

## The Effect of Dry Matter Allocation at the Early Seedling Stage on the Growth of Two Grass Species

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### 두 초본 종의 생장에 있어서 실생 초기의 물질분해 효과

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#### ABSTRACT

The growth of *Digitaria adscendens* and *Eleusine indica*, annual weeds common in Japan, was experimentally analyzed under varying nutrient conditions. Compared with *E. indica*, *D. adscendens* showed a higher relative growth rate(RGR) under low nitrogen availability, whereas there was no difference between the two under high nitrogen availability. Higher net assimilation rate(NAR) in *D. adscendens* than *E. indica* was responsible for high RGR in *D. adscendens* under the low nitrogen availability. The difference of NAR in the two species was induced not by leaf nitrogen content but by nitrogen use efficiency.

Under unfertilized conditions nitrogen uptake rate(NUR) was greater in *D. adscendens* than *E. indica*. Specific absorption rate in two species was similar, but root mass was greater in *D. adscendens* than *E. indica*. *D. adscendens* allocated more dry matter to roots than *E. indica* in earlier stage of seedlings. This contributed to higher root mass and in turn resulted in higher NUR in *D. adscendens* than that in *E. indica*. It is concluded that the larger allocation of dry matter to roots at early seedling stage in *D. adscendens* plays an important role in obtaining nitrogen for the continuation of growth under low nitrogen availability.

#### INTRODUCTION

It is generally acknowledged that there are two growth types in plants depending upon nutrient conditions of soil. One is slowly growing species which are predominant on infertile soil, and the other is rapidly growing species which are advantageous on fertile soil (Chapin, 1980). Some species inhabiting fertile soil cease to grow when nutrient availability of soil decreases(Rorison, 1968). The different performances among species to nu-

trient availability are related to plant growth and distribution (Bradshaw *et al.*, 1964).

Among nutrients, nitrogenous compounds are known to be the main limiting factor in coastal sand dunes (Kabaya, 1981; Kachi and Hirose, 1983). It is well known that small top-dressing of nitrogen is enough to change species composition in a natural plant community due to species differences in response to nitrogenous nutrients (Willis, 1963). Those plants which are capable to use nitrogen compounds efficiently can increase their growth rate and reproduction with increasing nitrogen availability (Chapin, 1980; Mooney and Gulmon, 1979). Consequently, two important points should be taken into consideration in the evaluation of growth of plants under poor nitrogen conditions. One is the capability to absorb nitrogen efficiently, and the other is the capability to use the absorbed nitrogen effectively.

In my previous papers, environmental factors affecting the distribution of *Digitaria adscendens* and *Eleusine indica* on coastal sand dunes in Japan was reported (Park, 1989a; Park, 1990). The results showed that poor nutrient conditions in soil was an important causal factor that determines the distribution of the two species, because they respond differently to infertile dune soil.

In this paper, the difference in growth response between *D. adscendens* and *E. indica* observed in the field is further analyzed experimentally with special reference to the efficiency of nitrogen utilization. These results will contribute to the understanding of how adaptative characteristics to nitrogen stress affect plant distribution in the field.

## MATERIALS AND METHODS

The experiment was carried out with two grass species, *D. adscendens* and *E. indica*. These species are known to show sympatric distributions in flatlands throughout Japan (Ohwi and Kitagawa, 1983). However, they show a quite different distribution in coastal sand dune areas though there are no differences in their life form and phenological schedules (Park 1989a). The distribution of *D. adscendens* extends into coastal sand dunes, whereas that of *E. indica* does not.

Seeds were collected from the Botanical Gardens of the University of Tokyo (Koishikawa), Tokyo, in August 1986. Seeds were germinated separately in petri-dishes in a growth chamber at temperatures of 25°C (day) and 20°C (night) with a 14 h light and 10 h dark lighting cycle of  $250 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Sand dune soil in which *D. adscendens* is distributed was used as soil medium for transplanting. On August 3, 1987 two seedlings at the first leaf stage were transplanted into each pot (16 cm in diameter and 20 cm in height) and then put on a concrete bench under vinyl roof. Transplanted seedlings were covered with translucent vinyl sheets for seven days to avoid possible damaging effects of strong sunlight and were well watered daily to the drip point. The sand used in the experiment retained little nitrogen : total N < 0.51, ammonium N < 0.003 and nitrate N < 0.002 mg nitro-

