論　文

The dynamics and longevity of leaves of two mangrove species, *Kandelia candel* and *Rhizophora apiculata*, in relation to plant density

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メヒルギとフタバナヒルギの葉群動態および葉の寿命に対する植えつけ密度の影響

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要　旨　メヒルギ（*Kandelia candel*）とフタバナヒルギ（*Rhizophora apiculata*）の生長におよぼす植栽密度効果について研究し，葉群動態と葉の寿命について解析した。要点は以下のとおりである。

1．メヒルギとフタバナヒルギの苗を砂20リットル，腐葉土10リットルを混合し，プラスチックポットにいれたものを培地として栽培した。培地にはHoagland nutrient solutionを施した。着葉数，葉痕数を測定し，展開葉数を求めた。また，各植栽密度ごとに葉の寿命を計算した。

2．シュートあたりの平均着葉数は植栽密度，樹種により大きく異なった。低密度区の個体のシュートあたりの着葉数は，高密度区のそれよりも多かった。一定期間中の展開葉数および落葉数はともに，メヒルギのほうがフタバナヒルギより多かった。

3．葉位および植栽密度による葉の寿命の変化は，メヒルギとフタバナヒルギで異なっていた。メヒルギの葉の平均寿命は低密度区のほうが，高密度区よりも長かった。また，葉位が低く早く展開した葉の寿命は，遅い時期に展開した高い葉位の葉よりも長かった。フタバナヒルギでは葉位の高い葉のほうが，葉位の低い葉よりも長い寿命を示した。

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Summary:

1. Two mangrove species, *Kandelia candel* (L.) Druce and *Rhizophora apiculata* Bl. were cultivated in plastic pots containing 20 liters of sand and 10 liters of leaf compost. All pots were subirrigated with Hoagland nutrient solutions. The numbers of standing leaves and leaf scars were counted, and also the number of flushed leaves were calculated. Longevity of leaves in various plant densities were also studied.
2. There were marked differences in the average number of leaves per shoot between densities and between species. The number of leaves attached to a shoot of lower density plants was greater than those of higher density plants. *Kandelia candel* produced more leaves per shoot than *Rhizophora apiculata* in the same period of growth, and the loss of leaves was greater in *Kandelia candel*.
3. Leaves of *Kandelia candel* and *Rhizophora apiculata* showed the differences in longevity between leaf position and between densities. The average longevity of *Kandelia candel* leaves of lower density was longer than that of high density. In earlier leaves, the lower position leaves had a longer longevity than those of the upper position. *Rhizophora apiculata* leaves showed a contrast trend of longevity to *Kandelia candel*, higher position leaves had a longer longevity than that of lower position.

Introduction

Attention has been paid to leaf dynamics of mangrove tree species from the view point of plant density. Leaf longevity in relation to plant density was examined by analyzing survivorship curve of leaf (flush, fall and standing) to understand the specific behavior in its living condition. Large amounts of data on leaf dynamics of various tree species have been collected (GILL and TOMLINSON, 1971; KIKUZAWA, 1978; MIYAJI and TAGAWA, 1979; MORIYA et al., 1985). However, few investigations of leaf number changes of mangrove tree species have been carried out.

The longevity of leaves in relation to plant density is not well documented. BAZZAZ and HARPER (1977) found in the artificial population of *Linum usitatissimun* that increasing density disturbed branching and promoted earlier leaf death. In cultivated annual *Glycine max* Merrill, leaf longevity was greater for leaves higher on the stem (MIYAJI and TAGAWA, 1979).

In this paper the authors describe the leaf survivorship curves and leaf longevity of *Kandelia candel* and *Rhizophora apiculata* as affected by plant density in cultivated conditions.

Materials and methods

Hypocotyls and cultivation

Hypocotyls of *Kandelia candel* (L.) Druce and *Rhizophora apiculata* Blume, were planted in plastic pots (size $32 \times 42 \times 30$cm) containing 20 litres of sand and 10 litres of leaf compost (KURAISHI and SAKURAI 1985). All pots were arranged at random in a green house at the College of Agriculture, Ehime University. The seedlings were evenly distributed and the density was regulated by changing the distance between individuals. The density of plants are 25, 44.4, 100 and 400 plants/m^2 (PATANAPONPAIBOON and OGINO 1987).

