

青藏高原东缘岷江冷杉天然群落的种群结构和空间分布格局

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摘要 岷江冷杉 (*Abies faxoniana*) 是青藏高原东缘亚高山顶极森林植被的优势种之一, 主要分布于岷江、大渡河和白龙江的上游地区。该文研究了岷江冷杉天然原始群落的种群结构和空间分布格局。样方大小为 100 m × 60 m。测定了所有个体的坐标及其胸径、高度和冠幅。将岷江冷杉按大小级分为 5 级, 即幼苗: $H < 0.33$ m; 幼树: $H \geq 0.33$ m, 且 DBH (胸径) < 2.5 cm; 小树: 2.5 cm \leq $DBH < 7.5$ cm; 中树: 7.5 cm \leq $DBH < 22.5$ cm 和 大树: $DBH \geq 22.5$ cm。采用了 Morisita 指数 (I_g)、方差均值比 (V/m)、聚块度指标 (m^*/m) 和空间点格局分析方法 (SP-PA) (采用了 Ripley 二次分析法) 4 种方法分析岷江冷杉的空间分布格局。结果表明: 1) 岷江冷杉种群结构稳定。因为其年龄结构表现为增长型, 幼苗幼树储备丰富, 密度分别为 $2\ 217 \cdot \text{hm}^{-2}$ 和 $2\ 683 \cdot \text{hm}^{-2}$, 可见岷江冷杉天然更新良好, 进而通过其“移动镶嵌循环”更新维持其种群的稳定性。在大小级结构图中的一些缺刻和年龄结构图中的“断代”现象, 是干扰的时空异质性在采样的时间和空间断面上的反映。2) 幼苗、幼树和小树在所有的研究尺度 (从 $1\ \text{m} \times 1\ \text{m}$ 到 $30\ \text{m} \times 30\ \text{m}$) 下都呈聚集分布。但中树和 大树基本上呈随机分布。3) 聚集强度随尺度的变化而变化。上述的前 3 种方法表明, 聚集强度随尺度的增加而减弱。但是, 空间点格局分析法表明, 岷江冷杉幼苗、幼树和小树的聚集强度首先随尺度的增加而增强, 达到一定高峰后, 随尺度的增加而减弱。4) 岷江冷杉的空间分布格局是与其自然环境长期作用的结果, 同时也反映了其种群天然更新的格局和机制。5) 4 种分析方法对格局的判别基本一致, 但空间点格局分析法更能反映出格局强度随尺度的变化的关系, 是值得推荐的一种分析空间分布格局的方法。使用空间点格局分析法的限制主要在于其计算和采样比较复杂。另外, 由于 Ripley 二次分析法对于“空白”的探测不敏感, 需要进一步做一些方法上的改进。

关键词 岷江冷杉 种群结构 空间分布格局 空间点格局分析

STRUCTURE AND SPATIAL PATTERN OF A NATURAL *ABIES FAXONIANA* POPULATION ON THE EASTERN EDGE OF QINGHAI-TIBETAN PLATEAU

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Abstract Minjiang fir (*Abies faxoniana*) (MJF) is a dominant tree species of sub-alpine forests on the eastern edge of Qinghai-Tibetan Plateau, and is mainly distributed over the upper reaches of the Minjiang, Dadu and Bailong Rivers. The population structure and spatial pattern of MJF was studied in a naturally occurring stand. In a 100 m × 60 m plot, the location of every tree was mapped, and the diameter at breast height (DBH), height and canopy area of each individual recorded. Trees were divided into five size classes: seedlings, height < 0.33 m; saplings, height ≥ 0.33 m, and $DBH < 2.5$ cm; small trees, 2.5 cm \leq DBH

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< 7.5 cm ; medium Trees , 7.5 cm \leq DBH < 22.5 cm ; and big trees , DBH \geq 22.5 cm. The spatial pattern of MJF was analyzed using four independent methods : the Morisita index (I_{δ}), variance to mean ratio (V/m), the congregation index (m^*/m) and the spatial point pattern analysis (SPPA) (Ripley 's second-order- analysis method). The results revealed that MJF was a stable population with an inverse J-shaped size structure indicating good natural regeneration. Seedlings and saplings were very abundant , with densities of 2 217 \cdot hm⁻² and 2 683 \cdot hm⁻² , respectively. Irregularities in the size structure histogram reflected past disturbances. The spatial analyses revealed that seedlings , saplings and small trees were clumped at most spatial scales studied which ranged from 1 m to 30 m , whereas the medium-sized trees and big trees were randomly distributed. The intensity of assemblage (IA) varied with scale. The first three methods indicated that IA decreased with increasing scale , but the SPPA method showed that the IA of seedlings , saplings and small trees first increased with increasing scale , and then declined at greater scales. We conclude that the spatial pattern of MJF in this subalpine forest resulted from long-term interactions between the MJF and its natural environment and mechanisms of natural regeneration that vary among species. The four different methods were very similar on the whole in their abilities to discriminate spatial patterns , but SPPA was superior in its ability to detect changes of IA with scale. Thus , we recommend SPPA for analyzing spatial patterns of populations. However , a limitation to using SPPA relates to the complexity of sampling and calculation required and some refinements in Ripley 's second-order-analysis are needed in order to better as it detect gaps.

Key words *Abies faxoniana* , Population structure , Spatial pattern , Spatial-point-pattern-analysis

At the eastern edge of Qinghai-Tibetan Plateau , a typical region called " high mountain and deep valley " , with various landforms , different altitude and multiple climate conditions , accommodates rich biodiversity and abundant of forest resources. The sub-alpine forest , especially the fir forest , is a peculiar climax vegetation type originated during the upheaval of the Qinghai-Tibetan Plateau , and was the principal component of the Southwest Forest District , which was the second largest one in China. Minjiang fir (*Abies faxoniana*) (MJF) forest is the one among them that had the largest area. It naturally distributed over valley , shade-slope or semi-shade slope between altitude 2 800 m and 4 200 m or so , monoclinal or mixed with other cold-temperate evergreen coniferous species , mainly over the upper branches of Minjiang River , Dadu River (belonged to Sichuan Province) and Bailong River , Taohe River (belonged to Gansu Province) and other regions at the western edge of Sichuan Basin (Collaborating Group for Vegetation of Sichuan , 1980 ; Editorial Board of Forests in Sichuan , 1992 ; Wu , 1980). It is not only the most important forest in producing timber , but also the most precious forest in holding water and reducing soil erosion , and also the habitat of many rare and endangered species. The systematic and deep study on them is important to the sustainable development of the region , biodiversity conservation and global change research.

Some research work had been done on MJF forest by many scholars , such as natural landscape , vegetation , soil , habitat types and the law of vegetation distribution along the gradient of altitude (Collaborating Group for Vegetation of Sichuan , 1980 ; Editorial Board of Forests

in Sichuan , 1992 ; Wu , 1980 ; Yang , 1959 ; Jiang , 1963a ; Zhang , 1983 ; Zhang *et al.* , 1981) , community structure , species composition characteristics (Jiang , 1963b ; Yang , 1980) , soil dynamics under canopy (Zhang *et al.* , 1979) , community functions of forest floor (Jiang , 1981) , natural regeneration below canopy (Yang , 1956) , rule of cone production , growth dynamics (Cao & Lin , 1991a ; Cao *et al.* , 1991b) , community ordination and quantitatively classification (Jiang , 1982 ; Jiang , 1994a ; 1994b) , early vegetation succession at clear-cut stand (Shi *et al.* , 1988). But little research on population structure and spatial pattern had being reported (Zhang , 1998 ; Wang *et al.* , 1998).

