論　文

Effect of Plant Density on the Growth of the Mangrove Species, *Kandelia candel* (L.) Druce

Pipat PATANAPONPAIBOON* and Kazuhiko OGINO**

マングローブ樹種，メヒルギの生長におよぼす植栽密度効果

ピパット　パタナポンパイブーン*・荻野　和彦**

要　旨　メヒルギ（*Kandelia candel*）の生長におよぼす植栽密度効果について研究をおこなった。要点は以下のとおりである。

1．メヒルギの苗を砂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。

2．植栽密度のちがいによって，直径（D），シュート長（L），$D^2 \cdot L$に差が生じた。結果は各植栽密度ごとに異なる生長曲線となってあらわれ，低密度区ほどはやい生長を示した。

3．シュートあたりの平均着葉数は生長とともに増加して最大値に達し，その後減少した。平均着葉数は低密度区のほうが高密度区よりも多くなった。

4．シュートあたりの平均積算展開葉数は低密度区と高密度区では差が生じなかった。

5．低密度区の葉の平均寿命は高密度区より長くなった。植栽密度が葉の寿命に影響をあたえ，高密度区の葉の平均寿命を短くしたものと考えられる。

Summary: The study on the effect of plant density on the growth of *Kandelia candel* seedlings is summarized as follows.

1) *Kandelia candel* seedlings were grown in plastic pots containing 20 litres of sand and 10 litres of leaf compost. Also, Hoagland nutrient solution was used to cultivate the *Kandelia candel* seedlings.

2) The difference in growth of plants in various plant densities were seen in the diameter of the stem (D), the height of the plant (L) and D^2L. The results show that the growth patterns between plant densities are different in curve, and the growth is greater in low plant density plots.

3) The mean number of leaves attached to a shoot progressively increased, reached the maximum and then decreased. The mean number of leaves on a shoot of a plant in the low density plot was greater than a plant in a high density plot.

4) The cumulative mean number of leaves which emerged on a shoot of low density

* Plant Resource Production, Bioresource Production Science,United Graduate School
連合農学研究科　生物資源生産学専攻　植物生産学講座

** Laboratory of Silviculture　造林学研究室

plant was similar to those of high density plants.

5) The mean longevity of leaves in a low density plot was longer than in a high density plot. That is, the plant density would affect longevity. Therefore, the leaves of high density plants had a shorter mean longevity.

Introduction

The mangrove forest plays a very important economic role and increased demand for land involving mangrove areas has led to the exploitation of mangrove forests. In order to recover mangrove forests, mangrove plantations should be introduced in the area where natural mangrove forest has been destroyed (AKSORNKOAE, S. 1976). To make the maximum utilization and conservation, more knowlege of the ecological processes of the mangrove community is required. At present, fundamental knowledge of the mangrove ecosystem, especially dealing with intraspecific competition or interaction among individuals of the same species, is very slight.

Intraspecific competition in cultivated plant population as controlled by spacing distance has long been a serious problem in agricultural practice (KIRA et al. 1953). Several experimental studies on plant competition have been carried out. CLEMENTS, WEAVER & H-ANSON (1929) carried out several experiments on intraspecfic competition. KIRA et al.(1953) proposed the results of experiments on intraspecific competition which are concerned with statistical analysis. As the materials in their experiment, cultivated varieties of vegetable and field crops such as soybean, radish and turnip were used. KONGSANGCHAI (1987) mentioned, in regard to the density of mangrove, that the density of a plantation forest was about two times great than natural forest, and a full density curve was proposed.

The present experiment is mainly concerned with the mangrove tree species, *Kandelia candel*, in the hope of analyzing interplant relation in the mangrove community of woody plants.

Materials and Methods

Plant Material : Hypocotyls and Cultivation

Hypocotyls of *Kandelia candel* (L.) Druce were collected from trees growing along the Kanna and Ukukubi Rivers, Okinawa, Japan. Hypocotyls were selected for uniform weight (8−13g.) and length (16−22 cm.). The hypocotyls were planted in plastic pots (size 32×42×30cm) 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 Faculty of Agriculture, Ehime University. These pots were subirrigated with tap water and the water level was maintained and changed weekly through drainage hole. The hypocotyls were kept in this way until the seedlings had first leaves. The tap water initially used to cultivate the hypocotyls was replaced with Hoagland nutrient solution. Water levels were maintained by addition of tap water every other day and the solution was changed weekly.

