles aislados a lo largo de secciones verticales de diferentes direcciones.

Seed source	Direction	N/D(m)/ΣA(m²)[1]	Min	Max	Mean [2]	SD	CV(%)
Woodland edge	Northeast	25	3552	4432	3904.0 a	465.7	11.9
	North	23	1884	4104	2669.3 ab	1244.3	46.6
	South	24	2064	3016	2420.0 b	519.4	21.5
	West	24	1224	2132	1668.0 b	454.3	27.2
Isolated tree	Northeast	26	1492	3596	2750.7 a	1111.2	40.4
	South	23	1420	2488	1985.3 a	536.8	27.0
	East	24	852	2132	1513.3 ab	641.1	42.4
	North	22	724	1628	1192.0 ab	452.8	37.9
	Southeast	22	708	1332	953.3 b	332.7	34.9
	Southwest	25	684	956	850.7 b	146.0	17.2

[1] N, number of samples; D, farthest distance; ΣA, cumulative area; (2) significant difference level of P<0.05 among different letters within the same seed source.
[1] N, número de muestras; D, distancia más alejada; ΣA, área acumulada; (2) diferencias significativas (P<0,05) entre letras diferentes dentro de la misma fuente de semillas.

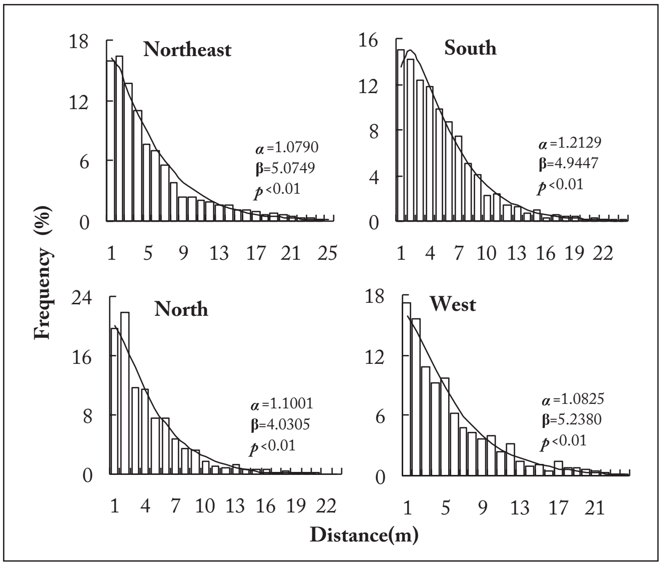

Fig. 1. The frequencies of observed average values (column) of the seed dispersal of *Ulmus macrocarpa* and the expected curves, the parameters of Weibull distribution in the woodland edges along vertical sections of different directions (***, most suitable level in $X_{2(\alpha)}$<0.900, the same below).

Fig. 1. Frecuencias de valores promedio observados (histogramas) de la dispersión de semillas de *Ulmus macrocarpa* y las curvas esperadas, los parámetros de la distribución de Weibull en los márgenes de los bosques a lo largo de secciones verticales de diferentes direcciones (***, nivel más adecuado en $X_{2(\alpha)}$<0,900, lo mismo es válido para la Figura 2).

and the expected values of the theoretical frequency from the Weibull distribution, and test its significance (Fig. 3 and 4). The relationship from the fitting curve reached levels of extreme significance (P≤0.01), so that it is effective and feasible to use the frequency of the seed distribution spectrum to estimate the parameters.

Pattern analysis of the seed dispersal by Weibull distribution parameters. If we relate the shape parameter (α) to the pattern of seed dispersal or the spatial expansion response of the population when estimating the parameters of the seed dispersal frequency of *U. macrocarpa* based on the density function of the Weibull distribution, then different ranges of α values will represent different spatial expansion responses of the population. In general, the parameter α will be divided into three cases: α<1, α>1, and α=1, which represent 'short-distance,' 'random-distance,' and 'long-distance' seed dispersal, respectively. The shape parameter (α) of the seed dispersal of *U. macrocarpa* based on the Weibull distribution in the 10 directions from the woodland edges and isolated trees all showed values of α>1. Therefore, we know that the population was 'long-distance' in its seed dispersal pattern, whether isolated trees or those at woodland edges, whether with or against the wind direction, under natural conditions in the Keerqin sandy lands. That is to say, the expansion response of *U. macrocarpa* populations in different directions will follow the same laws.

