TOPOGRAPHIC INFLUENCES ON THE POPULATION PERSISTENCE OF A TERTIARY RELICT DECIDUOUS TREE *EMMENOPTERYS HENRYI* OLIV. ON MT. TIANMU, EASTERN CHINA

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Abstract. Mt. Tianmu is one of the most important refugia of Tertiary relict plant taxa in Eastern China. We analyzed the habitat characteristics, community structure, demographic structure, and production methods of Tertiary relict deciduous forests at 1,100 m on Mt Tianmu (1,506 m), Zhejiang province, China. *Emmenopterys henryi* mostly occurred in unstable habitats with gap-formation or landslides, and these populations showed a sporadic regeneration pattern. *E. henryi* colonized and established at unstable sites by abundant wind-dispersed seeds. After colonization, *E. henryi* persisted for a long time and dominated in the canopy layer and even reached emergent layer due to its long lifespan and vegetative reproduction capability. It could thus be regarded as an undifferentiated climax pioneering species with an 'r-selected' life history that produced abundant minute seeds and experienced intermittent recruitment and often became pioneer species of secondary succession after moderate disturbance. Here, we discussed conservation strategies for Tertiary relict deciduous trees as climax pioneering species that accounted for the peculiarity of their habitat and population structure in broad-leaved forests.

Keywords: *habitat instability, root sucker, population structure, reproduction methods, regeneration strategy*

Introduction

Tertiary relict floras contain survivors from plant communities that were distributed throughout a large part of the Northern Hemisphere during much of the Tertiary (i.e. 65-15 million years ago (Ma)) (Milne and Abbott, 2002). They are now mainly restricted to warm humid areas (refugia) in southeastern and western North America, East Asia and southwest Eurasia (Milne and Abbott, 2002; Hampe and Arroyo, 2002). A number of deciduous broad-leaved ancient genera, considered to be Tertiary relicts, are found today in subtropical broad-leaved forests of China, such as *Davidia involucrate*, *Tetracentron sinense*, *Cercidiphyllum japonicum* var. *sinense*, *Euptelea pleiospermum*, *Ginkgo biloba*, *Cyclocarya paliurus*, *Emmenopterys henryi*, *Tapiscia sinensis*, *Fortunearia sinensis* etc. (Del Tredici, 1992; López-pujol et al., 2006; Gong et al., 2008; Wei et al., 2010; Wu et al., 2018). The current populations of these trees are very small and they usually coexist with other evergreen, deciduous and coniferous trees at relatively restricted ranges (Gong et al., 2008; Wu et al., 2018). During the

Quaternary glaciations, these ancient species experience severely reduced regeneration and survived while most other members of their group were wiped out (Tzedakis et al., 2002; Shen et al., 2002; Tang et al., 2011; Qian et al., 2016). A majority of these species are globally threatened now (López-Pujol et al., 2006). How these relict species survive and persist under current climate conditions or those of rapid climate change and frequent human activities became an important topic for rare and endangered species conservation (Calleja et al., 2009).

Emmenopterys henryi Oliv, belonging to the Rubiaceae family, is an endangered deciduous tree endemic to China (Zhang, 2016). It is characterized by a long lifespan, intermittent flowering with 2-4 year intervals, production of abundant wind-dispersed minute seeds (0.3-0.6 g per 1000 grains) and reduce competitive ability with other deciduous pioneer tree species and evergreen tree species during the juvenile stage (Wang et al., 2002). It is of ancient origin, a relic of the paleotropical flora of the Cretaceous Period, Mesozoic Era, and is considered valuable both for its unique position in the flora of China and in the systematic evolution of the Rubiaceae. *E. henryi* primarily occurs in ravines and mountain valleys at altitudes of 400-1400 m in southwestern China and the Yangtze River Valley. Populations of *E. henryi* have been affected by habitat destruction and over-exploitation in the wild. It has been listed as a threatened species within China due to its lower regeneration. Previous researches mainly focused on chemical components, seed physiology, community structure and genetic structure (Ma and He, 1989; Zhang et al., 2007; Li and Jin, 2008; Guo et al., 2017a,b; Ma et al., 2019). Kang et al. (2007), Guo et al. (2017a) and Ma et al. (2019) also reported that *E. henryi* regenerates through both sexual and asexual modes, but scientific analysis of its regeneration mechanism along the topographic gradients, has not been described. Further studies may be necessary to evaluate potential adaptation of populations to local environmental conditions.