gen per g air-dry sand. Twenty four pots of each species were divided into two groups according to nutrient levels. Twelve pots for each species were not supplied with any nutrient solution (unfertilized conditions) and the remainders received nutrient solution at 4-day intervals from 13 August to 29 August (fertilized conditions). The nutrient solution was given until water drained through the bottom of each pot. The nutrient solution contained macro- and micro-nutrients in the following weight ratio (ppm) (Takegawa, 1972) : N, 130.0; P, 60.0; K<sub>2</sub>O, 115.0; CaO, 115.0; MgO, 37.5; Fe, 4.85; Mn, 0.50; B, 0.25; Zn, 0.10; Cu, 0.10; Mo, 0.15. All pots were well watered every other day to run-off. During the experiment the daily maximum and minimum air temperature changed from 25.8 to 34.2°C and from 19.5 to 23.8°C, respectively. Eight plants of each species were harvested at each sampling time (13, 22 August and 2 September 1987), and separated into leaf, stem and root. Leaf area was determined with an automatic area meter (AAM-7, Hayashi-Denko). Roots were separated from soil by washing with running water on a fine sieve. Plant materials were oven-dried at 80°C for 48 hours and then their dry mass and total nitrogen content were determined. Total nitrogen content of plant materials were determined with N-C analyzer.

The statistical significance of difference between the means of groups was determined by Student *t*-test.

## RESULTS

Growth analysis was conducted with change of dry weight of the plant. Relative growth rate (RGR) was computed from the change of plant dry weight according to equation (1).

$$\text{RGR} = \frac{1}{W} \cdot \frac{dW}{dt} = \frac{\ln W_2 - \ln W_1}{t_2 - t_1} \quad (1)$$

where *W* stands for the total dry mass and *W*<sub>1</sub> and *W*<sub>2</sub> are *W* at time *t*<sub>1</sub> and *t*<sub>2</sub>, respectively. RGR of both species were small under unfertilized condition compared with the fertilized condition, although *D. adscendens* showed a higher RGR under unfertilized condition than fertilized condition in Days 9~20 (Table 1).

The two species showed no difference in RGR at their earlier seedling stage under both nutrient conditions. At the later seedling stage, however, RGR of the two species differed according to the nutrient conditions : RGR of *E. indica* was significantly higher than that of *D. adscendens* under fertilized conditions while RGR of *D. adscendens* was significantly higher under unfertilized conditions.

RGR can be analyzed into the product of net assimilation rate (NAR) and leaf area ratio (LAR) as follows (Hunt 1982):

**Table 1.** Relative growth rates of *D. adscendens* and *E. indica* under fertilized and unfertilized conditions. Each value represents mean of eight replicate plants with standard deviation.

Days	Relative growth rate(mg · dw mg · dw <sup>-1</sup> day <sup>-1</sup> )		
		Fertilized	
	<i>D. adscendens</i>		<i>E. indica</i>
0~9	0.21±0.06	NS	0.21±0.04
9~20	0.15±0.02	**	0.21±0.04
		Unfertilized	
	<i>D. adscendens</i>		<i>E. indica</i>
0~9	0.06±0.02	NS	0.04±0.03
9~20	0.18±0.02	***	0.10±0.01

\*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ , NS, not significant

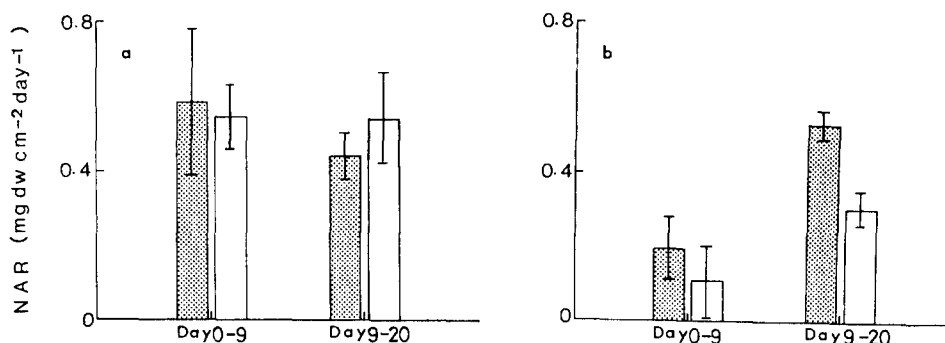
$$\frac{1}{W} \cdot \frac{dW}{dt} = \frac{1}{L} \cdot \frac{dL}{dt} \times \frac{L}{W} \quad (2)$$

