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The age of tropical rain-forest canopy species, Borneo ironwood (*Eusideroxylon zwageri*), determined by ^{14}C dating

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ABSTRACT: Using ^{14}C dating, the life span and growth rate of Borneo ironwood (*Eusideroxylon zwageri*, Lauraceae), which is a canopy tree species with extremely durable and decay-resistant wood distributed in tropical rain forests of South-East Asia, were studied. Timber segments collected from 15 logged stumps in Kubah National Park, Sarawak, Malaysia, were analysed by accelerator mass spectrometry and the obtained data were calibrated to determine the age of individuals. The ^{14}C dating turned out to be an effective method for estimating ages of long-lived trees, such as *E. zwageri*, in the aseasonal tropics because the estimated error was small compared with estimated age. We found that *E. zwageri* can live more than 1000 y and that the growth rate of this species was very slow, with a mean radial growth rate of 0·058 cm y^{-1}. The life span was much greater and the growth rate was much slower than those observed or estimated for trees of Dipterocarpaceae, the dominant family in this tropical forest. The long life span of this species may be caused by wood durability with a high specific gravity and abundant defensive compounds. Given equal carbon allocation, the high density and carbon-based defensive compounds may result in a reduced growth rate.

KEY WORDS: Borneo ironwood, ^{14}C dating, life history, long-lived tree, tree age, tropical rain forest

INTRODUCTION

A tree's life span provides critical information for understanding its life history strategy and population dynamics (Chambers *et al*. 1998). Also, it is an important parameter for estimating the regeneration cycle and turnover of forest ecosystems. In comparison with short-lived grasses or herbs, population growth rates of woody plants depend more heavily on the survival of adult individuals rather than fecundity or growth (Silvertown *et al*. 1993). In spite of the importance of tree life span for population dynamics, there are only a few such studies in tropical rain forests (Chambers *et al*. 1998, Clark & Clark 1992, Condit *et al*. 1995) unlike the case in temperate or boreal forests.

The age of temperate and boreal trees can be investigated by counting annual rings. In most cases, however, the trees in the humid tropics have no annual rings, or they have unclear and irregular rings because of the aseasonal climate. Tree age has been indirectly estimated in the tropics by extrapolating growth and mortality rates observed in permanent plots. This indirect method can result in large estimation errors because of the inherent variation in growth and mortality rates (Chambers *et al*. 1998, Mariaux 1981). Particularly for long-lived trees, the periods of direct observations are too short to estimate accurately the age of trees (Clark & Clark 1992, Condit *et al*. 1995).

The use of ^{14}C dating has helped researchers overcome this problem (Chambers *et al*. 1998, Stuiver *et al*. 1981). Stuiver *et al*. (1981) suggested that the most promising radio-isotope for growth rate determination in tropical trees is bomb-produced ^{14}C. There have been a few recent studies that determined growth rates of trees in tropical regions using this method (Mozeto *et al*. 1988, Worbes & Junk 1989). However, this bomb-produced ^{14}C method is applicable to wood increments only after the late 1950s because bomb-produced ^{14}C increased in the atmosphere by atomic-bomb tests that were conducted during the late 1950s and early 1960s (Stuiver *et al*. 1981).

For dating organic material before the 1950s, ^{14}C of natural origin is used for ^{14}C dating. As a part of a pioneer study to determine the age of older trees by this method, Chambers *et al*. (1998) revealed that some trees in an

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Amazonian rain forest were very old, with calibrated ages (± 80 y) ranging from 200 to 1400 y. However, other recent studies suggested that ^{14}C dating was inappropriate for applying to young samples because of large estimation errors (Ashton 1981, Stuiver *et al*. 1998, Worbes & Junk 1999). These studies demonstrated that there were long-lived trees in tropical rain forests and that ^{14}C dating was effective for determining ages of such trees that have particularly long life spans.

Borneo ironwood, *Eusideroxylon zwageri* Teijsm. & Binnend. (Lauraceae), is a canopy tree of tropical rain forests in some parts of South-East Asia. This species is known to have unique ecological characteristics such as high specific gravity and extremely hard timber, durable for decades or even a century (Whitten *et al*. 1984). These characteristics suggest that *E. zwageri* may have an extremely long life span, and thus ^{14}C dating could be applicable to determine the ages of *E. zwageri* individuals to help to elucidate its life history.