Therefore, this paper focuses on: (1) community structure, distribution pattern and demographic structure of main trees, and (2) the production methods of *E. henryi* population along the topographic gradients, to reveal that how they persisted as related to habitat. The inhabiting habitats, production methods and regeneration strategy of other similar relict trees have been compared to determine whether these relict trees have similar peculiarity for persistence at relatively restricted ranges.

Materials and Methods

Study site

The study was conducted at the Mt. Tianmu Nature Reserve (30°18'30'' ~ 30°21'37''N, 119°24'11'' ~ 119°27'11''E, Zhejiang Province, P. R. China), which is one of the most famous protected areas in China and throughout the world due to its remarkable number of large, rare and endangered plants. The foothill region is located at 300-350 m a.s.l., which gradually rises to 1,056 m a.s.l. Mt. Tianmu is characterized by a subtropical humid climate (Qian et al., 2002). According to records from weather stations at Chanyuan Temple (350 m a.s.l.) near the base and Xianrending (1,506 m a.s.l.) near the summit of Mt. Tianmu from 1987 to 1996, the average annual temperature is 14.5 °C and 9.0 °C, and the average annual precipitation is 1,739 mm and 1,751 mm for Chanyuan Temple and Xianrending, respectively (Da et al., 2009). Because the stratum was affected by tectonic movements and volcanic activity, the study area is made up of steep slopes and irregular terrain, especially many complex

landscape structures between 900 m and 1,100 m a.s.l. 90% of this area is covered with volcanic rock, and the zonal soils are comprised of red soils (below 600 m a.s.l.), yellow soils (600-1,200 m a.s.l.) and brown yellow soils (above 1,200 m a.s.l.) (Xia, 2004).

Data collection

The population size and distribution region of *E. henryi* on Mt. Tianmu is small by our survey on July to August 2010, which mainly concentrated on the mid-altitude region from 900 m a.s.l. to 1,200 m a.s.l. They were mainly distributed at roadsides, and in valleys, gravel mounds, cliffs, etc. Besides, we also founded that a few of seedlings and saplings of *E. henryi* grow on fallen log of the gap-maker. We established plots by patch sampling in twelve locations representing three micro-topographies (Table 1). Plot 1-4 (total 1,600 m²) was established in an old canopy gaps surrounded by old-growth *Cryptomeria fortunei*. These plots were located on hollow head with an average 20.0° incline. Plots 5-8 (total 1,600 m²) were established in flood terrace with an average 16.0° incline. Plot 9-12 (total 1,400 m²) was established in river bed on a seasonally active channel with a mean 23.8° incline. A more detailed description of these three microtopographies was shown in Table 2 by surveyed.

Table 1. The geological properties of 12 sampling plots

Plot	GPS position	Microtopography	Sampling area (m ²)	Altitude (m)	Slope (°)	Aspect
1	30°20'18.4", 119°25'44.8"	Hollow head	400	1062	15	S30E
2	30°20'32.3", 119°26'06.8"	Hollow head	400	1113	10	S65W
3	30°19'52.0", 119°25'45.6"	Hollow head	400	1000	30	NE45
4	30°20'25.5", 119°25'59.5"	Hollow head	400	980	25	S15E
5	30°20'29.8", 119°26'05.6"	Flood terrace	400	1097	10	N10W
6	30°20'29.8", 119°25'58.4"	Flood terrace	400	1080	14	S30W
7	30°21'33.5", 119°25'21.1"	Flood terrace	400	1050	15	NE30
8	30°20'20.8", 119°25'48.2"	Flood terrace	400	1020	25	S79E
9	30°20'27.5", 119°25'59.0"	River bed	400	1064	20	S15E
10	30°21'33.5", 119°25'33.7"	River bed	400	1050	23	NE50
11	30°19'54.3", 119°25'51.4"	River bed	400	856	30	NE45
12	30°20'18.4", 119°25'47.8"	River bed	200	975	22	S74E

Table 2. The characteristics of three different microtopographies

Habitat	Hollow head	Flood terrace	River bed
Situation	Upper gentle slope	Lower gentle Slope	Middle gentle slope
Litter cover	High	Low-high	Low
Soil depth	Deep	Medium	Shallow
Soil humidity	Low	High	Low
Disturbance type	Soil erosion	Soil erosion	Soil erosion
Physical stability	Relatively stable	Moderately unstable	Unstable