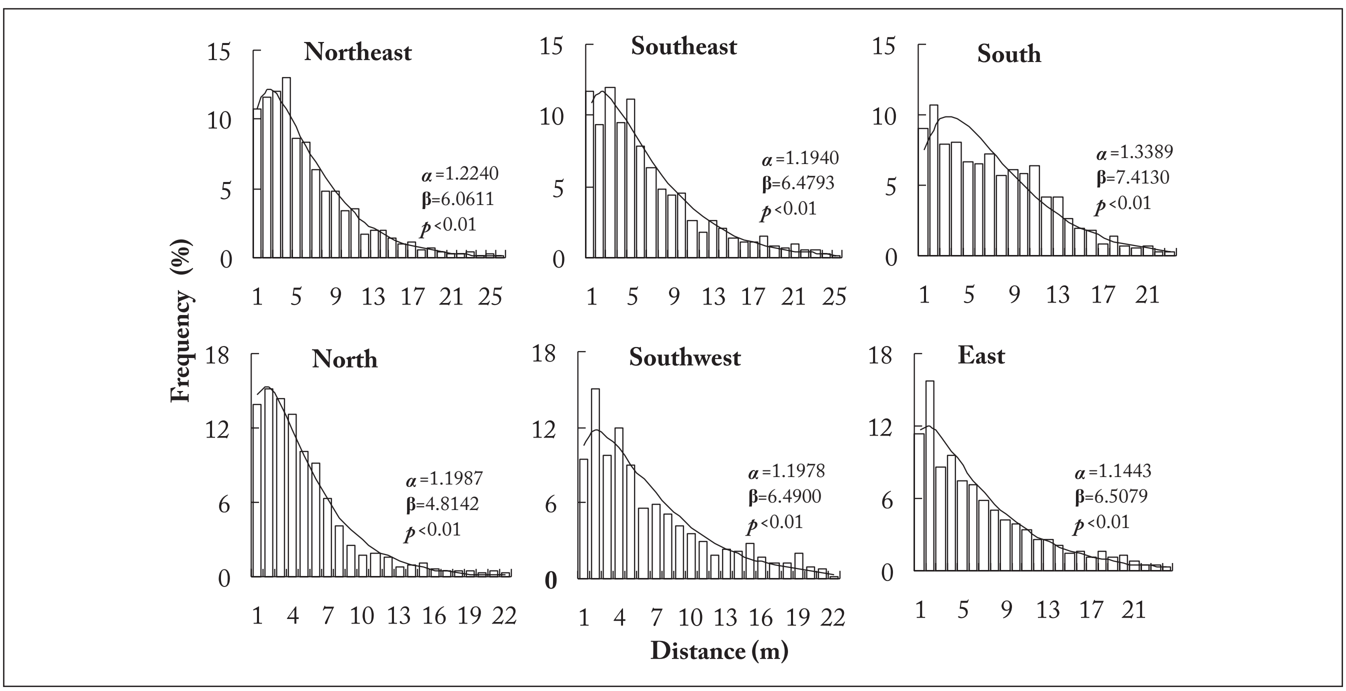

Fig. 2. The frequencies of observed average values (column) of the seed dispersal of *Ulmus macrocarpa* and the expected curves of Weibull distribution in the isolated trees along vertical sections of different directions.

Fig. 2. Frecuencias de valores promedio observados (histogramas) de la dispersión de semillas de *Ulmus macrocarpa* y las curvas esperadas de la distribución de Weibull en árboles aislados a lo largo de secciones verticales de diferentes direcciones. Ver texto de la Figura 1.

