Plant Morphological Characteristics and Resistance to Simulated Trampling

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ABSTRACT / The relationship between responses of plants to trampling and their morphological characteristics was studied in a glasshouse experiment. Thirteen species with four different growth forms were used in this experiment. They were five tussock species. *Chloris gayana, Eragrostis tenuifolia, Lolium perenne, Panicum maximum*, and *Sporobolus elongatus*; three prostate grasses, *Axonopus compressus, Cynodon dactylon*, and *Trifolium repens*, two herbaceous species, *Daucus glochidiatus* and *Hypochoeris radicata*; and three woody species, *Acacia macradenia, Acrotriche aggregata*, and *Sida rhombifolia*. These species were subjected to three levels of simulated trampling. For each species, measurements were taken of aboveground biomass, root biomass, leaf length, leaf width, leaf thickness, leaf number, broken leaf number and plant height. Overall, these measurements were greatest in the control plants, moderate in the level of light trampling, and the lowest in the level of heavy trampling. Biomass was used as a basis of the assessment of plant resistance to trampling. Three tussock species, *Eragrostis tenuifolia, Lolium perenne*, and *Sporobolus elongatus* had a high resistance. Woody and erect herbaceous plants were more intolerant to trampling. There appear to be two processes involved in the reduction of the plant parameters: direct physical damage with portions of the plants detached, and physiological changes, which slow down vegetative growth rates. Plant height was found to be the most sensitive indicator of trampling damage.

The selection of approprate trampling-resistant plants for pathways through natural or seminatural vegetation is one essential step in the management of areas used for outdoor recreation. When trampled areas or campgrounds have to be revegetated, it is also important to select species that will be more tolerant to human use, preferably members of the local flora. With these problems in mind we have examined the morphological characteristics of a range of species with the aim of providing some new criteria on which the selections may be based.

The relationship between the resistance of plants to trampling and morphological characteristics has been recognized (Bates 1935, Youngner 1961, Liddle 1975b, Jurko 1983, Kuss 1986, Cole 1988). Variations in the relative sensitivity of perennial plants to trampling appears to be strongly associated with plant morphology (Kuss 1986). Cole (1988) found that while all the species (more than 45) declined in cover as trampling intensity increased, some declined much more than others. He attributed this primarily to differences in the morphological characteristics of each species.

KEY WORDS: Plant morphology; Trampling; Resistance

Several studies in trampled areas have indicated that those plants that have a rosette form, tussock form, and bunched or low-spreading habits of growth are frequently identified as having trampling resistance (Naito 1969, Willard and Marr 1970, Liddle 1975a). Leaf size was also regarded as important by Kuss (1986). Cole (1988) commented that plant height is one of the most important morphological features that influence resistance. Internode length and shoot density were also noted to be important to plant wear by Shildrick (1974) and Canaway (1975).

Kuss (1986) regarded leaf size as one of those morphological characteristics that have the greatest influence on resistance to trampling. Leaf width of some turf grasses contributes significantly to the variation in wear tolerance among some turf grass species (Shearman and Beard 1975). Leaf length and thickness also have a considerable effect on plant resistance to trampling. The most trampling-resistant species have leaves that are either small or long and thin (Cole 1988). Shildrick (1974) mentioned that leaf number can affect wear tolerance, but no further information about the kind of relationship between them was offered.

Plant height is also one of the important factors affecting a plant's resistance to trampling. Pardhan and Tripathi (1983) reported that *Paspalum dilatatum* was more adversely affected by trampling due to its

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taller erect form than *Trifolium repens*, which grows as a prostrate plant. Cole (1988) reported that for some herbs, sensitivity to trampling increased with increased plant height. Liddle (1973) noted that the first visible effect of trampling is to reduce vegetation height. Kuss (1986) also noted that trampling damage to plants is reflected by significant reduction in height.

Other morphological characteristics, such as internode length and shoot density, were also noted to be important to plant wear (Shildrick 1974, Canaway 1975). Cole (1988) related the high resistance of *Berberis repens* to trampling to its high density of stems.

Although all morphological characteristics mentioned above have been reported to be related to plants' trampling resistance, the experiments from which these relationships were derived were carried out by different people under different conditions, and the trampling was at various intensities and frequencies. In addition, because most of these experiments were carried out on a community level, it is hard to avoid the effect of the interaction of plant species in relation to trampling. Take plant height as an example: although some experiments have shown that tall plants had more damage from trampling than did short plants, we do not know if the short plants are more resistant than tall plants because short plants may have been protected by tall plants from trampling, as reported by Cole (1988). To advance the understanding of the importance of plant morphological characteristics in the resistance to trampling, a comprehensive and quantitative study was carried out in the glasshouse, where one species of plant was grown in each pot as to be independent of the interactions between plant species. This morphological information may be used as a guide to the choice of plants in the planning and management of recreation areas.

