

## Studies on Matter Production of Edible Canna (*Canna edulis* Ker.)

### IV. Leaf unrolling and changes in leaf photosynthetic rates with growth under field conditions\*

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**Abstract** : Edible canna was grown from late April to November at either 0.5 m × 1 m or 3 m × 3 m spacing in the experimental field of the University of Tsukuba to clarify leaf area development and changes in leaf photosynthesis with leaf age and growth as a basis of high productivity. The leaves unrolled during a 6–9 day interval. In the middle growth stage, individual leaf area in the upper layers was larger than in the lower layers. On July 23 and August 16 when LAI attained 7 and 9, respectively, about 70% of the leaf area was occupied by the upper 4 leaves. The maximum net photosynthetic rate was 19.1  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (June 9) and the photosynthesis of the upper leaves did not become saturated at 1,000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD. The maximum rate, however, tended to decrease gradually with growth. After July, when plants began rapid growth, net photosynthetic rates of leaves in the canopy decreased rapidly with a decrease in light by mutual shading. Judging from the leaf area and net photosynthesis at each leaf position, the upper 4 leaves in the canopy substantially contributed to the dry matter production of this crop after the middle growth stage.

**Key words** : *Canna edulis* Ker., Edible canna, Field conditions, Leaf age, Leaf area, Leaf unrolling, Net photosynthetic rate.

**食用カンナの物質生産に関する研究 第4報** 圃場条件下における葉の展開および生育に伴う個葉光合成速度の推移: 加藤盛夫・今井 勝 (筑波大学農林学系)

**要旨** : 食用カンナの高生産力を解明するための基礎として、葉面積の形成と個葉光合成速度の葉齢および個体の生育に伴う変化を明らかにするため、0.5 m × 1 m (群落状態) および 3 m × 3 m (孤立状態) の栽植密度下で4月下旬から11月中旬まで筑波大学の実験圃場で栽培を行った。食用カンナは生育中期には6–9日間隔で大型の葉身を展開するため、LAIが7になる7月下旬、9になる8月中旬には、上位4葉までの葉身で全葉面積の約70%を占めていた。個葉の最大光合成速度は19.1  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (6月9日)であったが、生育が進むにつれて低下する傾向があった。個体群の下位葉では葉面積指数の拡大する7月以降になると主に相互遮蔽により光合成速度は急激に低下した。上位展開葉の光合成速度は1,000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD以上の光強度でも光飽和しなかった。葉冠内の葉面積構成及び各葉位の光合成速度から判断して、食用カンナ個体群では生育中期以降、上位4葉が乾物生産に大きな貢献をしていることが窺われた。

**キーワード** : *Canna edulis* Ker., 個葉光合成速度, 食用カンナ, 葉の展開, 圃場条件, 葉面積, 葉齢。

Edible canna (= achira, Queensland arrow-root) has not been improved by intensive selection or breeding, but is a highly productive crop in temperate to tropical regions<sup>7,9,12</sup>.

In previous papers, we reported that edible canna produced 2,600–4,000 g m<sup>-2</sup> whole plant biomass (dry weight basis)<sup>3,4</sup>. Such a high production was due to high crop growth

rates which were mainly attributed to high leaf area index (LAI) during the latter growth stages<sup>4,10</sup>.

We examined the gas exchange characteristics of leaves developed under controlled environments as the first step to clarify the matter production of edible canna<sup>11</sup>. However, leaf photosynthetic rates under natural conditions, in the field, have not been examined. In this experiment, we measured single leaf-photosynthetic rates which were affected by leaf age and plant growth under field conditions.

### Materials and Methods

The seed-rhizomes of edible canna (*Canna*

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*edulis* Ker. cv. Aokuki-kei) were planted at 0.5 m × 1 m spacing in 20 m × 20 m experimental fields of the University of Tsukuba in late April 1990 and 1991. The cultivation procedures were almost the same as described in a previous paper<sup>3)</sup>. However, as we found that edible canna required fairly large amounts of nutrients, especially potassium, for prosperous growth<sup>2)</sup>, 80 g m<sup>-2</sup> of potassium chloride (K<sub>2</sub>O=60%) was applied in addition to a compound chemical fertilizer (6 g m<sup>-2</sup> each of N, P<sub>2</sub>O<sub>5</sub>, and K<sub>2</sub>O). Before plowing, bark manure (2 kg m<sup>-2</sup>) in 1990 and poultry manure (125 g m<sup>-2</sup>) in 1991 were also scattered in the fields. In both years, six plants were grown at 3 m × 3 m spacing in adjacent plots. A three fold amount of compound chemical fertilizer was applied because these plants produced about a three fold amount of stems and rhizomes as compared to 0.5 m × 1 m spaced plants in previous experiment (data not shown). We defined the plants grown at 0.5 m × 1 m and 3 m × 3 m spacing as 'canopy' and 'isolated' plants, respectively.