Number of leaves flushed, falled, and standing

In each plant density, 20 shoots were selected and observations were carried out from July 5, 1986 to June 24, 1988 (*Kandelia candel*), from November 22, 1986 to June 24, 1988 (*Rhizophora apiculata*). The number of leaves attached to the shoot (standing leaves) and leaf scars were counted. The number of flushed leaves (emerged leaves) were calculated. Observations were repetitively carried out at two-week intervals. Every leaf was identified by its position on the axis from the lower to the upper part of the stem (node no. 1, 2, 3, ... etc.).

The number of leaves standing (L), falled (F) and flushed (N) were given by the Eq.(*1*) as follows,

$$L_n = L_{n-1} + N_n - \mathrm{F}_n \qquad (1)$$

where,

L_n stand for number of leaves attached to the shoot at n^{th} measurement,

L_{n-1} for number of leaves attached to the shoot at $n-1^{\text{th}}$ measurement,

N_n for number of leaves flushed during the period $n-1^{\text{th}}$ and n^{th} measurement, and

F_n for number of leaves fallen during the period of $n-1^{\text{th}}$ and n^{th} measurement.

Longevity of leaves

In order to understand the temporal arrangement of leaf flush and fall, we calculated the period of time (days) of each leaf attached on the shoot. We assumed the defoliation of leaves would take place from the lower node to the upper part of the stem. The sum of the period during with the individual leaf was attached alive on the shoot at position (node order), divided by the total number of leaves on that node, gives the average longevity of each leaf position, as follows;

$$E = 1/N \Sigma L_i t \qquad (2)$$

where,

E stand for average longevity of each leaf position,

N for the number of leaves flushed on that node,

L_i for the number of surviving leaves at that time period (t_i), and

t for the time interval.

The sum of longevity of each leaf position, divided by the comulative leaves flush, gives the mean longevity of the total leaves.

Results

Figure 1 shows the changes in leaf numbers flushed, fallen, and standing during a certain period of time per shoot according to the progress of time for the four plant densities.