The seedlings were evenly distributed and the density was regulated by changing the distance between individuals, as shown in Table 1.

Table 1. Outlines of experimental design

Space between plants (cm)	Density (No./m²)	Number of pots	Number of seedlings/pot
20	25	5	4
15	44.4	5	6
10	100	5	12
5	400	5	35

The hypocotyls of *Kandelia candel* were planted on June 4, 1986. Germination was good and uniform. The plants grew normally through the experimental period.

Growth Assessment

The diameter of the stem was measured at the first node level. The length of the shoot was measured from the first node level to the base of the apex. Measurements were started on July 5, 1986 and carried out about once every 7 days.

Number of standing leaves, leaf flush and leaf fall

Investigations were made in *Kandelia candel* seedlings on various plant density (25,44.4, 100 and 400 plants/m²). In each plant density, 20 shoots were selected and observations were carried out from July 5, 1986 to June 20, 1987. The number of leaves attached to the shoot (standing leaves), the number of flushed leaves (emerged leaves), the number of fallen leaves (defoliated leaves) were recorded every two weeks. At each observation, we defined the leaf flush as the time when the lamina expanded on a node. We determined the number of fallen leaves by the leaf scars on the shoot.

At each observation, the number of leaves attached to shoot could be obtained by an equation (1).

$$L_n = L_{n-1} + N_n - F_n \quad \cdots\cdots\cdots\cdots\cdots\cdots (1)$$

L_n=number of leaves attached to the shoot at n^{th} measurement

L_{n-1}=number of leaves attached to the shoot at $n-1^{th}$ measurement

N_n=number of leaves flushed during the period $n-1^{th}$ to n^{th} measurement.

F_n=number of leaves fallen on n^{th} measurement

Longevity of leaves

The empirical longevity of leaves or the duration of leaves attached to the shoot was the base of this experment. In order to understand the time sequence of leaf emergence and leaf fall, the empirical longevity of each leaf was calculated at each ordered leaf.

Leaf Area and Leaf Area Index (LAI)

The size of the leaves, width (W) and length (L) were measured for the same plants which were observed for the number of standing leaves every month. The leaf area (LA) was

calculated by allometric equation. The simple allometric equation was approximated by;

$LA=a(W\cdot L)^b$……(2)

The regression coefficient a and b were determined as shown in Table 2.

Table 2. Coefficients a, b of the allometric equation.

Plant density No./m²	*a*	*b*
25	0.61449	1.03129
44.4	0.53776	1.06414
100	0.43465	1.12163
400	0.6420	1.02344

The leaf area index (LAI), total leaf area (one side,m²) of each plant and density per square meter was calculated for each measurement time.

Results

Growth of the diameter of the stem

The diameter of the stem at the first node level of *Kandelia candel* seedlings in various plant densities are summarized in Figure 1. During the early measurement or from 31 to 59 days after planting, the stem diameter of plants in a high density plant grew similar to those in other plots and the increment rate of the stem diameter was similar to the curves for all four plant densities. But from August 9, 1986 (94 days after planting), the growth of the stem diameter of high density plants was slower than those of low density plants and as a result, the stem diameter of high density plants (400 plants/m²) was smaller than those of low density plants. The average stem diameter of low density plants was 0.95 cm. on June 20, 1987 (380 days after planting), but 0.70 cm. was the average stem diameter of high density plants.

Shoot elongation

The height of the stem from the first node level to the base of the apex are presented in Figure 1. With the progress of time the elongation of the shoots of the four plant densities increased. Figure 1 showed that shoot elongation for the four plant densities was apparently more rapid and similar in the earlier part of the measurement (during from 31 to 166 days after planting). But after 205 days (from December 27, 1986), the elongation of the shoot of low density plants (25 plants/m²) seemed to have grown faster than those of high density plants. That is, the growth increment of shoot elongation showed different curves for all four plant densities. As a result, the height of the stem of low density plants was higher than those of high density plants. On June 20, 1987 (380 days after planting), the average height of the stem of low density plants (25 plants/m²) was about 65.3 cm. but about 39.9 cm. high was found for high density plants (400 plants/m²).