Population structure and spatial pattern are two of the most important topics concerned by plant population scientists , and also the research hotspot over the recent years. Forest community has different rules at different temporal and spatial scales. Research on population structure and spatial pattern of the dominant species in forest community are very important to give insight to explore the mechanisms on the origin and sustainability of forest ecosystem , community stability , succession rules and the ecological and regeneration characteristics of the species.

Four methods were selected to test the scale and intensity of spatial pattern of MJF in order to discuss : 1) how does the spatial pattern vary with scale ? 2) how does the spatial pattern of different-sized MJF 's individuals vary with scale ? 3) population ' size structure and the developing trend of MJF , 4) Compare the advantages and disadvantages and the practicability of different methods aforementioned.

1 Research site and natural environment con-

ditions

The experiment was carried out at JiaBi Valley (31°43'N, 103°02'E), in the Miyaluo Forest District Eastern Sichuan, administratively belonging to Miyaluo Town, Li County, ABa Tibet-Qiang Peoples' Autonomic District of Sichuan Province. Geographically, it was lying at the upper reaches of Zagu'nao River, which is a big branch of Minjiang River, and at the eastern slope of Qionglai Mountain, and also belongs to the southeastern edge of Qinghai-Tibetan Plateau. The height difference between the bottom and the peak of the valley is 1 000 – 2 000 m, and the slope is mainly more than 35 degree.

The annual mean temperature, mean temperature for the warmest month, mean temperature for the coldest month, annual range of temperature, highest summer temperature and lowest winter temperature are 3.0 °C, 12.6 °C, -8.0 °C, 20.6 °C, 25.5 °C (in July) and -18.4 °C (in January), respectively. There are 7 months with monthly mean temperature (MMT) larger than 0 °C, and the accumulated temperature (AT) of these 7 months is 710 – 2 000 °C, and 5 – 6 months with MMT more than 5 °C, the AT of them is 1 500 °C or so, and 2 – 3 months with MMT more than 10 °C (July, August, or September). The annual mean precipitation (1 165.7 mm) is more than the evaporation (987.8 mm). The occurrence of high temperature synchronized with rainy seasons, which enhances the ecological effect of the precipitation, and implicates the rich biodiversity in this region.

The vegetation zones along vertical gradient are very evident. With the increasing of altitude, there are the coniferous-broadleaved mixed forest (2 400 – 2 700 m), fir forest (2 700 – 3 700 (3 900) m), sub-alpine shrub-meadow (3 700 (3 900) – 3 900 (4 100) m), alpine meadow (3 900 (4 100) – 4 400 m), alpine glacial drift vegetation (more than 4 400 m), and everlasting snow zone (some mountain peaks), with the soil belts changed from mountain dark brown forest soil, mountain brown dark coniferous forest soil, sub-alpine meadow soil, alpine meadow soil, alpine desert soil, to alpine tundra soil.

The soil under MJF forest is mountain brown dark coniferous forest soil, in which humus and total nitrogen content is very high, and the eluviation is not obvious.

At our MJF plot, the altitude is 3 250 m, the mean slope is 37.5°, the slope orientation is southwest 48°, the total vegetation coverage is very high, nearly up to 100%, and the partial coverage of tree, shrub and herb layer are 60%, 70% and more than 90%, respectively. The dominant arbor species are MJF, *Picea wilsonii*, *Picea asperata*, *Betula utilis* var. *sinensis*, and the sub-dominants are *Quercus aquifolioides*, *Acer* spp., *Tilia*

spp., *Tsuga chinensis*, etc. In shrub layer, there are many kinds of *Viburnum* and *Lonicera*, *Smilax stans*, *Sinarundinaria nitida*, many kinds of *Rubus*, etc. In herb layer, there are *Carex* spp., *Ophiopogon bodinier*, *Smilacian japonica*, *Clintonia udensis*, *Cacalia* spp., *Phlomis setifera*, *Ligularia* spp., etc. And there are many kinds of lianas such as *Actinidia kolomit*, *Schisan-dra chinensis*, *Clematis* spp., etc. In general, the community is characterized with very high species richness, distinct layers, and dark environment under canopy.

2 Research methods

2.1 Community traits and population density

The investigation on the community begun in August, 1998. The environment condition of the community, diameter at breast height (DBH), height, canopy area, height under live branch of those individuals taller than 1.4 m were recorded. And the locations of all individuals were mapped. Then the density of MJF and other arbor species were calculated.

2.2 Population dynamics and its spatial pattern

The plot area was 6 000 m² (60 m × 100 m). Two adjacent sidelines were put as coordinate axes, and coordinate (x, y) of every individual was measured at the location of its stem.

The size classification system was adopted as: I. seedlings (SD), height < 0.33 m; II. saplings (SP), height ≥ 0.33 m, and DBH < 2.5 cm; III. small trees (ST), 2.5 cm ≤ DBH < 7.5 cm; IV. middle trees (MT), 7.5 cm ≤ DBH < 22.5 cm; V. big trees (BT): DBH ≥ 22.5 cm (Jin, 1998).

The following four methods were selected to test the spatial pattern of MJF. 1) Morisita index (MI) I_0 (Jin, 1998; Wang *et al.*, 1998), 2) Ratio of variance vs. mean (V/m) (Wang *et al.*, 1998), 3) Congregation index (CI) m^*/m (Zhang, 1992), 4) Spatial point-pattern analysis (SPPA) (Zhang, 1997; Hou *et al.*, 1997; Wang *et al.*, 1998). We adopted Ripley's second-order-analysis method, the formulas were:

$$K(t) = \frac{A}{N \times N} \sum_{i=1}^N \sum_{j=1}^N ((1/W_{ij}) \times I_i(u_{ij})) (i \neq j) \quad (1)$$

$$h(t) = \sqrt{(K(t)/\pi) - t} \quad (2)$$

Where t is the scale, A is plot the area, N is the total number of points investigated, u_{ij} is the distance between two points, $I_i(u_{ij}) = 1$ when $u_{ij} \leq t$, and $I_i(u_{ij}) = 0$ when $u_{ij} > t$, $1/W_{ij}$ is a weighting factor to reduce the problem of edge effects, if the circle centered on i with radius t lies totally within the study plot then $W_{ij} = 1$, otherwise it is the proportion of the circle's circumference that lies within the plot.

We estimated the spatial pattern intensity of MJF of

different size (SD, SP, ST, MT, and BT) at the scale range from the grids 1 m × 1 m to 30 m × 30 m. And all the methods were calculated and modeled by computer program written in VB (Microsoft Visual Basic 6.0).

2.3 Size structure of MJF and its population dynamics

Age structure was substituted by size structure in analyzing the population structure and dynamics. We made age structure graphs by dividing the individuals shorter than 1.4 m into two groups: < 0.33 m and 0.33 – 1.4 m, and dividing the others into age groups according to

DBH every 2 cm.