(RGR)            (LAR)            (LAR)

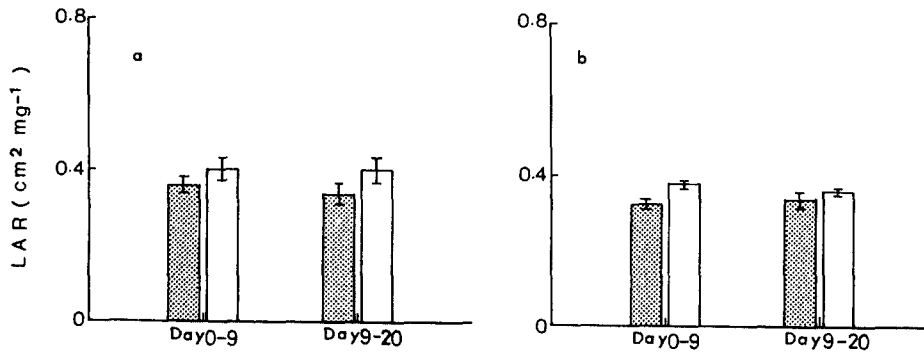
NAR was calculated using equation (3);

$$\text{NAR} = \frac{1}{L} \cdot \frac{dW}{dt} = \frac{1}{(L_2 - L_1)} \cdot \frac{(\ln L_2 - \ln L_1)(W_2 - W_1)}{(t_2 - t_1)} \quad (3)$$

Where L stands for leaf area and  $L_1$  and  $L_2$  are L at  $t_1$  and  $t_2$ , respectively. When an exponential increase in leaf area is assumed,  $(L_2 - L_1) / (\ln L_2 - \ln L_1)$  corresponds to mean leaf area between  $t_1$  and  $t_2$  (Williams 1946). NAR of both species were significantly higher under fertilized condition than under unfertilized condition ( $P < 0.01$  for *D. adscendens* and  $P < 0.001$  for *E. indica*), except for *D. adscendens* in Days 9~20 (Fig. 1). In



**Fig. 1** Changes in net assimilation rate of *D. adscendens* (dotted column) and *E. indica* (open column). a) Fertilized condition; b) unfertilized condition. Each short bar represents a standard deviation.



**Fig. 2** Leaf area ratio of *D. adscendens* (dotted column) and *E. indica* (open column). a) Fertilized condition; b) unfertilized condition. Each short bar represents a standard deviation.

Days 0~9 there was hardly any difference in NAR between *E. indica* and *D. adscendens* under fertilized condition, NAR was significantly different between the two species in Day 9~20 ( $P < 0.05$ ). An appreciable decrease in NAR from Days 0~9 to 9~20 in *D. adscendens* contrasts with relatively constant NAR in *E. indica*. Under unfertilized conditions, NAR in *D. adscendens* was higher than that in *E. indica* in both time periods. In particular, the difference was marked in Days 9~20 ( $P < 0.001$ ). The results showed that fertilization is effective in maintaining high NAR, except for *D. adscendens* in the second time period.

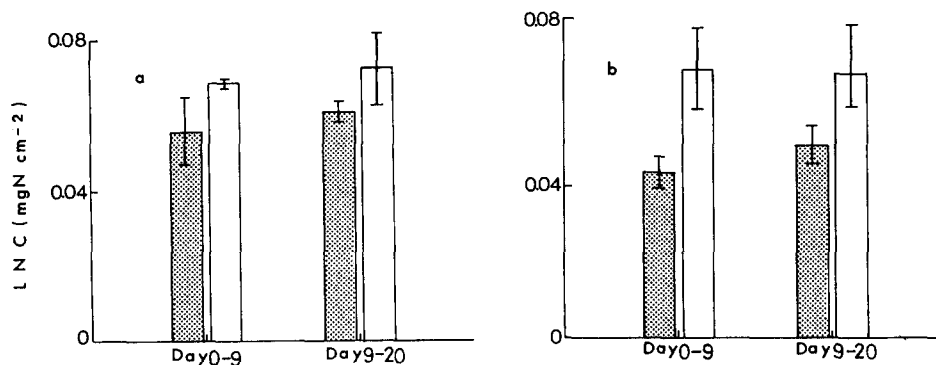
LAR was computed by dividing RGR by NAR (eqn. (2)) because LAR calculated in this way can be directly compared with parameters obtained for each growth period. However, calculated LAR was not much different from a mean of LAR obtained from actual samplings. LAR did not show any large variation at the two harvesting periods. *E. indica* showed slightly higher values than *D. adscendens* (Fig. 2). Fertilization increased LAR only slightly for both species. Thus, NAR is a main factor to determine the variations of RGR in Table 1.

