ORIGINAL ARTICLE

Effects of host tree size on the species richness and abundance of epiphyte assemblages in a Bornean lowland tropical forest

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ABSTRACT This study clarified the effects of host tree size on the numbers of epiphyte species and individuals on a tree, based on observation of 122 species and 2,162 individuals of epiphytes on 430 target trees in a Bornean primary lowland dipterocarp forest. We analyzed relationships of the diameter at breast height (DBH) of target host trees with the probability of epiphyte presence, number of epiphyte species on each target tree (species richness), number of epiphyte individuals on each target host tree (abundance), and cumulative number of epiphyte species. The probability of epiphyte presence was estimated by a generalized linear model (GLM) with a logistic distribution to be higher than 50% on trees with DBH > 40 cm. A GLM with a quasi-Poisson distribution showed that both species richness and epiphyte abundance increased exponentially with DBH. The most rapid increase was found for trees with DBH > 40 cm. Also, about half of all epiphyte species recorded in this study were only found on trees with DBH > 60 cm. These results suggest that in lowland tropical rainforests in the Southeast Asian tropics, large trees play an important role in maintaining the species diversity of epiphyte assemblages by providing them with habitats. Meanwhile, several epiphyte species were found only on trees with DBH ≤ 40 cm, suggesting that the small trees also provide essential habitats with such epiphyte species. Primary forests with various sizes of trees are necessary for conservation of the epiphyte assemblages.

Key words: forest canopy, Lambir Hills National Park, Southeast Asian tropics, spatial distribution, tropical rainforest

INTRODUCTION Vascular epiphytes (referred to as ‘epiphytes’ in this paper) are non-parasitic vascular plants that grow mainly on woody plants (Benzing 1990). Epiphytes comprise approximately 28,000 species and account for nearly 10% of the total number of vascular plant species in the world (Zotz 2013). They contribute greatly to local plant diversity, especially in humid tropical rainforest areas (Benzing 1990, Zotz 2016), sometimes exceeding 50% of the total number of plant species in a forest (Kelly et al. 1994). Epiphytes are especially abundant in forest canopies (Benzing 1990), and epiphyte assemblages are thus considered to play important roles in ecosystem functions therein, such as provision of essential habitats and food to arboreal organisms (Nadkarni and Matelson 1989, Ellwood and Foster 2004), and regulation of water and nutrition cycling in arboreal environments (Nadkarni et al. 2004).

To better understand the diversity and ecosystem functions of epiphyte assemblages, it is necessary to determine the environmental factors that affect the species richness and abundance of these assemblages, and to elucidate how these factors affect the within-forest spatial distributions of each epiphyte species. Tree size variation in a forest is considered to be among those factors because larger host trees provide epiphytes with a larger area suitable for their settling sites, with larger surface areas, more relatively flat areas at branch junctions (Taylor and Burns 2015, Woods et al. 2015, Wagner and Zotz 2020), and settling sites that are available for longer periods (Flores-Palacios and Garcia-Franco 2006).

The number of epiphyte species on a tree has been
shown to increase as tree size increases (Flores-Palacios and García-Franco 2006, Poltz and Zotz 2011, Wang et al. 2016), and the number of epiphyte individuals on a tree also has been shown to increase with tree size (Poltz and Zotz 2011, Wagner and Zotz 2020). The effects of tree size on epiphyte assemblages likely differs among forests at different sites because of variations in ecological and environmental conditions. For instance, Poltz and Zotz (2011) detected a linear relationship between the number of epiphyte individuals on a tree and tree size in a Neotropical lowland forest, whereas Wagner and Zotz (2020) found a non-linear relationship between these variables in another Neotropical lowland forest. However, at this time, the number of studies on such relationships is insufficient to identify clear patterns in these between-site variations. Hence, these relationships must be investigated in forests with different environmental conditions to accumulate information about between-site variations.

The abovementioned studies were conducted in the Neotropics (Flores-Palacios and García-Franco 2006, Poltz and Zotz 2011) and a montane forest in the Southeast Asian tropics (Wang et al. 2016). However, to our knowledge, no study has attempted to examine the effects of tree size on the species richness and abundance of epiphyte assemblages in lowland forests in the Southeast Asian tropics, where the species richness of epiphyte assemblages has been suggested to be notably high (Komada et al. 2020).