3 Results

3.1 The dominant species in arbor layer and their density

MJF, *Picea wilsonii*, *P. asperata* and *Betula utilis* var. *sinensis* dominated the plot, with densities of 7 633 · hm⁻², 2 667 · hm⁻², 2 350 · hm⁻², and 1 700 · hm⁻², respectively (Table 1).

Table 1 Composition and density of canopy tree in communities (No · hm⁻²)

Species	Total	SD + SP	Trees (ST + MT + BT)	SD	SP	ST	MT	BT
MJF	7 633	4 900	2 733	2 217	2 683	1 317	367	1 050
PW	2 667	1 633	1 033	683	950	333	233	467
PA	2 350	850	1 500	167	683	317	367	817
BS	1 700	717	983	267	450	533	300	150
Sum	14 350	8 100	6 249	3 334	4 766	2 500	1 267	2 484

MJF: Minjiang fir, *Abies faxoniiana* PW: *Picea wilsonii* PA: *Picea asperata* BS: *Betula utilis* var. *sinensis* SD: Seedlings SP: Saplings ST: Small trees MT: Medium trees BT: Big trees

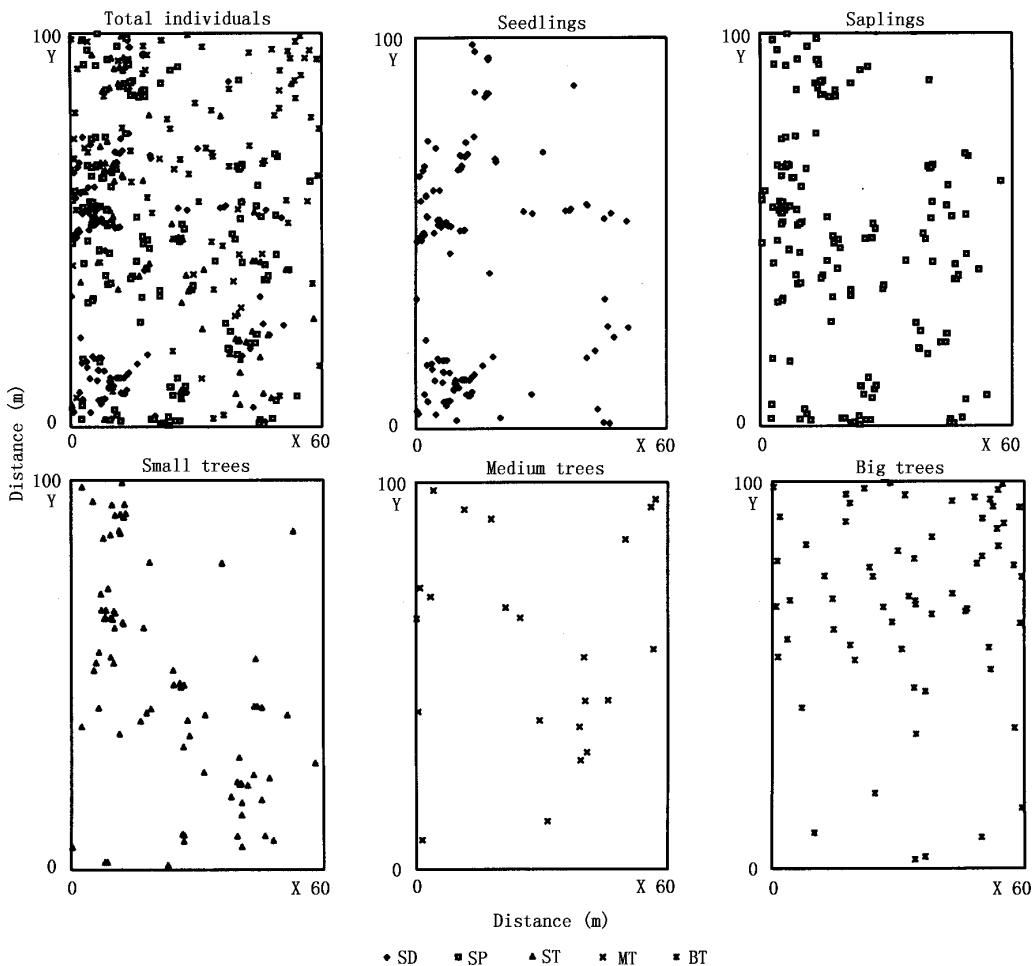


Fig. 1 Point maps of the SD, SP, ST, MT and BT of MJF
SD, SP, ST, MT, BT, MJF: See Table 1

MJF had the largest magnitude of dominance. The individual number of MJF was more than or equal to that of other three dominant arbor species in every size class. And the number of SD and SP were far more than that of other species, especially.

The densities of the SD, SP, ST, MT, BT of MJF were $2\ 217 \cdot \text{hm}^{-2}$, $2\ 683 \cdot \text{hm}^{-2}$, $1\ 317 \cdot \text{hm}^{-2}$,

$367 \cdot \text{hm}^{-2}$, $1\ 050 \cdot \text{hm}^{-2}$, respectively. The sum of seedling and SP was $4\ 900 \cdot \text{hm}^{-2}$, and that of ST, MT, BT was $2\ 733 \cdot \text{hm}^{-2}$ (Table 1).

The point maps of SD, SP, ST, MT, BT of MJF were shown in Fig. 1. The results of MI, V/m , CI and SPPA in determining the spatial pattern of MJF were similar on the whole (Table 2, 3, 4; Fig. 2).

Table 2 Morisita index (I_{δ}) and its test by F distribution of Minjiang fir ($F(p, n-1, \infty(1010))$)