The dates of emergence and unrolling of leaves on maternal shoots were recorded for five selected plants from each spacing. On July 23 and August 16 in 1991, five canopy plants were harvested and leaf areas were measured with an automatic area meter (Hayashi-denko, Model AAM-7).

Two or three plants were selected from each spacing for the measurement of leaf photosynthetic rate. In late May, when plants developed several leaves, the measurement of leaf photosynthetic rate was initiated and performed periodically until early August for the canopy plants and until late September for the isolated plants. Rate of net photosynthesis was measured with an open gas exchange measurement system using a portable infrared gas analyzer (Fuji Electric, Model ZFP D3). The air was drawn into a small leaf chamber (2 × 4 cm) by a pump through a rod at a height of 4 m. The flow rate of air into the chamber, which was clamped above and below the same section of a leaf, was maintained at 0.6 L min<sup>-1</sup>. As the leaves of edible canna were very large and elliptical (max. 50 cm-long and 25 cm-wide)<sup>4,7)</sup>, photosynthetic rate was measured at the central portion of a half hemisphere of a leaf at each leaf position. We did not disturb the

canopy structure during the photosynthetic measurements to maintain natural conditions. As it took about 30 seconds to measure photosynthesis (maximum difference of CO<sub>2</sub> between inlet and outlet of the chamber was 30 μmol mol<sup>-1</sup>) for each leaf, the temperature and vapor pressure in the leaf chamber were not controlled. Light intensity on the leaf surface was measured with a photosensor (Hamamatsu Photonics, Model S1133) equipped with the leaf chamber. The output from the photosensor was converted to photosynthetic photon flux density (PPFD) by comparing it with the data of a quantum sensor (LI-COR, LI-190SB). Net photosynthesis of all unrolled leaves on maternal and lateral shoots of selected plants were measured every 30-60 minutes.

Meteorological data were obtained from the Environmental Research Center of the University of Tsukuba adjacent to our experimental field. The changes in daily mean air temperature from late April to July were similar in both years, but during August in 1991 it was ca. 3.1°C lower than in 1990. Daily mean solar radiation (total short-wave radiation) from April to June in 1991 was 13% higher than in 1990. Precipitation from mid-August to October was much higher in 1991 (988.5 mm) than in 1990 (399.5 mm). However, plant growth and changes in leaf photosynthetic rate were similar in both years and the canopy structure was severely disturbed by a typhoon in August of both years. We mainly show the results obtained in 1991.

## Results

### 1. Interval of leaf unrolling on maternal shoot

Figure 1 shows the ontogenetic changes in the intervals of leaf unrolling on the maternal shoots in the canopy and isolated plants. The isolated plants developed 20 leaves on their maternal shoots. In the canopy plants, however, the emergence of new leaf was almost stopped because of the lodging by a typhoon, so that the measurement was ceased in August. The leaf blades became gradually larger toward the upper positions on the stems, and smaller toward the terminal leaves as reported<sup>4)</sup>. For the isolated plants, the intervals of leaf unrolling in the early growth stages were longer than in latter stages and averages

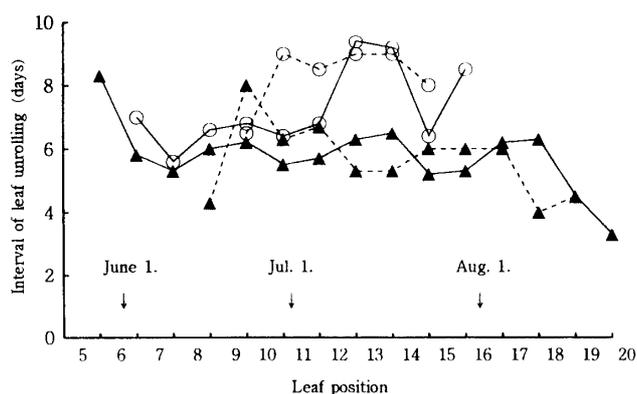


Fig. 1. Ontogenetic changes in intervals of leaf unrolling at each leaf position (counted upward from the base) on maternal shoots.