In the present study, we aimed to determine the effects of host tree size on epiphyte species richness and abundance on trees in a lowland forest in the Southeast Asian tropics. To achieve this, we conducted a census of all epiphyte individuals on 430 trees and then analyzed the relationship between the number of epiphyte species on a tree and the diameter at breast height (DBH) of host tree, and between the number of epiphyte individuals on a tree and DBH of host tree.

MATERIALS AND METHODS

Study site

All field surveys were conducted at Lambir Hills National Park (LHNP), Sarawak, Malaysia, located in the northwestern part of Borneo Island (4° 12’ N, 114° 02’ E, 150–458 m asl). The mean annual precipitation is approximately 2,600 mm (Kume et al. 2011) and the mean annual temperature is 27.0 °C at Miri Airport, which is located approximately 16 km northwest of LHNP (Kumagai 2005). Most of the area of LHNP is covered with primary lowland dipterocarp forests. The canopy height is approximately 50 m, and a fraction of emergent trees reach 70 m above the ground (Ashton 2005). The forest has a few building structures, including a canopy crane (rising 90 m above ground level) and several canopy towers (rising 30–60 m above ground level), constructed for ecological research and long-term biodiversity monitoring (Yumoto and Nakashizuka 2005). So far, 183 species of epiphytes have been found to occur at LHNP (Komada et al. 2020).

Field survey

We conducted a field census on epiphytes from August 2016 to September 2019, including 430 tree individuals belonging to >200 species growing in the primary lowland dipterocarp forests in LHNP. For the census, we selected 430 trees on which epiphytes were detectable from among trees in the study site that were 1.0 cm ≤ DBH ≤ 156.4 cm, as measured within 1 year before the census. Of the 430 trees, 98 were emergent trees or trees forming the uppermost layer of the forest canopy and DBHs of some of those trees reached the highest level of those observed in the forest. The remaining 332 trees did not reach the uppermost layer of the forest canopy, but formed the lower layers of the canopy or shrub layer; their crowns developed under the crowns of more than two other trees. After selecting the target trees, we measured their heights using a razor rangefinder (TruPulse 360; Laser Technology, Inc.) for trees ≥ 5 m tall and a surveying pole for trees < 5 m tall.

For the census, we used ropework and occasionally climbed the building structures to reach the core parts of the tree crown of the 98 taller trees, to observe all epiphytes on the trees. We were able to observe almost all epiphyte individuals on the 332 shorter trees from the ground. We checked all epiphyte individuals on each target tree using binoculars and then recorded the number of individuals of each epiphyte species, drawing sketches and taking photographs that captured the entire tree crown and its branching pattern. We also drew sketches and took photographs focusing on each epiphyte individual and noted its within-tree location. In the case of some rhizomatous species, it was difficult to distinguish one epiphyte individual from another, so we applied the methods of Sanford (1968) regarded a group of rhizomes that clearly separated from another as one individual for estimating the approximate number of individuals for such species. Every epiphyte individual whose stem length was less than 5% of the maximum stem length of the epiphyte species was excluded from all analyses, as well as every
hemiepiphytic individual whose root reached the ground.

We identified all recorded epiphyte individuals by referring to our previous inventory (Komada et al. 2020). Epiphytes to be classified into Asplenium nidus L. complex were treated as a single species because species-level identification in the field was not feasible.

**Statistical analysis**

Because there was a strong positive correlation between DBH and tree height (Fig. 1), DBH was considered a good indicator of tree size in this study.

To elucidate the relationship between epiphyte occurrence frequency and tree size, we performed generalized linear model (GLM) analysis with a logistic distribution, using binary data (absence or presence of epiphyte individuals on a tree) as the response variable and the log-transformed DBH value as the explanatory variable. We analyzed the association of the increasing cumulative number of epiphyte species with increased DBH by plotting the epiphyte species found on all trees with a DBH equal to or less than a given value.

To elucidate the relationship between the number of epiphyte species on a tree and tree size, we used GLMs with a quasi-Poisson distribution and log-link function, where the number of epiphyte species on each target tree was the response variable and the log-transformed value of the DBH was the explanatory variable.