Because the canopy layer forms at heights above 8 m in these plots, we expressed the strata of the forest as follows: tree layer, 8 m < height (H); subtree layer, 4 m ≤ H ≤ 8 m; shrub layer, 1.5 m ≤ H < 4 m; sapling, 0.5 m ≤ H < 1.5 m; seedlings, H < 0.5 m. In each whole plots, we recorded the species, measured the diameter at breast height (1.5 m above ground; DBH) and the height of trees ≥ 1.5 m. The quantities and heights of seedlings and saplings of *E. henryi* were also identified and measured.

The plantlets of *E. henryi* were classified into two types, true seedlings from seed-origin and root suckers from adventitious buds on lateral roots, identified by removing the litter and surface soil of lateral roots. Besides, individuals with own root systems in shrub or tree layer were also considered to be seed-orientated. Root suckers remained connected to parent tree for several years and could increase competitively and greater survival under adverse environmental conditions (Ky-Dembele et al., 2007; Beaudet and Messier, 2008).

Data analysis

The dominant species were identified by Ohsawa's dominance analysis method using the relative basal area (RBA) of each species. This analysis is based on the least deviation (d) between the share obtained by a given species, as a percentage of the total basal area (x_i), and its calculated share if all species were equally represented (x'):

$$d = 1/N \left\{ \sum_{i \in T} (x_i - x')^2 + \sum_{j \in U} x_j^2 \right\} \quad (\text{Eq.1})$$

where T is the number of 'top species' in a given dominant-number-model, U is the number of remaining species, and N is the total number of species. For example, in a community dominated by single species, $x' = 100/T$ (where $T=1$), the top dominant's share is 100%. If, however, two species share dominance, the top two dominants share 50%, or if there are three co-dominants, 33.3%, and so on. Species diversity was expressed by Shannon-Wiener Index.

For determining whether these Tertiary relict trees have similar regeneration mechanisms, more or less complete information on the inhabiting habitat, seed mass per 1000 grains, dispersal agent and production methods was available from literatures (Shang et al., 2016). The types of vegetative reproduction were clarified into five types. Seedling sprout means a plantlet of seed origin that was affected by shoot dieback, but re-sprouted from the root collar of the seedling; root sucker means a plantlet arising vertically from superficial lateral root; coppice means a plantlet arising from stumps of cut mature tree in response to logging or non-logging disturbances and which root diameter exceeds 10 cm; water sprout means a plantlet developed from the base of alive mature tree; layer means a plantlet developed from low hanging lateral branch (Ky-Dembele et al., 2007).

Results

Floristic characteristics

Within a total of nearly 4,600 m² plots in all habitats, 69 woody species belonging to 54 genera and 37 families were recorded (*Appendix A*). The tree life-forms were deciduous broad-leaved, evergreen broad-leaved, deciduous coniferous and evergreen coniferous, but only 9 species were evergreen. Of the deciduous species, 3 genera (*Pseudolarix*, *Emmenopterys* and *Cyclocarya*) were endemic to China, 7 genera (*Kalopanax*, *Acanthopanax*, *Ehretia*, *Corylopsis*, *Deutzia*, *Dendrobenthamia* and *Stachyurus*) were endemic to East Asia. Of the evergreen trees, one genus (*Cunninghamia*) was endemic to China, 3 genera (*Cryptomeria*, *Lithocarpus* and *Orixa*) were endemic to East Asia. Northern temperate deciduous broad-leaved genera such as

Petrocarya, *Acer* and *Viburnum*, pantropic genera and old-world temperate genera were also appeared. Besides, many relict species such as *E. henryi*, *Cyclocarya paliurus*, *Magnolia cylindrical*, *Pseudolarix amabilis* were co-existed in the community. Hence, the ancient and complexity of community were remarkable that with so many plants of diverse geographic distributions as well as Tertiary relicts.