Grids		Total		SD + SP		ST + MT + BT		SD		SP		ST		MT		BT	
Size (m × m)	Number	I_{δ}	F	I_{δ}	F	I_{δ}	F	I_{δ}	F	I_{δ}	F	I_{δ}	F	I_{δ}	F	I_{δ}	F
1 × 1	6 000	5.39	1.33 ^{*3}	10.73	1.48 ^{*3}	1.35	1.01	26.66	1.56 ^{*3}	13.98	1.35 ^{*3}	5.84	1.06 ^{*2}	0.00	1.00	0.00	0.99
2 × 2	1 500	3.55	1.78 ^{*3}	6.06	1.99 ^{*3}	1.91	1.10 ^{*2}	14.52	2.19 ^{*3}	6.52	1.59 ^{*3}	5.84	1.25 ^{*3}	0.00	0.99	1.54	1.02
3 × 3	660	2.91	2.31 ^{*3}	4.83	2.70 ^{*3}	1.43	1.11 [*]	10.30	2.86 ^{*3}	5.50	2.09 ^{*3}	3.52	1.29 ^{*3}	0.00	0.97	1.08	1.01
4 × 4	375	2.79	3.19 ^{*3}	4.49	3.74 ^{*3}	1.80	1.35 ^{*3}	6.96	3.10 ^{*3}	4.89	2.66 ^{*3}	4.75	1.78 ^{*3}	1.62	1.04	1.34	1.06
5 × 5	240	2.42	3.71 ^{*3}	3.61	4.19 ^{*3}	1.53	1.36 ^{*3}	6.86	4.24 ^{*3}	3.41	2.61 ^{*3}	3.51	1.82 ^{*3}	2.08	1.09	1.35	1.09
6 × 6	160	2.16	4.19 ^{*3}	3.21	4.96 ^{*3}	1.37	1.36 ^{*2}	6.32	5.31 ^{*3}	2.83	2.79 ^{*3}	3.06	1.99 ^{*3}	0.76	0.97	1.87	1.30 ^{*2}
7 × 7	112	2.21	5.75 ^{*3}	3.16	6.59 ^{*3}	1.55	1.73 ^{*3}	6.00	6.90 ^{*3}	2.44	3.01 ^{*3}	3.65	2.79 ^{*3}	1.96	1.16	1.30	1.14
8 × 8	84	1.98	6.03 ^{*3}	2.78	7.09 ^{*3}	1.44	1.77 ^{*3}	5.25	7.60 ^{*3}	2.12	3.08 ^{*3}	2.21	2.09 ^{*3}	1.10	1.02	1.99	1.58 ^{*3}
9 × 9	66	1.81	6.52 ^{*3}	2.47	7.59 ^{*3}	1.25	1.58 ^{*2}	4.24	7.58 ^{*3}	2.51	4.67 ^{*3}	1.87	2.02 ^{*3}	1.54	1.15	1.20	1.16
10 × 10	60	1.97	8.55 ^{*3}	2.83	10.10 ^{*3}	1.31	1.85 ^{*3}	4.20	8.17 ^{*3}	2.71	5.63 ^{*3}	2.01	2.33 ^{*3}	1.30	1.11	1.26	1.27
11 × 11	45	1.71	8.12 ^{*3}	2.33	9.78 ^{*3}	1.25	1.85 ^{*3}	3.74	9.23 ^{*3}	2.11	4.99 ^{*3}	1.63	2.09 ^{*3}	1.05	1.02	1.35	1.42
12 × 12	40	1.90	11.18 ^{*3}	2.65	13.05 ^{*3}	1.42	2.66 ^{*3}	4.18	11.53 ^{*3}	2.08	5.28 ^{*3}	2.13	3.21 ^{*3}	1.52	1.27	1.53	1.75 ^{*2}
13 × 13	28	1.55	9.11 ^{*3}	1.91	10.13 ^{*3}	1.23	2.10 ^{*3}	2.94	9.97 ^{*3}	1.69	4.66 ^{*3}	1.77	2.98 ^{*3}	1.65	1.38	1.16	1.24
14 × 14	28	1.59	10.50 ^{*3}	2.15	13.20 ^{*3}	1.23	2.23 ^{*3}	3.43	12.80 ^{*3}	1.77	5.42 ^{*3}	1.93	3.57 ^{*3}	1.64	1.42	1.38	1.74 [*]
15 × 15	24	1.69	13.19 ^{*3}	2.22	15.43 ^{*3}	1.28	2.61 ^{*3}	3.67	15.52 ^{*3}	1.81	6.14 ^{*3}	1.77	3.31 ^{*3}	1.24	1.16	1.23	1.48
16 × 16	18	1.46	11.83 ^{*3}	1.77	13.38 ^{*3}	1.25	2.89 ^{*3}	2.80	14.44 ^{*3}	1.57	5.91 ^{*3}	1.55	3.37 ^{*3}	1.06	1.06	1.38	1.83 [*]
17 × 17	15	1.52	14.81 ^{*3}	1.81	15.67 ^{*3}	1.22	2.82 ^{*3}	2.54	14.31 ^{*3}	1.70	7.68 ^{*3}	1.78	4.46 ^{*3}	0.86	0.86	1.31	1.77
18 × 18	15	1.45	13.91 ^{*3}	1.75	15.49 ^{*3}	1.19	2.75 ^{*3}	2.84	17.46 ^{*3}	1.50	6.23 ^{*3}	1.50	3.41 ^{*2}	0.75	0.73	1.36	2.05 [*]
19 × 19	15	1.47	15.19 ^{*3}	1.83	17.76 ^{*3}	1.24	3.43 ^{*3}	2.94	18.92 ^{*3}	1.55	7.05 ^{*3}	1.50	3.68 ^{*3}	0.95	0.93	1.42	2.42 ^{*2}
20 × 20	15	1.45	15.65 ^{*3}	1.88	19.36 ^{*3}	1.19	3.18 ^{*3}	2.97	19.61 ^{*3}	1.60	7.89 ^{*3}	1.48	3.65 ^{*3}	1.23	1.35	1.37	2.63 ^{*3}
21 × 21	8	1.25	12.46 ^{*3}	1.56	18.74 ^{*3}	1.08	2.09 [*]	2.32	21.61 ^{*3}	1.31	5.92 ^{*3}	1.16	2.23 [*]	0.97	0.94	1.40	2.65 ^{*2}
22 × 22	8	1.30	15.68 ^{*3}	1.57	20.54 ^{*3}	1.07	2.01 [*]	2.18	20.59 ^{*3}	1.39	7.95 ^{*3}	1.16	2.40 [*]	1.23	1.43	1.44	2.93 ^{*2}
23 × 23	8	1.30	17.05 ^{*3}	1.52	20.15 ^{*3}	1.13	3.22 ^{*2}	2.26	22.60 ^{*3}	1.29	6.66 ^{*3}	1.26	3.53 ^{*3}	1.33	1.71	1.28	2.35 [*]
24 × 24	8	1.29	17.77 ^{*3}	1.45	18.67 ^{*3}	1.22	5.06 ^{*3}	2.21	22.93 ^{*3}	1.20	5.07 ^{*3}	1.34	4.56 ^{*3}	1.29	1.67	1.29	2.51 [*]
25 × 25	8	1.25	16.63 ^{*3}	1.41	17.72 ^{*3}	1.20	5.07 ^{*3}	2.02	19.96 ^{*3}	1.20	5.52 ^{*3}	1.43	5.62 ^{*3}	1.31	1.80	1.27	2.74 ^{*2}
26 × 26	6	1.13	10.12 ^{*3}	1.21	11.74 ^{*3}	1.20	5.29 ^{*3}	1.59	15.10 ^{*3}	1.07	2.80 [*]	1.31	4.83 ^{*3}	1.43	2.20	1.51	4.06 ^{*2}
27 × 27	6	1.12	9.94 ^{*3}	1.23	12.38 ^{*3}	1.12	3.70 ^{*2}	1.53	13.69 ^{*3}	1.09	3.47 ^{*2}	1.16	3.03 ^{*2}	1.43	2.20	1.58	5.07 ^{*3}
28 × 28	6	1.15	11.88 ^{*3}	1.31	16.80 ^{*3}	1.08	2.92 [*]	1.57	14.57 ^{*3}	1.24	7.41 ^{*3}	1.22	3.78 ^{*2}	1.77	3.16 ^{*2}	1.49	4.72 ^{*3}
29 × 29	6	1.16	13.56 ^{*3}	1.32	18.07 ^{*3}	1.10	3.47 ^{*2}	1.58	15.27 ^{*3}	1.26	8.29 ^{*3}	1.24	4.26 ^{*3}	1.41	2.32 [*]	1.37	4.06 ^{*2}
30 × 30	6	1.17	14.91 ^{*3}	1.35	20.16 ^{*3}	1.09	3.53 ^{*2}	1.57	15.31 ^{*3}	1.31	9.91 ^{*3}	1.28	4.86 ^{*3}	1.19	1.61	1.34	4.20 ^{*3}