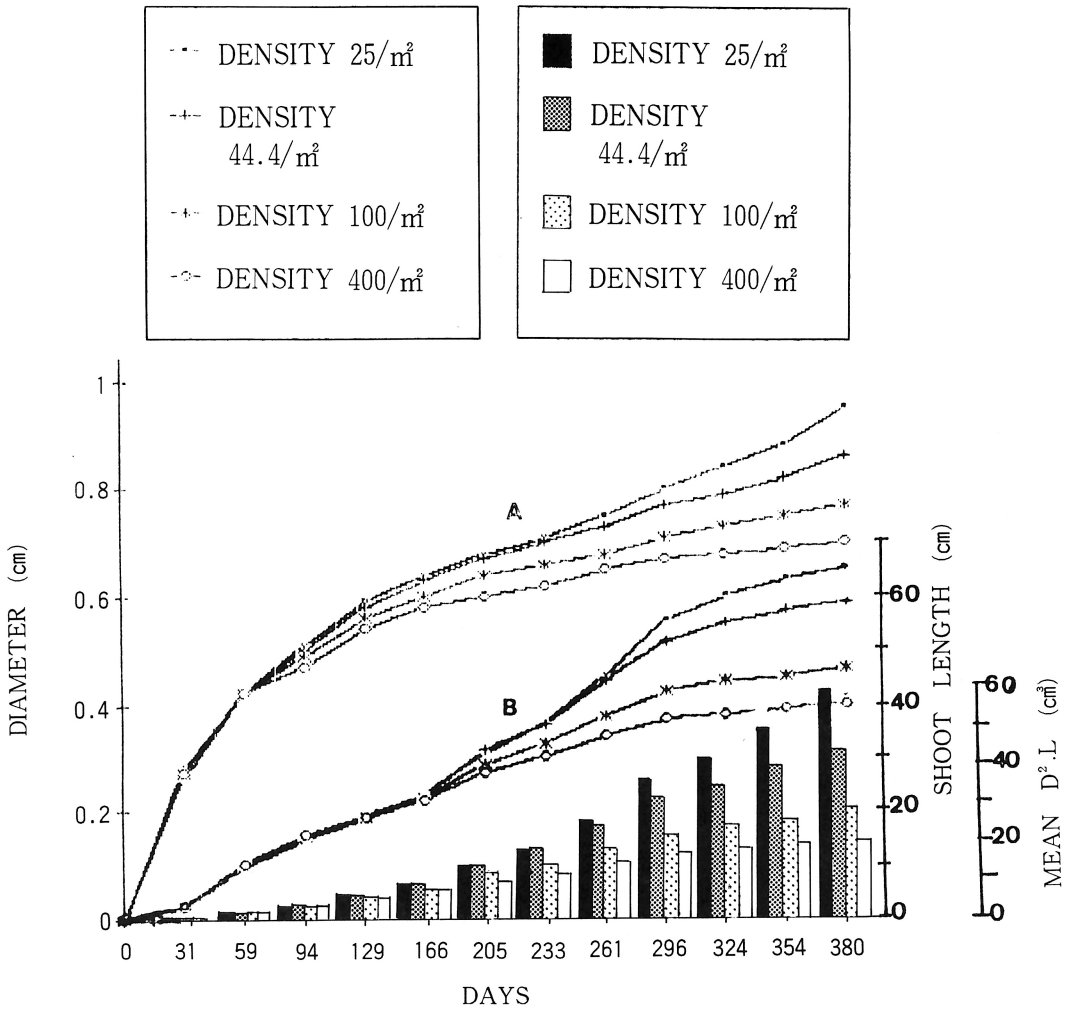

Figure 1. Growth curve of *Kandelia candel* seedling:
(A) mean diameter of stem
(B) mean shoot length
(C) mean $D^2 \cdot L$