The aim of this study is to estimate the life span and long-term average growth rate of *E. zwageri* using the ^{14}C dating method in order to understand its life history strategy and population dynamics. In this study, two specific questions are addressed: (1) is ^{14}C dating effective for life span estimation of this species? (2) If so, how long is the life span and how fast is the growth rate of *E. zwageri*? The ecological implications of these results are also discussed.

STUDY SPECIES

Eusideroxylon zwageri (Lauraceae) is distributed in the tropical rain forests of eastern and southern Sumatra, Bangka, Belitung, Borneo and the Sulu archipelago and Palawan (the Philippines). It is a canopy tree reaching 50 m in height, with a maximum diameter at breast height (dbh) of 220 cm (Whitten *et al.* 1984). It is called ‘ironwood’ because the specific gravity of mature trees is 0.8–1.19 at 15% moisture content (Kostermans *et al.* 1994), and it sinks in water at the higher specific gravity. Its wood is very hard and durable; it can resist rotting for up to 40 y even under direct contact with soil, and up to a century in dry conditions. It is resistant against bark beetles (Whitten *et al*. 1984), termite attacks and wood-rotting fungi (Kostermans *et al.* 1994). Because of these unique characteristics, ironwood timber is economically valuable as construction material in this region. Trees of this species have been selectively logged in the forests of Sarawak, and logged stumps can be seen even in a well-preserved forest.

METHODS

Sampling of wood tissue

To obtain data on the age and growth rate of adult *E. zwageri,* we sampled wood tissues in the lowland dipterocarp forest of Kubah National Park (1°37′N, 110°09′E), Sarawak, Malaysia. From the logged stumps of *E. zwageri* we removed wood samples (about 1 cm^3). We chose stumps that were still alive with sprouting shoots (the shoot diameter ranged from 2 cm to 18 cm) instead of from individuals that had already died many years ago because harvest dates could not be determined. Most of the stumps had a heart-rot hole so the centre points of many stumps could not be located. In such cases, we defined the centre point as being the intersection between the maximum diameter and the longest perpendicular axis of it. We collected wood tissues from 15 individuals at the innermost part of the stumps and measured the distance from the edge and from the assumed centre point to the sampling point. Approximately 1 cm was removed from the top of the stumps to avoid contamination, and the tissues underneath were sampled. For eight individuals, we took two or three samples per stump at different distances from the edge of the stump to check the variability of the estimation. In total we analysed 26 samples.

Accelerator mass spectrometry (AMS) ^{14}C measurement

For accurate ^{14}C age determination by accelerator mass spectrometry (AMS), dried samples were transformed to graphite which delivers an intense, long-lasting ion beam. To prepare the graphite, samples were cut into thin fragments, and then soaked in a 1.2 N HCl (80 °C) solution for 2 h to eliminate carbonates. Subsequently, the samples were soaked in a 1.2 N NaOH (80 °C) solution for 2 h to remove humic acids. This process was repeated until impurities were removed. After final soaking in 1.2 N HCl (80 °C) for 2 h, samples were repeatedly rinsed with sterilized water to attain complete neutrality. Subsequently, samples were burned, using a sealed quartz tube, and the resulting CO_2 gas was catalytically reduced to graphite on Fe powder in the presence of hydrogen gas by the method of Kitagawa *et al.* (1993).

Because of the fluctuation of ^{14}C density in atmospheric CO_2 in the past, ^{14}C age (A_{cb}, y before present (BP)) estimated on a half-life basis can deviate from actual calendar age. Therefore, we converted ^{14}C age to calendar age (hereinafter described as the calibrated age: A_{cal}, y BP). We converted A_{cb} to A_{cal} using calibration curves obtained by Stuiver *et al.* (1998) (University of Washington, Quaternary Isotope Lab, Radiocarbon Calibration Program). We referred to A_{cal} as calibrated age directly obtained by this calibration program plus 50 y because our samples were taken in AD 2000, 50 y after the standard year (AD 1950 = 0 y BP) of the Stuiver *et al.* (1998) calibration. Errors of A_{cb} using one standard error of three replicated measures for each sample were generally ± 20∼30 y. Errors of A_{cb} were also transformed to the calibrated range (CR) of A_{cal} per sample when the calibration was done

Table 1. Estimated age and radial growth rate for each individual of *E. zwageri*. The samples dated as after AD 1600 were excluded when growth rate and age were calculated (–) because their *CR* was too large for estimation. A, B, C indicate samples that were collected at different distances from the edge of the same individual