Materials and Methods

Species Utilized

This experiment used 13 species and was carried out from 27 September 1987 to 21 February 1988. The species were chosen for the following reasons: (1) they are all distributed in the subtropical or tropical areas of Queensland (Tothill and Hacker 1973) and most of them occurred in the two previously surveyed field sites (see Sun and Liddle, this issue); (2) these species can be divided into the four main morphological types mentioned below; (3) the seeds or seedlings of these species were available from either a commercial seed supplier or by transplanting from the field near Griffith University; and (4) some species, such as *Lolium perenne*, have been widely identified as trampling-resistant species (Edmond 1964, Fushtey and others 1983). The species and their morphology were as follows: *Chloris gayana, Eragrostis tenuifolia, Lolium perenne, Panicum maximum*, and *Sporobolus elongatus* are tussock grasses. *Axonopus compressus, Cynodon dactylon*, and *Trifolium repens* are prostrate grasses. *Daucus glochidiatus* and *Hypochoeris radicata* are herbaceous species. *Acacia macradenia, Acrotriche aggregata*, and *Sida rhombifolia* are woody species.

Plants of all 13 species were grown in separate 20-cm-diameter pots either from seeds or as transplanted seedlings. There were four plants in each pot of tussock species, six plants in each pot of prostrate species, and two plants in each pot of herbaceous and woody species. The seedlings of the three woody species and the two herbaceous species, *Daucus glochidiatus* and *Hypochoeris radicata*, were transplanted from the Griffith University campus. The work was carried out in a glasshouse, where the temperature range 28–30°C and the day length approximately 14 h, which to some extent simulated the subtropical environment of Brisbane.

Throughout the experiment the soil was kept at about two thirds field capacity by weighing and adding the appropriate amount of water to bring the overall weight of the pot to a known standard. Nutrient solutions of nitrogen, phosphorus, and potassium were made up according to Hewitt's stock solution (Hewitt 1966).

Treatments

The simulated trampling was based on the dropped weight method of Kellomaki and Saastamoinen (1975). This involved dropping an 18-cm-diamater circular 0.71-kg weight on the plants in 20-cm-diameter pots. The falling distance was 50 cm, and the force generated was similar to that of a human footfall (Kellomaki and Saastamoinen 1975). There were three trampling levels in this experiment: (1) control, zero drops of the weight; (2) light trampling, 10 drops of the weight at each trampling treatment; and (3) heavy trampling, 30 drops of the weight at each trampling treatment. Eight trampling treatments were applied over the length of the experiment at intervals of 10 days, starting on 29 November 1987 (35 days after seed germination).

Experimental Design

As each species was subjected to three levels of simulated trampling, three pots were required for each species making 3 × 13 (species) = 39 in each block. There were, therefore, 39 × 4 (block) = 156 pots in all.

The seeds of different species were sown into separate pots at different dates to minimize the expected difference in germination time determined in the preliminary experiment. The pots were initially positioned randomly within each block and then rerandomized every five days over the period of the experiment to minimize the potential location effect in the glasshouse.

Recording

The measurements of leaf length (millimeters), leaf width (millimeters), leaf thickness (millimeters), leaf number (per plant), and number of broken leaves (per plant), and plant height (millimeters) were taken before each of the eight trampling treatments. The plants in all pots were harvested on 21 February 1988, two days after the last trampling treatment. Plants were cut at the base in each pot and then dried and weighed to measure biomass (grams per pot). To assess the trampling damage, the live parts were carefully separated from the attached dead parts and were put in weighed aluminium trays. The roots in each pot were collected by sieving and carefully rinsing the soil. The aboveground live parts and root samples were oven dried at 105°C. Most green part samples were dried for 24 h, as they had reached a constant weight by that time. The aboveground samples of the relatively larger or woody plants of *Acacia macradenia, Acrotriche aggregata, Chloris gayana, Eragrostis tenuifolia, Panicum maximum,* and *Sporobolus elongatus* from the control pots and the samples of *Sida rhombifolia* from both the control and trampled pots and all the root samples were dried for 36 h.

Apart from the dead leaves, the physical damage to the leaves and the broken leaves caused by simulated trampling were visible at each time of measurement in this experiment. Only those leaves that were still alive were measured and used to calculate the percentage of broken leaves. The total number of leaves (per plant) reported here was the total number of live leaves recorded. This included some leaves that were broken but still alive.

Data Analyses

The data were analyzed by calculating the relative biomass or other parameters of the trampled plants as percentages of the control plants or, in the case of broken leaves, compared to total number of leaves in the pot.

As biomass is a comprehensive measurement of plant growth, the assessment of the resistance of the different species studied to simulated trampling was based on their biomass. Species with greater relative biomass had less loss and were more resistant to trampling.

The difference between species in relative biomass and in each of the morphological parameters at the time of the last measurement was tested by ANOVA (Byrkit 1987). The difference between any two species was further tested using the Tukey test (HSD, honestly significant difference) (Byrkit 1987). The species were grouped on the basis of LSD tests of each of their relative parameters.

Results

All the plants of *Acacia macradenia, Acrotriche aggregata,* and *Daucus glochidiatus* died after the first one to three light and heavy trampling treatments. The measurements of the morphological parameters of these three species in both light and heavy trampling levels are, therefore, absent in the following sections.