Mean $D^2 \cdot L$ for various plant densities

The $D^2 \cdot L$ or square of the stem circumference at the level of the first node multiplied by shoot length are shown in Figure 1. Early measurement (from 31 to 59 days after planting), showed that plants in both low density and high density plots were similar in the value of average $D^2 \cdot L$. But from 94 days, the mean $D^2 \cdot L$ of low density plants became slightly higher than the high density plants and the difference was most remarkable between low density plants and high density plants with respect to the progress of time. Figure 1 shows that the low plant density plot had a higher value of $D^2 \cdot L$ than high plant density, which corresponded to the increment of diameter and height. The $D^2 \cdot L$ of low plant density reached 60.3 cm^3 on June 20, 1987 (380 days after planting) but the $D^2 \cdot L$ of high plant density (400 plant/m^2) was about 21.0 cm^3.

Survivals of Leaves

Figure 2 shows the changes in leaf number per shoot according to the progress of time for the four plant densities. 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 and decreased thereafter. These results show that the maximum number of leaves attached to a shoot of a low density plant (25/m²) was 16 (261 days after planting), of plant density

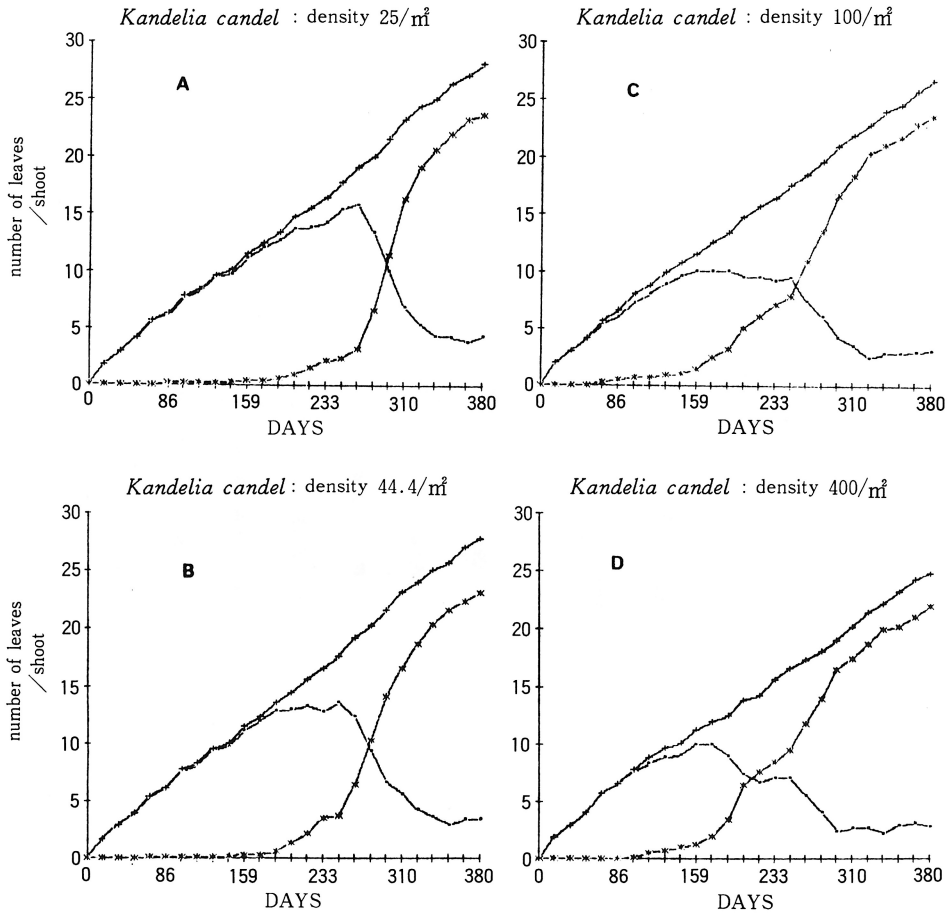

Figure 2. Changes in leaf number of four different plant densities of *Kandelia candel* seedling. (A) 25 plants/m², (B) 44.4 plants/m², (C) 100 plants/m² and (D) 400 plants/m²

—+— Emergence curve, indicating cumulative mean number of emerged leaves per shoot