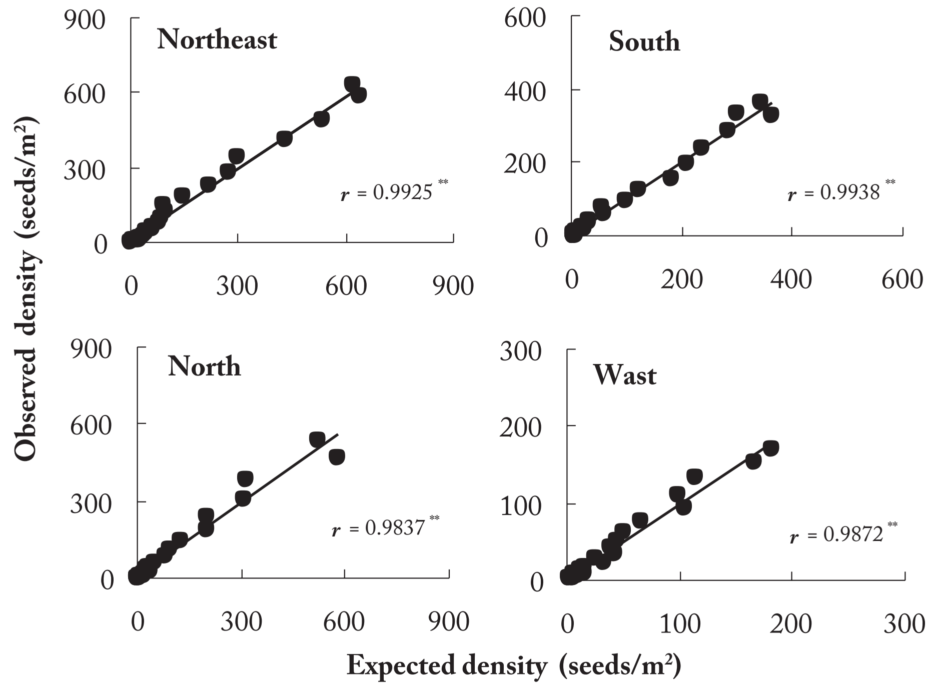

Fig. 3. Correlation between observed average values of the seed densities of *Ulmus macrocarpa* and the restored expected values through theoretical frequency of Weibull distribution in the isolated trees along vertical sections of different directions (**, the significant level of P<0.01, the same below).

Fig. 3. Correlación entre valores promedio observados de las densidades de semilla de *Ulmus macrocarpa* y los valores esperados restaurados a través de la frecuencia teórica de la distribución de Weibull en los árboles aislados a lo largo de secciones verticales de diferentes direcciones (**, P<0,01, lo mismo es válido para la Figura 4).

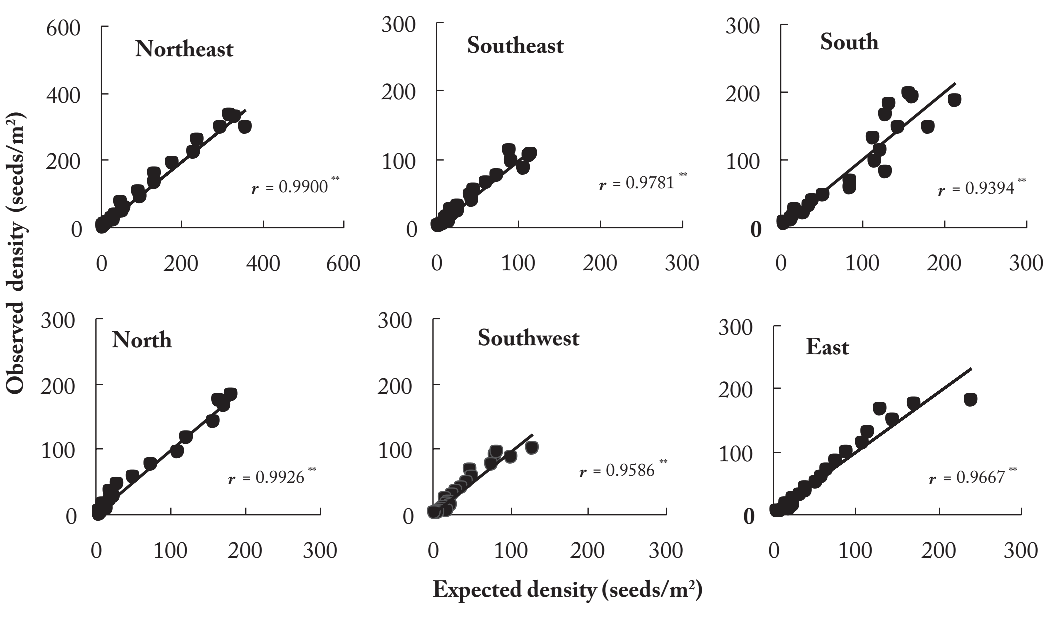

Fig. 4. Correlation between observed average values of the seed densities of *Ulmus macrocarpa* and the restored expected values through theoretical frequency of Weibull distribution in the isolated trees along vertical sections of different directions.

Fig. 4. Correlación entre valores promedio observados de las densidades de semillas de *Ulmus macrocarpa* y los valores esperados restaurados a través de la frecuencia teórica de la distribución de Weibull en los árboles aislados a lo largo de secciones verticales de diferentes direcciones.