Biomass

For each species, the control plants had both the greatest aboveground biomass and root biomass, while heavily trampled plants had the lowest biomass (Table 1). The relative biomass of both lightly and heavily trampled plants differed among species (Figure 1). However, the differences were only significant for the relative biomass of heavily trampled plants. *Eragrostis tenuifolia* and *Chloris gayana* had the greatest and the lowest relative biomass of lightly trampled plants, respectively. *Eragrostis tenuifolia, Lolium perenne,* and *Sporobolus elongatus* had the greatest relative biomass after heavy trampling. *Axonopus compressus* and *Chloris gayana* had moderate values, while *Cynodon dactylon, Hypochoeris radicata, Panicum maximum, Sida rhombifolia,* and *Trifolium repens* had the lowest values (to 105 days).

Leaf Length

The measurements of mean leaf length of the control plants showed that *Acrotriche aggregata* had the shortest leaves of the 13 species while *Panicum maximum* had the longest leaves (Figure 2a). The leaf length of each species increased with age. For most species the leaf length increased markedly over the first four measurements (between age 35 days and 65 days) and changed little over the last four measurements.

Over the period of the experiment, the plants of each species grown in control pots had the longest leaves, while those grown in heavily trampled pots

Table 1. Mean biomass (dry weight g/pot) of species measured at end of experiment and ANOVA test of biomass in three levels of trampling

Species	Trampling level			ANOVA (F test)[a]
	Control	Light trampling	Heavy trampling	
Acrotriche aggregata				
Aboveground parts	1.222	0.000	0.000	
Root parts	4.033	0.000	0.000	
Acacia macradenia				
Aboveground parts	2.340	0.000	0.000	
Root parts	2.600	0.000	0.000	
Axonopus compressus				
Aboveground parts	7.877	3.456	0.691	0.854**
Root parts	1.786	0.960	0.215	0.463*
Chloris gayana				
Aboveground parts	15.400	3.203	0.947	7.505**
Root parts	3.445	1.092	0.322	0.462**
Cynodon dactylon				
Aboveground parts	15.480	2.290	0.161	7.417**
Root parts	2.247	1.293	0.148	0.563**
Eragrostis tenuifolia				
Aboveground parts	13.819	7.031	3.649	9.404**
Root parts	9.001	2.601	2.059	0.247**
Daucus glochidiatus				
Aboveground parts	4.510	0.000	0.000	
Root parts	0.933	0.000	0.000	
Hypochoeris radicata				
Aboveground parts	3.581	1.069	0.062	1.356**
Root parts	1.305	0.575	0.062	0.067**
Lolium perenne				
Aboveground parts	4.477	1.831	1.111	0.139**
Root parts	1.661	0.785	0.369	0.073**
Panicum maximum				
Aboveground parts	12.964	4.474	0.277	0.686**
Root parts	4.343	1.875	0.386	1.276**
Sida rhombifolia				
Aboveground parts	2.937	1.024	0.030	2.937**
Root parts	1.399	0.606	0.167	0.066**
Sporobolus elongatus				
Aboveground parts	11.573	4.278	2.457	1.610**
Root parts	3.731	2.244	0.945	0.140**
Trifolium repens				
Aboveground parts	3.164	0.513	0.008	0.173**
Root parts	1.317	0.378	0.024	0.085**

[a]**, significant at 0.025 level; *significant at 0.05 level.

had the shortest leaves. Both the relative leaf length of lightly trampled plants and the relative leaf length of heavily trampled plants varied significantly with the species (Table 2). *Lolium perenne* had the greatest relative leaf length after light trampling. *Cynodon dactylon, Eragrostis tenuifolia, Sporobolus elongatus,* and *Trifolium repens* had moderate values, while *Axonopus compressus, Chloris gayana, Panicum maximum,* and *Sida rhombifolia* had the lowest values. After heavy trampling, *Cynodon dactylon, Eragrostis tenuifolia, Lolium perenne,* and *Sporobolus elongatus* had high relative leaf length while *Axonopus compressus, Chloris gayana, Hypochoeris radicata, Panicum maximum, Sida rhombifolia, Trifolium repens* had low values.

Leaf Width

The leaf width of the control plants differed depending on the species, and for seven species markedly increased with age (Figure 2b). *Sida rhombifolia* and *Hypochoeris radicata* had the widest leaves of all species throughout the experiment. *Daucus glochidiatus, Panicum maximum,* and *Trifolium repens* also had relatively wide leaves. The other species had narrow leaves.