Stump no.	Sample position	Cutting height (cm)	Diameter of trunk (cm)	Distance from the edge (cm)	Distance from the centre (cm)	^{14}C age (Acb y BP)	Error of age (±y)	Calibrated age (A_{cal} y BP)	Calibrated range (CR y)	Radial growth rate (cm y^{-1})	Estimated tree age (y) including heart-rot)			
											(1)	(2)	(3)	(4)
1	A	110	77.5	28	10.8	298	21	< 400	117	–	–	–	–	–
	B			18	20.8	213	21	< 400	139	–	–	–	–	–
2	A	194	92.0	39	7.0	497	81	573	118	0.068	676	588	690	639
3	A	210	121.0	42	18.5	885	20	838	136	0.050	1207	877	1146	1011
	B			21	39.5	701	23	710	15	0.030	2045	792	1368	1080
4	A	165	73.5	36	1.3	629	24	634	92	0.057	656	699	717	708
	B			20	16.8	235	21	< 400	137	–	–	–	–	–
5	A	110	126.0	52	10.5	595	21	655	84	0.079	787	694	847	770
	B			25	38.0	304	21	462	118	0.054	1164	545	1099	822
6	A	230	90.5	36	9.3	633	30	632	95	0.057	794	716	851	784
	B			26	19.3	574	22	662	79	0.039	1152	707	988	847
	C			16	29.3	377	21	518	145	0.031	1465	579	1006	792
7	A	120	60.8	25	5.4	443	19	558	11	0.045	678	569	648	609
8	A	140	98.0	28	21.0	565	21	598	80	0.047	1047	642	948	795
	B			18	31.0	726	23	717	13	0.025	1952	782	1234	1008
	C			8	41.0	189	19	< 400	280	–	–	–	–	–
9	A	280	122.5	60	1.3	323	21	440	120	0.136	449	479	497	488
	B			40	21.3	176	23	< 400	279	–	–	–	–	–
	C			20	41.3	237	20	< 400	14	–	–	–	–	–
10	A	300	75.0	37	0.0	495	19	572	21	0.065	572	572	572	572
11	A	120	108.5	35	19.3	560	20	597	80	0.059	925	637	918	777
12	A	220	68.0	30	4.0	410	20	548	35	0.055	621	556	615	586
13	A	90	110.5	55	0.3	486	20	568	18	0.097	571	569	572	570
	B			30	25.3	469	23	563	15	0.053	1037	616	984	800
14	A	110	51.5	24	1.8	220	18	< 400	139	–	–	–	–	–
15	A	180	124.0	33	29.0	386	20	522	37	0.063	981	582	1005	794

(1) By using calculated growth rate; (2) by using maximum growth rate from literature; (3) by using minimum growth rate from literature; (4) by using average growth rate from literature.

(Stuiver & Becker 1986). After around AD 1600, the fluctuation of ^{14}C density in the atmosphere became large (Stuiver *et al*. 1998) resulting in a large *CR* of A_{cal}. Therefore, only samples whose A_{cal} was older than 400 y BP were used to estimate growth rate and age.

Growth rate

We estimated the growth rate of the sampled *E. zwageri* trees (stumps) by dividing the radial distance between the sampling point and the trunk edge by the A_{cal} of each sample (Table 1). We excluded the samples whose A_{cal} was younger than 400 y BP (after AD 1600), because *CR* was too large to estimate growth rate accurately.

Age estimation of each individual

Because the stumps did not have centre parts, the obtained $A_{\rm cal}$ underestimated the actual age. To improve estimates, we added the age corresponding to the distance from assumed centre to sampling point, which included the heart-rot cavity, to $A_{\rm cal}$. We estimated the time that individuals took to grow to the sampling point in four ways: (1) the radial growth rate obtained by ^{14}C dating of the outer part of the hole of the same individual; (2) the maximum radial growth rate listed in the literature (0.48 cm y^{-1}), which was measured for young trees in an open nursery (Kostermans *et al*. 1994); (3) the minimum radial growth rate listed in the literature (0.06 cm y^{-1}), which was measured for saplings planted under shade in a secondary forest (Kiyono 1997); and (4) the average radial growth rate listed in the literature (0.27 cm y^{-1}) (Kiyono 1997, Kostermans *et al*. 1994). We also excluded the samples whose A_{cal} was younger than 400 y BP (after AD 1600) in this analysis.