* 3 : $p < 0.001$ * 2 : $p < 0.01$ * : $p < 0.05$ I_{δ} : Morisita index F : value of F test on Morisita index V/m : Variance vs. mean t : Value of t test on V/m m^*/m : Congregation index SD, SP, ST, MT, BT : See Table 1

3.2 Population spatial pattern and dynamics

3.2.1 Pattern intensity (intensity of assemblage) with different scale

IA (intensity of assemblage) of MJF varied with scale or size of sampling grids. As the result of MI, V/m and CI, IA decreased with increasing scale, on the whole (Table 2 – Table 6). But as the result of SPPA, IA of SD, SP and ST, it increased with increasing scale, but after some scale, decreased with increasing scale. The scales with largest IA of SD, SP and ST, were 12 m, 11 m, and 5 m, respectively. And for ST, there were other two scales with second largest IA, 10 m and 21 m

(Fig. 2).

3.2.2 Scale of pattern and IA in different size classes

IA was also varied among different size classes of MJF. 1) MI (I_{δ}): SD, SP and ST were clumped under the scale from 1 m × 1 m to 30 m × 30 m with $p \geq 99\%$. 9% ($p \geq 95\%$ or $p \geq 99\%$ under a few scales) by F test. MT had a random or regular distribution usually. But BT distributed randomly or regularly when the scale is less than 5 m × 5 m, and then clumped with the increasing of scale. 2) V/m : The result of V/m with t test was almost the same as that of MI. 3) CI: SD, SP and ST clumped under all the scales tested, but IA decreased

Table 3 *V/m* and its *t* test of Minjiang fir

Grids		Total		SD + SP		ST + MT + BT		SD		SP		ST		MT		BT	
Size (m × m)	Number	<i>V/m</i>	<i>t</i>	<i>V/m</i>	<i>t</i>	<i>V/m</i>	<i>t</i>	<i>V/m</i>	<i>t</i>	<i>V/m</i>	<i>t</i>	<i>V/m</i>	<i>t</i>	<i>V/m</i>	<i>t</i>	<i>V/m</i>	<i>t</i>
1 × 1	6 000	1.33	18.31 ^{*3}	1.48	26.02 ^{*3}	1.01	0.52	1.56	30.92 ^{*3}	1.35	18.95 ^{*3}	1.06	3.45 ^{*3}	1.00	-0.19	0.99	-0.57
2 × 2	1 500	1.78	21.32 ^{*3}	1.99	27.08 ^{*3}	1.10	2.70 ^{*2}	2.19	32.61 ^{*3}	1.59	16.14 ^{*3}	1.25	6.90 ^{*3}	0.99	-0.38	1.02	0.61
3 × 3	660	2.31	23.80 ^{*3}	2.70	30.80 ^{*3}	1.11	1.92	2.86	33.82 ^{*3}	2.09	19.71 ^{*3}	1.29	5.34 ^{*3}	0.97	-0.58	1.01	0.14
4 × 4	375	3.19	29.93 ^{*3}	3.74	37.42 ^{*3}	1.35	4.74 ^{*3}	3.10	28.78 ^{*3}	2.66	22.76 ^{*3}	1.78	10.69 ^{*3}	1.04	0.48	1.06	0.78
5 × 5	240	3.71	29.62 ^{*3}	4.19	34.91 ^{*3}	1.36	3.92 ^{*3}	4.24	35.40 ^{*3}	2.61	17.64 ^{*3}	1.82	8.94 ^{*3}	1.09	1.04	1.09	1.00
6 × 6	160	4.19	28.44 ^{*3}	4.96	35.28 ^{*3}	1.36	3.19 ^{*2}	5.31	38.46 ^{*3}	2.79	15.92 ^{*3}	1.99	8.79 ^{*3}	0.97	-0.27	1.30	2.68 [*]
7 × 7	112	5.75	35.42 ^{*3}	6.59	41.66 ^{*3}	1.73	5.47 ^{*3}	6.90	43.94 ^{*3}	3.01	14.94 ^{*3}	2.79	13.36 ^{*3}	1.16	1.17	1.14	1.05
8 × 8	84	6.03	32.43 ^{*3}	7.09	39.22 ^{*3}	1.77	4.93 ^{*3}	7.60	42.55 ^{*3}	3.08	13.37 ^{*3}	2.09	7.05 ^{*3}	1.02	0.13	1.58	3.76 ^{*3}
9 × 9	66	6.52	31.49 ^{*3}	7.59	37.56 ^{*3}	1.58	3.29 ^{*2}	7.58	37.52 ^{*3}	4.67	20.95 ^{*3}	2.02	5.81 ^{*3}	1.15	0.86	1.16	0.93
10 × 10	60	8.55	41.00 ^{*3}	10.10	49.42 ^{*3}	1.85	4.60 ^{*3}	8.17	38.93 ^{*3}	5.63	25.14 ^{*3}	2.33	7.22 ^{*3}	1.11	0.58	1.27	1.48
11 × 11	45	8.12	33.41 ^{*3}	9.78	41.16 ^{*3}	1.85	4.01 ^{*3}	9.23	38.59 ^{*3}	4.99	18.70 ^{*3}	2.09	5.11 ^{*3}	1.02	0.10	1.42	1.99
12 × 12	40	11.18	44.97 ^{*3}	13.05	53.21 ^{*3}	2.66	7.32 ^{*3}	11.53	46.50 ^{*3}	5.28	18.91 ^{*3}	3.21	9.75 ^{*3}	1.27	1.19	1.75	3.32 ^{*2}
13 × 13	28	9.11	29.80 ^{*3}	10.13	33.53 ^{*3}	2.10	4.03 ^{*3}	9.97	32.95 ^{*3}	4.66	13.46 ^{*3}	2.98	7.27 ^{*3}	1.38	1.41	1.24	0.88
14 × 14	28	10.50	34.91 ^{*3}	13.20	44.82 ^{*3}	2.23	4.51 ^{*3}	12.80	43.37 ^{*3}	5.42	16.23 ^{*3}	3.57	9.45 ^{*3}	1.42	1.56	1.74	2.70 [*]
15 × 15	24	13.19	41.33 ^{*3}	15.43	48.92 ^{*3}	2.61	5.46 ^{*3}	15.52	49.25 ^{*3}	6.14	17.42 ^{*3}	3.31	7.82 ^{*3}	1.16	0.56	1.48	1.62
16 × 16	18	11.83	31.58 ^{*3}	13.38	36.10 ^{*3}	2.89	5.52 ^{*3}	14.44	39.19 ^{*3}	5.91	14.31 ^{*3}	3.37	6.92 ^{*3}	1.06	0.16	1.83	2.43 [*]
17 × 17	15	14.81	36.55 ^{*3}	15.67	38.80 ^{*3}	2.82	4.80 ^{*3}	14.31	35.22 ^{*3}	7.68	17.68 ^{*3}	4.46	9.16 ^{*3}	0.86	-0.38	1.77	2.05
18 × 18	15	13.91	34.15 ^{*3}	15.49	38.33 ^{*3}	2.75	4.62 ^{*3}	17.46	43.56 ^{*3}	6.23	13.84 ^{*3}	3.41	6.38 ^{*3}	0.73	-0.71	2.05	2.78 [*]
19 × 19	15	15.19	37.54 ^{*3}	17.76	44.34 ^{*3}	3.43	6.44 ^{*3}	18.92	47.41 ^{*3}	7.05	16.00 ^{*3}	3.68	7.09 ^{*3}	0.93	-0.19	2.42	3.76 ^{*2}
20 × 20	15	15.65	38.77 ^{*3}	19.36	48.57 ^{*3}	3.18	5.77 ^{*3}	19.61	49.23 ^{*3}	7.89	18.22 ^{*3}	3.65	7.00 ^{*3}	1.35	0.93	2.63	4.30 ^{*3}
21 × 21	8	12.46	21.45 ^{*3}	18.74	33.18 ^{*3}	2.09	2.05	21.61	38.55 ^{*3}	5.92	9.20 ^{*3}	2.23	2.31	0.94	-0.11	2.65	3.08 [*]
22 × 22	8	15.68	27.46 ^{*3}	20.54	36.56 ^{*3}	2.01	1.88	20.59	36.65 ^{*3}	7.95	13.01 ^{*3}	2.40	2.61 [*]	1.43	0.80	2.93	3.61 ^{*2}
23 × 23	8	17.05	30.03 ^{*3}	20.15	35.83 ^{*3}	3.22	4.15 ^{*2}	22.60	40.41 ^{*3}	6.66	10.60 ^{*3}	3.53	4.73 ^{*2}	1.71	1.34	2.35	2.52 [*]
24 × 24	8	17.77	31.36 ^{*3}	18.67	33.05 ^{*3}	5.06	7.59 ^{*3}	22.93	41.02 ^{*3}	5.07	7.61 ^{*3}	4.56	6.67 ^{*3}	1.67	1.26	2.51	2.83 [*]
25 × 25	8	16.63	29.25 ^{*3}	17.72	31.28 ^{*3}	5.07	7.61 ^{*3}	19.96	35.47 ^{*3}	5.52	8.46 ^{*3}	5.62	8.65 ^{*3}	1.80	1.49	2.74	3.26 [*]
26 × 26	6	10.12	14.42 ^{*3}	11.74	16.98 ^{*3}	5.29	6.78 ^{*2}	15.10	22.30 ^{*3}	2.80	2.85 [*] 4.88 ^{*0.5}	2.20	1.90	4.06	4.84 ^{*2}		
27 × 27	6	9.94	14.13 ^{*3}	12.38	18.00 ^{*3}	3.70	4.27 ^{*2}	13.69	20.07 ^{*3}	3.47	3.91 [*]	3.03	3.20 [*]	2.20	1.90	5.07	6.43 ^{*2}
28 × 28	6	11.88	17.20 ^{*3}	16.80	24.98 ^{*3}	2.92	3.04 [*]	14.57	21.45 ^{*3}	7.41	10.13 ^{*3}	3.78	4.39 ^{*2}	3.16	3.42 [*] 4.73 ^{*0.89}	2.89 ^{*2}	
29 × 29	6	13.56	19.86 ^{*3}	18.07	26.99 ^{*3}	3.47	3.90 [*]	15.27	22.57 ^{*3}	8.29	11.52 ^{*3}	4.26	5.15 ^{*2}	2.32	2.08	4.06	4.83 ^{*2}
30 × 30	6	14.91	22.00 ^{*3}	20.16	30.29 ^{*3}	3.53	4.01 [*]	15.31	22.63 ^{*3}	9.91	14.08 ^{*3}	4.86	6.10 ^{*2}	1.61	0.97	4.20	5.06 ^{*2}

