SPECIAL FEATURE   Interspecific segregation and attraction in forest birds

Prey distribution and foraging preference for tits

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Abstract   We examined the abundance and distribution of prey in four different height strata and eight tree species in a temperate forest, and analyzed the influence on foraging preference by three breeding tit (*Parus*) species. Densities of arthropod prey for tits in canopy foliage varied with tree species but not with height. Most of them were Lepidoptera larvae. Also, interspecific differences in choice of foraging substrate were found between tree species but not in height. These results demonstrate that tree species composition is a more important habitat factor than foliage height profile for coexistence of different tit species in forests. We examined four different measures of prey abundance to find how tits chose tree species. The largest species, the Great Tit *P. major*, preferred the tree species with high total biomass, and the intermediate-sized Willow Tit *P. montanus* preferred those with high density per leaf area. Concentrated searching for prey on a few tree species with high total biomass may be a useful strategy for inflexible perch-gleaners such as *P. major*, and finer-scale searching on each leaf may be more practical for agile foragers such as *P. montanus* which often hang-glean to reach less accessible food. In spite of these differences, both species gained benefits from choosing the tree species on which they foraged most efficiently. In contrast, the smallest species, the Coal Tit *P. ater*, frequently foraged on food-poor tree species. Of the three tit species, *P. ater* was the most generalized forager, using diverse techniques on a variety of tree species and specializing at capturing small prey quickly. These foraging patterns may make it possible for the smallest species to coexist with the other tit species.

Key words   Foraging efficiency, Foraging technique, *Parus*, Prey distribution, Tree species preference

As habitat factors determining bird species diversity in forests, some researchers have emphasized the importance of vertical foliage distribution (MacArthur & MacArthur 1961; Recher 1969) and others have emphasized tree species composition (Rice et al. 1984; Verner & Larson 1989). Either of these factors could help different species co-exist in different forests, and it remains unclear whether one or both factors provides a general mechanism for coexistence. Holmes et al. (1979) proposed a hypothesis that tree species composition determines bird species diversity within guilds, the presence and size of which are determined by foliage height distribution. Hino (1985) supported this idea in part by a correlation analysis between habitat variables and bird communities in shelterbelts of Hokkaido, but we need to know how bird species partition height strata and tree species based on food availability in forests.

Many studies have shown the different use of height strata and/or tree species among insectivorous bird species within the same guild (Hartley 1953; MacArthur 1958; Morse 1970; Lack 1971; Alatalo 1982; Hino 1998). Few studies, however, have examined prey abundance and distribution although the need for such studies has been recognized for many years (Wiens 1984; Morrison et al. 1990). Holmes and his colleagues demonstrated that foraging by birds on three different tree species was influenced by the prey abundance on and foliage structure of each tree species and the species-specific ability of the

birds (Holmes & Robinson 1981; Holmes & Schultz 1988). Their conclusion was somewhat speculative, however, because they examined only three species of trees. Moreover, the prey distributions and their effects on bird foraging at different height strata have never been studied in forest habitats.

In this paper, we examine the abundance and distribution of prey in four different height strata and eight tree species in a temperate forest, and analyze the influence on foraging preference by three breeding tit (*Parus*) species. We then reveal interspecific differences in the degree to which prey abundance determines foraging preference, and relate it to searching-pattern constraints on foraging techniques of each species.

METHODS

1) Vegetation

This study was conducted in the Nakagawa Experimental Forest of Hokkaido University, northern Hokkaido, Japan (44°49′N, 142°16′E). A 6-ha study plot (200 m×300 m) was established along the mountain ridge (c. 350 m in altitude). This plot largely consists of deciduous broad-leaved trees dominated by *Quercus mongolica* and *Betula ermanii* with <10% of conifers *Picea jezoensis* and *Abies sachalinensis* (Appendix). Canopy height is 15–20 m. The understory is dominated by high density of two bamboo species *Sasa kurilensis* and *Sasa senanensis* 1.0–1.5 m in height.