—·— Survivorship curve, indicating mean number of leaves actually persisting on the shoot

—×— Leaf fall curve indicating cumulative mean number of leaves fallen from the shoot

44.4/m² it was 14 (247 days), of plant density 100/m² it was 10 (191 days) and of plant density 400/m² it was 10 (173 days). On June 20, 1987 (380 days after planting), the actual number of leaves attached to a shoot of plant density 25, 44.4, 100 and 400 per m² were 5, 4, 3 and 3 respectively plants (400/m²), defoliation reached a maximum on December 27 1986 (205 days after planting) but the low density plant (25/m²) reached a maximum on March 21 and April 11, 1987 (from 289 to 310 days after planting).

Empirical longevity of leaves

Empirical longevity of leaves or the observation of the duration of a leaf attached to the shoot for all four densities of *Kandelia candel* seedlings are presented in Table 3 and Figure 3. The empirical longevity of leaves of plant density 25/m² range from 57 to 217 days, of plant density 44.4/m² range from 57 to 191 days, of plant density 100/m² range from 41 to 155 days and of plant density 400/m² range from 41 to 151 days. The average longevity of leaves is long for low density (25/m²), at about 133 days and short for high density (400/m²) at about 92 days. The results show that the leaves of each plant density which emerged in the early period of growth had a longer longevity than those in the later period of growth.

Table 3. Empirical longevity of Leaves of *Kandelia candel* seedlings.

Density No./m²		25	44.4	100	400
Time of leaf flush	days		days		
Jun. 4,86	planted	-	-	-	-
Jul. 5,86	31	212	186	155	155
Jul. 19,86	45	217	191	155	150
Aug. 2,86	59	217	191	145	142
Aug. 16,86	73	207	191	150	134
Aug. 29,86	86	186	181	150	124
Sep. 13,86	101	186	171	153	124
Sep. 27,86	115	173	160	142	109
Oct. 11,86	129	160	150	132	119
Oct. 25,86	143	142	137	122	111
Nov. 10,86	159	137	127	111	103
Nov. 24,86	173	124	116	101	96
Dec. 14,86	191	109	101	91	80
Dec. 27,86	205	101	93	83	75
Jan. 10,87	219	88	83	72	62
Jan. 24,87	233	78	75	60	54
Feb. 7,87	247	67	67	54	47
Feb. 21,87	261	62	67	47	47
Mar. 7,87	275	57	57	41	41
Mar. 21,87	289	60	60	44	36
Apr. 11,87	310	67	70	47	36