SD, SP, ST, MT, BT: See Table 1 *3, *2, * : See Table 2

Table 4 Congregation index (*CI*, *m/m*^{*}) of Minjiang fir

Grids		Total	SD + SP	ST + MT + BT	SD	SP	ST	MT	BT	Grids		Total	SD + SP	ST + MT + BT	SD	SP	ST	MT	BT
Size (m × m)	Number	<i>m</i> [*] / <i>m</i>	<i>m</i> [*] / <i>m</i>	<i>m</i> [*] / <i>m</i>	<i>m</i> [*] / <i>m</i>	<i>m</i> [*] / <i>m</i>	<i>m</i> [*] / <i>m</i>	<i>m</i> [*] / <i>m</i>	<i>m</i> [*] / <i>m</i>	Size (m × m)	Number	<i>m</i> [*] / <i>m</i>	<i>m</i> [*] / <i>m</i>	<i>m</i> [*] / <i>m</i>	<i>m</i> [*] / <i>m</i>	<i>m</i> [*] / <i>m</i>	<i>m</i> [*] / <i>m</i>	<i>m</i> [*] / <i>m</i>	<i>m</i> [*] / <i>m</i>
1 × 1	6 000	5.38	10.70	1.34	26.47	13.90	5.78	0.05	0.02	16 × 16	18	1.48	1.81	1.26	2.89	1.60	1.58	1.06	1.39
2 × 2	1 500	3.55	6.05	1.90	14.43	6.49	5.78	0.04	1.53	17 × 17	15	1.56	1.86	1.24	2.64	1.75	1.82	0.86	1.32
3 × 3	660	2.91	4.82	1.43	10.24	5.48	3.49	0.04	1.08	18 × 18	15	1.49	1.80	1.21	2.96	1.54	1.52	0.75	1.38
4 × 4	375	2.79	4.49	1.79	6.93	4.88	4.71	1.60	1.34	19 × 19	15	1.50	1.89	1.25	3.07	1.59	1.53	0.95	1.44
5 × 5	240	2.42	3.61	1.53	6.84	3.40	3.48	2.03	1.35	20 × 20	15	1.48	1.94	1.20	3.10	1.64	1.50	1.24	1.39
6 × 6	160	2.16	3.21	1.37	6.31	2.83	3.05	0.77	1.86	21 × 21	8	1.29	1.64	1.09	2.50	1.35	1.18	0.97	1.44
7 × 7	112	2.22	3.17	1.56	6.00	2.44	3.64	1.92	1.30	22 × 22	8	1.34	1.65	1.08	2.34	1.45	1.18	1.24	1.48
8 × 8	84	1.99	2.79	1.45	5.27	2.12	2.21	1.09	1.98	23 × 23	8	1.34	1.59	1.15	2.43	1.33	1.30	1.36	1.31
9 × 9	66	1.82	2.49	1.25	4.27	2.53	1.87	1.52	1.20	24 × 24	8	1.33	1.51	1.25	2.37	1.22	1.39	1.32	1.32
10 × 10	60	1.99	2.86	1.31	4.23	2.72	2.01	1.29	1.26	25 × 25	8	1.29	1.46	1.23	2.16	1.23	1.49	1.34	1.30
11 × 11	45	1.73	2.35	1.26	3.78	2.13	1.64	1.05	1.35	26 × 26	6	1.15	1.26	1.24	1.70	1.08	1.37	1.48	1.59
12 × 12	40	1.93	2.69	1.43	4.24	2.10	2.15	1.51	1.54	27 × 27	6	1.15	1.27	1.14	1.63	1.11	1.19	1.48	1.68
13 × 13	28	1.57	1.94	1.24	2.99	1.71	1.79	1.63	1.16	28 × 28	6	1.18	1.37	1.10	1.67	1.29	1.26	1.86	1.57
14 × 14	28	1.61	2.19	1.23	3.50	1.79	1.95	1.63	1.39	29 × 29	6	1.19	1.39	1.12	1.69	1.31	1.29	1.47	1.44
15 × 15	24	1.72	2.27	1.29	3.77	1.84	1.79	1.23	1.24	30 × 30	6	1.20	1.42	1.11	1.68	1.36	1.33	1.22	1.40