- 1) ○, Canopy plant ; ▲, isolated plant ; —, 1990 ; ----, 1991.
- 2) Data are averages of 5 plants.

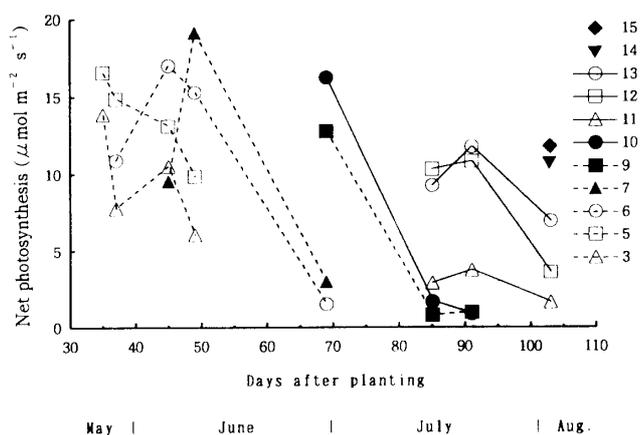


Fig. 2. Changes in net photosynthetic rates of individual leaves on maternal shoots in the canopy plants (1991).

- 1) Data points are averages measured between 10:00-14:00 on clear days at each leaf position for 2-3 plants under natural conditions.
- 2) Number at each symbol indicates the leaf position counted upward from the base.

were 7 days in the canopy plants and 6 days in the isolated plants. The interval of the middle growth stages was 2-3 days longer in the canopy plants than in the isolated plants.

## 2. Leaf area distribution

Table 1 shows the leaf area distribution on the stems in the canopy plants. Leaf area are shown as uppermost and 2nd leaves, 3rd and 4th leaves, and lower leaves counted downward from the top of the maternal and lateral shoots. As reported in the previous paper<sup>4)</sup>,

during the middle growth stage, the 8th to 15th leaves (counted upward from the base) exceeded 50 cm in length and 20 cm in width. Then the leaf area distribution of the upper layer was larger than the lower layer. On July 23, when the maternal shoot had 12 leaves and LAI reached 7.2, the total leaf area of the upper two leaves occupied 37% of the whole plant. Individual leaf area in upper leaves was larger than in lower leaves, i.e. 1,510 cm<sup>2</sup> for upper two, 1,300 cm<sup>2</sup> for middle two and 670 cm<sup>2</sup> for lower leaves. On August 16, when the maternal shoot had 16 leaves and LAI reached 9.0, the upper two leaves occupied 33% of leaf area of plant, though the average area of them decreased to 1,340 cm<sup>2</sup>.

## 3. Changes in leaf photosynthetic rates with growth

Figs. 2 and 3 show the changes in average net photosynthetic rates of leaves on maternal shoots measured between 10:00-14:00 on clear days in the canopy and isolated plants, respectively.

The changes in single leaf photosynthetic rates with aging were similar to the pattern reported in the controlled environments<sup>1)</sup>, i.e., photosynthetic rate was low on the day of leaf unrolling, attained its maximum after several days and then gradually declined. The maximum net photosynthetic rate observed in this experiment was 19.1  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in the 7th (counted upward from the base) leaf on June 9 (Fig. 2), which was higher than the values reported in previous papers<sup>10,13)</sup>. Photosynthetic rates of the uppermost leaves were 16.2 on June 29 (10th leaf), 11.8 on July 21 (13th leaf) and 11.6  $\mu\text{mol m}^{-2} \text{s}^{-1}$  on August 2 (15th leaf) in the canopy plants (Fig. 2), and 14.4 on July 8 (10th leaf), 16.1 on July 24 (12th leaf), 12.5 on August 9 (15th leaf) and 14.1  $\mu\text{mol m}^{-2} \text{s}^{-1}$  on August 28 (17th leaf) in the isolated plants (Fig. 3).