NAR was further divided into the following two components, nitrogen use efficiency (NUE), which represents dry matter produced per total nitrogen contents of leaves in a plant ( $L_n$ ), and leaf nitrogen content (LNC) (Hirose, 1984), as follows.

$$\frac{1}{L} \cdot \frac{dW}{dt} = \frac{1}{L_n} \cdot \frac{dW}{dt} \times \frac{L_n}{L} \quad (4)$$

(NAR)            (NUE)            (LNC)

Nitrogen content per unit leaf area (LNC) was the mean of values determined at the beginning and end of growth period. LNC of *E. indica* remained nearly constant, irrespective of nutrient conditions and growth periods (Fig. 3). In contrast, *D. adscendens* showed larger variations depending upon the availability of nutrients; 0.056 and 0.061 mg N cm<sup>-2</sup> in fertilized condition and 0.044 and 0.051 mg N cm<sup>-2</sup> in unfertilized condition. Leaves of *E.*

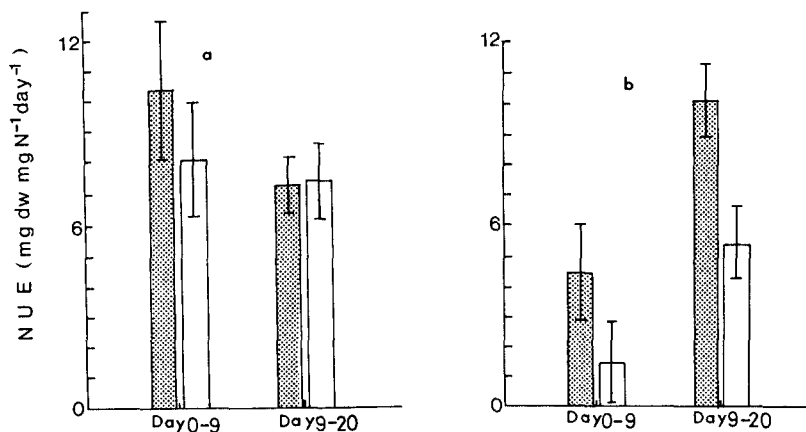


**Fig. 3** Leaf nitrogen per unit area of *D. adscendence* and *E. indica*. a) Fertilized condition; b) unfertilized condition. Dotted column for *D. adscendence* and open column for *E. indica*. Each short bar indicates a standard deviation.

*indica* always contained larger amounts of nitrogen than those of *D. adscendens*.

In NUE which was calculated from NAR and LNC using eqn. (4), both species showed great improvements of NUE under fertilized condition (Fig. 4). The sole exception was *D. adscendens* on Days 9~20, which showed a high NUE even under unfertilized condition. Fertilization treatments yielded similar NUE values for both species. Under unfertilized conditions, both species showed a consistent increase in NUE during the second growth period, and *D. adscendens* showed a particularly large NUE on Days 9~20. The data indicate that NUE was maintained at high levels in both species under fertilized condition, but were lowered under unfertilized condition, particularly in *E. indica*.

Similar analysis was done for nitrogen uptake rate as follows (Hirose, 1984):



**Fig. 4** Nitrogen use efficiency of *D. adscendence* (dotted column) and *E. indica* (open column). a) Fertilized condition; b) unfertilized condition. Each short bar represents a standard deviation.

$$\text{NUR} = \frac{dN}{dt} = \frac{N_2 - N_1}{t_2 - t_1} \quad (5)$$

Where  $N_1$  and  $N_2$  stands for the total nitrogen contents of plants at  $t_1$  and  $t_2$ , respectively. Fig. 5 compares nitrogen uptake rate (NUR), i.e. amounts of nitrogen absorbed per unit time per plant. NUR of both species increased significantly with the increase of nutrient availability. Under fertilized condition, *E. indica* showed significantly higher uptake rate than *D. adscendens* in Days 9~20 ( $P < 0.01$ ), though there was no clear difference between them in Days 0~9. On the other hand, under unfertilized condition, NUR in *D. adscendens* was significantly higher than that in *E. indica* in Days 9~20 ( $P < 0.01$ ).