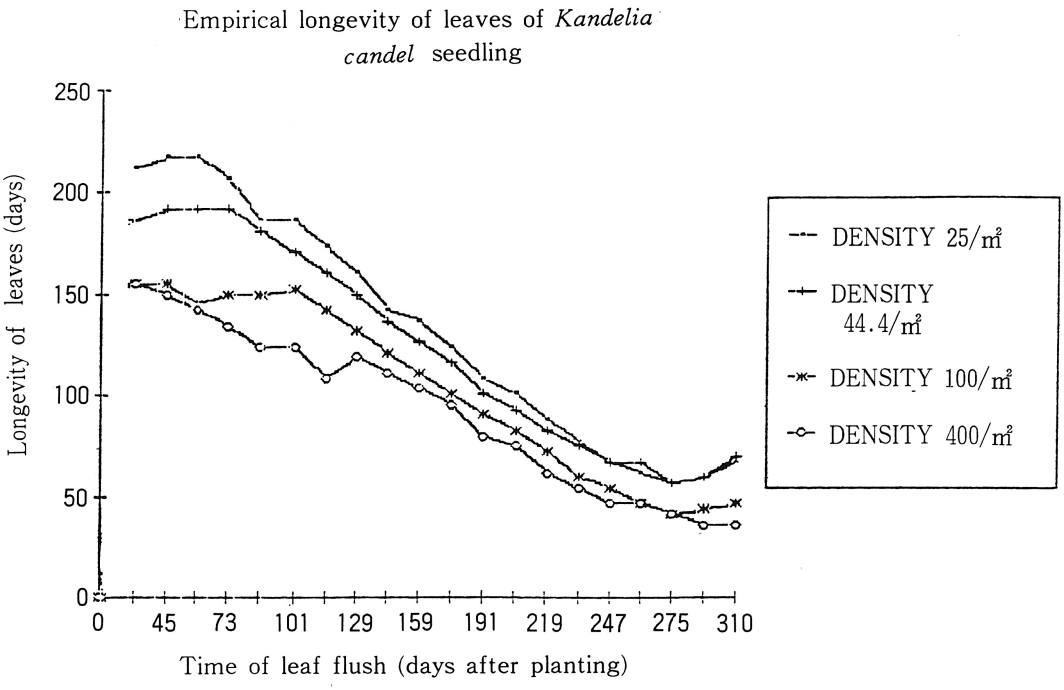

Figure 3. Changes in empirical longevity of leaves of four different plant densities of *Kandelia candel* seedling at each observation.

Leaf area and leaf area index (LAI)

The results of leaf area per plant and leaf area index (LAI) of *Kandelia candel* seedlings in four plant densities are presented in Figures 4 and 5. As seen in Figure 4, the leaf area per plant of four plant densities were low at early measurement and tended to increase. Plant density 25, 44.4 and 100/m^2 increased in the leaf area per plant from 143 days after planting and had high value (866, 689 and 420 square centimeter respectively) on the 261st days and declined to 616, 364 and 147 cm^2 respectively on the 324th day and then increased up to value of 747, 392 and 160 cm^2 respectively on the 380th day after planting. The leaf area of plants in a density of 400/m^2 gradually increased from early measurement and reached a high value (263cm^2) on the 233rd day and declined to 93cm^2 on the 289th day and then increased up to 103cm^2 on the 380th day.

Changes in leaf area index (LAI) of *Kandelia candel* seedlings in the four densities are indicated in Figure 5. The results show that LAI of plant density 400/m^2 were low at early measurement and reached a peak where the LAI was 10.5 on the 233rd days and tended to decline to 3.7 on the 289th days. Plant density 25, 44.4 and 100/m^2 gradually increased in the LAI and had a high value (2.2, 3.1 and 4.2 respectively) on the 261st day and decreased to 1.5, 1.6 and 1.5 respectively on the 324th day and then increased.

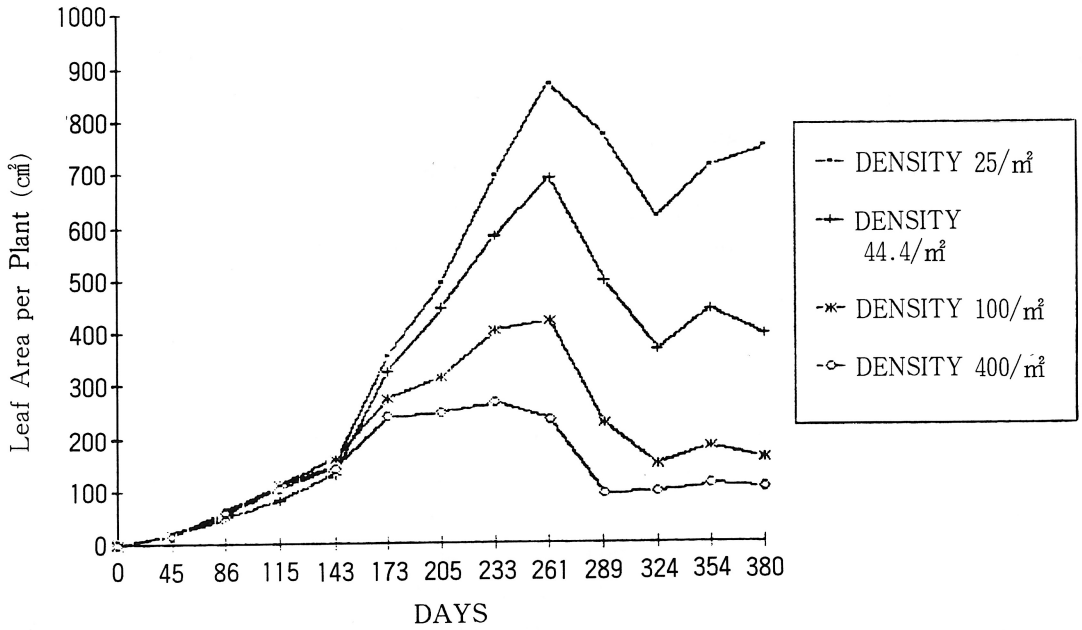

Figure 4. Leaf area per plant of *Kandelia candel* seedling at each measurement time.