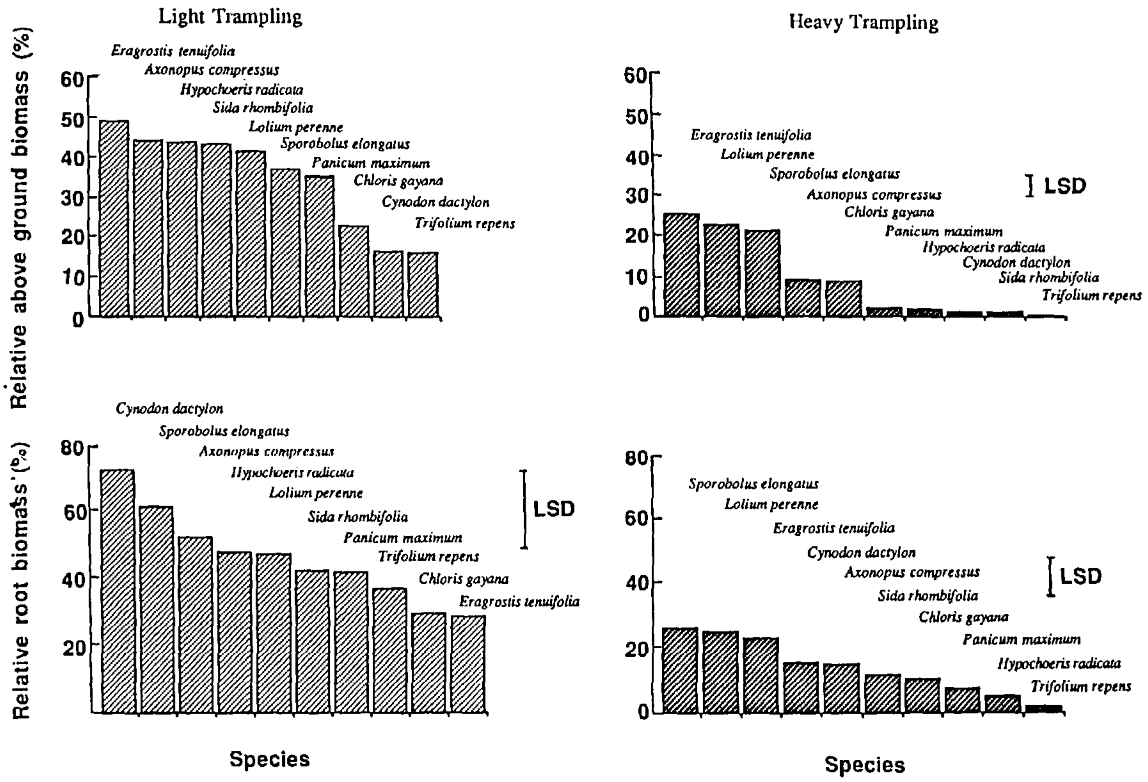

Figure 1. The relative aboveground biomass of both lightly and heavily trampled plants of the ten species that survived trampling calculated as a percentage of controls.

Overall, for each species the leaf width was greatest in the control, moderate in light trampling, and lowest in heavy trampling. The relative leaf width of both lightly and heavily trampled plants varied significantly among species (Table 2). After light trampling, *Axonopus compressus, Chloris gayana, Eragrostis tenuifolia, Lolium perenne, Sporobolus elongatus, Trifolium repens* had the greatest relative leaf width. *Cynodon dactylon* and *Panicum maximum* had moderate values. *Sida rhombifolia* had a low value, while *Hypochoeris radicata* had the lowest value. After heavy trampling, *Axonopus compressus, Chloris gayana, Cynodon dactylon, Eragrostis tenuifolia, Lolium perenne,* and *Sporobolus elongatus* had the greatest relative leaf width. *Hypochoeris radicata, Panicum maximum,* and *Sida rhombifolia* had moderate values, while *Trifolium repens* had the lowest value.

Leaf Thickness

The leaf thickness of the control plants of each species increased slightly with age (Figure 2c). *Hypochoeris radicata* had the thickest leaves of all 13 species over the period of this experiment, while *Cynodon dactylon* had the thinnest leaves.

The leaf thickness of each species was different between the three trampling levels. Overall, it was greatest in the control plants, moderate in lightly trampled plants, and lowest in heavily trampled plants. The relative leaf thickness of both lightly and heavily trampled plants varied significantly among species (Table 2). After light trampling, *Eragrostis tenuifolia, Lolium perenne, Panicum maximum,* and *Sporobolus elongatus* had the greatest relative leaf thickness. *Axonopus compressus, Chloris gayana,* and *Hypochoeris radicata* had moderate values, while *Cynodon dactylon, Sida rhombifolia,* and *Trifolium repens* had the lowest values. After heavy trampling, *Eragrostis tenuifolia, Lolium perenne,* and *Sporobolus elongatus* had the greatest relative leaf thickness of heavily trampled plants. *Axonopus compressus, Chloris gayana, Cynodon dactylon, Panicum maximum,* and *Trifolium repens* had moderate values. *Hypochoeris radicata* and *Sida rhombifolia* had the lowest values.

