PHOTOSYNTHETICA 37 (1): 123-130, 1999

Differences in field gas exchange and water relations between a C_3 dicot (*Plantago asiatica*) and a C_4 monocot (*Eleusine indica*)

T. KOBAYASHI*, K. OKAMOTO, and Y. HORI

Laboratory of Ecology, Department of Environmental Sciences, Faculty of Science, Ibaraki University, Mito 310-8512, Japan

Abstract

Field gas exchange and water potential in the leaves of a C_3 dicot, *Plantago asiatica* L., and a C_4 monocot, *Eleusine indica* Gaertn., which dominate in trampled vegetation in eastern Japan were surveyed during the growing periods for two consecutive years. Net photosynthetic rate (P_N) of *E. indica* increased with photosynthetic photon flux density (PPFD) and leaf temperature (T_L). P_N was not saturated at PPFDs above 1500 μmol m^{-2} s^{-1} and at T_L above 30 °C. On a sunny day in mid summer, maximum P_N was two times higher in *E. indica* than in *P. asiatica* [42 *vs*. 20 μmol(CO_2) m^{-2} s^{-1}], but their transpiration rate (E) and the leaf water potential (Ψ_L) were similar. Soil-to-leaf hydraulic conductance, which probably plays a role in water absorption from the trampled compact soil, was higher in *E. indica* than in *P. asiatica*. The differences in photosynthetic traits between *E. indica* explain why *E. indica* communities more commonly develop at heavily trampled sites in summer than the *P. asiatica* communities.

Additional key words: diurnal pattern; intercellular CO_2 concentration; leaf conductance; leaf water potential; micro-habitat; photosynthesis; seasonal dominance; soil-to-leaf hydraulic conductance; trampling tolerance; transpiration.

Received 21 June 1999, *accepted* 4 November 1999.

**Present address*: Japan Science and Technology Corporation, The Center for Forest Decline Studies, Hiroshima Technoplaza, 3-13-26 Kagamiyama, Higashi-Hiroshima 739-0046, Japan. Fax: +81 824 20 0520; e-mail: eco@ipc.hiroshima-u.ac.jp

Abbreviations: C_i - intercellular CO_2 concentration; E - transpiration rate; g_L - leaf conductance to water vapour; P_{max} - maximum net photosynthetic rate; P_N - net photosynthetic rate; PPFD - photosynthetic photon flux density; T_L - leaf temperature; VPD - leaf-to-air vapour pressure deficit; Ψ_L - leaf water potential.

Acknowledgements: We thank Profs. Dr. Y. Yamamura and Dr. M. Shiyomi for advice and encouragement in the course of this study. Dr. S. Kawarasaki, Mr. K. Maeda, Ms. A. Maeda, and Dr. K. Urayama provided invaluable field assistance. Thanks are also due to Dr. A. Ishida, Mr. H. Ozawa, and Prof. Dr. H. R. Bolhàr-Nordenkampf for critical advice and valuable suggestions. The study site was kindly made available by Mito City.

Introduction

The perennial C_3 dicot *Plantago asiatica* and the summer-annual C_4 monocot *Eleusine indica* are trampling tolerants (Ikeda and Okutomi 1990, 1992, 1995, Kobayashi *et al.* 1999) and dominate trampled vegetation in the North-Kanto district, eastern Japan (Okuda 1986). These species grow sympatrically but show different phenologies. The growing period of *P. asiatica* is early spring to late autumn, and the plant flowers continuously during most of this period (Yamazaki 1981). In contrast, *E. indica* has a shorter growing period (early summer to autumn), and flowers after mid summer (Ohwi 1982). Therefore, matter production in *E. indica* should be much more strongly supported by sunlight and high temperature than it is in *P. asiatica.*

Since trampled vegetation is low and shows poor coverage, not only does the temperature near the soil surface rise markedly (up to 40-50 °C), but also soil drying accompanied by the loss of free water occurs at open habitats in summer (Tachibana 1976, Kobayashi *et al.* 1997). Therefore the dominant species at trampled habitats may tolerate drought. However, under simulated soil drying, seedling survival of trampling tolerants (*P. asiatica* and *E. indica*) was lower than that of trampling intolerants [the perennial C_3 dicot *Artemisia princeps* Pamp. and the summer-annual C_4 monocot *Digitaria adscendens* (H.B.K.) Henr.], which dominate areas adjacent to trampled habitats (Kobayashi and Hori 1999). These observations suggest that plants can not tolerate both trampling and drought.