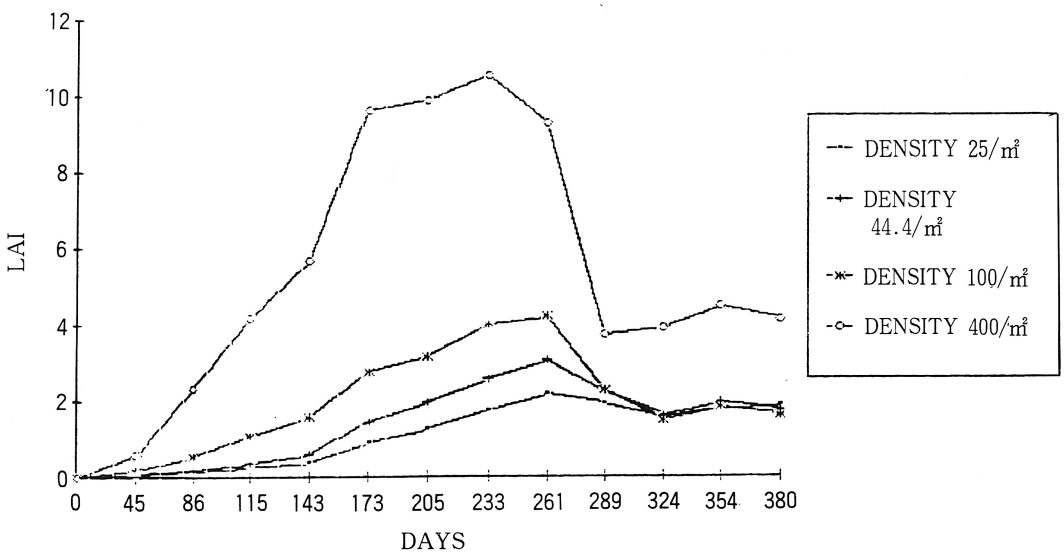

Figure 5. Changes in leaf area index (LAI) of *Kandelia candel* seedling in various plant densities at each measurement time.

Discussion

Diameter of stem, Plant height and $D^2 \cdot L$

In early measurement, the growth of the *Kandelia candel* seedlings in the low density plot was similar to those of high density plots but after the middle of measurement, the size of plants in low density plots was larger than those of high density plots, as seen in Figure 1. According to HOZUMI, et al. (1955) in the earlest stage of development immediately after germination, the size of the plant largely depends upon the growth potential inherent in the seed or the amount of nutrient stored in the seed grain. When plants are closely spaced, however, interaction between individuals soon begins to affect the growth of each plant. Figure 1(A) indicates that the average diameter of stems for the four densities became varied from 94 days after planting. Also Figure 1(B) and 1(C) show the apparent differences in the average plant height and mean $D^2 \cdot L$ from 166 days. The effect of plant density upon the plant growth is apparent, plant growth in a low density plot is generally higher than in a high density plot.

KIRA,OGAWA and SAKAZAKI (1953) pointed out that plots with high density had small mean values of both fresh and dry weight. An experiment on the soybean showed that the mean values of plant weight became significantly higher with decreasing density.

HOZUMI, KOYAMA and KIRA (1955) reported that the fresh weight of a shoot that was measured at the experiment was found to be fairly well correlated with the square of the stem circumference at the level of the level of the first node above ground (D) multiplied by shoot length (L). In the case of *Kandelia candel*, the growth in $D^2 \cdot L$ of seedlings in a high density plot was less than low plant density (Figure 1). So it can be said, the mean plant weight of plots with high density is smaller than low plant density plots.