Total Number of Leaves

The results of total number of leaves on control plants for the 13 species are shown in Figure 2d. In

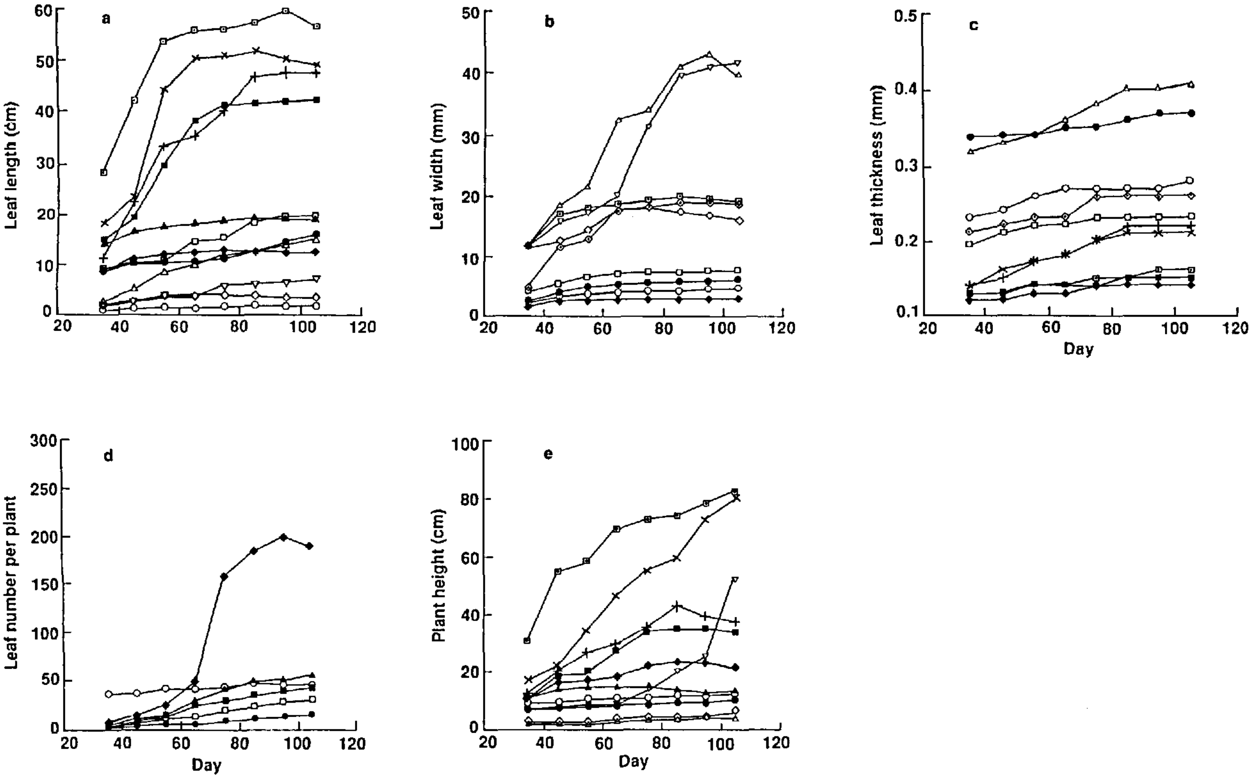

Figure 2. The growth of control plants over the experimental period. **(a)** Leaf length; •, *Acacia macradenia*; □, *Axonopus compressus*; X, *Chloris gayana*; ◆, *Cynodon dactylon*; ■, *Eragrostis tenuifolia*; ◇, *Daucus glochidiatus*; △, *Hypochoeris radicata*; ▲, *Lolium perenne*; ⊡, *Panicum maximum*; ▼, *Sida rhombifolia*; +, *Sporobolus elongatus*; ○, group includes *Acrotriche aggregata, Trifolium repens*. **(b)** Leaf width; symbols as for **a** except •, group includes *Acacia macradenia, Cynodon dactylon, Sporobolus elongatus*, and ○, group includes *Acrotriche aggregata, Lolium perenne, Sida rhombifolia*. **(c)** Leaf thickness; symbols as for **a** except ○, *Acrotriche aggregata*; ◇, group includes *Daucus glochidiatus, Lolium perenne, Eragrostis tenuifolia, Trifolium repens*. **(d)** Leaf number; symbols as for **a** except ○, *Acrotriche aggregata*; •, group includes *Acacia macradenia, Daucus glochidiatus, Hypochoeris radicata, Sida rhombifolia*. **(e)** Plant height; symbols as for **a** except ○, group includes *Acrotriche aggregata, Axonopus compressus, Daucus glochidiatus*.

general, the total number of leaves of each species increased as the age increased. However, this increase was very small for *Acacia macradenia* and *Acrotriche aggregata*. *Cynodon dactylon* had the greatest number of leaves of all the species throughout the experiment. *Acacia macradenia* had the least number of leaves.

Each species, except for *Hypochoeris radicata* and *Panicum maximum*, had the greatest number of leaves on the control plants, an intermediate number on lightly trampled plants, and the lowest number on heavily trampled plants. The relative total leaf numbers of both lightly and heavily trampled plants were significantly different among species (Table 2). After light trampling, *Hypochoeris radicata* had the greatest relative total number of leaves. *Axonopus compressus, Chloris gayana, Cynodon dactylon, Eragrostis tenuifolia, Lolium perenne, Panicum maximum, Sida rhombifolia*, and *Sporobolus elongatus* had moderate values. *Trifolium repens* had the lowest value. After heavy trampling, *Sporobolus elongatus* had the greatest relative total number of leaves. *Chloris gayana, Eragrostis tenuifolia*, and *Lolium perenne* had high values. *Axonopus compressus* had a moderate value. *Hypochoeris radicata* had a low value. *Cynodon dactylon, Panicum maximum, Sida rhombifolia*, and *Trifolium repens* had the lowest values.