E. henryi could establish them on different microtopography along habitat instability and become a dominant. In the hollow head with relatively stable, was co-dominated by *P. amabilis*, *C. fortunei* and *E. henryi*; the relative dominance value of *E. henryi* was 15.2-67.6%. In the flood terrace with moderately unstable, *C. fortunei*, *E. henryi* and *P. amabilis* were co-dominant; the relative dominance value of *E. henryi* was 23.7-57.2%. In the river bed, *E. henryi* as the first dominant was co-dominated with *C. fortunei* and the relative dominance value reached to 41.9-97.0%.

Height-class distribution with increasing habitat instability

The height-class frequency distribution of all woody species is shown in Fig. 1. In the hollow head, the number of evergreen individuals was more than deciduous and the ratio of evergreen/deciduous was 1.16. Evergreen species such as *Cyclobalanopsis gracilis*, *Lithocarpus harlandii* and *C. fortunei* were found in the shrub, subcanopy and canopy layers. Besides, deciduous trees *E. henryi* and *C. paliurus* were also found in all three layers, and the former even reaching the emergent layer (above the canopy, more than 20 m). In the flood terrace, the number of evergreen individuals was decreased, and the ratio of evergreen/deciduous reached to 0.48. They mainly appeared in shrub and subcanopy layer (below 10 m) while *E. henryi* were found in all layers. In the river bed, although *C. fortunei* could reach the emergent layer, evergreen individuals including *L. harlandii* and *C. fortunei* were rare and mainly confined to the shrub layers. The canopy, subcanopy and shrub layers of the forest were occupied by *E. henryi* and other deciduous trees such as *Alangium chinense* and *Bothrocaryum controversum*.

Figure 1. Height-class frequency distribution of all individuals and main populations with increasing. Dominant species are indicted by an asterisk

Population structure with increasing habitat instability

These communities include unimodal, sporadic and L types of size-class frequency distribution (Fig. 2). The unimodal type, with a single peak in the intermediate or large size-classes, and fewer if any individuals in small size-classes, suggests a weak regeneration pattern. Evergreen trees *L. harlandii*, *C. gracilis* and *Cunninghamia lanceolata* located on valley and *C. fortunei* appeared in all three habitats were of this type. The sporadic type, with more than one peak in the size-classes, indicates the possibility of good regeneration. *E. henryi* occurred in all three microtopography were of this sporadic type, but the number of populations decreased along habitat instability. Active regeneration is suggested by the L type having the highest frequency in small DBH classes. In hollow head and flood terrace habitats, evergreen trees *L. harlandii*, *C. gracilis* and *C. lanceolata* was of this type, indicating that these evergreen canopy species were suppressed by the dominant deciduous species but their populations could develop.

Figure 2. Size-class frequency distribution for the *E. henryi* population and main evergreen tree with increasing habitat instability

Sprouts ratio of *E. henryi* population at different habitat

Although the reproduction of *E. henryi* was by means of seeds at many habitats, such as gravel mound, canopy gap and fallen-log by our investigation, the resprouter by root sucker were also abundant at hollow head and river bed habitat (Fig. 3). In the hollow head, 23 stems (including 14 seedlings and 9 saplings) were found to regenerate successfully from root suckers and 9 individuals were true seedlings or assumable seed-orientated trees. And 2 of these individuals were located on fallen-log. In the river bed, 6 stems originated from root suckers and 6 individuals were true or assumable seed-orientated trees. The suckering stems accounted for 72% of all stems in the hollow head, while 50% in river bed.

Figure 3. Vegetative mode of *E. henryi* population in hollow head and river bed

Discussion

Reproductive strategy and population persistence of E. henryi in relation to micro-topography

The distribution of *E. henryi* on Mt. Tianmu was primarily at unstable habitats, such as hollow head valleys, flood terrace, fallen logs and gravel-mounds. This was similar to other Tertiary relict species, such as *Euptelea polyandra* in warm-temperature forest of Japan (Sakai and Ohsawa, 1993), *Euptelea pleiospermum*, *Cercidiphyllum japonicum* and *Davidia involucrata* in subtropical evergreen broad-leaved forests of western China (Tang and Ohsawa, 2002; Wei et al., 2010; Wu et al., 2018), *Frangula alnus* subsp. *Baetica* and *Prunus lusitanica* in Iberian Peninsula of Spain (Hampe and Arroyo, 2002; Calleja et al., 2009; Pardo et al., 2018). All these trees seem to require very particular unstable habitats where competition from other trees is limited.