Vegetation was surveyed in the study plot in July 1990. Species, numbers of individuals and DBH (diameter at breast height) were recorded for all trees > 5 cm in DBH. The relative importance value (IV) of each tree species was calculated as the percentage of basal area (the sum of cross sectional areas of trunks determined from DBH), which is closely correlated with leaf surface area (Holmes & Robinson 1981). To determine the foliage distribution (in percentage cover) at five different height strata (0–3.6 m, 3.6–7.2 m, 7.2–10.8 m, 10.8–14.4 m, 14.4 m+), four categories of foliage volume (0: none, 1: 1–33%, 2: 34–66%, 3: 67–100%) were recorded by eye at 459 points, averaged and multiplied by 30% for each stratum.

2) Insect distribution

All arthropods, most of which were Lepidoptera larvae (97.6% in dry weight), were collected and counted from 300 leaves per unit, and their body lengths were measured in the laboratory. The dry weight (W, mg: 60°C, 48 h) of an arthropod was estimated from the body length (L, mm) with the following equation: $W=0.033L^{2.52}$ (r=0.92, P<0.001, N=180). This equation was determined with a part of the samples (W, mg). For statistical analyses, the dry weights were transformed to $\ln(W+0.5)$ to reduce skewness.

The abundance of arthropods in the canopy foliage at different height strata was examined in June 1990. We collected samples directly from a nine-storied tower (14.4 m high and 10 m square) built of steel pipes near the study plot. This tower gave access to six trees of *Quercus mongolica* and seven of *Betula ermanii*, which were two dominant species. We chose two units randomly for arthropods sampling from each tree species at each story in June. The unit samples from both species were combined and averaged for each of the same height strata as foliage distribution except the 0–3.6 m stratum for which no foliage was accessible. The expected percentage of prey biomass at each height stratum was calculated based on the average dry weight multiplied by the foliage volume to compare with the foraging height use by birds.

The abundance of arthropods in the canopy foliage of different tree species was examined in June 1991. We collected samples from the branches 1–3 m in height with a clipping method. The tree species examined were the eight species >2% in IV (Appendix): *Quercus mongolica*, *Betula ermanii*, *Kalopanax pictus*, *Picea jezoensis*, *Abies sachalinensis*, *Tilia japonica*, *Acer mono* and *Phellodendron amurense*. We used four different measures of arthropod abundance as determinants of tree species selection by birds because the tree density and the leaf area varied among tree species. The two indices of density were the average dry weight (mg) per 100 leaves (D_a) and per 1 m²–leaf area (D_b), and the two indices of total biomass in the study site were $D_a \times IV$ (T_a) and $D_b \times IV$ (T_b), respectively. To calculate D_b, we collected 25 leaves randomly from three trees of each species and measured their areas with a digitizer. We treated one shoot with a node for two conifer species and one leaflet for *Phellodendron amurense* with compound leaves as one piece of leaf.

3) Bird foraging

Observations were made in the morning (0600–1100 hours) and in the afternoon (1400–1700 hours) in June and July 1990 and in June 1991. The target

species were three breeding tit species, Great Tit *Parus major*, Willow Tit *P. montanus* and Coal Tit *P. ater*, the densities of which were 21.7, 34.8 and 43.5 pairs/100 ha, respectively (Hino & Nakano 1992). Body size was largest in *P. major*, medium in *P. montanus* and smallest in *P. ater* (14.1 g, 10.7 g, 8.5 g in Nakamura 1978). Each time a bird was observed foraging for prey (including active searching), we recorded the height and tree species, and the prey length estimated in 5 mm intervals using beak size as a standard. We also differentiated between three types of feeding technique (perch-gleaning, hang-gleaning or sally-hovering; Remsen & Robinson 1990). To avoid bias from repeated observations of the same individuals, we collected data from individuals in different territories in the study area. In 1991, foraging time (searching and handling) was timed for each tree species. Foraging efficiency (mg/min) was calculated as a total dry weight of prey (estimated by body length) divided by the total foraging time for each tree species. Foraging rate was also calculated as the number of prey capured per minute.

Tree species preference was calculated with ln (r_i/p_i), where r_i was the proportion used by birds and p_i was the IV/100 for each tree species i. For the diversity of the tree species and feeding technique used by birds, we used the Simpson's diversity index: $1/\Sigma p_i^2$, where pi was the proportion of a category i. Correlation analyses were conducted to reveal which indices of food abundance on different tree species were related to the preferences and the foraging efficiencies by each tit species. We considered $P<0.1$ as significance level owing to small sample sizes (5–6).