To elucidate the relationship between the number of epiphyte individuals on a tree and tree size, we used the same GLMs, where the number of individuals of all epiphyte species on each target tree was the response variable and the log-transformed value of the DBH was the explanatory variable.

We calculated McFadden pseudo $R^2$ (McFadden 1974) for each GLM as a measure of goodness of fit. All analyses were performed using R software (version 4.0.5; R Core Team, 2021).

**RESULTS**

Approximately 20% (86 ind.) of the 430 target trees hosted at least one epiphyte individual, representing 2,162 individuals of 122 species in total; the remaining 80% (344 ind.) of trees hosted no epiphytes. A species list with taxonomic names is shown in Table S1.

The epiphyte presence probability significantly increased with an increase in the log-transformed DBH ($p<0.001$). The regression line indicated that the probability increased non-linearly and exceeded 50% as the DBH reached 42.6 cm (Fig. 2).

The number of epiphyte species on each target tree significantly increased with increases in the log-transformed value of DBH ($p<0.001$). The regression line showed a notably rapid increase in the number of species as DBH reached approximately 40 cm, followed by an exponential increase without saturation even as the DBH reached the maximum value (Fig. 3). Among trees with DBH ≤ 40 cm, those hosting ≥3 epiphyte species accounted for 0.3% and the mean number of epiphyte species was 0.1, whereas among trees with DBH > 40 cm, the percentage was 42% and the mean number of epiphyte species was 4.6 (Fig. 3).

Similarly, the number of individuals of all epiphyte species on each target tree significantly increased with the increase in log-transformed DBH ($p<0.001$). The regression line showed a notably rapid increase in the number of epiphyte individuals as the DBH exceed approximately 40 cm, followed by a non-linear and exponential increase without saturation even after the DBH exceeded 150 cm (Fig. 4). Among trees with DBH ≤ 40 cm, those hosting >10 epiphyte individuals accounted for 0.3% and the mean value of epiphyte individuals was 0.2, whereas among trees with DBH > 40 cm, trees hosting >10 epiphyte individuals accounted for 42%, the mean number of individuals was 22 and the number of epiphyte individuals rarely exceeded 150 (Fig. 4).
The cumulative number of species did not reach 23 (19% of the total number of species) until the DBH reached 40 cm; it increased approximately threefold when the DBH reached about 60 cm, accounting for 50% of the total number of epiphyte species (Fig. 5). Of all epiphyte species, 81% were found on trees with DBH \( \leq 40 \) cm (Fig. 5).

Among trees with DBH \( \leq 40 \) cm, 21 out of 340 trees (6%) hosted at least one epiphyte individual, and the total number of epiphyte species occurred on trees with DBH \( \leq 40 \) cm was 22. Of these, five epiphyte species, i.e., *Asplenium* sp., *Hoya lacunosa* Blume, *Hoya mitrata* Kerr, *Hydnophytum formicarum* Jack, and *Poikilospermum* sp., were recorded only on trees with DBH 7–22 cm. The numbers of individuals of those five species were one in *Asplenium* sp., *Hoya mitrata*, *Hydnophytum formicarum*, and *Poikilospermum* sp. and five in *Hoya lacunosa*, respectively.

**DISCUSSION**

Similar to the six previous studies on the effects of tree size on epiphyte species richness and/or epiphyte individuals on trees in a Neotropical montane forest (Flores-Palacios and Garcia-Francisco 2006), Neotropical lowland forests (Zotz and Schultz 2008, Poltz and Zotz 2011,
Wagner and Zotz (2020), and an Asian subtropical montane forest (Wang et al. 2016), our study detected positive correlations between epiphyte species richness and tree size, and between epiphyte abundance and tree size (Figs. 3 and 4). These results are consistent with the assumption that larger trees provide epiphytes with more spaces that would be suitable as settling sites, including spaces with larger surface areas and/or greater numbers of the relatively flat areas that develop at branch junctions (Taylor and Burns 2015, Woods et al. 2015, Wagner and Zotz 2020), and spaces that are available for a longer time (Flores-Palacios and García-Franco 2006). In addition, the larger trees provide epiphytes with a greater variety of microhabitats with good light intensity and water availability, enabling multiple epiphyte species with different habitat preferences to co-occur on a tree (Woods et al. 2015).