In the present study, we examined gas exchange and water relations of two trampling tolerants, *P. asiatica* and *E. indica*, in the field over two consecutive years. We also discuss the differences in seasonal dominance and micro-distribution between these two species.

Materials and methods

The study site was an open trampled habitat at a flat playground in Mito City, North-Kanto district, eastern Japan (36°23'N, 140°28'E, 20 m a.s.l.). The vegetation was dominated by *P. asiatica* but it was over-dominated by *E. indica* in mid-summer. Subordinate species were *Zoysia japonica, Poa annua, Polygonum aviculare,* and *Digitaria violascens*. The hardness at the soil surface was *ca.* 235 000 kg m^{-2}, reflecting frequent trampling in this site. The soil water potential remained above -0.1 MPa (free water available) during the growing season (spring to autumn).

Microclimatic values from sunrise to sunset were measured on 20 June, 7 August, and 3 October in 1995, and on 26 May, 27 June, 8 August, and 10 October in 1996. Photosynthetic photon flux density (PPFD, 400-700 nm) was measured with a quantum sensor (*IKS-25, Koito*, Yokohama, Japan). Leaf and air temperatures were measured with copper-constantan thermocouples (*K*-type, 0.1 mm in diameter, *Hayashi-Denko*, Tokyo, Japan). Wind speed was measured with a hot wire anemometer (model *6611*, *Kanomax*, Suita, Japan). These values were stored at 1 min intervals in a data-logger (*Thermodac-E, Eto-Denki*, Tokyo, Japan). Relative air humidity was measured with an Assman psychrometer (*THERM 2286-2, Nippon Medical & Chemical Instruments*, Osaka, Japan) and recorded hourly. Leaf-to-air vapour pressure deficit (VPD) was calculated using Goff-Gratch formation for saturated water vapour pressure (Goff and Gratch 1946).

Diurnal changes in gas exchange and leaf water potential during the above measurements were measured under field conditions, using a portable gas exchange system (*LI-6200, Li-Cor*, Lincoln, NE, USA) and pressure bomb (*PMS-600*, Plant Moisture Stress, Corvallis, OR, USA; Boyer 1995). Fully-developed leaves were chosen for measurements of four or five plants. For the gas exchange measurements in the early morning, dew on the leaf surface was gently wiped with soft paper before measurements. For the measurements of leaf water potential (Ψ_L), the leaves were sealed to the pressure bomb. In *P. asiatica*, the leaves were sealed around the petiole and in *E. indica*, the leaves were sealed around the blade. Leaf intercellular CO_2 concentration (C_i), leaf transpiration rate (E), and leaf conductance to water vapour (g_L) were determined according to Field *et al.* (1989) and Pearcy *et al.* (1989). Only *P. asiatica* was measured from May to June because the seedlings of *E. indica* occurred after mid-June.

Results and discussion

Diurnal patterns: The diurnal pattern of gas exchange and leaf water potential were clearly different between *P. asiatica* and *E. indica* on 7 August in 1995 (a clear day in mid-summer). On this day, the maximum PPFD reached 2000 μmol m^{-2} s^{-1} at about noon (Fig. 1). Passage of a cloud mass in the sky temporarily decreased PPFD at around 10:00 h. Air temperature increased gradually until 13:00 h and reached a maximum of 34 °C. Soil surface temperature rose considerably (to 50 °C). The difference in air and leaf temperature (T_L) was less than 2 to 3 °C in both species during midday. VPD increased to 2.3 kPa at 13:00 h. In the afternoon, VPD was slightly greater in *E. indica* because of its higher T_L. The wind was relatively calm (<3.5 m s^{-1}) throughout the day.