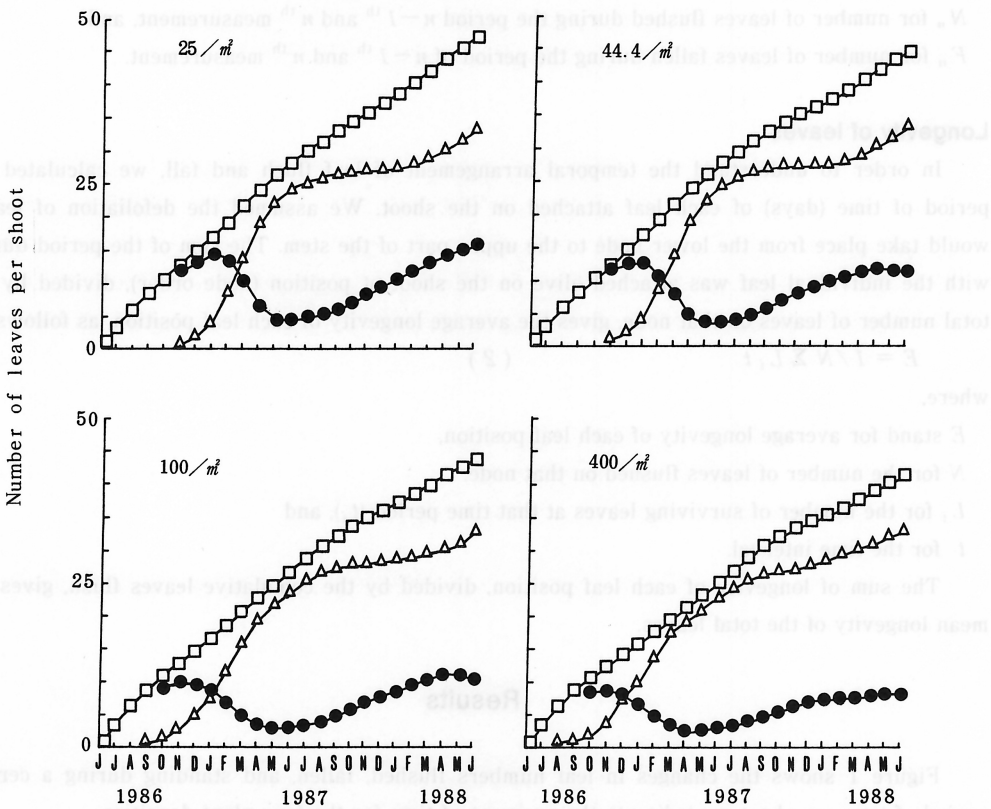
Kandelia candel

The first leaf of *Kandelia candel* emerged in early July 1986. The number of leaves attached to a shoot increased at first, reached a maximum at the end of the year, decreased to a minimum in April or May next year and gradually increased thereafter. The maximum numbers of leaves attached to a shoot were 16 (February, 1987), 14 (December, 1986), 10 (November, 1986) and 10 (November, 1986) for plant densities 25, 44.4, 100 and 400 plants/m^2, respectively. The minimum numbers of leaves attached to a shoot were 5 (May, 1987) to 3 (March, 1987) for lower to

higher densities, respectively. The curves of standing leaves showed that the average number of leaves attached to a shoot of lower density plants are greater than those of higher density plants.

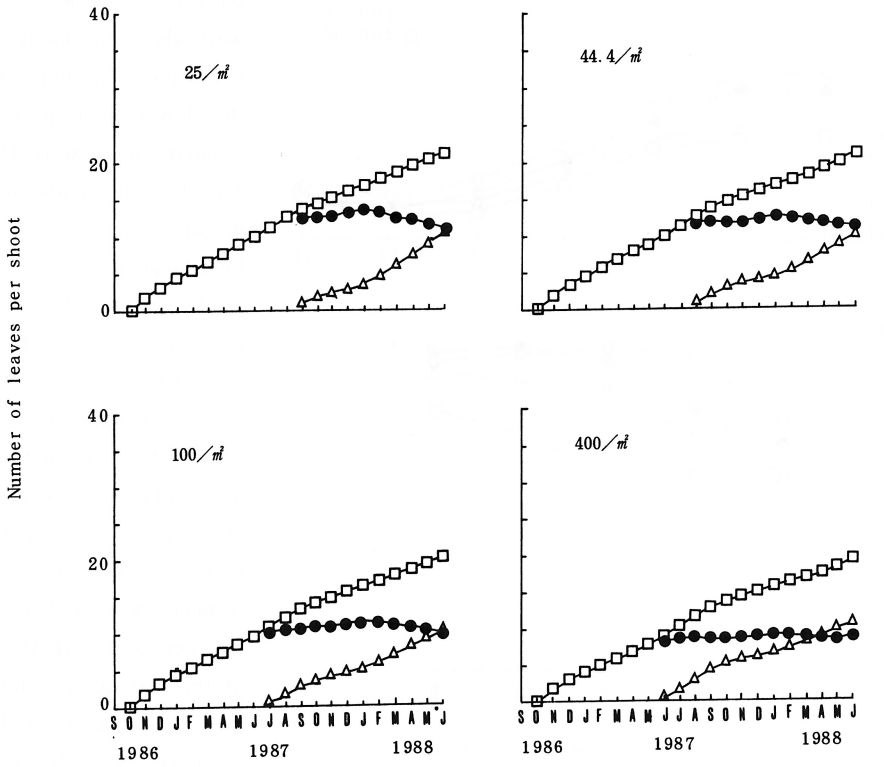
The patterns of leaf flush of the four densities showed similar curves. New leaves were produced throughout the year. The patterns of leaf fall were different between lower and higher density plots, therefore the number of standing leaves attached to a shoot were different. The leaves of lower density plots (25/m²) began to fall in November, 1986 and falling increased during February and May, 1987, while high density plots (400/m²) began as early as in September, 1986 and increased during November, 1986 and March, 1987. The results indicated that leaves of higher density plots fall earlier than those of lower density plots.

Rhizophora apiculata



(a) *Kandelia candel*

Fig. 1 Changes in leaf number of four different plant densities
●, standing leaves, indicating mean number of leaves actually persisting on the shoot;
□, leaves flush, indicating cumulative number of flushed per shoot;
△, leaf fall curve, indicating cumulative number of leaves fallen from the shoot;
(a) *Kandelia candel* (b) *Rhizophora apiculata*



(b) *Rhizophora apiculata*

As shown in Fig. 1b, leaves of *Rhizophora apiculata* opened in November, 1986 (81 days after planting) and also new leaves were produced throughout the year, but losses were greater in August and September, 1987. The leaves attached to a shoot gradually increased, reached a maximum in January, 1988 and decreased thereafter. The maximum numbers of leaves attached to a shoot were 14, 13, 12 and 10 for plant densities 25, 44.4, 100 and 400 plants/m^2, respectively. The patterns of leaf flush of the four densities showed similar curves. The patterns of leaf fall were different between higher density and lower density plots, therefore the number of standing leaves were different. The leaves of higher density plots (400/m^2) began to fall in June, 1987 and increased during August and September, 1987, while low density plots (25/m^2) began later in August, 1987 and falling increased in September, 1987.