RESULTS

Estimation accuracy of ^{14}C dating

The mean *CR* of A_{cal} for 19 samples (the samples whose A_{cal} was younger than 400 y BP were excluded) was about 70 y with a range of 11–145 y. As A_{cal} becomes smaller, particularly after AD 1600, relative *CR* (CR/A_{cal}) becomes larger (Figure 1). Thus, as Stuiver *et al*. (1998) pointed out, estimates after AD 1600 are of limited use. However, the A_{cal} obtained before AD 1600 had small enough relative *CR*s (1–30%) accurately to estimate age.

Growth rate

The radial growth rate estimated by ^{14}C dating was 0.058 ± 0.025 cm y^{-1} (mean ± 1 SE) with a maximum and minimum of 0.136 and 0.025 cm y^{-1}, respectively (Table 1). There was no significant correlation between A_{cb} and radial distance from stump edge to sample point, suggesting a large variation in growth rate among individuals (Figure 2). This variation was not caused by the estimation errors from ^{14}C dating, which were small, but from the distribution of growth rate among individuals, which were highly variable (Ashton 1981).

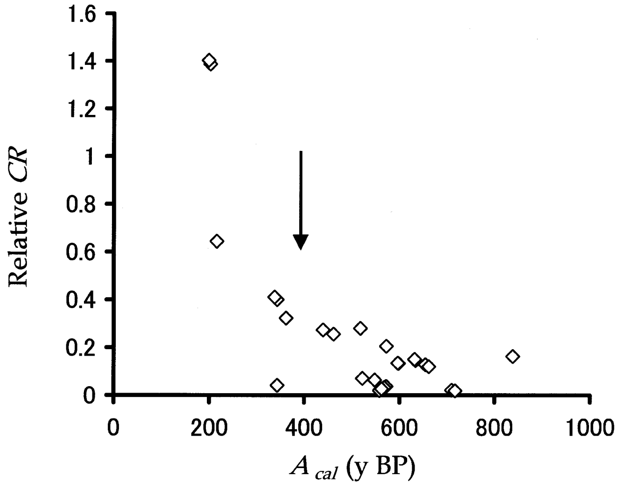

Figure 1. Relative *CR* of ^{14}C dating. Estimation errors become large after AD 1600, shown by an arrow.

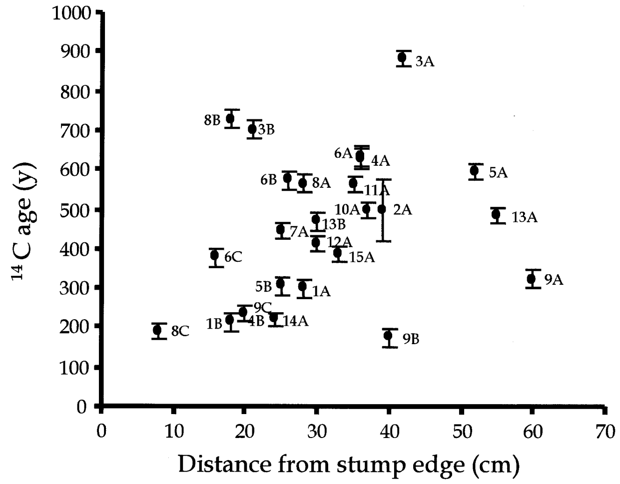

Figure 2. The relationship between ^{14}C age (A_{cb}) and the distance from trunk edge (cm). The number indicates stump and A, B, C indicate samples collected at different distances from the edge of the same numbered individual. The error bar indicates one standard error of three replicated measurements.

Age estimation of each individual

The maximum A_{cal} of the sample, at the inner edge bordering the hole that originated from heart-rot within the trunk, directly obtained by ^{14}C dating was 838 y BP for an individual with a 121-cm diameter (Table 1; tree no. 3). The estimated age of an individual varied among the four different methods to estimate the age corresponding to the distance from assumed centre to sampling point. Even using the maximum growth rate listed in the literature to estimate the age corresponding to the rotten heart of the trunk, the estimated age of the oldest individual was 877 y. When we used the minimum radial growth rate described in the literature and the calculated growth rate by ^{14}C dating, the estimated ages of many individuals whose diameter ranged from about 90 to 120 cm were more than 1000 y.