Bird classification followed the Ornithological Society of Japan (2000)

RESULTS

1) Foraging height

In *Quercus mongolica* and *Betula ermanii* in 1990, the average dry weight of arthropods per 100 leaves was 32.2 mg ($\pm$28.6 SD, N=14) in the canopy foliage >3.6 m in height. The dry weights did not differ significantly among four height strata ($F_{3,24}=0.72$, P=0.55), nor in comparisons between pairs of different strata (F-test with Bonferroni correction, P>0.20, Table 1). The foliage volume varied from 38% to 58% in percentage cover among height strata. The estimated biomass of prey was least in the top stratum (14.4 m+) and greatest in the stratum immediately below (10.8–14.4 m), with a threefold difference between the two values (Table 1). χ^2-analyses revealed that the tit species all foraged made use of each stratum in proportion to the distribution of prey biomass in the study site, with no significant difference between species ($\chi^2=15.1$, df=8, P>0.05).

2) Foraging tree species

In 1991, the average dry weights of arthropods per 100 leaves (D_a) varied greatly among tree species from the lowest in *Picea jezoensis* through the highest in *Kalopanax pictus* (Table 2). However, the orders of each species changed when we used different indices of prey abundance. In terms of dry weight per 1 m^2 (D_b), the highest values were obtained for *Betula ermanii* and then *Tilia japonica*, with large-leafed,

Table 1. Prey abundance and foraging uses by tits at each height stratum

Height category (m)	Foliage (%)	Caterpiller biomass		Bird foraging use (%)		
		Dry weight per 100 leaves (mg)[1]	Expected biomass (%)[2]	*P. major*	*P. montanus*	*P. ater*
14.4–	38.6	22.0±13.9 (4)	14.1	6.3	13.1	25.0
10.8–14.4	58.1	43.7±44.0 (8)	42.1	37.5	33.8	32.4
7.2–10.8	55.8	25.1±15.5 (8)	23.2	29.2	26.2	19.4
3.6–7.2	38.1	32.8±18.3 (8)	20.7	27.1	22.8	17.6
0–3.6	57.2	–	–	0.0	4.1	5.6
No. of observations				48	145	108
χ^2-value (df=3)[3]				6.63	5.17	5.16

[1] Mean±SD (no. of sample size).

[2] Percentages based on (Dry weight per 100 leaves)×(Foliage %) in the height categories 2–5.

[3] Comparisons of bird foraging use to expected prey biomass in the height categories 2–5. Neither values were significant (P>0.05).

Table 2. Four indices of prey abundance on each tree species

Tree species	D_a: Dry weight per 100 Leaves (mg)	D_b: Dry weight per 1 m^2 (mg)	T_a: Total biomass $D_a \times IV^1$	T_b: Total biomass $D_b \times IV^1$
QM	27.7	36.9	977.5	1303.4
BE	99.0	293.0	3089.5	9140.6
KP	182.4	137.4	1312.9	989.4
PJ	2.8	10.3	13.2	49.3
AS	11.3	47.7	38.3	162.3
TJ	71.7	155.0	186.5	402.9
AM	29.3	53.9	61.5	113.1
PA	7.4	35.6	14.9	71.2

[1] Importance Values (%) in Appendix.

Table 3. Foraging uses and preferences of tits on each tree species

Tree species	P. major		P. montanus		P. ater	
	Use (%)	Preference	Use (%)	Preference	Use (%)	Preference
QM	28.0	0.26	15.1	−0.07	26.0	0.21
BE	50.0	0.74	50.0	0.74	28.0	0.33
KP	8.0	0.48	9.3	0.58	0.0	−0.69
PJ	2.0	−0.69	0.0	−0.69	18.0	1.45
AS	0.0	−0.69	8.1	1.06	10.0	1.24
TJ+AM+PA	6.0	0.35	11.6	0.80	12.0	0.83
No. of observations	50		86		50	
Simpson's diversity	2.94		3.36		5.15	

Kalopanax pictus (Appendix) falling to third place. Indices of total biomass (T_a and T_b), as expected, were high in the two dominant species, *Betula ermanii* and *Quercus mongolica* (>30% in IV, Appendix).

