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Effects of trampling and competition on plant growth and shoot morphology of *Plantago, Eragrostis* and *Eleusine* species

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SUMMARY

Plant growth and shoot morphological patterns of three weeds, *Plantago asiatica, Eragrostis ferruginea* and *Eleusine indica*, were compared between monoculture and multispecies mixed culture along a trampling gradient. Total dry weights of these species were markedly lower in mixed culture than those in monoculture at all trampling levels, indicating intense multispecies competition. Differences in the total dry weights between monoculture and mixed culture, however, decreased with increasing trampling intensity, suggesting that trampling reduces the intensity of competition from neighbours. Differences in sizes and numbers of shoots and leaves were significant between the target species but there were little differences in their responses to trampling and multispecies competition. In response to trampling in monoculture, the maximum lengths of leaves and shoots decreased but the numbers of leaves and tillers increased significantly as trampling intensity increased. In response to competition, both the lengths and numbers of leaves and tillers were significantly smaller in mixed culture than in monoculture. These results suggest that there is a trade-off relationship between trampling tolerance and competitive ability, and these species prefer less-competitive habitats resulting from trampling.

Key-words: competitive ability, morphological response, trade-off, trampling tolerance, tread community.

INTRODUCTION

Trampling is one of the important factors affecting floristic composition in semi-natural grasslands and tread communities occur in heavily trampled habitats such as footpaths (e.g. Liddle & Greig-Smith 1975b; Tüxen 1977; Mucina *et al.* 1991). Blom (1977) investigated the effects of trampling and soil compaction on seedling establishment of *Plantago* species; *P. major* and *P. media* showed higher tolerance to trampling but relatively high mortality in the untrampled turves with dense vegetation. Pradhan &

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Nomenclature: Ohwi & Kitagawa (1983).

Table 1. Trampling treatments and their terminology

Trampling level	T0	T1	T2	T3	T4
No. tramplings per day	0	1	1	1	4
No. trampling days per week	0	0·5	1	4	4

Tripathi (1983) revealed that trampling reduced the growth of *Paspalum dilatatum*, superior species with an erect form under no trampling, much more than that of *Trifolium repens* and caused the coexistence of these two species. In our early study, we also found that tread community species such as *Plantago asiatica* were tolerant to trampling but markedly suppressed by an erect herb, *Ambrosia artemisiifolia* var. *elatior*, under no trampling (Ikeda & Okutomi 1990). Therefore, it can be hypothesized that there is a trade-off relationship between trampling tolerance and competitive ability; thus, the species tolerant to trampling have inferior competitive abilities under low trampling but predominate in plant communities in heavily trampled habitats.

To test this hypothesis, we carried out experimental studies in which plant growth and shoot morphological patterns were compared between monoculture and multispecies mixed culture along a trampling gradient and examined the relative importance of trampling and competition on the organization of a tread community. We used three weeds, *Plantago asiatica, Eragrostis ferruginea* and *Eleusine indica*, which are common species of tread communities developed on dry-mesic soils in Japan (Miyawaki 1964; Okuda 1978; Okutomi *et al.* 1987). Total vegetation covers of the tread communities vary markedly from 30 to 90%. *P. asiatica* is a perennial herb and *Er. ferruginea* is a perennial grass, occurring in various trampled and open habitats such as footpaths and school grounds. *El. indica* is an annual grass characteristic of habitats more heavily trampled than the formers, adjacent to bare grounds (Okuda 1978; Okutomi *et al.* 1987).

MATERIALS AND METHODS

The experimental site was an abandoned field in the farm of Tokyo University of Agriculture and Technology, Tokyo, Japan (35°41′N and 139°29′E). Annual mean air temperature and precipitation measured at the Farm in the experimental year, 1986, were 15·2°C and 1458 mm, respectively (Japan Meteorological Agency 1987), and the soil type of the site was 'andosol' originated from volcanic ash (National Land Agency of Japan 1976). Prior to the experiments, the field was well ploughed and all plant parts were removed by hand, although buried seeds were left in the soil (Ikeda & Okutomi 1990). We arranged the experimental quadrats (1 m^2) at random in the site.

Table 1 shows the trampling treatments. On 25 April 1986, we began the treatment for each quadrat. 'Trampling' was carried out by one man weighing about 65 kg with flat, rubber-soled shoes (*c.* 0·34 kg cm^{-2}). One 'trampling' involved subjecting the entire area of the quadrat to equal trampling.