P_N increased in the morning and peaked at about noon (Fig. 2). No midday depressions of P_N were found in either *E. indica* or *P. asiatica*. Maximum photosynthetic rate (P_{max}) was two times higher in *E. indica* than in *P. asiatica* [42 *vs.* 20 μmol(CO_2) m^{-2} s^{-1}]. g_L peaked in the early morning (08:00) and decreased gradually in both species. *P. asiatica* had g_L values above 0.5 mol m^{-2} s^{-1} from 09:00 to 16:00 h and showed higher values than did *E. indica* over most of the day. Minimum C_i was 251 μmol mol^{-1} in *P. asiatica* and much lower (137 μmol mol^{-1}) in *E. indica*. E peaked at 14:00 h and there were little obvious differences between *P. asiatica* and *E. indica* [a maximum of 14 mmol(H_2O) m^{-2} s^{-1}]. Diurnal Ψ_L values were also similar in both species. Ψ_L was decreased in the morning and reached a minimum at 13:00 h (-1.8 MPa).

Differences in light and temperature responses of photosynthesis between C_3 and C_4: The photosynthetic traits of each species in 1996 were similar to those observed in 1995. In *P. asiatica*, P_N saturated at a PPFD of 500-1000 µmol m^{-2} s^{-1} and a T_L of *ca.* 26 °C (Fig. 3). In contrast, in *E. indica* P_N was still not saturated at PPFDs above 1500 µmol m^{-2} s^{-1} and at T_L above 30 °C. P_N more strongly depended on irradiance and T_L in the C_4 monocot *E. indica* than in the C_3 dicot *P. asiatica* (Fig. 3). These results were consistent with the general differences in photosynthetic traits between C_3 and C_4 plants (Ishikawa *et al.* 1990, 1996, Larcher 1995, Lambers *et al.* 1998). In addition, the present results of field measurements paralleled our previous laboratory-based findings, *i.e.*, that photosynthesis of *E. indica* is much more dependent on PPFD and T_L than photosynthesis of *P. asiatica* (Kobayashi and Hori 1999).

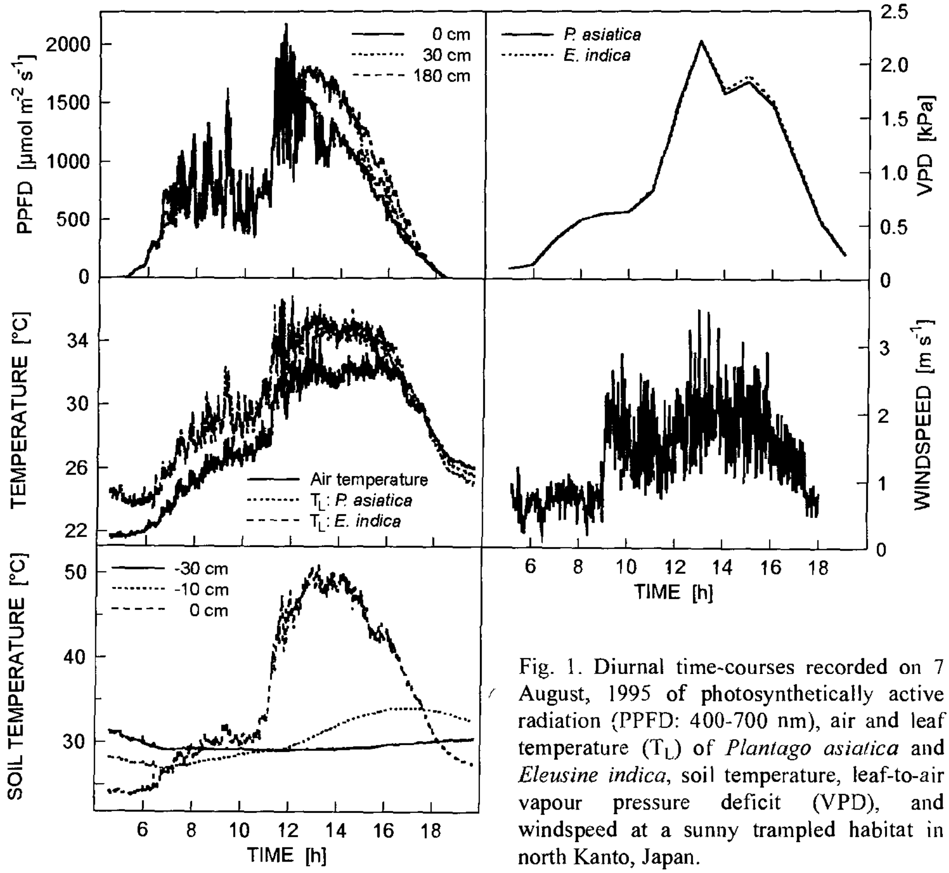

Fig. 1. Diurnal time-courses recorded on 7 August, 1995 of photosynthetically active radiation (PPFD: 400-700 nm), air and leaf temperature (T_L) of *Plantago asiatica* and *Eleusine indica*, soil temperature, leaf-to-air vapour pressure deficit (VPD), and windspeed at a sunny trampled habitat in north Kanto, Japan.