The uppermost leaves in the canopy plants showed a gradual decrease in photosynthetic activity with growth. After July, when the plants began rapid growth, photosynthetic rates of lower positioned leaves in the canopy decreased rapidly. For example, photosynthetic rate at the 10th leaf was 16.2  $\mu\text{mol m}^{-2} \text{s}^{-1}$  on June 29 (average PPFD on the leaf surface was 1,296  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and it decreased to 1.7  $\mu\text{mol m}^{-2} \text{s}^{-1}$  on July 15 (average PPFD on the leaf surface was 70  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ),

which corresponded to 18% of the uppermost leaf. Also, on July 21, photosynthetic rates in the 13th, 12th, 11th, 10th and 9th (counted upward from the base) leaves were 11.8, 10.8, 3.7, 0.9 and  $1.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ , respectively (Fig. 2). Corresponding PPFD on leaf surfaces were 986, 796, 697, 53 and  $45 \mu\text{mol m}^{-2} \text{s}^{-1}$ , respectively.

In the isolated plants, on the other hand, photosynthetic rates decreased slower than in the canopy plants. For example, photosynthetic rate at the 11th leaf was  $17.3 \mu\text{mol m}^{-2} \text{s}^{-1}$  on July 24 (average PPFD on the leaf surface was  $1,306 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) and on August 14 (21 days later), it was  $10.4 \mu\text{mol m}^{-2} \text{s}^{-1}$  (60% of July 24) (Fig. 3). Average PPFD on the leaf surfaces were 1,087, 1,357, 1,328, 1,210, 706, 990, 1,091 and  $562 \mu\text{mol m}^{-2} \text{s}^{-1}$  for the 15th, 14th, 13th, 12th, 11th, 10th, 9th and 8th leaves, respectively.

#### 4. Photosynthesis in relation to light intensity

Fig. 4 shows photosynthetic rates of the canopy plants measured at each leaf position from 9:00-16:00 on July 21 plotted against PPFD on the leaf surface. The rapid decrease in photosynthetic rates of lower leaves was attributed to a decrease in PPFD by mutual shading. At high light intensities, however, the rates in the lower leaves were still lower than those in the upper leaves.

Fig. 5 shows photosynthetic rates of the isolated plants measured at each leaf position from 10:00-16:00 on August 9 plotted against PPFD on the leaf surface. The pattern of light responses of the upper 4 leaves were similar. For leaves lower than the upper 4 leaves, photosynthetic rates were lower than those of the upper leaves at high light intensities. However, at low light intensities, the rates were similar to those of the upper leaves. In controlled environments there was no light saturation at  $1,000 \mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD<sup>1)</sup>. Similarly in this study, the rate was not saturated when PPFD exceeded  $1,000 \mu\text{mol m}^{-2} \text{s}^{-1}$ .

#### Discussion

It was emphasized that edible canna was soil conservative because of its rapid leaf growth which covered the ground surface and protected from erosion<sup>5)</sup>. This is attributed to having large leaves on shoots periodically.

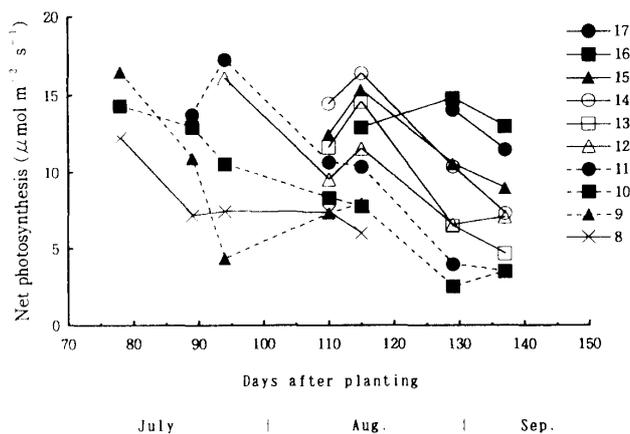


Fig. 3. Changes in net photosynthetic rates of individual leaves on maternal shoots in the isolated plants (1991).

1) Data points are averages measured between 10:00-14:00 on clear days at each leaf position for 2-3 plants under natural conditions.

2) Number at each symbol indicates the leaf position counted upward from the base.

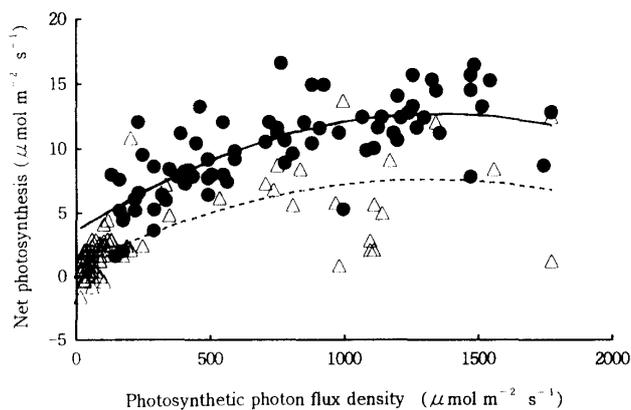


Fig. 4. Light responses of leaf photosynthesis in the canopy plants.