We used monoculture (three target species) and mixed culture within each trampling level. In mixed culture, 500 seeds of each of seven species were sown by hand into each experimental quadrat on 23–25 April 1986. These were composed of six tread community species and a non-tread community species, *A. artemisiifolia* var. *elatior* (Table 2). In monoculture, 500 seeds of either *P. asiatica, Er. ferruginea* or *El. indica*

Table 2. Species used in monocultures[1] and mixed cultures[2], and their ecological characteristics: a, annual; w, winter annual; p, perennial; g, grass; h, herb

Plant species	Life history	Community
Eleusine indica[1,2]	ag	ED
Plantago asiatica[1,2]	ph	EP
Eragrostis ferruginea[1,2]	pg	EP
Pennisetum alopecuroides[2]	pg	EP, RH
Digitaria violascens[2]	ag	ED
Poa annua[2]	wg	EP, ED
Ambrosia artemisiifolia var. *elatior*[2]	ah	RH

EP, Eragrostio ferrugineae-Plantaginetum asiaticae (Miyawaki 1964).
ED, Eleusino indicae-Digitarietum violascentis (Okuda 1978).
RH, roadside herb community.

were sown by hand into each experimental quadrat on 23–24 April 1986. In the monocultures, the emerging seedlings of other species were removed by hand throughout the experiment. No seedlings were removed from the mixtures, not even those from seed bank species.

In September 1986, we dug up all plants including their roots within a subquadrat (0·5 m × 0·5 m) in the centre of the experimental quadrat. Then we measured shoot length, tiller number, maximum leaf length and leaf number of all plants, and weighed them including their roots after drying at 85°C for more than 48 h.

We also monitored the soil hardness and the water content of surface soils every 2 weeks. Soil hardness (kg cm^{-2}) was measured using a Yamanaka soil hardness tester (Yamamura Co. Ltd, Japan, Model YH-62) with 20 replications for each trampling level. To monitor the soil water content, surface soils (0–2 cm depth) were systematically sampled on the outside of the subquadrats with five replications for each trampling level. Water content (% dry weight) was determined by drying the soils at 105°C for more than 24 h.

RESULTS

Soil physical properties

Soil hardness increased significantly with increasing trampling intensity (Fig. 1a; $P<0{\cdot}01$ using Friedman's test). It also varied seasonally with a maximum value in August and the fluctuation of soil hardness was greater as trampling intensity increased (Fig. 1a). The trampling treatments had also significant effects on the soil water contents when the first (25 April, prior to trampling treatments) and second (13 May) data were excepted (Fig. 1b; $P<0{\cdot}05$ using Friedman's test).

Plant growth patterns

In monoculture, there were significant effects of trampling on the shoot length, maximum leaf length, tiller number and leaf number (Table 3; $P<0{\cdot}01$ using two-way ANOVA). As trampling intensity increased, the shoot length and maximum leaf length decreased (Fig. 2) but the numbers of tillers and leaves increased (Figs 3 and 4). There were also significant interactions between effects of trampling and species on the numbers of tillers and leaves (Table 3; $P<0{\cdot}01$ using two-way ANOVA). Only for *Eleusine*,

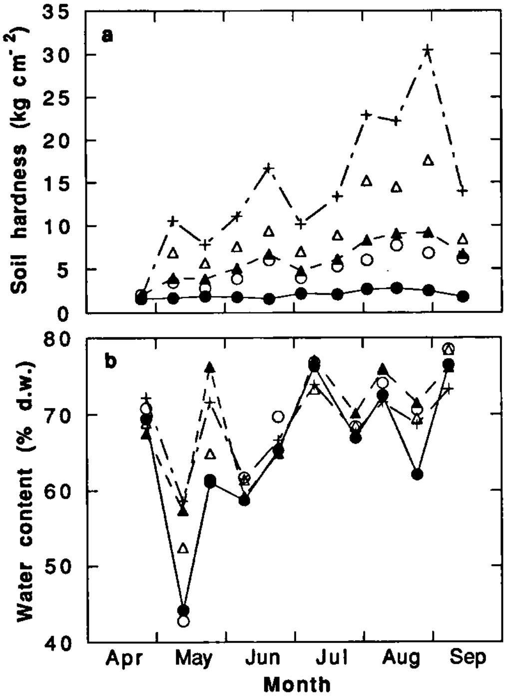

Fig. 1. Seasonal changes in mean soil hardness (a, n=20) and mean water content of surface soil (b, n=5) at five trampling levels: T0 (●, no trampling), T1 (○, one trampling every 2 weeks), T2 (▲, one trampling every week), T3 (△, four tramplings every week) and T4 (+, 16 tramplings every week).