NUR can further be described as product of specific absorption rate of nitrogen (SAR) and root mass (RW) as follows (Hirose, 1984):

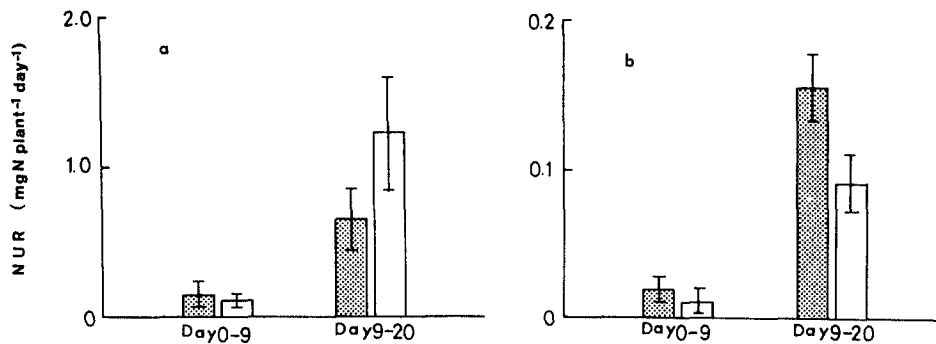
$$\frac{dN}{dt} = \frac{1}{W_r} \cdot \frac{dN}{dt} \times W_r \quad (6)$$

(NUR)    (SAR)    (RW)

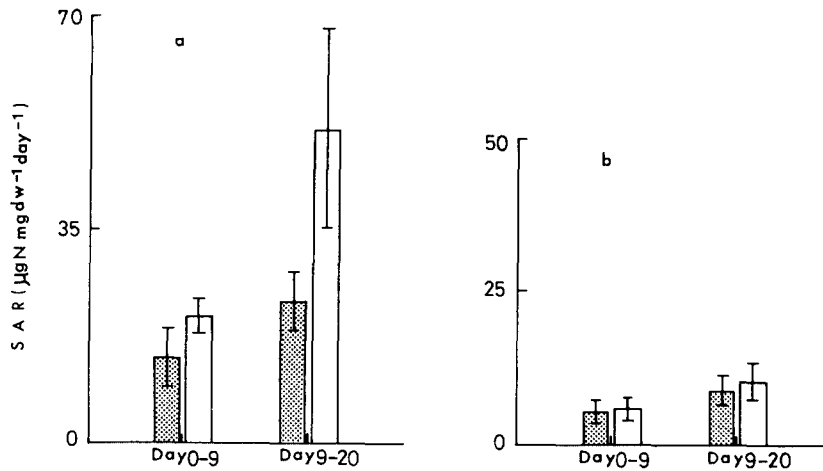
Where SAR, the amount of nitrogen absorbed per unit root dry mass per unit time, represents the efficiency of nitrogen uptake by roots (Hunt, 1982). SAR was calculated with the following equation based on the assumption of exponential increase in root mass with time.

$$\frac{1}{W_r} \cdot \frac{dN}{dt} = \frac{(\ln W_{r2} - \ln W_{r1})}{(t_2 - t_1)} \times \frac{(N_2 - N_1)}{(W_{r2} - W_{r1})} \quad (7)$$

In which  $W_{r1}$  and  $W_{r2}$  represent root mass at time  $t_1$  and  $t_2$ , respectively. In response to the improvement of nutrient availability, SAR increased significantly in both species, and



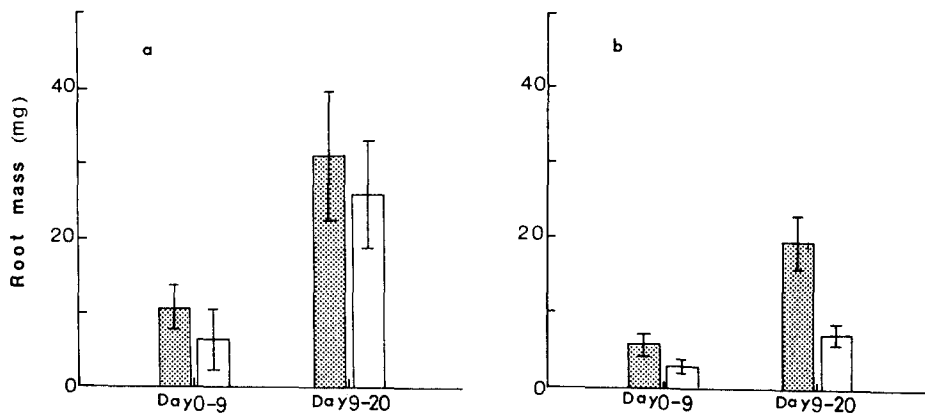
**Fig. 5** Nitrogen uptake rate of *D. adscendens* (dotted column) and *E. indica* (open column). a) Fertilized condition; b) unfertilized condition. Each short bar indicates a standard deviation. Note that the scale in the fertilized conditions is 10 times larger.