At those unstable habitats, the deciduous pioneer tree *E. henryi* could colonize firstly by mean of abundant minute seeds production (0.3-0.6 g per 1,000 grains) after moderate disturbance (Kang et al., 2007; Shang et al., 2016). Their populations experienced intermittent recruitment as shown by the sporadic type of stem-diameter class frequency distribution, while evergreen trees regenerated more weakly along habitat instability (Fig. 2). At hollow head and flood terrace habitat with lower unstable, *E. henryi* can dominate in the canopy layer and even reach the emergent layer due to its long life span (Fig. 1; Appendix A). When these habitats become more stable, the evergreen trees *L. harlandii*, *C. gracilis* and *C. lanceolata* may become dominants according to the regeneration pattern (Fig. 2). At river bed habitat with frequent landslide, *E. henryi* could recruit well due to the possibility of good regeneration while other evergreen trees were not (Fig. 2). Here, the *E. henryi* dominated forest in the river bed on Mt Tianmu could be regarded as a topographic climax phenomenon formed in an area of landslide disturbances.

The results of this investigation showed that asexual reproduction resprouted by long-distance root (root sucker) was the important mechanism of seedling recruitment of *E. henryi* population (Fig 3, Guo et al., 2017a). The suckering stems accounted for 72% of all plantlets in hollow head compared to 50% in river bed. This is because although *E. henryi* can colonize at different habitats by the active production of seeds, the seed germination and seedling establishment are influenced by environmental filtering (Zhang et al., 2007; Guo et al., 2017b). The seed germination and seedling recruitment of *E. henryi* at current conditions are hampered by the thick layer of leaf litter in gentle slope habitat except for fallen-log, which agrees with previous findings that seedlings produced by small seeds may be unable to emerge in sites with thicker litter layers (Carlton and Bazzaz, 1998; Castro et al., 1999). After the stage of seedling-establishments, a light-demanding deciduous pioneer tree, *E. henryi* can not compete with modern deciduous pioneer tree species and evergreen tree species due to its reduced competitive ability during the juvenile stage (Zhang et al., 2007; Pulido et al., 2008). On the other hand, resprouts arising from vegetative reproduction grow faster than newly established seedlings due to their well-established root system (Ky-Dembele et al., 2007), providing better resistance to stress in their first years (Deiller et al., 2003), and a stronger competitive advantage (Beaudet and Messier, 2008). It can be considered that root suckers probably contribute to the survival and maintenance of *E. henryi* population by reducing vulnerability to severe disturbance and recruitment failure (Guo et al., 2017a).

Ohsawa (1991) have suggested that most sporadic type species who experienced intermittent recruitment can be regarded as a kind of pioneers in the climax forests and called ‘undifferentiated canopy components’ that between a nomadic pioneer and a climax species. *E. henryi* populations have experienced intermittent recruitment in hollow head and flood terrace habitat with relatively stable (Fig. 2). Moreover, *E. henryi* is a deciduous pioneer tree that characterized by a long life span, intermittent flowering with 2-4 year intervals, and production of abundant wind-dispersed minute seeds (0.3-0.6 g per 1,000 grains). Thus we suggested that *E. henryi* can be regarded as an undifferentiated climax pioneering species with an ‘r-selected’ life history.

Persistence mechanism of Tertiary relict deciduous trees as climax pioneering species

A large number of deciduous broad-leaved trees of ancient genera, considered to be Tertiary relicts, occurred in the mid-altitude region of subtropical mountains (Table 2; Shang et al., 2016). The Tertiary relict trees seem to require very particular unstable habitats that mainly distributed on valley, forest edges, steep slopes and stream banks (Table 3). This is probably due to the importance of differential growth, differential survival and differential dispersal of species as well as its evolutionary factor (Pullio, 2008; Qian et al., 2016).

Since the Quaternary era, the distribution, population size and regeneration capacity of many Tertiary relict plant species has changed greatly (Tzedakis, 2002; Calleja et al., 2009; Zhang et al., 2016). Owing to their reduced competitive ability with modern floras and their ecophysiology (Pulido et al., 2008), these species need to colonize on ‘safe sites’ where competition from other species is limited (Tang and Ohsawa, 2002). The environmental stochasticity in unstable habitats could provide more opportunity for regeneration of seed-orientated species and decrease interspecific competition (García, 2003). Therefore, Tertiary relict trees would recruitment intermittent by abundant minute wind-dispersal seeds (Table 2; Zhang et al., 2007; Li et al., 2008).