However, the effects of tree size on the two attributes addressed in this study seem to be considerably different from those documented in previous studies in terms of the linearity of the regression relationships. The present study suggests that the species richness of epiphyte assemblages increases exponentially with tree size, whereas earlier studies suggested that the attribute increased only in a linear fashion. Our results showed that trees with DBH ≤ 40 cm rarely hosted >3 species (0.3 %), and the mean number of epiphyte species was nearly zero, whereas among trees with DBH > 40 cm, due to a rapid non-linear increase, 42 % hosted >3 species, and the mean number of epiphyte species was 4.6. However, previous studies showed that even trees with DBH ≤ 20 cm frequently hosted >5 species, and that the species richness of epiphytes showed a continuous linear increase with increased DBH (Flores-Palacios and García-Franco 2006, Poltz and Zotz 2011, Wang et al. 2016). The difference was more remarkable for trees whose DBHs were close to the maximum values within their study site. As the regression lines indicate, the value of the attribute was not saturated even as the DBH approached the maximum. By contrast, Wang et al. (2016) showed that the values reached saturation when the DBH reached a maximum, and Flores-Palacios and García-Franco (2006) and Poltz and Zotz (2011) showed that the values displayed signs of saturation. The effects of tree sizes on the abundance of epiphyte assemblages in this study also seems to differ from those in previous studies, in terms of the linearity of the regression relationships. The current study suggests that the abundance of epiphyte assemblages increases exponentially as tree size increases, whereas the preceding studies suggested that this attribute did not necessarily increase in a non-linear fashion. One study suggested that epiphyte abundance showed a non-linear exponential increase (Wagner and Zotz 2020), consistent with our results, whereas another suggested that the increase was linear (Poltz and Zotz 2011). Our results showed that trees with DBH ≤ 40 cm rarely hosted >10 epiphyte individuals, and the mean number of epiphyte individuals was nearly zero. Additionally, we showed that even after the rapid exponential increase around 40 cm DBH, the number of epiphyte individuals rarely exceeded 150. However, previous studies showed that trees with DBH < 40 cm frequently hosted >10 individuals, with some hosting >100 individuals. Furthermore, the number of epiphyte individuals frequently exceeded 300 and may have reached around 2,000 in trees whose DBHs were near the maximum (Poltz and Zotz 2011, Wagner and Zotz 2020).

These differences in findings imply that, in the lowland forests of the Southeast Asian tropics, characteristic relationships between epiphyte assemblages and tree size may exist. For instance, in the forests, it might be possible that degree of large host preference of epiphyte assemblages is higher than those in the other forests. In addition, the epiphyte assemblages in this forest might have higher degree of light dependency than those in the other forests. In this forest, all individuals of trees with number of epiphyte species >5 in our study site were emergent or upper canopy trees (Fig. S1). On such trees, most of epiphyte individuals inhabited relatively sunny crown parts.
(approximately more than 25 m above ground height), and epiphyte individuals inhabiting shaded trunk parts were quite a few (Authors pers. obs.). The number of studies in the Southeast Asian tropics, however, remains insufficient. Furthermore, studies that target a sufficiently large number of tree species co-occurring in a forest are also extremely limited. Thus, further investigation is needed to determine whether our results are consistent across the region, and whether the trends shown in prior studies persist for large numbers of tree species in each forest.

Although the reasons for the differences in linearity and saturability shown in this study remain to be determined, it seems that differences among study sites in tree species composition may differentially affect the epiphyte species richness on trees. The epiphyte species composition on a tree has been shown to differ by tree species (Callaway et al. 2002, Adhikari et al. 2012, Wagner and Zotz 2020), and is influenced by the different chemical traits of bark (Adhikari et al. 2012, Wagner et al. 2015) and branching architecture (Wagner et al. 2015) among tree species. In addition, Werner et al. (2012) suggested that epiphyte abundance on a tree is influenced by forest dynamics, stand structure, and the within-forest climate. Thus, it is plausible that one or more of these factors could modulate the effects of tree size on the species richness and abundance of epiphyte assemblages in our site and others. These questions need to be examined in future studies. Investigating the effects of host tree size on ontogeny of epiphytes may help a deeper understanding of the effects of host tree size on epiphyte assemblages and the among-site differences of the effects.