**Fig. 6** Specific absorption rate of nitrogen of *D. adscendence* (dotted column) and *E. indica* (open column). a) Fertilized condition; b) unfertilized condition. Each short bar represents a standard deviation.

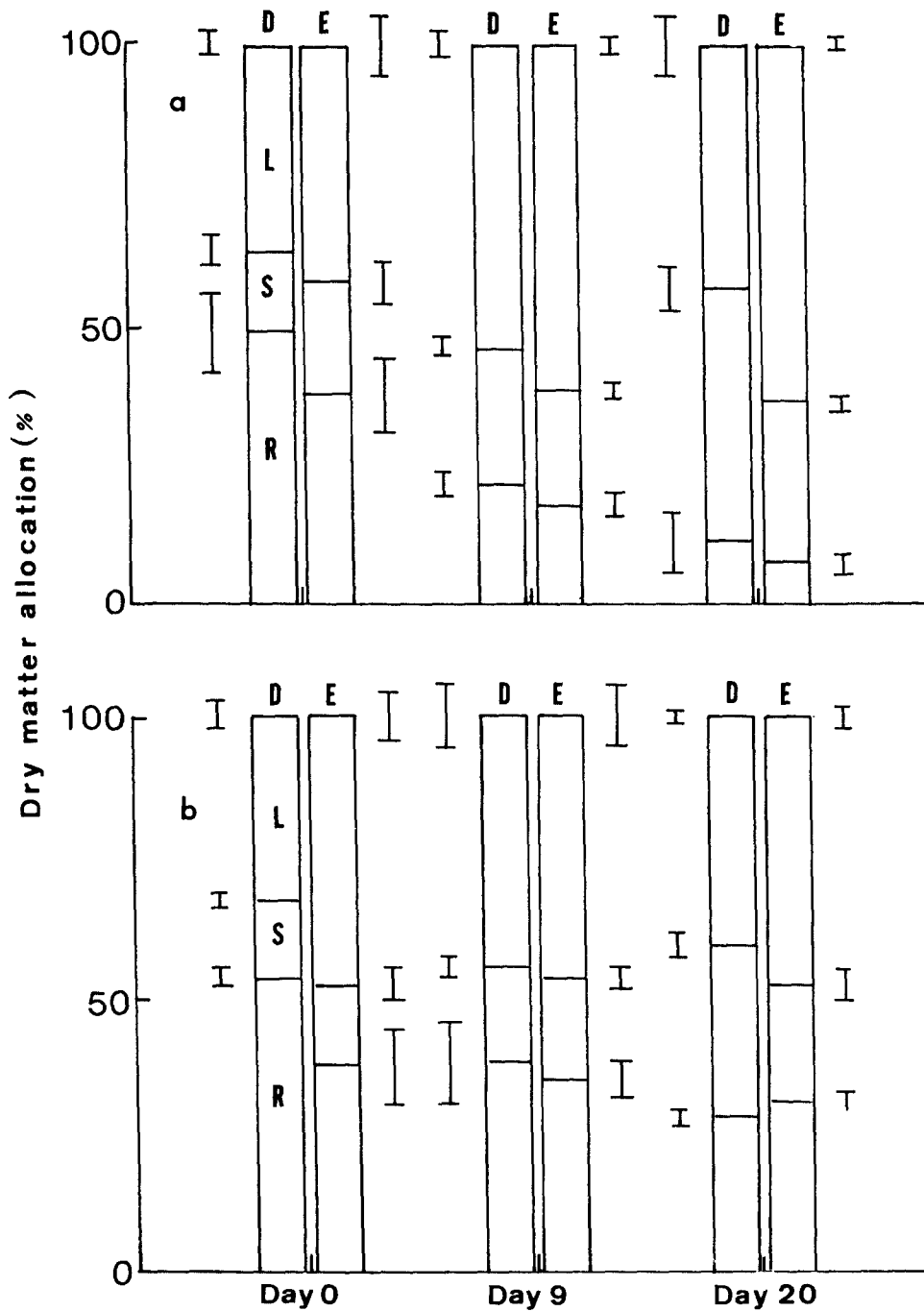
in particular in *E. indica* (Fig. 6). Differences in SAR of the two species became marked in the latter period of the experiment under fertilized condition, whereas no such a difference was noticed under unfertilized condition.