Water use in a C_4 trampling tolerant: A more gentle slope of the regression line between *E* and Ψ_L represents a higher soil-to-leaf hydraulic conductance when soil water potential is high (Tinklin and Weatherley 1966, Jones 1992, Kobayashi 1994, Ito *et al.* 1995). The hydraulic conductance was higher in *E. indica* than in *P. asiatica*

(Fig. 4). When *E. indica* is subjected to trampling, its culms and roots develop larger cell internal spaces surrounding the vascular bundle (Takahashi 1994). Such anatomical traits of *E. indica* might contribute to an effective water passage through the plant. Increasing soil-to-leaf hydraulic conductance probably plays an important role in water absorption from trampled compact soil with a low water conductivity.

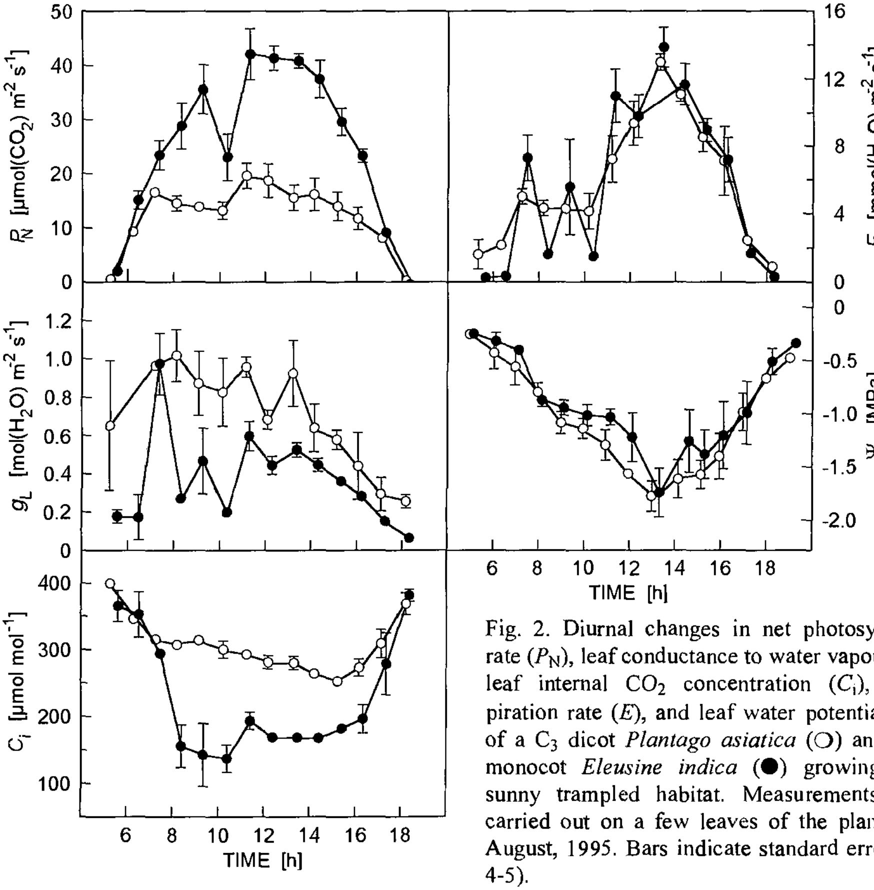

Fig. 2. Diurnal changes in net photosynthetic rate (P_N), leaf conductance to water vapour (g_L), leaf internal CO$_2$ concentration (C_i), transpiration rate (E), and leaf water potential (Ψ_L) of a C$_3$ dicot *Plantago asiatica* (○) and a C$_4$ monocot *Eleusine indica* (●) growing in a sunny trampled habitat. Measurements were carried out on a few leaves of the plant on 7 August, 1995. Bars indicate standard error (n = 4-5).