Longevity of leaves

The longevity of leaves of every order are presented in Fig. 2. The average longevity of leaves of lower density was longer than that of higher density. The leaves of *Kandelia candel* flushed in the earlier period of growth, or leaves of lower order had a longer longevity than those

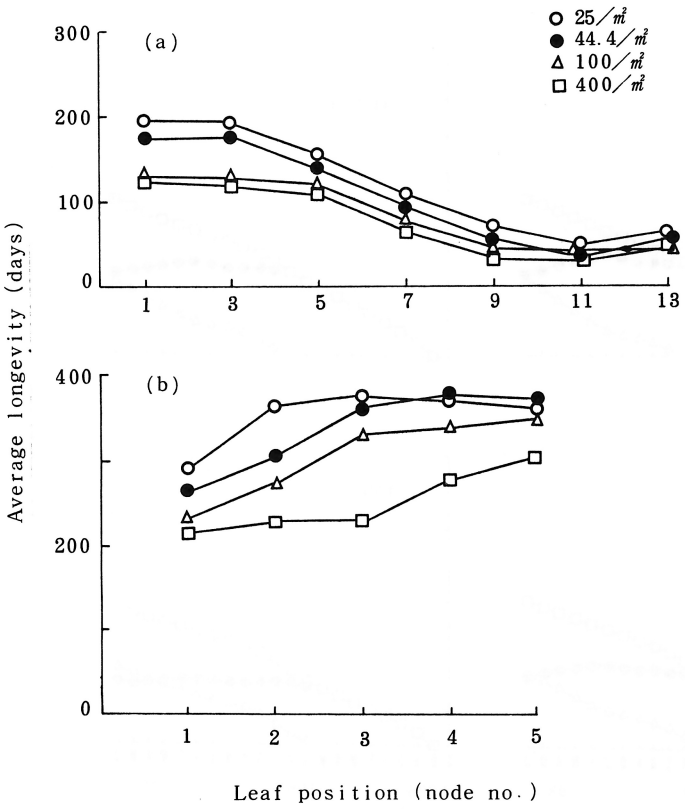


Fig. 2 Average longevity of leaves and their positions on the stem
(a) *Kandelia candel* (b) *Rhizophora apiculata*

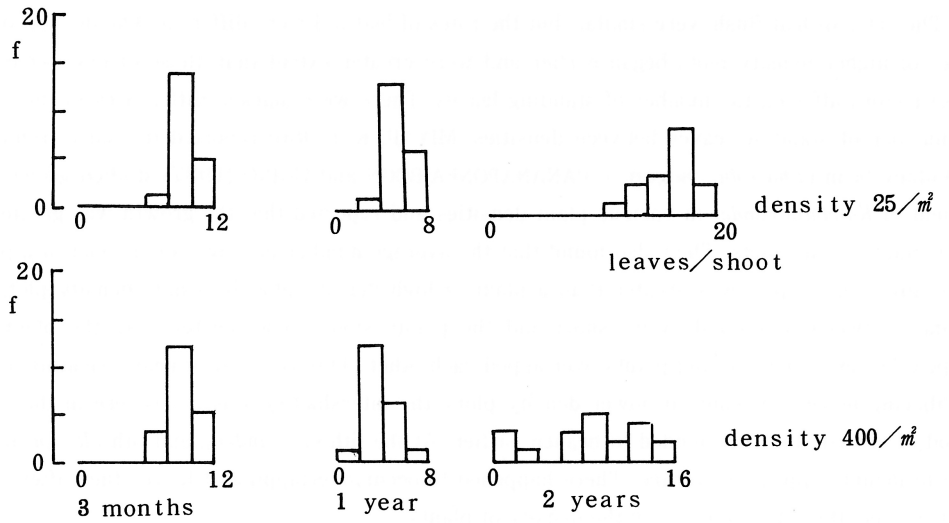
in the later period. The difference between the plots were also remarkable in earlier leaves. The longevities of the lower leaf position of *Kandelia candel* were 198 and 134 days in the low and high density plots, respectively. Leaf longevity decreased with the height of leaf on the stem from the lower to the upper part of the stem. The longevities of the upper leaves were 65 and 50 days in the lower and higher density plots, respectively. As with the longevity of leaves in *Rhizophora apiculata*, leaf longevity increased with the height of the leaf on the stem (Fig. 2b). The longevity of the lower leaves was 289 and 233 days, but the longevity of the leaves in the upper part was 365 and 307 days in the low and high density plots, respectively. *Rhizophora apiculata* showed a contrast trend of longevity to *Kandelia candel*, the leaves of higher position on the stem had a longer longevity than those in lower position. In general leaf longevity is greater for leaves of low plant density. As the results in Fig. 2 show, leaves of *Rhizophora apiculata* had a longer longevity than leaves of *Kandelia candel*.