Number of leaves and Longevity of leaves

In this study, there were differences in the average of the number of leaves attached to a shoot mong the four densities (as seen in Figure 2). The patterns of leaf flush (emergent) were similar to each other, but the patterns of leaf fall (defoliation) were different according to plant density. The defoliation of leaves (leaf fall) of high density plants reached a maximum earlier than those of low density plants . This means that the leaves of the high plant density plot fell rapidly from the time of leaf flush which corresponds to MIYAJI, K. 1986.

As seen in Table 3 and Figure 3, the longevity of leaves of *Kandelia candel* seedlings are different according to the density of the plot. Empirical longevities of leaves examined in this study were 133, 124, 103 and 92 days for plant density 25, 44.4, 100 and 400/m^2 respectively. The leaves in the low density plot (25/m^2) had a longer longevity than those in the high density plot (440/m^2). MIYAJI, K. (1986) examined the mean longevities of leaves of the kidney bean (*Phaseolus vulgaris*) and reported that the upper leaves at high density had a much shorter mean longevity.

Leaf area and leaf area index (LAI)

Changes in leaf area per plant of the four plant densities are presented in Figure 4. These results showed that the leaf area per plant in the low density plot are larger than those in the high density plot. Plant density 25, 44.4 and 100/m^2 had a high value of leaf area per plant about 866, 689 and 420 cm^2 on the 261st day, but a plant density of 400/m^2 reached a high value (263cm^2) on the 233rd day.

As seen in Figure 5, the maximum value of LAI was 10.5 (233 days after planting) in the high density plot (400/m^2) and 2.2 (261 days after planting) in the low density plot (25/m^2).

It is apparent that leaf size of plant on high density is smaller than plant on low density, and also, plant on high density, the number of leaves are less than low plant density.

Acknowledgements

We would like to express our sincere thanks to Prof. S. KURAISHI (Hiroshima University) for his kind suggestion for a culture medium. We are also indebted to Dr. T. NAKASUGA (University of the Ryukyus) for providing the hypocotyls of *Kandelia candel* for this study, to Dr. A. IKEMOTO(Kochi University) for his kind advice and to Dr. I. NINOMIYA and Mr. A. TSUJITA (Ehime University) for their kind assistance in the experimental work.

References

1) AKSORNKOAE, S. : Structure of mangrove forest at Amphoe Khlung, Changwat Chantaburi, Thailand. Kasetsart Univ. For. Bull. **38**:1−42. Bangkok, 1976.

2) CLEMENTS, F. E., WEAVER, J. E. and HANSON H.C : Plant Competition. Carnegie Institution of Washington, 1929.

3) DOWNTON, W. J. S. Growth and Osmotic Relation of the Mangrove *Avicennia marina* as Influenced by Salinity. Aust. J. Plant Physiol. **9** : 519−28, 1982.

4) HOZUMI, K., KOYAMA, H. and KIRA, T.: Intraspecific Competition among Higher Plants. Ⅳ. A preliminary account on the interaction between adjacent individuals. J. Inst. Polytech. Osaka City Univ. Ser. D. **6**:121−130, 1955.

5) KIKUZAWA, K. : Emergence, defoliation and longevity of alder (*Alnus hirsuta* Turcz.) leaves in a deciduous hardwood forest stand. J. Ecol. **28** : 299−306, 1978.

6) KIRA, T., OGAWA, H. and SAKAZAKI, N. : Intraspecfic Competition among Higher Plants. I. Competition-yield-density interrelationship in regularly dispersed population. J. Inst. Polytech. Osaka City Univ.Vol.**4** No.1 D : 1−16, 1953.

7) KURAISHI, S. and SAKURAI N. : Cultivation Conditions for *Kandelia candel* seedlings. Studies on the mangrove ecosystem. Nodai Research Institute. Tokyo University of Agriculture : 94−101, 1985.

8) MIYAJI, K. : A new life table of leaves of *Phaseolus vulgaris* L. in relation to their position with in the canopy and plant density. Ecol. Res. 1(3) : 303−322, 1986.

9) MORIYA, H. *et al.* : Ecological Studies on the Vegetation of Mangrove Forests in Thailand. 147−152, 1985.

(Received August 31, 1987)