The line showing the cumulative number of epiphyte species according to increases in DBH indicates that nearly half of all observed epiphyte species were found to occur only on trees of >60-cm DBH. This suggests that thicker and taller host trees largely contribute to maintaining the species diversity of epiphyte assemblages in the study site. Such information about the cumulative increase in epiphyte species could aid the conservation of epiphyte assemblages not only in lowland forests in the Southeast Asian tropics, but also in forests in other regions. However, this relationship has yet to be sufficiently examined in many forests. The issue of how the frequency distribution of tree size in a forest affects species richness in the entire forest should be investigated at various sites to facilitate biodiversity conservation. The results show that among trees with DBH ≤ 40 cm, the percentage of individuals of trees with epiphytes is only 6%. In addition, the results showed that there are rare epiphyte species that specifically inhabit trees with DBH ≤ 40 cm, and all of those species were recorded with number of individuals five or less. This suggests that thinner and shorter trees are necessary as habitats of specific epiphyte species, and that such trees are also contributing to maintaining epiphyte species diversity in the study site. Therefore, it can be considered that preserving forests composed of various sizes of trees is essential for the conservation of the epiphyte assemblages in lowland forests in the Southeast Asian tropics.

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Effects of tree size on epiphytes in a Bornean forest

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APPENDICES

Table S1. List of 122 epiphyte species recorded from 430 target trees. *Schefflera littoralis* (Miq.) Harms. listed in Komada et al. (2020) is shown as *Heptapleurum littoralis* (Miq.) Harms. here, following the latest taxonomic concept of the genus (Lowry and Plunkett 2020).

| Taxonomic name | Taxonomic name |
|----------------|----------------|
| **LYCOPHYTA** | **Bulbophyllum sp. 1** |
| Huperziaceae | **Bulbophyllum sp. 2** |
| *Huperzia carinata* (Desv. ex Poir.) Trevis. | **Bulbophyllum sp. 3** |
| *Huperzia nummularifolia* (Blume) Jermy | **Bulbophyllum sp. 4** |
| *Huperzia phlegmaria* (L.) Rothm. | Coelogyne foerstermannii Rchb. f. |
| **PTERIDOPHYTA** | Coelogyne sp. |
| Aspleniacae | **Cymbidium finleysonianum** Wall. ex Lindl. |
| *Asplenium auriculatum* Sw. | **Dendrobium aloifolium** (Blume) Rehb. f. |
| *Asplenium nidus* Species Complex | **Dendrobium grootingsii** J. J. Sm. |
| *Asplenium sp.* | **Dendrobium leonis** Rchb. f. |
| **Davalliaceae** | **Dendrobium pinifolium** Ridl. |
| *Davallia denticulata* (Burm. f.) Mett. & Kuhn | **Dendrobium cf. hymenanthum** Rchb. f. |
| *Davallia repens* (L. f.) Diels. | **Dendrobium sp. 1** |
| **Lomariopsidaceae** | **Dendrobium sp. 2** |
| *Humata repens* (L. f.) Diels. | **Dendrobium sp. 3** |
| **Polypodiaceae** | **Dendrobium sp. 4** |
| *Aglomorpha speciosa* (Blume) M. C. Roos. | **Dendrobium sp. 5** |
| *Drynaria quercifolia* (L.) J. Sm. | **Dendrochilum sp.** |
| *Drynaria sparsisora* (Desv.) T. Moore. | **Diplocaulobium cf. brevicolle** (J. J. Sm.) Kraenzl. |
| *Goniophlebium percussum* (Cav.) W. H. Wagner & Grether | **Eria leiophylla** Lindl. |
| *Lecanopteris sinuosa* (Hook.) Copel. | **Eria pannea** Lindl. |
| *Lecanopteris sp.* | **Eria sp. 1** |
| **Lomariopsidaceae** | **Eria sp. 2** |
| *Lecanopteris sinuosa* (Hook.) Copel. | **Eria sp. 3** |
| **Lomariopsidaceae** | **Eria sp. 4** |
| *Lecanopteris sp.* | **Eria sp. 5** |
| **Lomariopsidaceae** | **Eria sp. 6** |
| *Lecanopteris sp.* | Liparis sp. |
| **Lomariopsidaceae** | **Luisia sp.** |
| *Lecanopteris sp.* | Phalaenopsis *cornu-cervi* (Hasselt ex Hassk.) Blume & Rchb. f. |
| **Pteridaceae** | Rhynchochilus *sp.* |
| *Haplopteris angustifolia* (Blume) E. H. Crane | **Thrisspermum sp.** |
| *Haplopteris ensiformis* Sw. | **Trichoschizys sp.** |
| **MONOCOTYLEDONEAE** | **Vanda sp. 1** |
| **Araceae** | **Vanda sp. 2** |
| *Amydrium medium* (Zoll. & Moritzi) Nicolson | Pandanaceae |
| *Scindapsus beccarii* Engl. | **Benstonea sp.** |
| *Scindapsus coriaceus* Engl. | Zingiberaceae |
| *Scindapsus cf. glaucescens* (Engl. & K. Krause) Alderw. | **Anomum roseissquamosum** Nagam. & S. Sakai |
| *Scindapsus sp.* 1 | EUDICOTYLEDONEAE |
| *Scindapsus sp.* 2 | Apocynaceae |
| **Orchidaceae** | Dischidia *cochleata* Blume |
| *Bromheadia cf. truncata* Seidenf. | **Dischidia hirsuta** (Blume) Decne. |
| *Bromheadia sp.* | **Dischidia major** (Vahl) Merr. |
| *Bulbophyllum auratum* (Lindl.) Ridl. | **Dischidia cf. nummularia** R. Br. |
| *Bulbophyllum limbatum* Lindl. | **Phalaenopsis cornu-cervi** (Hasselt ex Hassk.) Blume & Rchb. f. |
Table S1. Continued.