Mean longevity of total leaves of *Rhizophora apiculata* were about 275 and 220 days, while that of *Kandelia candel* were 121 and 83 days for plant densities 25 and 400 plants/m^2, respectively.

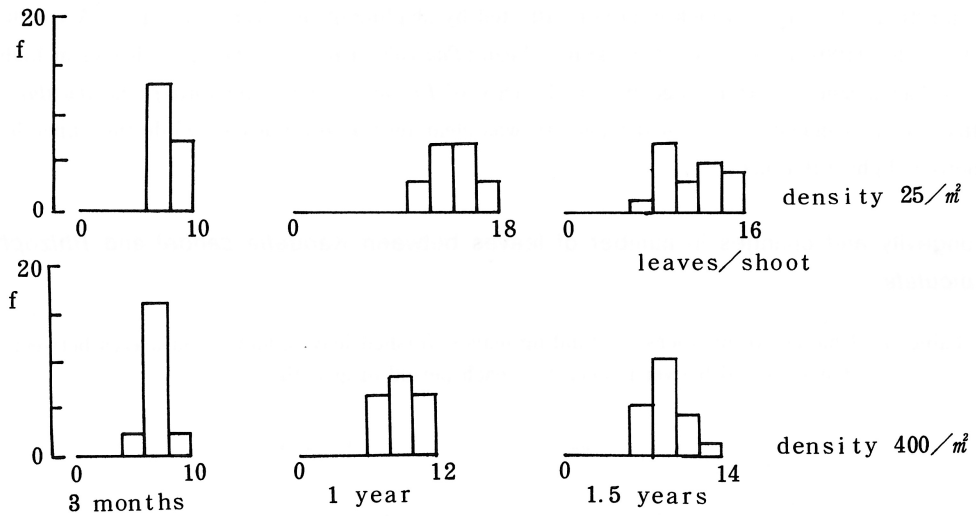
Frequency distribution of the standing leaves

The frequency distribution of the standing leaves are given in Fig.3 in the form of the histogram. The time trend in the type of histogram was reported. The initial distribution followed the symmetrical normal types and passed into the asymmetric types with the progress of time. The frequency distribution was quite similar between low plant density and high plant density in the early period of growth in *Kandelia candel* and *Rhizophora apiculata*. The distribution on low density plots of *Kandelia candel* showed a bell-shaped curve, but their modes slightly shifted rightwards at about two years after planting. The distribution in high density plots of the same day showed a relatively slight deviation from the symmetry. Frequency distribution curves of standing leaves of

Rhizophora apiculata showed a similar type throughout the whole period (Fig. 3b). No deviation of mode, either to the left nor to the right, could be observed.



(a) *Kandelia candel*



(b) *Rhizophora apiculata*

Fig. 3 Frequency distribution of standing leaves per shoot, f is the frequency or the number of individuals per class (class interval = 2)
(a) *Kandelia candel* (b) *Rhizophora apiculata*