Number of Broken Leaves

The percentage of leaves that were broken in both light trampling and heavy trampling varied significanty among species (Table 2). After light trampling, *Chloris gayana* and *Panicum maximum* had high percentage of broken leaves, while the other species had low values. After heavy trampling, *Hypochoeris radicata, Panicum maximum*, and *Sida rhombifolia* had the greatest values. *Axonopus compressus, Chloris gayana, Eragrostis tenuifolia, Lolium perenne*, and *Sporobolus elonga-*

Table 2. Relative morphological parameters of both lightly and heavily trampled plants (%) of each species measured before the last trampling treatment and results of statistical analysis

Species	Leaf length	Leaf width	Leaf thickness	Leaf number	Broken leaf number	Plant height
Axonopus compressus						
Light trampling	58.5	99.7	95.7	66.6	25.3	38.1
Heavy trampling	40.1	83.0	73.9	35.8	40.6	16.3
Chloris gayna						
Light trampling	54.2	94.5	95.2	68.6	63.6	20.0
Heavy trampling	44.5	82.2	81.0	51.0	48.9	16.3
Cynodon dactylon						
Light trampling	67.8	81.0	92.9	53.6	23.5	65.8
Heavy trampling	59.5	70.0	76.9	12.5	24.7	58.7
Eragrostis tenuifolia						
Light trampling	74.5	98.6	100.0	76.1	22.0	53.3
Heavy trampling	70.4	97.6	100.0	57.1	53.9	41.5
Hypochoeris radicata						
Light trampling	49.5	49.7	96.3	129.2	21.5	66.0
Heavy trampling	28.9	39.3	59.9	26.4	95.1	44.0
Lolium perenne						
Light trampling	87.3	98.3	100.0	65.2	18.3	54.1
Heavy trampling	84.3	94.1	100.0	56.0	39.7	54.8
Panicum maximum						
Light trampling	49.8	81.8	98.4	122.5	82.6	12.5
Heavy trampling	35.7	46.0	85.9	16.6	100.0	4.6
Sida rhombifolia						
Light trampling	57.5	59.2	92.3	71.8	27.5	45.7
Heavy trampling	30.0	36.1	53.9	15.8	73.2	8.2
Sporobolus elongatus						
Light trampling	71.5	95.2	100.0	87.3	28.2	49.5
Heavy trampling	65.9	94.0	100.0	71.4	46.5	47.2
Trifolium repens						
Light trampling	74.8	98.0	92.4	28.4	10.8	51.5
Heavy trampling	34.6	16.3	68.3	9.7	9.1	16.7
F test[a]						
Light trampling	11.84**	31.9**	7.6**	45.8**	23.9**	41.3**
Heavy trampling	9.8**	26.4**	61.7**	47.2**	8.5**	36.1**

[a] **Significant at 0.025 level.

tus had moderate values. *Cynodon dactylon* and *Trifolium repens* had the lowest values.

Plant Height

The heights of control plants of all 13 species recorded over the experiment are shown in Figure 2e. *Panicum maximum* and *Chloris gayana* were the tallest species, while *Hypochoeris radicata* was the shortest in this experiment.

The plant height of each species differed among the three levels of trampling. The plants of each species were tallest in the control, moderately tall after light trampling, and shortest after the heavy trampling. The relative plant height of both lightly and heavily trampled plants varied significantly among species (Table 2). After light trampling, *Cynodon dactylon* and *Hypochoeris radicata* had the greatest relative plant height. *Axonopus compressus, Eragrostis tenuifolia, Lolium perenne, Sida rhombifolia, SPorobolus elongatus,* and *Trifolium repens* had moderate values. *Chloris gayana* and *Panicum maximum* had the lowest values. After heavy trampling, *Cynodon dactylon, Eragrostis tenuifolia, Hypochoeris radicata, Lolium perenne,* and *Sporobolus elongatus* had the greatest relative plant height. *Axonopus compressus, Chloris gayana, sida rhombifolia,* and *Trifolium perenne* had moderate values. *Panicum maximum* had the lowest value.

Discussion

Biomass

Since the growth of plant roots was restricted by the pots, the results of the root measurement are considered to have little value, but the fact that root biomass of each species declined with trampling intensity in this experiment suggests the importance of studying the effect of trampling on the root growth in field conditions. Only aboveground biomass is discussed in this article and is simply called biomass.

Because the difference in the relative biomass of lightly trampled plants among all species that survived trampling was not significant, these species seem to have similar resistance to trampling. However, these species did have different resistances to trampling according to their relative biomass after heavy trampling. Light trampling was not sufficient to allow this difference to occur. This suggests that comparisons of the resistances of species to trampling based on the light trampling information may be misleading.