Table 3. Known distribution habitat, vegetation regeneration strategies, and dispersal agent of the main relict deciduous tree in China's subtropical forests

Relict deciduous trees	Main habitats	Seed mass (g/1,000)	Dispersal agent	Vegetative mode
<i>Annamocarya sinensis</i>	Valley, stream bank	9000-13000	Mammals	Water sprout; Coppice
<i>Bretschneidera sinensis</i>	Humidity valley, stream bank	715-780	Wind	Coppice
<i>Camptotheca acuminata</i>	Stream bank, forest edge	34-45	Wind	Water sprout
<i>Cercidiphyllum japonicum</i>	Steep slope, valley, stream bank	0.75-0.9	Wind	Water sprout
<i>Cyclocarya paliurus</i>	Steep slope, creek valley, forest edge	200	Wind	Water sprout
<i>Davidia involucrata</i>	Steep slope, ravine	3400-5500	Mammals	Water sprout; Coppice
<i>Eucommia ulmoides</i>	Valley, dry ravines	58-130	Wind	Root sucker; Coppice
<i>Halesia macgregorii</i>	Steep slope	125-220	Birds	Water sprout
<i>Liquidambar formosana</i>	Valley, stream bank	4.3-6.4	Wind	Water sprout
<i>Liriodendron chinense</i>	Valley	22-35	Wind	Coppice
<i>Nyssa sinensis</i>	Valley, stream, steep slope	125-240	Birds	Water sprout
<i>Pteroceltis tatarinowii</i>	Foothill, forest edge, river bed	21-28	Wind	Water sprout
<i>Tetracentron sinensis</i>	Valley, hillside, rocky ravine	0.1-0.15	Wind	Coppice

Note: Sources: Shang et al., 2016

On the other hand, Tertiary relict trees could sprout new shoots in subtropical area of China, including water sprouts, coppices, and root suckers (Table 2). It seems to allow the population to recruitment quickly after disturbance. This supplemental mechanism for population persistence is similar to that of *E. henryi* in our study, *E. polyandra* in Japan and *Rhododendron ponticum* in Mediterranean, which allocate more resources to sprouts than to reproduction by seeds (Sakai et al., 1995; Mejías et al., 2002).

These characteristics are coincident with the general tendency that the Tertiary relict deciduous trees survive and persist well in the unstable scree slopes where competition is not severe, but are unable to thrive in the stable habitats where competition is more rigorous (Tang and Ohsawa, 2002). Consequently, minute easily-dispersed seeds and seedling recruitment supplemented with vegetative reproduction seem to be most important reasons why Tertiary relict deciduous trees have been able to persist at a given site after frequent disturbance (Milne and Abbott, 2002).

Conclusion

Many of Tertiary relict deciduous trees regarded as an undifferentiated climax pioneering species with an 'r-selected' life history has very few individuals remaining. They are of high conservation concern due to their rarity and their phylogenetic uniqueness, and are therefore very important to China and the world. Responsible conservation efforts should aim to maintain present populations of these species and expand their distribution by creating new habitat. Firstly, restoration efforts should focus both on preserving habitats by protecting valley bottoms, stream habitats, and hollows, and also on preserving or restoring the natural disturbance regime. Secondly, we should prohibit salvage logging or clearing of fallen trees so that this wood can

provide opportunities for the recruitment of seedlings. Thirdly, in order to maintain sufficient genetic variation in a small area, it is important to increase the population of true seedlings (i.e. not resprouts) through protection of seedlings and/or increasing the sowing density. Moreover, plantations could function as starting points for the natural restoration of extirpated populations in unstable habitats. These measures, together with effective legal protections against human disturbance, might help to improve the long-term persistence of Tertiary relict trees in subtropical area of China during future changes in climate.