RW for each growth period was estimated by dividing NUR by SAR (eqn. 6). Fertilization greatly stimulated the root growth of both species as shown in Fig. 7. *D. adscendens* maintained larger root mass than *E. indica* throughout the experiment under both nutrient conditions. Differences between the two species were more pronounced



**Fig. 7** Root mass calculated from nitrogen uptake rate and specific absorption rate of nitrogen in *D. adscendence* (dotted column) and *E. indica* (open column). a) Fertilized condition; b) unfertilized condition. Each short bar represents a standard deviation.





**Fig. 8** Bar graphs showing relative allocation of dry matter into leaves, stems and roots. a) Fertilized condition; b) unfertilized condition. "D" and "E" at the top of each column represents, *D. adscendens* and *E. indica*, respectively. Each short bar by each column represents a standard deviation.

under unfertilized condition.

Fig. 8 illustrates dry matter allocation among different parts of plants. Differences between the two species were already observed on Day 0: about 50% of the total dry matter was allocated to roots for *D. adscendens* and to leaves for *E. indica* irrespective of fertilization treatment. Particularly, under unfertilized condition, *E. indica* maintained nearly constant allocation percentages for leaves and roots throughout the experiment, whereas *D. adscendens* increased dry matter allocated to leaves and stems with plant growth.

## DISCUSSION

Under unfertilized condition, RGR of *E. indica* was significantly lower than that of *D. adscendens* on day 9~20. Under fertilized condition, however, RGR of *E. indica* became higher than that of *D. adscendens* during the same period (Table. 1). Deficiency of available nitrogen in soil in the field has been reported to be a primary causal factor to limit plant growth (Kabaya, 1981; Kachi & Hirose, 1983). Slow growth of *E. indica* under unfertilized condition may therefore be related to deficiency of available nitrogen in soil collected from the sand dune (Park, 1989a).

The differences in RGR of *E. indica* and *D. adscendens* observed under unfertilized condition can be ascribed to difference in NAR of the two species (Fig. 1). NAR has long been thought to be relatively constant irrespective of in species (Heath and Gregory, 1938; Williams, 1946). However, recent experiments showed that there are wide variations in NAR among species, particularly, in monocots (Hunt, 1982). The present result that NAR largely varied depending upon fertilization is also contrary to the early notion.

NAR, which represents averaged net production of plants per unit leaf area, is related to photosynthetic capacity of leaves (Evans, 1972). Photosynthetic capacity of leaves is often well related to LNC (Sage and Pearcy, 1987). There are several reports which show linear relationships between exchange rates of carbon dioxide at light saturation (CER) and leaf nitrogen contents (LNC) (Field et al., 1983; Gulmon and Chu, 1981). However, the relationship at high leaf nitrogen contents is not linear in some cases (Nevins and Loomis, 1970; Gulmon and Chu, 1981). It was also shown that the ratio of CER to leaf nitrogen content (so called instantaneous nitrogen use efficiency) is higher in  $C_4$  plants than in  $C_3$  plants (Brown, 1978). Since NAR is an integration of net photosynthesis of plant for a long period of time rather than the maximal rate of photosynthesis, plots of NAR against leaf nitrogen content show a saturation-type curve with a positive interception on the abscissa. Such a relationship has been demonstrated in *Polygonum cuspidatum* by Hirose (1984). However, this type of analysis has not yet been conducted in  $C_4$  plants, to which the two plant species used here belong (Downton, 1975).

NAR is divided into NUE and LNC (Hirose, 1986). Here, NUE denotes the ratio of NAR

to LNC. In spite of its lower LNC (Fig. 3), *D. adscendens* showed higher NAR than *E. indica* under unfertilized conditions. This is ascribed to large NUE in *D. adscendens* than *E. indica*. The difference may be at least partly attributed to the fact that *D. adscendens* shows a slightly higher stomatal conductance than *E. indica* even under well-watered conditions (Park 1989b). On the other hand, larger LNC in *E. indica* than *D. adscendens* indicate that *E. indica* requires more nitrogen than *D. adscendens* to make a unit leaf area. LNC of *E. indica* was constant irrespective of nutrient conditions and growth periods, whereas that of *D. adscendens* was variable depending upon nitrogen availability (Fig. 3). Thus, *E. indica* has a lower plasticity than *D. adscendens* in response to nutrient conditions. Because an excess nitrogen accumulation in leaves reduces NUE, lower NUE in *E. indica* may also be attributed to its high LNC.