CONCLUSION

The seed dispersal of *U. macrocarpa* was continuous in distance. The seed dispersal distance ranged from 23 to 25 m for woodland edges and from 22 to 26 m for isolated trees, and the distance of seed dispersal was longest to the northeast. The total number of seeds accumulated per unit area for woodland edges and isolated trees was the largest, and reached the farthest distance to the northeast, and was the smallest and reached the shortest distance to the west, southwest, and southeast. Therefore, the population will expand to the northeast and north directions more easily than to the southwest and west directions.

The coefficient of variation of the total number of seeds per unit area ranged from 11.9% to 46.6% along the repeated sampling sections in the same direction for woodland edges and isolated trees. This may be due to differences in the microtopography of the surface and the mobility of the seed, causing some seeds to be dispersed twice.

The frequency of the number of seeds per unit area from the base of the tree is suitable for the Weibull distribution for woodland edges and isolated trees. The shape parameters of the fitting curves for different directions were all $\alpha>1$, so that the population was 'long-distance' in its seed dispersal pattern and its spatial expansion response. This is characteristic of an anemochorous plant under natural conditions in the Keerqin sandy lands.

ACKNOWLEDGEMENTS

We thank Dr. Bai Yunpeng, Dr. Li Haiyan and Dr. Zhang Wei for help with the field survey.

REFERENCES

Bai, Y.G. & J.T. Romo (1997). Seed production, seed rain, and the seedbank of fringed sagebrush. *Journal of Range Management* 50: 151-155.

Chen, H., R.H. Zhen & W. Hong (1992). Simulating of Weibuli distribution with spatial distribution pattern of pine caterpillar population. *Journal of Fujian College of Forestry* 12: 359-363.

Dow, B.D. & M. V. Ashley (1996). Microsatellite analysis of seed dispersal and parentage of samplings in bur oak, *Quercus macrocarpa*. *Molecular Ecology* 5: 615-627.

Drake, D.R. (1998). Relationships among the seed rain, seed bank and vegetation of a Hawaiian forest. *Journal of Vegetation Science* 9: 103-112.

Fang, J.Y. & M. Kan (1987). Estinatiog diameter distribution with the Weibull distribution function. *Journal of Beijing Forestry University* 9: 261-269.

Fang, K. T. &J.L. Xu (1987). Statistical Distribution. Beijing: Science Press; pp. 152-164.

Godoy, J.A. & P. Jordano (2001). Seed dispersal by animals: Exact identification of source trees with endocarp DNA microsatellites. *Molecular Ecology* 10: 2275-2283.

Han, D. Y., Y.P. Bai, Y.J. Zhao, Y.H. Dong & J.D. Li (2008). Community structure of the *Ulmus macrocarpa* var. mongolica forest in the sandy land of Songnen grassland [J]. *Journal of Northeast Normal University (Natural Science Edition)* 40: 107-111.

Han, Y.Z. & Z.Q. Wang (2002). Spatial pattern of manchurian ash seed dispersal in secondary hardwood forests. *Chinese Journal of Plant Ecology* 26: 51-57.

Harper, J.L. (1977). Population Biology of Plants. Academic Press, London, pp. 12-15.

He, T.H., G.Y. Rao., R.L. You & D.M. Zhang (1999). The spatial distribution pattern and seed dispersal mechanism for the population of *Ophiopogon xylorrhizus*, an endangered Plant. *Chinese Journal of Plant Ecology* 23: 181-186.

He, T.H., S.L. Krauss., B.B. Lamont, B.P. Miller & N.J. Enright (2004). Long-distance seed dispersal in a metapopulation of *Banksia hookeriana* inferred from a population allocation analysis of amplified fragment length polymorphism data. *Molecular Ecology* 13: 1099-1109.

Hong, L.X., G.J. Du, Q.R. Zhang & B.T. Liu (1995). Weibull D. B. H. distributions and their dynamic predictions in the natural uneven-aged evergreen broad-leaf juvenile forest. *Chinese Journal of Plant Ecology* 19: 29-42.

Howe, H.F. & J. Smallwood (1982). Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13: 201-228.

http://www.weather.com.cn/cityintro/101060605.shtml.

Huang, J.Y., R.D. Li, L.Z. Qi, & J.H. Ding (1989). Application of Weibull Distribution Function and Rayleigh Density Function in Established Forecast Model of BPH Population Fluctuation. *Chinese Journal of Rice Science* 3: 67-72.

Levine, J.M. & D.J. Murrell (2003). The community-level consequences of seed dispersal patterns. *Annual Review of Ecology, Evolution y, and Systematics* 34: 549–574.