Tree species preferences for foraging differed among tit species (Table 3). *P. major* foraged on the lowest diversity of tree species, preferring *Betula ermanii* and avoiding conifers. *P. montanus* showed opposing preferences for each of the two coniferous species, preferring *Abies sachalinensis* and avoiding *Picea jezoensis*. *P. montanus* also made preferential use of deciduous species except *Quercus mongolica*. *P. ater* foraged on the greatest diversity of tree species, but showed special preferences for each of the two coniferous species and avoided *Kalopanax pictus*. Foraging efficiencies on each tree species also differed among the tit species (Table 4). *P. major* captured prey on *Betula ermanii* and *Quercus mongolica* most effectively. *P. montanus* did so on *Betula ermanii* and *Kalopanax pictus*, and *P. ater* on *Acer mono*.

Correlation analyses were conducted to reveal which indices of food abundance on different tree species (Table 2) were related to the preferences (Table 3) and foraging efficiencies (Table 4) of each tit species (Table 5). *P. major* foraged preferentially on the tree species with high total biomass in the study site (T_a and T_b). *P. montanus* foraged preferentially on tree species with high dry weight per leaf area (D_b). In both species, the indices of prey abundance for the tree species where they foraged most efficiently were consistent with those they preferred, although this relationship was not significant (Table 5). On the other hand, *P. ater* did not show positive relationships with any of the indices, but tended to avoid foraging on the tree species with high values of D_a and T_a (Table 5).

3) Foraging technique

P. major was a specialized perch-gleaner, *P. montanus* foraged most frequently by hang-gleaning, and *P. ater* used both perch- and hang-gleaning with the same frequency. The diversity of foraging techniques

Table 4. Foraging efficiencies of tits on each tree species

Tree species	P. major		P. montanus		P. ater	
	Efficiency (mg/min)	Time (sec)	Efficiency (mg/min)	Time (sec)	Efficiency (mg/min)	Time (sec)
QM	28.6	457	5.5	384	14.4	672
BE	34.9	1185	46.4	1241	12.0	748
KP	21.9	83	44.3	265	–	–
PJ	0.0	36	–	–	4.9	253
AS	–	–	21.9	219	5.9	97
TJ+AM+PA	5.0	201	36.1	409	49.2	162
All species	28.9	2018	34.7	2631	14.8	1932

Table 5. Results of correlation analyses between foraging preferences (Table 3) or efficiencies of tits (Table 4), and four indices of caterpiller abundance on each tree species (Table 2)

	N	D_a	D_b	T_a	T_b	Preference
Preference						
P. major	6	NS	NS	+	(+)	
P. montanus	6	NS	(+)	NS	NS	
P. ater	6	–	NS	–	NS	
Efficiency						
P. major	5	(+)	NS	+	+	(+)
P. montanus	5	NS	(+)	NS	NS	NS
P. ater	5	NS	NS	NS	NS	NS

Positive correlation: $+P<0.05$, $(+)$ $0.05<P<0.1$; Negative correlation: $-P<0.05$; NS: $P>0.1$.
N: sample size.

Table 6. Foraging techniques of tits

Foraging technique	P. major	P. montanus	P. ater
Perch-gleaning	85.4	23.3	41.9
Hang-gleaning	2.4	58.3	40.0
Sally-hovering	12.2	18.3	18.1
Number of observations	41	120	105
Simpson's diversity	1.34	2.33	2.71

was highest in *P. ater* and lowest in *P. major* (Table 6).

In total, foraging efficiency was high in *P. montanus* and *P. major*, and low in *P. ater* (Table 4). This difference was related to prey size captured by each tit species: *P. ater* caught significantly smaller prey (9.0 mg±20.4 SD, N=53) than *P. montanus* (23.8 mg±35.4 SD, N=64, U-test with Bonferroni's correction: z=−3.21, P<0.05) or *P. major* (27.8 mg± 40.8 SD, N=35, z=−2.62, P<0.005). On the con-

trary, foraging rate was highest in *P. ater* (1.65), the second in *P. montanus* (1.46) and lowest in *P. major* (1.04). The species with the most diverse technique took prey at the fastest rate (r=0.99, P<0.05, N=3).

DISCUSSION

During the breeding season, densities of arthropod prey for tits varied with tree species but not with height. The three tit species showed interspecific differences in their use of tree species but not in use of height. These quantitative results demonstrate that tree species composition is a more important habitat factor than foliage height profile for coexistence of different tit species in forests. Similar results were found by Holmes et al. (1979) in North American forests and by Hino (1985) in northern Japanese shelterbelts. These studies show that tree species composition determines bird species diversity within guilds, though abundance may be affected further by foliage height distribution.