The anatomical characteristics of *E. indica* that are related to trampling tolerance might also influence other aspects of its water relations. On each day of the measurements, the Ψ_L values of *E. indica* and *P. asiatica* decreased to a similar extent at midday (Fig. 5). Kobayashi and Hori (1998) reported that the leaves of *E. indica*, which have thick and/or rigid cell-walls, based on their high bulk modulus of elasticity, can reduce Ψ_L rapidly with a slight decrease in leaf water content. Under high T_L and VPD in summer, transpiration of *E. indica* must be as great as that of *P. asiatica* (see Fig. 2) but in *E. indica* water loss from the leaf would be partly compensated by the lower Ψ_L, which increases the water uptake ability in the leaf. However, in order to maintain high *E*, the soil water content must be sufficient.

E. indica even though it is a C_4 plant. The growth of *E. indica* plants is much more affected by unwatered treatment than is the growth of *Digitaria adscendens* (Park 1989, 1990), which is a C_4 monocot that is trampling intolerant (Ikeda and Okutomi 1990, Kobayashi *et al.* 1999).

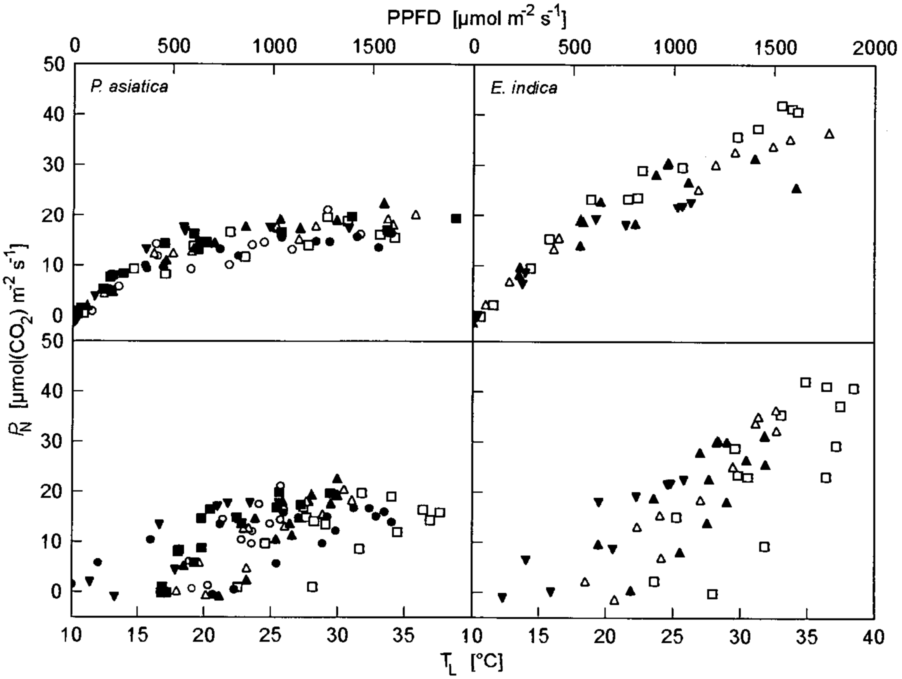

Fig. 3. Photosynthetic responses to photosynthetic photon flux density (PPFD) and to leaf temperature (T_L) of a C_3 dicot *Plantago asiatica* and a C_4 monocot *Eleusine indica* recorded during 7 d (○ - 20 June 1995; □ - 7 August 1995; Δ - 3 October 1995; ● - 26 May 1996; ■ - 27 June 1996; ▲ - 8 August 1996; ▼ - 10 October 1996) of the growing periods.