Eragrostis tenuifolia, Lolium perenne, and *Sporobolus elongatus* were the most resistant to trampling in this experiment. *Axonopus compressus* and *Chloris gayana* were moderately resistant. *Cynodon dactylon, Hypochoeris radicata, Panicum maximum, Sida rhombifolia,* and *Trifolium repens* were the least resistant. Since all the above species survived the trampling treatments, they are considered trampling-tolerant species. Conversely, *Acacis macradenia, Acrotriche aggregata,* and *Daucus glochidiatus* are trampling-intolerant species. Of the most resistant species, *Lolium perenne* has been reported to be highly resistant to trampling (Edmond 1964, Van der Horst and Kamp 1974, Fushtey and others 1983). Frenkel (1972) also found that *Eragrostis tenuifolia, Eleusine indica, Sporobolus poiretii, Paspalum notatum,* and *Cynodon dactylon* were species present in "treaded" sites in tropical areas. The reason that *Cynodon dactylon* frequently appeared in "treaded" sites was not, however, discussed. High recovery of this species (Sun and Liddle 1991) may have played an important role.

Leaf Length

Simulated trampling in this experiment caused a reduction in leaf length for all the species. O'Connor (1956) reported that the average leaf length of *Dactylis glomerata* was reduced from 9.1 to 5.8 cm by the trampling effect. The reduction in leaf length may mainly be attributed to the physical damage of leaves. In addition, trampling may also cause an inhibition to leaf growth (Goryshina 1983).

For *Chloris gayana, Eragrostis tenuifolia, Panicum maximum,* and *Sporobolus elongatus,* light trampling can so reduce their leaf length that the additional trampling would cause little further decrease. However, for *Axonopus compressus, Cynodon dactylon, Sida rhombifolia,* and *Trifolium repens* the leaf length appeared to be linearly associated with trampling intensity. Bratton (1985) reported that the leaf length of *Cypripedium accule,* an orchid, was reduced as the trampling intensity increased. The effect of trampling intensity on the growth of leaf length is, therefore, different depending on species. The reason that some species reached a maximum reduction in leaf length with only light trampling appeared to be fragility of their leaves rather than a physiological reaction, but this explanation is not totally consistent with the other morphological changes observed in this experiment.

In both light and heavy trampling levels, *Cynodon dactylon, Eragrostis tenuifolia, Lolium perenne,* and *Sporobolus elongatus* has less reduction in leaf length than the other species. However, the reason for *Cynodon dactylon* occurring in this group may be different from that of *Eragrostis tenuifolia, Lolium perenne,* and *Sporobolus elongatus.* The trampled plants of *Cynodon dactylon* produced some new leaves over the ten-day intervals between each two trampling treatments. These new leaves were relatively longer than the broken leaves when measured. For *Eragrostis tenuifolia, Lolium perenne,* and *Sporobolus elongatus* the strength of the leaves was a contributing factor.

Leaf Width

For *Chloris gayana, Hpochoeris radicata, Panicum maximum,* and *Sida rhombifolia,* the physical damage by trampling was the direct cause of the reduction in growth of leaf width. It was evident that these species had the greatest percentage of leaves that were broken. For a species like *Trifolium repens* the reduction may be mainly attributed to the inhibition caused by trampling of the growth of leaflet width as this species had the lowest percentage of leaflets that were broken. That *Hypochoeris radicata, Panicum maximum, Sida rhombifolia,* and *Trifolium repens* had both greater loss in leaf or leaflet width and relatively wider leaves or leaflets than the other species studied suggests that species with broad leaves may be affected more by trampling than the species with narrow leaves with respect to growth of leaf width.

Leaf Thickness

It was noticeable that for most species studied, the leaf thickness of even heavily trampled plants was only 15% less than the control by the end of the experiment. The reduction in leaf thickness of trampled plants may not, therefore, be a main factor contributing to the great reduction in biomass of trampled plants.

Hypochoeris radicata and *Sida rhombifolia* had both the thickest leaves and the lowest relative leaf thickness after heavy trampling. This suggests that the effect on leaf thickness caused by trampling may be greater for the species with thicker leaves than for the species with thinner leaves.

Total Leaf Number

That *Cynodon dactylon* rapidly produced a large number of leaves over the experimental period reflects its fast growth. Similarly, the smallest increase in leaf number that occurred in the two woody species, *Acacia macradenia* and *Acrotriche aggregata*, is a reflection of their slow growth.

The result that trampled plants had less leaves than control plants in this experiment confirms the work of Bowles and Maun (1982) and Jurko (1983). Bowles and Maun (1982) mentioned that trampling caused the loss of a large proportion of leaves. *Pinus mugo* was found by Jurko (1983) to have a reduction in number of needles at trampled sites. Serious leaf damage was explained by Bowles and Maun (1982) as the reason for leaf loss. In the present study, both direct damage on leaves and indirect damage such as breaking of stems were the main contributors to the loss of leaves. In addition, trampling may also have caused an inhibition of leaf development. In general, leaf number appears to be negatively correlated with trampling intensity. Bratton (1985) reported that the plants of *Cypripedium acaule* near roads and easy access trails had fewer leaves per shoot than at greater distance.