1) Data points indicate measurements of upper and lower leaves on maternal and lateral shoots between 9:00-16:00 on July 21, 1991.

2) Regression lines are for uppermost 2 leaves (●, solid line:  $Y = -5 \times 10^{-6} X^2 + 0.0135 X + 3.57$ ,  $R^2 = 0.56$  ( $n = 75$ )) and for lower leaves ( $\triangle$ , dotted line:  $Y = -4 \times 10^{-6} X^2 + 0.0105 X + 0.75$ ,  $R^2 = 0.52$  ( $n = 98$ )), respectively.

Long-lived, large leaf area (LAI > 9 for 2 months) which was distributed among tall stands (2.5-2.8 m height) with good light interception was reported to be an important characteristic in dry matter production of

edible canna<sup>4</sup>). It was also reported that a high LAI (6–10) of edible canna during the latter part of ontogenesis was important<sup>10</sup>). The distribution of maximum leaf area was in the middle or lower layers during early growth stages, but as growth proceeded, it shifted to the upper layers<sup>4</sup>). In this study, the leaves unrolled during 6–9 day-intervals (Fig. 1). In the canopy plants, leaf unrolling was delayed compared to the isolated plants in the latter growth stage (Fig. 1), probably due to rapid stem elongation or insufficient nutrient uptake.

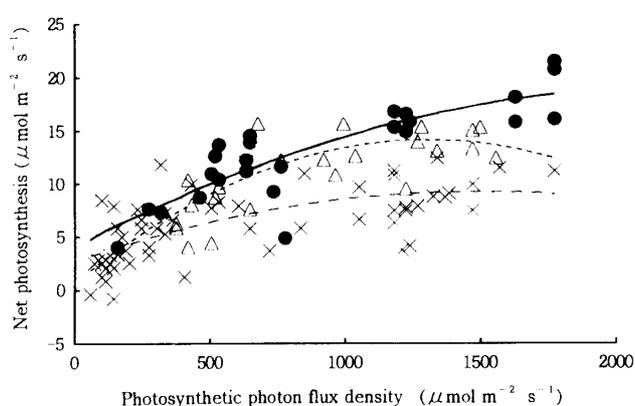


Fig. 5. Light responses of leaf photosynthesis in the isolated plants.

1) Each data were obtained at each leaf position of maternal and lateral shoots between 10:00–16:00 on Aug. 9, 1991.

2) Regression lines are for uppermost 2 leaves (●, solid line:  $Y = -3 \times 10^{-6}X^2 + 0.0135X + 3.98$ ,  $R^2 = 0.72$  ( $n = 26$ )), 3rd and 4th leaves (△, dotted line:  $Y = -8 \times 10^{-6}X^2 + 0.0208X - 0.09$ ,  $R^2 = 0.64$  ( $n = 24$ )) and lower leaves (×, broken line:  $Y = -3 \times 10^{-6}X^2 + 0.0089X + 2.66$ ,  $R^2 = 0.43$  ( $n = 60$ )), respectively.

In the middle growth stages, the position of maximum density of leaf area shifted to the upper layers<sup>4</sup>). On July 23 and August 16 (LAI was 7 and 9, respectively) in the present experiment, about 70% of leaf area was occupied by the upper 4 leaves on maternal and lateral shoots (Table. 1). During this stage, such distribution was attributed to the facts that the size of the upper leaves was larger than lower leaves and that lower leaves senesced with the decrease of light penetration by mutual shading.

In this study, we examined leaf photosynthetic rates with growth in the canopy and isolated plants. After July, when LAI began to increase rapidly, photosynthetic rates at the lower leaf positions decreased rapidly in the canopy plants. The rates of lower leaves were much lower than the uppermost 2 leaves (Fig. 2). For example, photosynthetic rates of the 4th and 5th leaves (counted downward from the top) decreased to about 10% of the uppermost leaf and corresponding light intensities also decreased to less than 10% of the uppermost leaf on July 21. On the other hand, the decline of the rates of lower leaf positions was gradual in the isolated plants (Fig. 3). As shown in the results on August 14, the light intensities on leaf surfaces at lower positions were not much lower than the uppermost leaf. Therefore, this decline in photosynthetic rates was caused by the decline of light intensity in the canopy. It was reported that in rice populations, light intensity at the leaf surface was a leading factor regulating single-leaf photosynthesis under field conditions<sup>6</sup>). In edible canna, much solar radiation reached to the ground in the early growth stages because of small LAI but in the latter growth stages, the absorption

Table 1. Canopy leaf area distribution on the stem at the middle growth stage (1991)<sup>1)</sup>.