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APPENDIX

Appendix A. Floristic composition and RBA (%) of the woody plant in the sample plots

Parameters	Genus distribution	Plot											
		1	2	3	4	5	6	7	8	9	10	11	12
Microtopographic type		Hollow head				Flood terrace				River bed			
Plot area (m ²)		400	400	400	400	400	400	400	400	400	400	400	200
Number of plants		186	113	83	123	96	104	244	118	66	280	120	82
Maximum height (m)		35	35	15.5	30	24	36	13	18	32	9	15.5	16
Maximum DBH (cm)		101	69	40.8	129	109	81	18.5	28.5	100	18	59.3	65.8
Average DBH		4.2	5	6.9	7.2	6.2	5	5.9	6.5	5.7	3.3	7.4	6.3
Average Height		5	7	10.3	7.8	8.5	6.9	5.6	6.2	8	3.4	11.8	7.8
Total basal area (m ² /100m ² plot)		4037	5154	2497	6129	5023	3465	2383	1944	4005	1387	2088	4330
Deciduous Coniferous Tree													
<i>Pseudolarix amabilis</i>	China	47.3*	18.1*				37.2*						
Deciduous Broadleaved Tree													
<i>Emmenopterys henryi</i>	China	15.5*	35.3*	67.6*	15.2*	23.7*	33.7*	40.2*	57.2*	41.9*	70.7*	86.9*	97.0*
<i>Bothrocaryum controversum</i>	NTem		0.1	8.2*	<0.1		0.7	5.4		0.4	14.7*	4.1	0.1
<i>Acer henryi</i>	NTem			0.1	<0.1		0.4			0.1	<0.1	<0.1	<0.1
<i>Acer mono</i>	NTem				<0.1					0.2	<0.1	0.3	0.4
<i>Cyclocarya paliurus</i>	China	7.8	1.9	<0.1	3.3		1.1	5.1	13.9*				
<i>Quercus aliena</i> var. <i>acutiserrata</i>	NTem		5.4				0.9						
<i>Toxicodendron vernicifluum</i>	EAs,NAm,dis			5.0	0.3	4.8			1.1				
<i>Kalopanax septemlobus</i>	EAs		2.4										<0.1
<i>Liquidambar acalycina</i>	EAs,NAm,dis	1.4	17.1*										
<i>Padus obtusata</i>	NTem		4.4	4.2									
<i>Ilex macropoda</i>	PanTr			0.1									
<i>Acanthopanax evodiaefolius</i>	EAs				<0.1								
<i>Acer palmatum</i>	NTem		<0.1	3.6									
<i>Acer olivaceum</i>	NTem					<0.1	0.1		0.7				
<i>Acer davidii</i>	NTem					0.2			<0.1				
<i>Ehretia thyrsoiflora</i>	EAs					6.2		1.9	5.0				
<i>Juglans cathayensis</i> var. <i>formosana</i>	NTem						2.2						

Parameters	Genus distribution	Plot											
		1	2	3	4	5	6	7	8	9	10	11	12
<i>Cladrastis wilsonii</i>	EAs,NAM,dis						<0.1		4.2				
<i>Nyssa sinensis</i>	EAs,NAM,dis						2.1						
<i>Fraxinus insularis</i>	NTem								0.1				
<i>Celtis sinensis</i>	PanTr						0.2						
<i>Celtis chekiangensis</i>	PanTr						3.0		4.7				
<i>Alangium chinense</i>	Old World Tr						2.2			1.7	6.5		0.7
<i>Magnolia cylindrica</i>	EAs,NAM,dis						2.0			1.1	<0.1	6.2	<0.1
<i>Diospyros glaucifolia</i>	PanTr									1.0			
<i>Pistacia chinensis</i>	Med to TrAs, Aus.SAM,dis							6.2		0.3			
Deciduous Broadleaved Shrub													
<i>Lindera glauca</i>	TrAs	0.3	0.3		0.9	0.6		0.7					0.1
<i>Symplocos paniculata</i>	PanTr		<0.1		0.1	<0.1	<0.1	<0.1		<0.1	0.1		
<i>Hydrangea chinensis</i>	EAs,NAM,dis		<0.1		0.1	0.2	<0.1	0.1		<0.1	1.9		0.1
<i>Lonicera hemsleyana</i>	NTem		0.1		0.1		0.2	1.1			0.1	0.1	
<i>Lonicera modesta</i>	NTem			<0.1	<0.1	<0.1	<0.1	<0.1					
<i>Euonymus hamiltonianus</i>	NTem		<0.1		0.1			<0.1	0.1				
<i>Dendrobenthamia japonica</i> var. <i>chinensis</i>	EAs	2.1	0.9					2.5	0.7				
<i>Mallotus japonicus</i> var. <i>floccosus</i>	Old World Tr				<0.1	0.1		0.4	2.4				
<i>Lindera fruticosa</i>	TrAs				<0.1	<0.1							
<i>Meliosma flexuosa</i>	TrAs,TrAm,dis		<0.1			0.1		0.1	<0.1				
<i>Meliosma oldhamii</i>	TrAs,TrAm,dis	0.1		9.3*	0.1	0.2		<0.1	7.8				
<i>Clerodendrum trichotomum</i>	PanTr					<0.1		<0.1					
<i>Callicarpa giraldii</i>	PanTr	<0.1		0.5	0.2	0.1	0.2	0.1	0.4				
<i>Styrax obassia</i>	PanTr				0.2								
<i>Corylopsis glandulifera</i>	EAs	<0.1	<0.1										
<i>Viburnum dilatatum</i>	NTem	<0.1	0.1	<0.1	<0.1								
<i>Viburnum erosum</i>	NTem								0.6				
<i>Rhamnus utilis</i>	Cos					<0.1	<0.1	<0.1	0.3				
<i>Rhamnus globosa</i>	Cos					<0.1	<0.1	<0.1	0.6				