Table 3. Results of two-way ANOVA testing the effects of trampling, species and trampling × species interaction on the shoot length, maximum leaf length, tiller number and leaf number in monoculture

		P			
		Length		Number	
Effects	d.f.	Shoot	Leaf	Tiller	Leaf
Trampling (A)	4	<0·01	<0·01	<0·01	<0·01
Species (B)	2	<0·01	<0·01	<0·01	<0·01
A × B	8	0·20	0·13	<0·01	<0·01
Error	240				

no significant effect of trampling was observed on the number of tillers because of the high variance in the numbers (Fig. 3; P=0·16 using one-way ANOVA). These results indicate that trampling reduced the leaf and tiller sizes of these species but enhanced their numbers.

On the other hand, there were significant effects of culture on both the lengths and numbers (Table 4; P<0·01 using three-way ANOVA); they were smaller in mixed culture than in monoculture (Figs 2–4). There were also significant interactions between the effects of culture and species on the shoot length and maximum leaf length (Table 4;

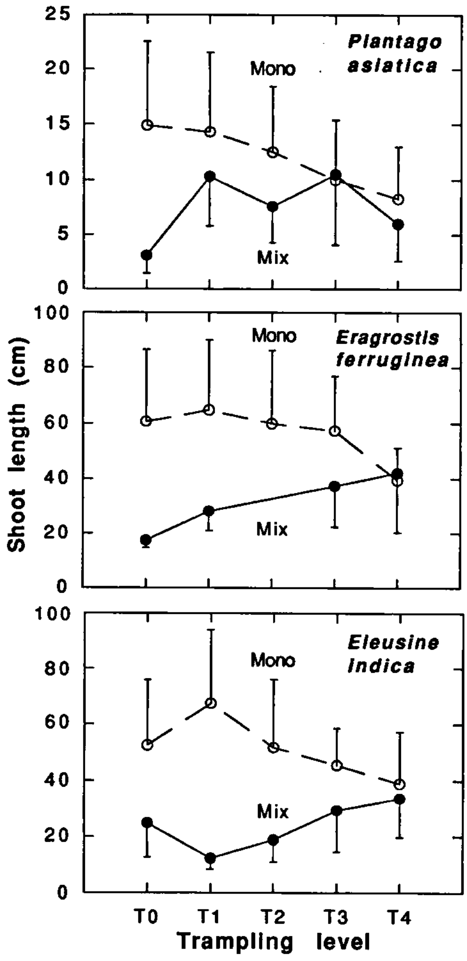

Fig. 2. Mean shoot length (+1 SD) for *Plantago asiatica, Eragrostis ferruginea* and *Eleusine indica* in monoculture (○) and mixed culture (●) along a trampling gradient.

$P<0{\cdot}01$ using three-way ANOVA). However, the effects of culture were significant on all the features tested for each species separately ($P<0{\cdot}05$ using two-way ANOVA). These results indicate that neighbours of other species reduced both the sizes and numbers of shoots and leaves of the target species.

Total dry weights of *Plantago, Eragrostis* and *Eleusine* species were markedly larger in monoculture than those in mixed culture at all treatments (T0–T4), indicating that intense multispecies competition occurred (Fig. 5). These differences decreased with increasing trampling intensity (Fig. 5). In mixed culture, *Ambrosia* dominated in the T0 treatment with a mean shoot length of 178 cm, and *Digitaria adscendens* (mean shoot length of 39–83 cm) and *Setaria faberi* (mean shoot length of 68–174 cm), annual grasses originating from buried seeds, predominated at low trampling (T0–T2). In addition, even in monoculture the maximum dry weights were not observed at no trampling (T0) but at light (T1) or heavy (T3) trampling (Fig. 5). The above results suggest that the intensity of multispecies competition was reduced as trampling intensity increased.