Under unfertilized condition, *D. adscendens* exhibited higher NUR than *E. indica*. Generally, NUR is given as the product of SAR and RW (Hirose, 1984). The result of this study clearly shows that the different NUR of the two species under unfertilized condition is due to the differences in root mass between *E. indica* and *D. adscendens*. Under nutrient-stressed conditions, plants usually adjust their dry matter allocation so as to maximize nutrient uptake (Chapin, 1980; Hirose, 1987). The two species showed larger dry matter allocation to roots under unfertilized condition than under fertilized condition. In particular, *D. adscendens* allocates more dry matter to roots than *E. indica* in earlier stage of the experiment, although the difference become smaller in the later stages (Fig. 8). Consequently, *D. adscendens* developed a larger root system than *E. indica* (Fig. 7), which in turn resulted in larger NUR in *D. adscendens* than *E. indica*. Fig. 6 shows clearly that SAR does not contribute to the difference in NUR between *D. adscendens* and *E. indica*.

Takano and Tsunoda (1971) suggested that there are two types of rice plants which have different nitrogen requirement for the grain yield in Japan; one is japonica type which requires relatively large quantities of nitrogen to increase crop yield and the other is indica type which requires less nitrogen than japonica type. The present work shows that *E. indica* requires more nitrogen for their leaf growth than *D. adscendens*, like the japonica type of rice. This difference in nitrogen requirements between the two species corresponds closely with their habitat where they occur (Park, 1989a).

In conclusion, *D. adscendens* showed larger RGR than *E. indica* under unfertilized conditions. This could be attributed to higher NAR in *D. adscendens*. In relation to nitrogen use, nitrogen in the leaf was used more efficiently in photosynthesis in *D. adscendens* than in *E. indica*, while the efficiency of absorption in roots (SAR) did not differ between these two species. The larger allocation of dry matter to roots at small seedling stage in *D. adscendens* seems to play an important role in obtaining enough nitrogen for the continuation of considerable growth even under unfertilized conditions.

## 적 요

해안 사구에서의 바랭이와 왕바랭이의 생장의 차를 규명하기 위해 영양실험을 실시하고, 사구에서 식물생장에 가장 크게 영향을 미치는 질소의 흡수와 이용에 착안하여 생장해석을 실시하였다. 생장해석의 결과, RGR, NAR은 시비조건에서는 두 종 사이에 유의차가 없었다. 그러나 무시비구에서는 바랭이의 RGR과 NAR이 왕바랭이의 RGR과 NAR 보다 높게 나타났다. 바랭이의 잎의 질소 함량은 무시비구에서  $0.044 \sim 0.051 \text{ mg cm}^{-2}$ , 시비구에서  $0.056 \sim 0.061 \text{ mg cm}^{-2}$ 로 이용할 수 있는 질소량에 따라 잎의 질소 함량도 변화했다. 이와는 반대로 왕바랭이는 시비조건에 관계없이  $0.069$ 에서  $0.073 \text{ mg cm}^{-2}$ 로 거의 일정한 질소함량을 나타내었다. 질소이용효율도 시비구에서는 두 종사이에 차이가 없었으나 무시비구에서는 바랭이가 높게 나타났다.

무시비구에서의 질소흡수속도는 바랭이가 높았다. 이것은 질소흡수속도의 두 요소인 specific absorption rate(SAR)와 root mass(RW) 중 두종에서 비슷한 값을 나타낸 SAR 보다 바랭이에서 큰 값을 나타낸 RW가 질소흡수속도에 더욱 크게 기여한 것을 나타낸다. 또한 바랭이의 RW가 왕바랭이보다 큰 것은 실생초기의 물질분배에 있어서 왕바랭이가 건물량의 많은 부분을 잎에 분배하는데 비해 바랭이는 뿌리에 많이 분배했기 때문이다. 이러한 결과는 빈영양 토양에서의 식물생장에 실생초기의 물질분배 패턴이 큰 영향을 미친다는 것을 나타내고 있다.

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