Our results suggest that each tit species responded to a different measure of prey abundance in selecting tree species for foraging. The largest species, *P. major* preferred the tree species with high total biomass in a forest, and the intermediate-sized, *P. montanus* preferred those species with high average density per leaf area. This interspecific difference may be related to their searching patterns associated with foraging technique. *P. major* was a specialized perch-gleaner taking prey mainly from the upper surface of leaves, as reported in other studies (Morse 1978; Hino 1993). *P. montanus* hang-gleaned more frequently but also foraged by perch-gleaning and sally-hovering. Since most of caterpillars are found on undersides of leaves (Greenberg & Gradwohl 1980; Holmes & Schultz 1988), hang-gleaning would be a

more effective (but energy-expensive) technique for birds to access them. Thus, *P. montanus* are expected to forage on different tree species more flexibly than *P. major* while searching for prey from tree to tree, as indicated by using more diverse species of trees and fine-scale searching on each leaf. On the other hand, concentrated searching for prey on a small number of tree species with high total biomass may be useful for less flexible perch-gleaners like *P. major* because prey accessibility is constrained (Holmes & Robinson 1981; Holmes & Schultz 1988). In spite of these differences, both species gained benefits from choosing the tree species where they foraged most efficiently (as reported by Partridge 1976a, b).

In contrast, the smallest species, *P. ater* often used food-poor tree species. We can suggest two possible reasons to explain this observation. One possibility is that interference competition from the larger species may deny *P. ater* access to the most profitable foraging sites. Many studies have shown that *P. ater* are forced to food-poor substrates in the presence of the other tit species (Alatalo et al. 1985; Alatalo & Moreno 1987; Suhonen et al. 1993; Fyhn & Sorensen 1997). These studies all were conducted in winter when interspecific competition was severe owing to scarcity of food resources. Our study indicates that interspecific competition may also play an important role for foraging-site selection by tits during the breeding season. The other possibility is that *P. ater* with a morphology adapted to conifers (Partridge 1976b), may forage on *Picea jezoensis* and *Abies sachalinensis* frequently regardless of prey abundance. This could be partly true but *P. ater* was neither a specialized nor an efficient forager on conifers. Goldcrests *Regulus regulus*, which also bred in low density in the study site (4.3 pairs/km^2, Hino & Nakano 1992), are known as specialized foragers in conifers (Nakamura 1980). This species foraged on coniferous trees much more frequently (83% in 1990, 55% in 1991) and more efficiently (20.4 mg/min) than *P. ater*, with more frequent sally-hovering (56%) (Hino et al. unpubl. data). Of the three tit species, *P. ater* was the most generalized forager. This species took prey from a variety of tree species with diverse foraging techniques: by perch-gleaning like *P. major*, hang-gleaning like *P. montanus* and sally-hovering like *Regulus regulus*. Instead of low foraging efficiency, *P. ater* captured small prey with high speed. This flexible foraging pattern may make it possible for this smallest tit species to coexist with the other tit species.

REFERENCES

Alatalo RV (1982) Multidimensional foraging niche organization of foliage-gleaning birds in northern Finland. Ornis Scand 13: 56–71.

Alatalo RV & Moreno J (1987) Body size, interspecific interactions, and use of foraging sites in tits (Paridae). Ecology 68: 1773–1777.

Alatalo RV, Gustafsson L, Linden M & Lundberg A (1985) Interspecific competition and niche shifts in tits and the goldcrest: an experiment. J Anim Ecol 54: 977–984.

Fyhn M & Sorensen L (1997) Niche shifts of coal tits *Parus ater* in Denmark. J Avian Biol 28: 68–72.

Greenberg R & Gradwohl J (1980) Leaf surface specialization of birds and arthropods in Panamanian forest. Oecologia 46: 115–124.

Hartley PHT (1953) An ecological study of the feeding habits of the English titmice. J Anim Ecol 22: 261–288.

Hino T (1985) Relationships between bird community and habitat structure in shelterbelts of Hokkaido, Japan. Oecologia 65: 442–448.

Hino T (1993) Interindividual differences in behaviour and organization of avian mixed-species flocks. In: Kawanabe H, Cohen JE & Iwasaki K (eds), *Mutualism and community organization*. pp 87–94. Oxford University Press, Oxford.