Discussion

Relationship between leaf longevity and density of planting

The rates of leaf flush were similar, but the rates of leaf fall were different. The defoliation of leaves of higher density plots began earlier and were greater extent than those of lower density. These factors affected the number of standing leaves. There were marked differences in the average number of standing leaves between densities. MIYAJI, K. (1986) reported the same trend for the kidney bean (*Phaseolus vulgaris*). PANANAPONPAIBOON and OGINO (1987) studied growth increment of *Kandelia candel* in various plant densities and reported that the growth was greater in lower plant density plots. They also found that the average number of leaves on a shoot of a plant in the low density plot was greater than a plant in high density plot. In a high density plot, the distance between individuals were short and the plants stood close together. As the plant developed, leaves of neighboring plants overlapped each other. This resulted in heavy shading of the neighboring leaves. In plants in lower density plots, the intershading was not severe in the early period of growth, but they tended to branch earlier. At the 6th (*K. candel*), and 5th (*R. apiculata*) node branching appeared average. There happened to occur overlapping of leaves thereafter. Leaf number was affected negatively by the density of plants.

Leaves of the lower node showed a significant difference in relation to longevity. MIYAJI and TAGAWA (1979) reported that density may influence the longevity through the CO_2 assimilation-respiration relationship which is greatly affected by shading of the overlying leaves. According to MIYAJI, K. (1986) in the case of the kidney bean (*Phaseolus vulgaris*), the upper leaves at high density had a much shorter longevity. In the case of *Kandelia candel* and *Rhizophora apiculata*, the effect of plant density on the leaf longevity was clear on the lower leaves while the upper leaves showed slight differences.

Longevity and changes in number of leaves between *Kandelia candel* and *Rhizophora apiculata*

Table. 1 Changes in numbers of standing leaves, flushed leaves, and fallen leaves between densities and between species, at each period of growth

Period of growth	*K. candel*						*R. apiculata*					
	LD			HD			LD			HD		
	L	AN	AF	L	AN	AF	L	AN	AF	L	AN	AF
3 months	8.4	8.5	0.1	8.4	9.2	0.8	3.7	3.7	0.0	3.4	3.4	0.0
6 months	13.9	14.8	0.9	7.3	14.2	6.7	6.7	6.7	0.0	6.0	6.0	0.0
1 year	4.6	28.2	23.6	2.8	25.0	22.2	13.3	14.0	0.7	8.4	12.7	4.3
1.5 year	9.3	37.0	27.7	6.8	34.4	27.6	12.7	19.0	6.3	8.5	16.6	8.1
2 years	15.5	47.0	31.5	8.5	41.4	32.9	–	–	–	–	–	–
Mean longevity	121 days			83 days			275 days			220 days		

LD : low density (25 plants/m²)
HD : high density (400 plants/m²)
L : average number of standing leaves per shoot
AN : cumulative leaves flush per shoot
AF : cumulative leaves fall per shoot

Kandelia candel is a small mangrove tree. It has no remarkable buttress or pneumatophore. On the other hand, *Rhizophora apiculata* is a large tree, with the trunk supported by lateral adventitious stilt roots. The trees stand very densely and make a pure forest stand. According to Table 1, there are marked differences in the number of leaves between the two species. *Kandelia candel* produced a larger number of leaves than *Rhizophora apiculata* in the same time. Consequently, the loss of leaves was greater in *Kandelia candel* than *Rhizophora apiculata*. GILL and TOMLINSON (1971) stated that the number of leaves on the shoot may accect the production of future leaves through the supply of assimilates and it may affect the leaf fall through shade induced senescence. The number actually present in any circumstance is a reflection of the balance among all these processes. As the results show in Figure 1 and Table 1, the leaf fall of *Kandelia candel* occurred in the early period of growth, but for *Rhizophora apiculata* it occurred in the later period. Both species are evergreen and there are usually about 3–6 pairs of leaves on each shoot with the lowermost pair beginning to fall. Leaf fall of *Kandelia candel* had a markedly seasonal trend as was shown in Fig. 1a, but those of *Rhizophora apiculata* had no remarkable seasonal trend, as seen in Fig. 2b.

Leaf longevity varies broadly between plant density and between species. As the results show in Fig.2 and Table 1, lower leaves of *Kandelia candel* in low density plots had a longer longevity than those in high density plots, while upper leaves were slightly different in longevity. On the other hand, *Rhizophora apiculata* leaves increased in longevity from the lower to the upper part of the stem, and also leaves of low density plots had longevity longer than those of high density. The comparison of the two species showed that the leaves of *Rhizophora apiculata* had a longer mean longevity than *Kandelia candel*. On the other hand, the average number of leaves flush and leaf fall were greater in *Kandelia candel* than in *Rhizophora apiculata*.

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