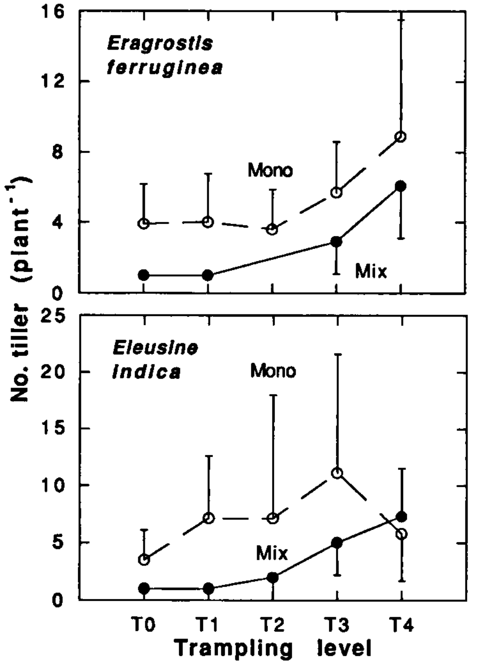

Fig. 3. Mean tiller number (+1 SD) for *Eragrostis ferruginea* and *Eleusine indica* in monoculture (○) and mixed culture (●) along a trampling gradient.

Table 4. Results of three-way ANOVA testing the effects of trampling, culture, species and these interaction on the shoot length, maximum leaf length, tiller number and leaf number in monoculture and mixed culture

		P			
		Length		Number	
Effects	d.f.	Shoot	Leaf	Tiller	Leaf
Trampling (A)	4	0·27	0·02	<0·01	<0·01
Culture (B)	1	<0·01	<0·01	<0·01	<0·01
Species (C)	2	<0·01	<0·01	<0·01	<0·01
A × B	4	<0·01	<0·01	0·22	0·14
A × C	8	0·80	0·34	<0·01	<0·01
B × C	2	<0·01	<0·01	<0·01	<0·01
A × B × C	8	0·01	<0·01	0·25	0·03
Error	351				

In addition, plant densities at harvest time varied among treatments (T0–T4); those (mean ± S.D.) of *Plantago, Eragrostis* and *Eleusine* in monoculture were 390 ± 138, 349 ± 117 and 188 ± 63 m^{-2}, respectively, while densities of 332 ± 99 m^{-2} were found in mixed culture (including all species). The densities of the target species were markedly lower in mixed culture than those in monoculture at all treatments.

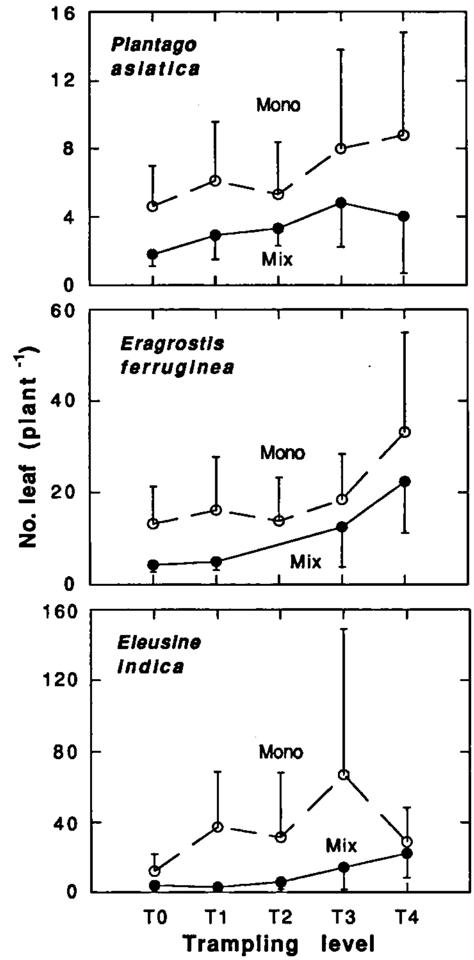

Fig. 4. Mean leaf number (+1 SD) for *Plantago asiatica, Eragrostis ferruginea* and *Eleusine indica* in monoculture (○) and mixed culture (●) along a trampling gradient.

DISCUSSION

The species grown in monoculture showed reduced sizes of shoots and leaves due to trampling (Fig. 2), confirming earlier observations with other species (e.g. Liddle 1975; Bratton 1985). On the contrary, we also found an increase in the numbers of shoots and leaves by trampling (Figs 3 and 4). Liddle & Greig-Smith (1975b) revealed that shoot damage or soil compaction enhanced the tiller number of *Festuca rubra*, while there were little effects when the two treatments were applied together. Pradhan & Tripathi (1983) found that moderate trampling enhanced the leaf number of *Paspalum dilatatum* but heavy trampling reduced it. The increase of shoots and leaves can complement the loss in those sizes by trampling. Thus, our results suggest that high trampling tolerance of the tread community species (*Plantago, Eragrostis* and *Eleusine*) is partly attributable to the morphological complementarity in response to trampling.