Michael, E. (1985). Seed Ecology. Chapman and Hall, New York. Pp. 57-116.

Moles, A.T. & D.R. Drake (1999). Potential contributions of the seed rain and seed bank to regeneration of native forest under plantation pine in New Zealand. *New Zealand Journal of Botany* 37: 83-93.

Nathan, R. & H.C. Muller-Landau (2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution* 15: 278-285.

Nathan, R. (2003). Seeking the secrets of dispersal. *Trends in Ecology and Evolution* 18: 275.276.

Nathan, R. (2006). Long-distance dispersal of plants. *Science* 313: 786-788.

Okubo, A. & S.A. Levin (1989). A theoretical framework for data analysis of wind dispersal of seeds and pollen. *Ecology* 70: 329-338.

Peart, D.R. (1989). Species interactions in a successional grassland. I. Seed rain and seedlings recruitment. *Journal of Ecology* 77: 236-251.

Sagnarda, F., C. Pichota, P. Dreyfusa, P. Jordano & B. Fady (2007). Modelling seed dispersal to predict seedling recruitment: recolonization dynamics in a plantation forest. *Ecological Modelling* 203: 464-474.

Schnabel, A., J.D. Nason & J.L. Hamrick (1998). Understanding the population genetic structure of *Gleditsia triacanthos* L.: seed dispersal and variation in female reproductive success. *Molecular Ecology* 7: 819-832.

Schupp, E.W., P. Jordano & J.M. Gomez (2010). Seed dispersal effectiveness revisited: a conceptual review. *New Phytologist* 188: 333-353.
Shen, Z.H., N. Lu & J. Zhao (2004). The topographic pattern of seed rain of a mountain mixed evergreen and deciduous forest community. *Acta Ecologica Sinica* 24: 1981-1987.
Silvertown, J.W. (1982). Introduction to Plant Population. Lomgman, New York. Pp. 20-22.
Silva, M.G. & M. Tabarelli (2001). Seed dispersal, plant recruitment and spatial distribution of *Bactris acanthocarpa* Martius (Arecaceae) in a remnant of Atlantic forest in northeast Brazil. *Acta Oecologica* 22: 259-268.
Wu, C.Z. & W. Hong (1997). Study on Weibull model for species abundance distribution of *Tsoongiodendron odorum* forest. *Journal of Fujian College of Forestry* 17: 21-24.
Xiao, Z.S. Z.B. Zhang & Y.S. Wang (2005). Effects of seed size on dispersal distance in five rodent-dispersed fagaceous species. *Acta Oecologica* 28: 221-229.
Xing, F., Y, H. Wang & J. X. Guo (2004). Spatial distribution patterns and dispersal mechanisms of the seed population of *Stellera chamaejasme* on degraded grasslands in Inner Mongolia, *China. Acta Ecologica Sinica* 24 : 143-148.
Zou, L., Z. Xie, Q.M. Li, C.M. Zhao & C.L. Li (2007). Spatial and temporal pattern of seed rain of *Abies fargesii* in Shennongjia Nature Reserve, Hubei. *Biodiversity Science* 15: 500-509.
Yang, Y.F., Y.P. Bai, J.D. Li & L. Li (2010). Spatial patterns of the seed dispersal in *Hemiptelea davidii* woodland in Keerqin sandy land, China. *Chinese Journal of Applied Ecology* 21: 1967-1973.
Yang, Y.F (1990). The study on seed dispersal of *Puccinellia tenuiflora* on alkalization meadow in the Songnen Plain of China. *Acta Ecologica Sinica* 10: 288-290.
Yang, Y.F. & L. Zhu (1994). Pattern of seed dispersal of *Hordeum brevisubulatum* of alkalizied meadow in Songnen Plain of China. *Acta Botania Sinica* 36: 636-644.
Yang, Y.F. & L. Zhu (1995). Analysis on the mechanism of seed dispersal of *Puccinellia chinampoensis* on alkalized meadow in Songnen Plain of China. *Acta Botania Sinica* 37: 222-230.
Yu, S.L., N.J. Lang, M.J. Peng & L. Zhao (2007). Research advances in seed rain. *Chinese Journal of Ecology* 26: 1646-1652.
Zhang, Y.B., J.W. Li, H. Zhang, D.L. Zou, F.P. Wu, C.L. Cheng, J.Q. Li & S.Y. Li (2005). Spatiotemporal patterns of seed dispersal in *Populus euphratica*. *Acta Ecologica Sinica* 25: 1994-2000.