| Taxonomic name          | Taxonomic name                        |
|-------------------------|---------------------------------------|
| *Dischidia* sp. 1       | *Plethiandra tomentosa* G. Kadereit   |
| *Dischidia* sp. 2       | Moraceae                              |
| *Dischidia* sp. 3       | *Ficus aurantiaca* Miq.               |
| *Dischidia* sp. 4       | *Ficus binnendijkii* Miq. var. *latifolia* Corner |
| *Dischidia* sp. 5       | *Ficus deltoidea* Jack                |
| *Dischidia* sp. 6       | *Ficus dubia* Wall. ex King           |
| *Hoya lacunosa* Blume   | *Ficus kerkhovenii* Koord. & Valeton  |
| *Hoya miriata* Kerr     | *Ficus stricta* Miq.                  |
| *Hoya cf. finleysonii* Wight | *Ficus stupenda* Miq.               |
| *Hoya cf. mappigera* Rodda & Simonsson | *Ficus subgelderii* Corner     |
| *Hoya cf. sigillatis* T. Green | *Ficus xylophylla* Wall. ex Miq.       |
| *Hoya sp. 1*            | *Ficus* sp. 1                         |
| *Hoya sp. 2*            | *Ficus* sp. 2                         |
| *Hoya sp. 3*            | *Ficus* sp. 3                         |
| Araliaceae              | *Ficus* sp. 4                         |
| *Heptapleurum litorale* (Miq.) Boerl. | Oxalidaceae                              |
| Ericaceae               | *Daption racemosum* Korth.            |
| *Vaccinium* sp.         | Primulaceae                           |
| Gentianaceae            | *Embelia* cf. *coriacea* Wall. ex A. DC. |
| *Fagraea ceilanica* Thunb. | Rubiaceae                               |
| *Fagraea* sp.           | *Hydnophyllum formicarum* Jack        |
| Gesneriaceae            | *Psychotria* sp. 1                    |
| *Aeschynanthus* angustifolius* (Blume) Steud. | *Psychotria* sp. 2                   |
| Melastomataceae         | *Psychotria* sp. 3                    |
| *Pachycentria* constricta* Blume | Uricaceae                              |
| *Pachycentria* glauca* Triana | *Pokilospermum suaveolens* (Blume) Merr. |
| *Pachycentria* pulverulenta* (Jack) G. Clausing | *Pokilospermum* sp.                   |
| *Pachycentria* sp. 1    | Unidentified family                   |
| *Pachycentria* sp. 2    | unidentified eudicot sp.              |

Fig. S1. Relationships between DBH and epiphyte species richness on a tree. Each symbol indicates the forest stratum, where major part of crown of each target tree exists.