Light trampling enhanced the total dry weights of the tread community species (Fig. 2), in accordance with previous studies on plant cover (Lieth 1954; Ikeda & Okutomi

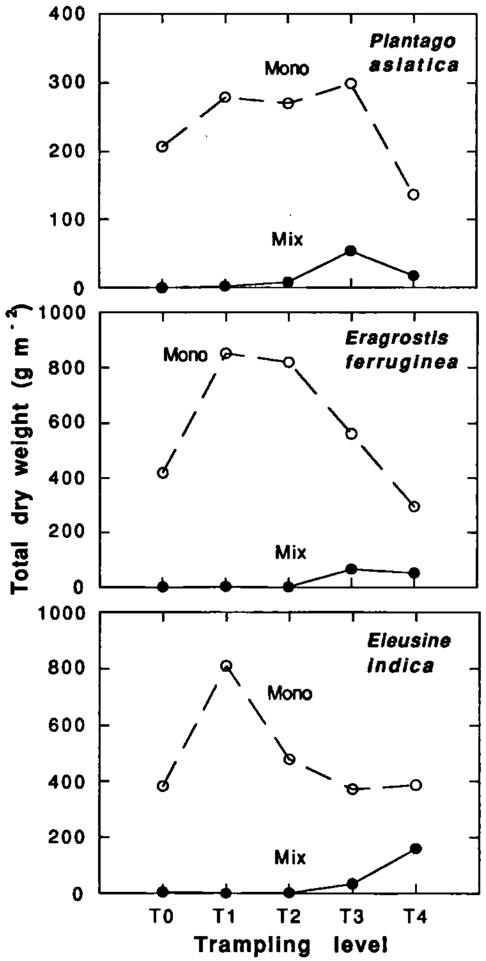

Fig. 5. Total dry weight (including roots) for *Plantago asiatica*, *Eragrostis ferruginea* and *Eleusine indica* in monoculture (○) and mixed culture (●) along a trampling gradient.

1990, 1992) and seedling emergence (Harper *et al.* 1965; Blom 1976, 1977). There are some reports of soil compaction promoting plant growth due to soil water rising by capillary attraction (Lieth 1954; Blom 1976), thus increasing the availability of water (Liddle & Greig-Smith 1975a) and probably also of nutrients resulting from mass flow (Nye & Marriott 1969).

Competition is another factor determining floristic composition in grassland communities. We found that heterospecific neighbours reduced both the sizes and numbers of shoots and leaves as well as the plant biomass for the tread community species (Figs 2–5). Plant densities at harvest time were relatively similar among the cultures, except for the lower density of *Eleusine* in monoculture under some treatments. Therefore, in most cases the decrease in their growth and morphological traits in mixed culture under low trampling cannot be attributable to density dependence but probably results from shading by the heterospecific neighbours with larger plant sizes, such as *Ambrosia, Digitaria* and *Setaria*. Individual plant size is an important characteristic of competitive ability and hierarchy in communities (Miller & Werner 1987; Goldberg & Fleetwood 1987; Gaudet & Keddy 1988). Thus, the tread community species are considered to have inferior competitive abilities. This confirms our early findings that roadside species with large plant sizes such as *Ambrosia* outcompeted the tread community species under low trampling (Ikeda & Okutomi 1990, 1992), and supports our hypothesis on the trade-off relationship between trampling tolerance and competitive ability.

Novoplansky *et al.* (1990) revealed that *Portulaca oleracea* seedlings avoided growing towards their neighbours by sensing the spectral composition (red/far-red ratio) of light and reducing their shoot growth in the direction of their neighbours. The plastic shoot growth to avoid their neighbours seems to be a good strategy under intense competition. However, no plastic responses of shoot growth to their neighbours were observed for the tread community species, suggesting that these species also have low avoidability from neighbours. On the other hand, we found that trampling reduced the intensity of competition from neighbours (Fig. 5). Pradhan & Tripathi (1983) revealed that trampling reduced the competitive ability of *Paspalum dilatatum*, thus allowing the coexistence with *Trifolium repens*. As in our early studies (Ikeda & Okutomi 1990, 1992), the roadside herbs were susceptible to trampling and trampling released the tread community species from competitive suppression by the roadside herbs. Therefore, trampling can be considered one of the factors controlling the competitive interactions within semi-natural grassland communities and the trade-off relationship between trampling tolerance and competitive ability may play an important role in the community organization.

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