Hino T (1998) Mutualistic and commensal organization of avian mixed-species flocks in a forest of western Madagascar. J Avian Biol 29: 17–24.

Hino T & Nakano S (1992) Breeding bird community of a deciduous broad-leaved forests in northern Hokkaido, Japan. Res Bull Hokkaido Univ For 49: 195–200 (in Japanese with English summary).

Holmes RT, Bonney RE Jr & Pacala SW (1979) Guild structure of the Hubbard Brook bird community: a multivariate approach. Ecology 60: 512–520.

Holmes RT & Robinson SK (1981) Tree species preferences of foraging insectivorous birds in a northern

hardwoods forest. Oecologia 48: 31–35.

Holmes RT & Schultz JC (1988) Food availability for forest birds: effects of prey distribution and abundance on bird foraging. Can J Zool 66: 720–728.

Lack D (1971) *Ecological isolation in birds*. Blackwell Scientific Publications, Oxford.

MacArthur RH (1958) Population ecology of some warblers of northeastern coniferous forest. Ecology 39: 599–619.

MacArthur RH & MacArthur J (1961) On bird species diversity. Ecology 42: 594–598.

Morrison ML, Ralph CJ, Verner J & Jehl JR Jr (1990) *Avian Foraging: theory, morphology, and applications*. Allen Press, Lawrence.

Morse DH (1970) Ecological aspects of some mixed-species foraging flocks of birds. Ecol Monogr 40: 119–168.

Morse DH (1978) Structure and foraging patterns of flocks of tits and associated species in an English woodland during the winter. Ibis 120: 298–312.

Nakamura T (1978) A study of Paridae community in Japan IV: Ecological segregation of species by the difference of use of bill in space and technique. Misc Rept Yamashina Inst Ornithol 10: 94–118 (in Japanese with English summary).

Nakamura T (1980) Ecological separation and adaptive space of warbler guild inhabiting the coniferous forest in Shiga Heights. Bull Inst Nature Edc Shiga Heights 19: 45–59.

Partridge L (1976a) Individual differences in feeding efficiencies and feeding preferences of captive Great Tits. Anim Behav 24: 230–240.

Partridge L (1976b) Field and laboratory observations on the foraging and feeding techniques of blue tits (*Parus caeruleus*) and coal tits (*P. ater*) in relation to their habitats. Anim Behav 24: 534–544.

Recher HF (1969) Bird species diversity and habitat diversity in Australia and North America. Am Nat 103: 75–80.

Remsen JV Jr & Robinson SK (1990) A classification scheme for foraging behavior of birds in terrestrial habitats. In: Morrison ML, Ralph CJ, Verner J & Jehl JR Jr (eds) *Avian Foraging: theory, morphology, and applications*. pp 144–160. Allen Press, Lawrence.

Rice J, Anderson BW & Ohmart RD (1984) Comparison of the importance of different habitat attributes to avian community organization. J Wildl Manag 48: 895–911.

Suhonen J, Halonen M & Mappes T (1993) Predation risk and the organization of the *Parus* guild. Oikos 66: 94–100.

The Ornithological Society of Japan (2000) *Check-list of Japanese birds: 6 ed*. OSJ, Obihiro.

Verner J & Larson TA (1989) Richness of breeding bird species in mixed-conifer forests of Sierra Nevada, California. Auk 106: 447–463.

Wiens JA (1984) Resource systems, populations, and communities. In: Price PW, Slobodchikoff CN & Gaud WS (eds) *A new ecology*. pp 397–436. John Wiley Sons, New York.

Appendix Average leaf area ($\pm$SD, N$=$25) and importance value (IV) of each tree species

Code	Tree species	Leaf area (cm^2)	Importance value (%)
QM	*Quercus mongolica*	75.0±49.5	35.3
BE	*Betula ermanii*	33.8±12.1	31.2
KP	*Kalopanax pictus*	132.7±106.1	7.2
PJ	*Picea jezoensis*	26.8±12.3	4.8
AS	*Abies sachalinensis*	23.6±15.9	3.4
TJ	*Tilia japonica*	49.3±19.7	2.6
AM	*Acer mono*	54.4±26.4	2.1
PA	*Phellodendron amurens*	20.9±14.1	2.0