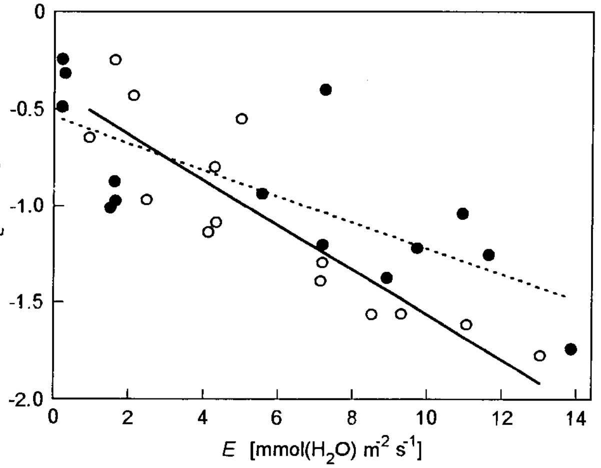

Fig. 4. Transpiration rate (E) *vs.* leaf water potential (Ψ_L) for *Plantago asiatica* (○) and *Eleusine indica* (●) on 7 August, 1995. The slope of regression line between E and Ψ_L represents the soil-to-leaf hydraulic resistance. Ψ_L (*P. asiatica*) = -0.4 - 0.12 E (r^2 = 0.79, n = 14); Ψ_L (*E. indica*) = -0.5 - 0.07 E (r^2 = 0.57, n = 14).

Seasonal dominance and micro-habitats: The differences in photosynthetic traits between *E. indica* and *P. asiatica* well explain the differences between these trampling-tolerants in seasonal dominance and micro-habitats. In mid summer, *E. indica* assimilates effectively and thus would grow vigorously under high irradiance and high temperature. On the other hand, in *P. asiatica*, the diurnal patterns of P_N were roughly constant throughout the growing season (values not shown) and P_{max} was similar during two successive years (see Fig. 3). This enables *P. asiatica* to produce biomass successfully for a longer growing period. Trampling tolerance, which is characterized by a larger plant size and a higher growth rate under trampling, was larger in *E. indica* than in *P. asiatica* due to the tougher organs in *E. indica* (Kobayashi *et al.* 1999). These results support the finding of Okuda (1986) that *E. indica* communities develop more often at heavily trampled sites in summer than do the *P. asiatica* communities.

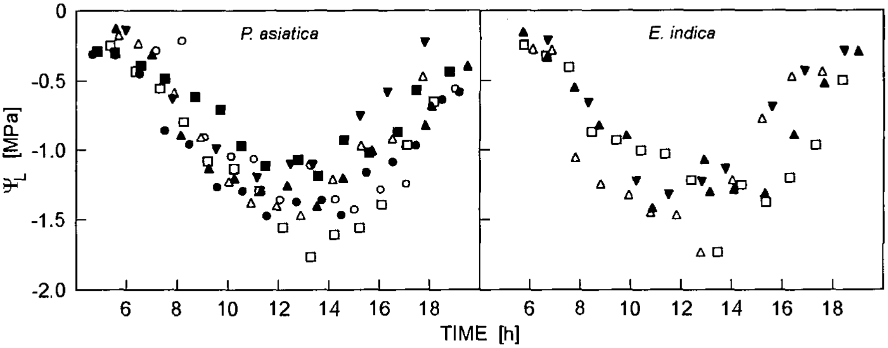

Fig. 5. Diurnal changes in leaf water potential (Ψ_L) of *Plantago asiatica* and *Eleusine indica* recorded during 7 d of the growing periods in 1995 and 1996 (for symbols see legend to Fig. 3).

References

Boyer, J.S.: Measuring the Water Status of Plants and Soils. - Academic Press, San Diego 1995.

Field, C.B., Ball, J.T., Berry, J.A.: Photosynthesis: principles and field techniques. - In: Pearcy, R.W., Ehleringer, J., Mooney, H.A., Rundel, P.W. (ed.): Plant Physiological Ecology. Pp. 209-253. Chapman & Hall, London 1989.

Goff, J.A., Gratch, S.: Low-pressure properties of water. - Trans. amer. heat. vent. Eng. **52**: 95-121, 1946.

Ikeda, H., Okutomi, K.: Effects of human trampling and multispecies competition on early-phase development of a tread community. - Ecol. Res. **5**: 41-54, 1990.

Ikeda, H., Okutomi, K.: Effects of species interactions on community organization along a trampling gradient. - J. Veg. Sci. **3**: 217-222, 1992.

Ikeda, H., Okutomi, K.: Effects of trampling and competition on plant growth and shoot morphology of *Plantago, Eragrostis* and *Eleusine* species. - Acta bot. neerl. **44**: 151-160, 1995.