DISCUSSION

Based on this study, we believe that the ^{14}C dating method is effective for determining the life span of long-lived trees like *E. zwageri* when the age of a given tree is more than 400 y old. Up to AD 1600, the *CR* of A_{cal} (11–145 y) was small enough to discuss the estimated life span of this species (probably more than 1000 y at maximum). The method was not accurate enough to reconstruct the history of a given tree, but it was sufficient for estimating the life span.

The mean radial growth rate estimated by the ^{14}C dating was close to the lower estimations found in the literature before, which is that of saplings planted in a secondary forest (Kiyono 1997). Generally speaking, the growth rate of a tree changes with its life history. The growth rates of seedling or sapling stages were very slow. Trees are expected to have their highest growth rate at middle-sized stages, and then the metabolic rate (balance between gross production and respiration) and reproduction gradually begin to limit their growth as an individual becomes bigger (Bazzaz *et al.* 1987, Enquist *et al.* 1999). Because the growth rates estimated in this study were the long-term growth rates, which include the long slow-growing period in the later stages of the life history, these were close to the lowest estimation in the literature.

Among the four methods for estimating the additional age originating from heart-rot, the method which uses the radial growth rate of saplings grown in the understorey seems the most plausible estimation. The individuals we studied grew up in relatively dark conditions (in the understorey of the forest) when they were young. In fact, we can see the seedlings and saplings of this species surviving in the understorey of the forest (Kurokawa, pers. obs.). The estimated ages of many individuals were more than 1000 y when using the radial growth rate of saplings in an understorey for estimating the age corresponding to the distance from assumed centre to sampling point. Thus, we can conclude that the determined maximum life span of *E. zwageri* is more than 1000 y.

In order to know the ecological traits of *E. zwageri* in the dipterocarp forest, we compared some traits i.e. growth rate, life span and specific gravity of *E. zwageri* with those of Dipterocarpaceae and Leguminosae (Fabaceae) species, which commonly occur in primary forests in South-East Asia, gathered from earlier reports

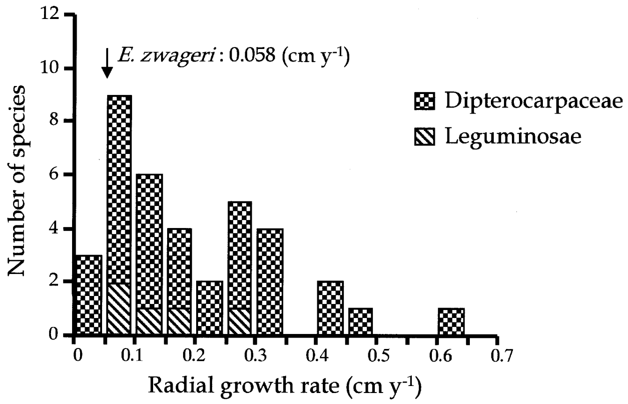

Figure 3. Frequency distribution of mean radial growth rate in 37 species of Dipterocarpaceae and Leguminosae. The data were obtained for trees whose diameter ranged from 10 to 310 cm (but most of them are more than 100 cm in dbh) in an 8-ha plot in Lambir Hills National Park, Sarawak, Malaysia. The arrow indicates the value obtained by ^{14}C dating in this study.

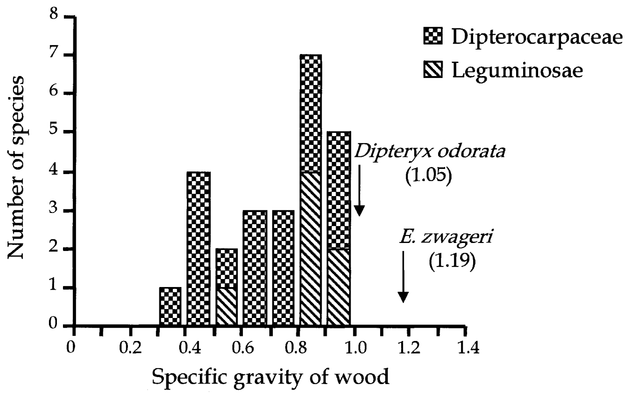

Figure 4. Frequency distribution of specific gravity of wood in 25 species of Dipterocarpaceae and Leguminosae. The specific gravity estimates, which are values of commercial timbers of South-East Asia, were obtained from the literature (Sudo 1970). The values for a long-lived (> 1200 y) neotropical tree, *Dipteryx odorata*, and *E. zwageri* (> 1000 y, in this study) are indicated by arrows.