Eragrostis tenuifolia, Lolium perenne, and *Sporobolus elongatus* had both the greatest relative leaf number and relative biomass after heavy trampling. In contrast, *Cynodon dactylon, Hypochoeris radicata, Panicum maximum, Sida rhombifolia*, and *Trifolium repens* had both the lowest relative leaf number and lowest relative biomass. These results suggest that the ability of plants to maintain their leaves when trampled may be positively related to their resistance to trampling. The function of plant leaves to conduct photosynthesis apparently plays an important role. However, the trampled plants in this experiment appeared to have maintained their leaf numbers in different ways. Since none or few of the tillers of *Eragrostis tenuifolia, Lolium perenne*, and *Sporobolus elongatus* were broken by trampling (Sun unpublished data), the direct damage to the leaves was the main cause of the reduction in their leaf numbers.

Percentage of Broken Leaves

One of the visible impacts of trampling on plants was the injury to leaves. The degree of injury varies with both trampling intensity and plant species. In general the degree of leaf damage may increase as trampling intensity increases.

The leaves of the various species studied may have had different strengths and anatomical structures, which affected the amount of damage. The differences in leaf size and leaf number may also play a role. Broad leaves may be more easily damaged by trampling, particularly heavy trampling, than narrow leaves. Grabherr (1982) suggested that broad-leaved grasses are easily damaged and are not trampling tolerant. In the present study, *Chloris gayana, Hypochoeris radicata*, and *Panicum maximum*, which had relatively large leaves, had more broken leaves than the other species when subjected to trampling. However, this may be because their leaves were weaker than the other species. Of all the species, *Cynodon dactylon* and *Trifolum repens* had the lowest percentage of leaves that were broken. This may have been because these two species had tougher leaves than the other species. However, the real reason may have been that the damaged leaves of these species died shortly after trampling and were not included in the measurements of leaf number. This is supported by the fact that their total numbers of leaves were much lower than the control plants. In addition, *Cynodon dactylon* developed some new leaves during the ten-day intervals between any two trampling treatments. This increased the number of undamaged leaves and thus reduced the percentage of leaves that were recorded as broken for this species.

Plant Height

Deans (1968) found that there was a reduction in height of plants towards the greatest area of impact. In the present study, even light trampling caused a significant reduction in plant height for all the species. Sankey and Mackworth-Praed (1969) observed a considerable reduction in the height of grass after the slight trampling. This suggests that plant height is sensitive to trampling and thus can be used as an indicator of trampling.

The plant height was reduced by trampling in different ways, depending on species. The reason *Cynodon dactylon* had the greatest relative plant height after both light and heavy trampling may be explained by its rapid development of new shoots during ten-day intervals. The tillers of *Eragrostis tenuifolia, Lolium perenne*, and *Sporobolus elongatus* were bent by trampling from the base without breaking (Sun unpublished data). This bending led to a reduction in plant height for these species. The decline in plant height of *Chloris gayana* and *Panicum maximum* was mainly attributed to the breaking of their tillers by trampling, although their tillers were also bent towards the soil surface.

Chloris gayana and *Panicum maximum*, the tallest plants in this experiment, had the greatest reduction in plant height after both light and heavy trampling. This suggests that trampling may cause a greater proportional decrease in plant height for tall plants than for short plants. A study to compare the three distinct height types of *Poa pratensis* showed that a low spreading form appeared to be best adapted to the trampled site, whereas tall plants survived best in the untrampled treatment.

Conclusion

The results of the present experiment suggest that plants can be divided into two types, tolerant and intolerant, on the basis of their responses to trampling. These two types appear to be strongly associated with plant morphological characteristics. Woody and erect herbaceous plants are more likely to be intolerant compared with tussock and prostrate grasses. In general, trampling-tolerant species can be classified as having high, moderate, and low resistance to trampling. Plant morphology also plays an important role in influencing the resistance of trampling-tolerant species to trampling.

Although not all the tussock species are resistant to trampling, tussocky species are most likely to have high resistance. In general, the prostrate form appears to be less resistant than tussock species. Herbaceous plants with broad leaves may be also less resistant than tussock species. The erect herbaceous and woody forms are the least resistant to trampling.

Trampling caused quantitative changes in various aspects of vegetative growth, such as the growth of leaves, stems, and plant height. It appears that there are two major processes involved in these changes, one where the plants are uninjured and another where the plants are injured. The changes without or with only little physical damage are regarded as uninjured change, such as the reduction in plant height and the increase in tiller number or the trampled plants of *Eragrostis tenuifolia, Lolium perenne*, and *Sporobolus elongatus*. This would appear to be a physiological response to trampling impacts. The changes with marked physical damage are regarded as the injured change, such as the reduction in leaf length and leaf width of all the species in this experiment. Uninjured changes in plants when subjected to trampling would favor their resistance to trampling.

For the same species, the effect of trampling on the growth of different vegetative parts, such as leaf, stem, and plant height, is different. In general, the growth of plant height may be more affected by trampling than that of the other vegetative parameters we measured, while leaf thickness may be least affected. Plant height, therefore, can be used as a sensitive indicator that the vegetation has been subjected to trampling.

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