Parameters	Genus distribution	Plot											
		1	2	3	4	5	6	7	8	9	10	11	12
<i>Photinia beauverdiana</i>	EAs,NAm,dis					<0.1	0.5						
<i>Meliosma veitchiorum</i>	TrAs,TrAm,dis					0.4							
<i>Styrax confusus</i>	PanTr					<0.1							
<i>Aralia chinensis</i>	EAs,NAm,dis					<0.1	0.1			0.1			
<i>Viburnum plicatum</i> var. <i>tomentosum</i>	NTem					0.2	0.1	<0.1		<0.1		0.4	
<i>Sambucus williamsii</i>	NTem,STem,dis					<0.1	<0.1			0.3			<0.1
<i>Phyllanthus glaucus</i>	PanTr					<0.1	<0.1			0.1	2.0		<0.1
<i>Lindera praecox</i>	TrAs					<0.1	0.1	3.0					0.1
<i>Deutzia glauca</i>	EAs					<0.1	<0.1	0.1			<0.1		
<i>Picrasma quassioides</i>	TrAs & Tr Am dis									<0.1			
<i>Stewartia gemmata</i>	EAs,NAm,dis			0.2						1.0	2.7	0.8	
<i>Stachyurus chinensis</i>	EAs									0.1	1.2	0.1	
Evergreen Coniferous Tree													
<i>Cryptomeria fortunei</i>	EAs	16.7*	0.3		61.3*	53.4*	0.3			49.1*			
<i>Cunninghamia lanceolata</i>	China	0.1	0.6		11.6*	3.8	<0.1	17.0*		1.4			
Evergreen Broad-leaved Tree													
<i>Lithocarpus harlandii</i>	EAs	1.0	2.7		5.5	5.4	5.5	15.8*		0.8	<0.1	0.9	0.7
<i>Cyclobalanopsis gracilis</i>	NTem	<0.1					1.1						
<i>Litsea coreana</i> var. <i>sinensis</i>	TrAs,TrAm,dis			1.2	<0.1	<0.1			0.1				
<i>Cyclobalanopsis myrsinifolia</i>	NTem	0.1	8.4*	<0.1	0.6	<0.1	0.1		<0.1				
Evergreen Broad-leaved Shrub													
<i>Daphniphyllum macropodum</i>	TrAs to Tr Af	7.6	1.8		0.2	0.4	5.9			0.4			0.5
<i>Elaeagnus pungens</i>	NTem		<0.1		<0.1		<0.1	0.4					
<i>Orixa japonica</i>	EAs				0.1		<0.1						
<i>Eurya hebeclados</i>	TrAs,TrAm,dis								0.1				
<i>Pittosporum illicioides</i>	Old World Tr												0.2

Note: RBA-relative percent of basal area. Dominant species of each stands are indicated by an asterisk. E-East, N-North, S-South, As-Asia, Tem-Temperate, Cos-Cosmpolitan, Aus-Australasia, Tr-Tropic, Am-America, Med-Mediterranea, dis-disjuncted (Wu, 1991). Dominant species are indicted by an asterisk