(Sudo 1970; data obtained in a 8-ha plot in Lambir Hills National Park, Sarawak, Malaysia). The growth-rate data were calculated by dividing the increase in diameter by number of years. Those species have similar maximum height as *E. zwageri* and potentially co-occur with *E. zwageri*.

The radial growth rate of *E. zwageri* obtained in this study was nearly comparable to the most slow-growing species of Dipterocarpaceae and Leguminosae (Figure 3). In the forest, *E. zwageri* seedlings and saplings tend to occur in relatively dark conditions (Kurokawa, unpubl. data). Dipterocarp species have a large variation in radial growth rate. There are species whose radial growth rate is about six times as large as that of *E. zwageri*. On the other hand, there is a species whose radial growth rate is slower than that of *E. zwageri*. This variation suggests that dipterocarp species occupy various habitats in the forest, or have wide genetic variation in growth rates within genera, or both.

The age at maximum size of various dipterocarp species was estimated by Nicholson in 1965 to range from 60 to 570 y among individuals whose maximum diameter ranged from approximately 0.4 to 1.6 m (Whitmore 1975). These age values were estimated from girth measurements. The indirect methods of estimating age based on girth measurements may have large errors of estimation; even then, the age of *E. zwageri* estimated by ^{14}C dating in this study (more than 1000 y) is thus considerably older than that of the dipterocarp species in Nicholson's report.

Long-lived trees were also found in an Amazonian rain forest by applying a similar ^{14}C dating method (Chambers *et al.* 1998). Their study revealed that *Dipteryx odorata* Willd. (Leguminosae) can live for about 1200 y. The two species, *E. zwageri* and *D. odorata*, have some common traits. The specific gravity of these long-lived tree species is very high (*E. zwageri*: 1.19, *D. odorata*: 1.05) (Figure 4) and their wood is very hard and durable (Kitano 1984, Kiyono 1997). There seems to be a positive correlation between wood density, durability and life span (Loehle 1988). While it is very important for plants to defend their leaves against herbivores, Loehle (1988) suggested that the strong structural and chemical defensive support for their bodies against breakage and pathogens plays a big role in determining the longevity of woody plants. These defences result from high wood density (Loehle 1988), and investing in lignin (Wainhouse *et al.* 1990) and carbon-based defensive chemicals (Coley 1986, Zucker 1983) in their wood, which decrease decay and insect attack (Loehle 1988). If there was no catastrophic fire, the major cause of mortality of adult trees is breakage resulting from decayed wood (Loehle 1988). This could be applicable to long-lived species such as *E. zwageri* even if it took a long time to decay their wood. Especially in a region with a high decay rate such as the tropics, it seems that wood resistance to decay contributes significantly to the longevity of trees. However, investment in increased wood density (Enquist *et al.* 1999) or defensive compounds (Bazzaz *et al.* 1987, Coley 1986, 1988; Coley *et al.* 1985, Gulmon & Mooney 1985, Zucker 1983) decreases the growth rate. Coley *et al.* (1985) suggested that plants with inherently low growth rates in resource-poor habitats invest more in defence than those with high growth rates in more favourable conditions. This study's results showed the very slow growth rate of *E. zwageri* (Table 1, Figure 3); furthermore, its seedlings occur in relatively dark conditions in dipterocarp forest and present low growth rates compared with dipterocarp species (Kurokawa, unpubl. data). *Eusideroxylon zwageri* may manage to live through unfavourable conditions by large investment in defence.

Loehle (1988) also suggested that a tree with strong structural support and well-defended tissue should be selected strongly if continued reproduction of the adult tree is advantageous. Longevity is an important parameter contributing to increased tree fitness as suggested by Silvertown *et al*. (1993). They suggested that the population growth rates of woody plants depend heavily on the survival of adult individuals, that is, long-period fecundity by matrix analysis of plant demography. Actually, our estimation reveals that *E. zwageri* individuals become reproductively active after they are 40–200 y old, based on calculations using the diameter of mature trees and from minimum to maximum growth rates, which were found in the literature (Kiyono 1997, Kostermans *et al*. 1994). Consequently, *E. zwageri* may continue reproducing for 800 y or more from the first reproduction to its maximum age, and the period is probably much longer than that of dipterocarp species. These characteristics such as long life span of *E. zwageri* may be a strategy to increase its fitness in a dipterocarp forest even if its growth rate is very slow.

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