SD, SP, ST, MT, BT: See Table 1

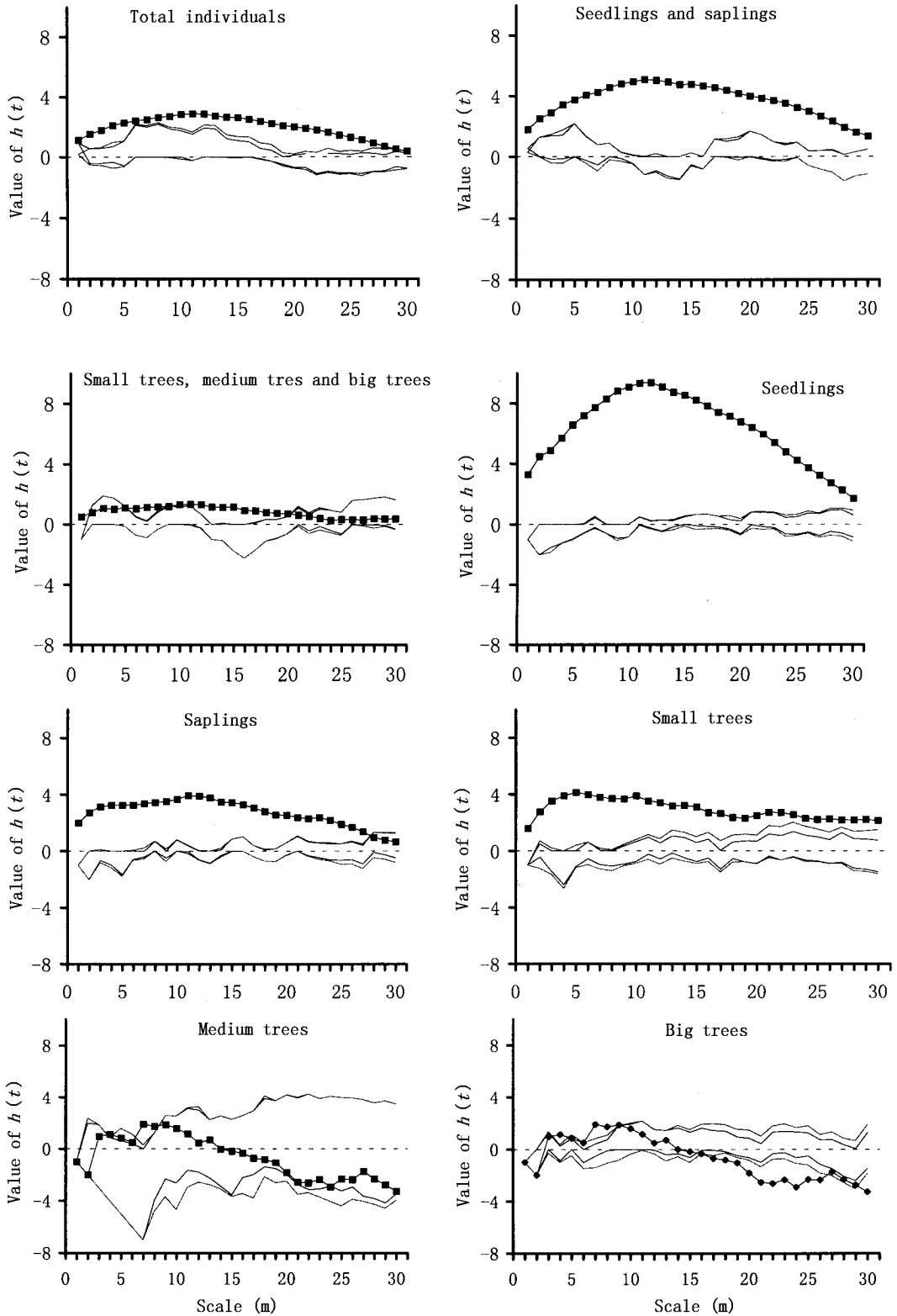


Fig.2 Spatial point pattern analysis and its Monte Carlo test on Minjiang fir

The pointed curve was the result of SPPA. The other four curves were the upper and lower envelop curve with the trust degree of 95% and 99% respectively. The broken line was the theoretical line that random pattern happened

with the adding of scale. The rule of the pattern of MT was not obvious, that the pattern was regular under some small scales or some moderate scales, and clumped under

other scales. 4) SPPA: The result tested by Monte Carlo method was also similar with that of the three above methods, but the trend that the scale of pattern and IA varied

with the change of scale, which was different from that demonstrated in section 3.2.1 (Fig. 2).

3.3 Population size structure and population dynamics

The population size structure was inverse "J" shape on the whole, although not so regular because there was a nick at MT. The individuals of SD and SP were very abundant, which indicated that the population was stable and can regenerate continuously. The phenomenon that individuals of MT were few but that of BT were more, was mainly caused by long life span of MJF that can be seen from Fig. 4 (Fig. 3; Fig. 4).

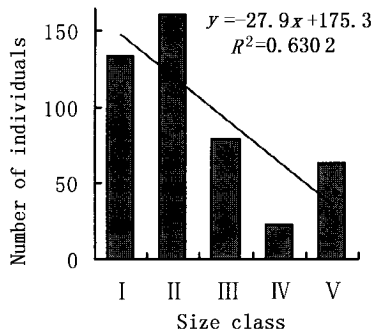


Fig. 3 Histogram of different size classes of the MJF individuals

I : Height < 0.33 m II : Height \geq 0.33 m, and DBH < 2.5 cm
 III : 2.5 cm \leq DBH < 7.5 cm IV : 7.5 cm \leq DBH < 22.5 cm V : DBH \geq 22.5 cm

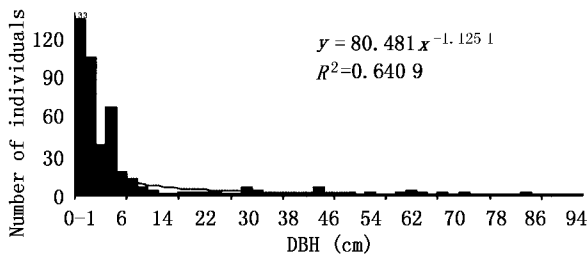


Fig. 4 Histogram of different DBH classes of the MJF individuals

4 Discussion

4.1 Spatial pattern of the population of MJF

4.1.1 Effects of scale on spatial pattern

Population spatial pattern usually varied with the change of scale in time and space. Because individuals of plants took up some continuous three-dimensional space, we had to define the unit of scale and then the method of investigation before carrying out research on their spatial pattern. Many scholars had measured spatial pattern under single scale with the investigation of the single unit, the result of which could only express the pattern at that scale, and the pattern under other scales could not be known. In the case of the block method of Greig-Smith, different size of grids had been adopted. Because the size of the block was double of the first smaller block, the spatial pattern between the two blocks could not be measured with the increasing of blocks, much information of spatial pattern had been omitted. But the methods we

adopted overcame these defects. For every individual of MJF was pointed out in a map, we could sample with different scales. The point mapping method must be applied to a plot big enough to contain sufficient number of grids, although this had brought much difficulty in field investigation.