Date	Stem number	Leaf number on maternal shoot	Leaf area distribution			Average single leaf area		
			Upper	Middle	Lower <sup>2)</sup>	Upper	Middle	Lower
			(cm <sup>2</sup> /plant)			(cm <sup>2</sup> /leaf)		
July 23	7	12	13,400 (37%)	13,100 (36%)	9,500 (27%) <sup>3)</sup>	1,510	1,300	670
Aug. 16	7	16	14,900 (33%)	16,300 (36%)	14,000 (31%)	1,340	1,440	1,260

1) Data are averages of 5 plants.

2) 'Upper', 'Middle' and 'Lower' indicate the sum or average leaf area of the 1st and 2nd, the 3rd and 4th, and the lower leaves counted downward from the uppermost expanded leaf, respectively.

3) Percentage of each layer to the total leaf area of the plant.

of light by the canopy became large and the light intensity at the ground level declined, e. g., less than 1% of the top of the canopy<sup>4)</sup>. In the present experiment, the upper 4 leaves in the canopy plants could contribute most to dry matter production judging from leaf area and photosynthetic rates at each leaf position in the middle growth stage.

Oka et al.<sup>10)</sup> suggested that a high LAI supported the high productivity of edible canna irrespective of the low photosynthetic rates of single leaves. Fig. 2 shows the average photosynthetic rates measured from 10:00–14:00 on clear days at different leaf positions on maternal shoots in the canopy plants. The maximum photosynthetic rate ( $19.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) observed on June 9 was much higher than their report<sup>10)</sup> and comparable to other  $C_3$  crops<sup>8)</sup>. However, the maximum rate decreased with growth. This might be due to either nutrient limitation (non-topdressing) or water supply (non-irrigation) or both. Another possible cause in summer was high leaf temperatures that could decrease the photosynthesis in edible canna. In the previous study conducted under controlled conditions, the optimum temperature was  $28^\circ\text{C}$ <sup>1)</sup>. Leaf temperatures often exceeded  $30^\circ\text{C}$  on clear days under field conditions and in extreme case, the midday depression of photosynthesis was also observed at the upper leaves on sunny days in 1990 and 1991, though these data were not included in the figures.

Light responses of photosynthesis of upper leaves in isolated plants (without saturation at  $1,000 \mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD) were similar to responses observed under controlled conditions<sup>1)</sup>. Photosynthetic rates of lower leaves were lower than those of upper leaves at higher PPFD (Fig. 4, 5), which related to a decrease in photosynthetic capacity with aging, and these leaves seemed to adapt to the low light regime.

In the canopy of edible canna, the position of maximum leaf area density shifted to the upper layers with growth<sup>4)</sup> because the upper leaves were larger (Table 1) and the leaf senescence moved gradually up the stem with the decline of light intensity in the lower layers. Subsequently, the photosynthetic rates at each leaf position decreased rapidly and the rates in lower leaves of the canopy were much

lower than those of upper leaves (Fig. 2, 3). In a previous experiment, however, the high LAI in the latter growth stages was supported by long-lived lower leaves under good weather conditions<sup>3,4)</sup>. These leaves could adapt to low light regime and could maintain low photosynthetic rates for a long period under such conditions. In rice populations, it has also been reported that the lowest, old leaves under shade are still autotrophic<sup>11)</sup>. Actually, in 1987, when the final dry weight of whole plant was  $39.7 \text{ t ha}^{-1}$ , the high LAI (ca. >9) was sustained for about 2 months during the latter growth stage<sup>3,4)</sup>. However, final dry weight of whole plant was  $24.3 \text{ t ha}^{-1}$  in 1990. We observed that more leaves at the lower positions were sustained in the canopy in 1987<sup>4)</sup> than in 1990 and 1991 (data not shown). Therefore, the contribution of lower leaves could also be important in higher production of edible canna.

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\*\* In Japanese with English summary or abstract.