Ishikawa, S.-I., Furukawa, A., Oikawa, T.: Photosynthetic responses to drought conditions in three coastal dune plants in relation to their zonal distribution. - Aust. J. Bot. **44**: 381-391, 1996.

Ishikawa, S.-I., Oikawa, T., Furukawa, A.: Photosynthetic characteristics and water use efficiency of three coastal dune plants. - Ecol. Res. **5**: 377-391, 1990.

Ito, S., Sakuta, K., Gyokusen, K.: Distribution of hydraulic resistance in seedlings, sprouts and an adult tree of *Pasania edulis* Makino. - Ecol. Res. **10**: 143-149, 1995.

Jones, H.G.: Plants and Microclimate. 2nd Ed. - Cambridge University Press, Cambridge 1992.

Kobayashi, T.: [Studies on ecology and water relations of revegetation plants in the Mu-Us sandy district, China.] - Tech. Bull. Fac. Hort. Chiba Univ. **48**: 239-381, 1994. [In Jap.]

Kobayashi, T., Hori, Y.: [Comparative study of photosynthesis and water relation traits between *Eleusine indica* and *Digitaria adscendens* (Poaceae) with special reference to a difference in their dominance along a trampling intensity.] - J. Weed Sci. Tech. **43** (Suppl.): 264-265, 1998. [In Jap.]

Kobayashi, T., Hori, Y.: Photosynthesis and seedling survival of weeds with different trampling susceptibilities under contrasting light and water conditions. - J. Weed Sci. Tech. **44**: 195-204, 1999.

Kobayashi, T., Hori, Y., Nomoto, N.: Effects of trampling and vegetation removal on species diversity and micro-environment under different shade conditions. - J. Veg. Sci. **8**: 873-880, 1997.

Kobayashi, T., Ikeda, H., Hori, Y.: Growth analysis and reproductive allocation of Japanese forbs and grasses in relation to organ toughness under trampling. - Plant Biol. **1**: 445-452, 1999.

Lambers, H., Chapin, F.S., Pons, T.L.: Plant Physiological Ecology. - Springer, Berlin 1998.

Larcher, W.: Physiological Plant Ecology. 3rd Ed. - Springer, Berlin 1995.

Ohwi, J.: [Poaceae.] - In: Satake, Y., Ohwi, J., Kitamura, S., Watari, S., Tominari, T. (ed.): Wild Flowers of Japan. Herbaceous Plants I. Monocotyledoneae. Pp. 85-126. Heibonsha, Tokyo 1982. [In Jap.]

Okuda, S.: [Trittgesellschaften.] - In: Miyawaki, A. (ed.): Vegetation of Japan. Vol. 7. Kanto. Pp. 269-272. Shibundo, Tokyo 1986. [In Jap.]

Park, Y.-M.: Factors limiting distribution of *Digitaria adscendens* and *Eleusine indica* on coastal sand dunes in Japan. - Ecol. Res. **4**: 131-144, 1989.

Park, Y.-M.: Effects of drought on two grass species with different distribution around coastal sand-dunes. - Func. Ecol. **4**: 735-741, 1990.

Pearcy, R.W., Schulze, E.-D., Zimmermann, A.E.: Measurement of transpiration and leaf conductance. - In: Pearcy, R.W., Ehleringer, J., Mooney, H.A., Rundel, P.W. (ed.): Plant Physiological Ecology. Pp. 137-160. Chapman & Hall, London 1989.

Tachibana, H.: Changes and revegetation in sphagnum moors destroyed by human treading. - Ecol. Rev. **18**: 133-210, 1976.

Takahashi, K.: [Adaptive strategies for trampling in weeds at school grounds.] - Bull. Studies Okayama-Asahi **15**: 57-68, 1994. [In Jap.]

Tinklin, R., Weatherley, P.E.: On the relationship between transpiration rate and leaf water potential. - New Phytol. **65**: 509-517, 1966.

Yamazaki, T.: [Plantaginaceae.] - In: Satake, Y., Ohwi, J., Kitamura, S., Watari, S., Tominari, T. (ed.): Wild Flowers of Japan. Herbaceous Plants III. Sympetalae. Pp. 85-126. Heibonsha, Tokyo 1981. [In Jap.]