4.1.2 Spatial pattern on different size class of the population of MJF

Trees usually have the trait of long life. During different growth phases, they had different ability to take up space, holding different size of space, and taking up different position of community. The SD, SP, and ST of MJF took up the lower and smaller space of the community. The competition among individuals and with other species in shrub layer and herb layer was very severe due to the trait of seed disseminate, regime of disturbance and approach of regeneration (mainly was gap regeneration), so the spatial distribution was aggregation. In the case of MT, they took up the middle space of the community, and the survival of them was the result of competition among the individuals during different growth phases. The spatial pattern was random because the intensive competition had passed. BT, taken up the upper space of the community, and hold even bigger space size, should be more important in stabilizing the community and its environment. The survival of them was the result of the outgrowth of the long life individual in MT, so the pattern was usually random too. The heterogeneity of the environment had great impact on the spatial pattern of plant, that the more heterogeneity, the more impact.

4.1.3 Factors affecting the spatial pattern of the population of MJF

The origin of population's spatial pattern was determined by the characteristic of the species, and closely related with the habitat environment. Seed disseminate trait, regeneration approach, and shade-tolerant or not were the main factors of a species' self-character that affect the generation of spatial pattern. The habitat environmental factors included biologic factors such as self-toxic, allelopathy, competition for resources etc., and non-biologic factors such as soil, microclimate and micro-geomorphology etc. The factors that affect the spatial pattern of SD, SP and ST were mainly parent trees, regeneration approach, seed rain, germination condition, density of the same species, the competition among individuals of different species and impact of animals etc. (Wang *et al.*, 1999; Wu *et al.*, 2002). The density of SD, SP and ST of MJF were very great, which were $2\ 217 \cdot \text{hm}^{-2}$, $2\ 683 \cdot \text{hm}^{-2}$, $1\ 317 \cdot \text{hm}^{-2}$, so the competition among individuals may be very intense. The main generation approach of MJF was seed germination within forest gap, so SD, SP and ST, situated in the lower layer of the community, not only were affected by the individuals of the same arbor species or not, but also would compete for light resources with the plant in shrub layer, herb layer and

lichen layer. Thus, the main factor affecting the spatial pattern of the SD, SP and ST was the competition for light resource. The spatial pattern of MT and BT was mainly the result of the competition among the individuals in the middle or upper layer of the community of the same species or not on one hand, on the other hand, the competition for light resources was one of the important factor since the soil condition and water resource were abundant in the site of MJF. As the result of competition, the decrease of density caused by self-thinning and hetero-thinning, not only created better light condition for the individuals among the middle and upper layer, but also let the SD, SP and ST in lower layer and the plants in shrub layer and herb layer obtain sufficient light. Then the whole community could accommodate lots of species and the individuals at different growth phases, so that it can keep the condition of "multi-layer and hetero-ages". The competition among the individuals of arbor species in middle and upper layer made less of the density of MT and BT, which were $367 \cdot \text{hm}^{-2}$ and $1\ 050 \cdot \text{hm}^{-2}$, respectively, far less than that of SD, SP and ST, so the spatial pattern was random.

4.2 Age structure of MJF and its dynamics

4.2.1 Regeneration approach of the population of MJF

MJF had three main regeneration approaches: forest gap regeneration, wave regeneration along the forest edge and the regeneration under forest canopy. The forest gap regeneration was the main approach within community. Wave regeneration along the forest edge was the main approach for forest restoration after large-scale disturbance and for forest self-expanding. The regeneration under canopy was the most important approach that should not be omitted due to the shade tolerant characteristics of MJF, and sometimes it was the important supplement for forest gap regeneration, and usually combined with forest gap regeneration make the community recycle regenerate smoothly. From the figures of size structure and DBH structure, we can see the phenomena of "age gap", i.e. the nick that cause by the number of individuals of SD less than that of SP, that of MT less than that of BT and the nicks within the graph of DBH structure. The phenomenon was closely related with the regeneration approach and disturbance regime of MJF. The difference in frequency and intensity of disturbance caused heterogeneity in time and space within the shifting mosaic regeneration. And the heterogeneity embodied in the section of time and space was the nicks among the DBH structure graph and the "age gap" phenomenon among age structures.

4.2.2 Developing trend of the population of MJF

MJF forest was a climax of sub-alpine vegetation, distributed over the eastern edge of Qinghai-Tibetan Plateau at the upper branches of Minjiang River and Dadu River within Sichuan Province and at the upper branches of Bailong River and Tao River in the southern part of

Gansu Province. The primitive community had great stability and richness of biodiversity. The figures of size structure and DBH structure showed that the pool of SD and SP were very rich. The age structure was the growing type, and due to the intensive competition, relatively few individuals could grow adult into the canopy layer. The phenomenon of "age gap" also indicated the cyclic death of naturally aging, which need more investigation and research on the age rings of the stem of MJF. This phenomenon was greatly related with the type, frequency and intensity of disturbance. The heterogenous disturbance of MJF forest included wind, snow suppression, dilapidation, landslip and plant diseases and insect pests etc. The endogenous disturbance included natural aging and death, suppress under canopy, competition among species, and so on. The cyclic regeneration mainly determined by the self-characteristics of the species. The drive power mainly came from endogenous disturbance, but the heterogenous disturbance let the cyclic trait be blurry and not determinate.

4.3 Comparison of different methods

All the four methods aforementioned could examine the spatial pattern under different scales. We pointed all the individuals in the plot in a map, and the results were similar on the whole, as mentioned in section 3.2. SPPA calculated the covariance between every point, the spatial pattern determined by SPPA maybe more accuracy and more adjacent to the reality. Furthermore, the pattern intensity calculated by SPPA could express the relationship between population's assemblage intensity and the variation of scales. So through SPPA, we can find out the scale that the population had greatest congregation, then we can analysis the reason further more. For example, from the phenomena that the scale with greatest congregation of the total MJF, the SD-SP, and the SP was 11 m, that of SD was 12 m, that of ST was 5 m and then the two scales with next greater assemblage intensity were 10 m and 21 m, and that of trees (including ST, MT and BT), MT, and BT all were 9 m (Fig. 2), we can confer that the diameter of the common patch in the community was 11 m, that of SD and SP was 12 m and 11 m, respectively, that of ST was 5 m, next common was 10 m and 21 m, that of MT and BT was 9 m. From this conference, we can also infer the common size of forest patch, which need more research and study. Some refinement should be made, because Ripley's second-order-analysis method does not do well in detecting gaps (Dale-Mark, 1999).

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