Effects of Herbivores on the Competition of C3 and C4 Graminoids

Toshinori OKUDA

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I. INTRODUCTION

Distribution, abundance and productivity of plants depend on several environmental factors and these dependencies are altered by the difference of life forms and physiological function systems of each plant species.

Herbivore pressure has been described as a significant environmental factor influencing on both the vegetation as a whole and productivity of individual species throughout the literature. Herbivore grazing can take a plant species from a dominant to a minority component of the flora and make room for invasion by other species (Harper 1969). However, relatively few studies have been conducted to evaluate the herbivore's effect on plants in relation to the life forms or physiological function systems of plants.

The discovery of a new photosynthetic process, C4 cycle of CO_2 fixation system by Kortschak et al.(1965) and its detailed description by Hatch and Slack (1966) have stimulated intensive study of the differences in photosynthetic efficiency in the plant species (Brown 1978). Higher CO_2 uptake rates in leaves of plants with C4 photosynthesis results from a high concentration of CO_2 in the cells surrounding the vascular bundle in which the pentose phosphate CO_2 fixation cycle (C3) is operative (Hatch 1971; Black 1973). This higher concentration of CO_2 at the site of ribulose diphosphate (RuDP) consequently reduces the

O_2 inhibition on ribulose diphosphate carboxylase (RuDPC) which is generated by the process of photorespiration.

The higher photosynthetic capacity in leaves of species with C4 photosynthesis is believed to create some advantages in certain environments and much ecological interest has focused on the adaptive significance of the C4 plants and their competitive relationship to species possessing C3 photosynthetic pathways. C4 plants typically have higher optimum temperature for growth and photosynthesis, a higher water-use efficiency and a higher level of irradiance required for light saturation (Bjorkman 1971; Black 1971).

These characteristics of C4 plants have been supported by several ecological observations which have shown that the C4 pathway appears to be advantageous in environments characterized by high light intensities, high temperatures, and limited soil moisture (Cooper 1965; Downton and Tregunna 1968; Welkie and Caldwell 1970; Gifford 1974; Redmann 1975; Doliner and Jolliffe 1979), and that abundance of C4 plants is correlated with one or a combination of these factors mentioned above (Teeri and Stowe 1976; Ehleringer 1978; Eickmeir 1978; Stowe and Teeri 1978; Tieszen et al. 1979b; Boutton 1980). Nitrogen use efficiency has also been found to be greater in C4 plants than in C3 plants particularly under the conditions of low soil nitrogen supply (Wilson and Haydock 1971; Christie 1981).

Attempts have also been undertaken to correlate macroscale patterns in climate with broad geographic patterns in a majority of C4 species. Reports of Teeri and Stowe (1976) and Stowe and Teeri (1978) suggested that high minimum temperatures during the growing season have the strongest correlation with the relative abundance of C4 species in regional flora. It appears that C4 grasses and dicots increase in abundance at lower latitudes. Elevation of habitat is also determinant of the distribution of C4 species (Tieszen et al. 1979b; Bouton 1980; Rundel 1980). Apparently C4 species decrease in their importance at higher elevations.

These plant geographical researches have led to experimental studies examining the competitive nature of C4 plants over C3 plants in relation to temperature and nitrogen supply (Christie and Detling 1982). Although this type of experimental design represents only a small proportion of the total floristic and geographic composition of the world's C4 flora (Teeri and Stowe 1976), it explains the physiological advantages of C4 plants over C3 palnts in relation to their ecological competitions.

Few attempts, however, have focused on the C3 and C4 plant distribution and its ecological significance related to herbivore influence. Several authors have documented the difference in herbivore preference for C3 and C4 species but not the relationship between the abundance of C3 and C4 species and herbivore preference. Only a limited amount of data is available showing that the distribution of C3 and C4 species can be attributed to the defoliation or clipping by herbivores in either field observation or experimental design.

The present study was conducted to develop the idea of how herbivores relate to the distribution of C3 and C4 plants i.e., to what extent do herbivores affect the competition between the two types of plants in an attempt to address the following hypothesis: The relative abundance of C3 and C4 plants is dependent primarily on herbivore grazing (direct influence) and secondarily on the modification of the environment by herbivores (indirect influence). Direct influences are the defoliation by herbivores or selective grazing which ultimately reduce or induce the competition of C3 and C4 plants. Indirect influences refer to, for example, maintenance of open canopy which leads to high temperatures above ground, high bulk density and hardness of soil. As a results, those alternations induce the evaporation of water from the soil and the lower water and nutrient holding capacities, which ultimately affect the replacement from C3 to C4 plant-dominance. Furthermore, when the plants are subjected under the high pressure of herbivores, physiological responses of C3 and C4 plants to the moisture and temperature gradient are strictly dependent on grazing intensity.

The second hypothesis is that this replacement of dominance between the C3 and C4 species consistently occurrs in most of the region on the biosphere even if they were under the different ecosystem and climate. Thus, the broad geographical patterns of C3 and C4 species potentially have some coevolutional aspects with the herbivory history. To examine this hypothesis, competitive distribution-patterns of C3 and C4 species were assessed and compared between in the semi-arid short grass steppe in the cool temperate zone in the United States and semi-natural grassland in the warm to cool temperate climate zone of Japan with high precipitation.

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III. STUDY AREAS

The present research was conducted at seven study areas. One of these areas is the Central Plains Experimental Range (CPER) at Pawnee National Grassland, Colorado in the United States and the remaining six are semi-natural grasslands in the southwestern part of Japan: Nara Park, Miyajima Island, Mt. Azuma of Hiroshima Prefecture, the Oita Prefecture Animal Husbandry Range (OPAHR) on Mt. Kuju, Mt. Aso, and Toi Misaki Point (Figs. 1-a and 1-b). Locality, soil type, herbivore, climate and vegetation type of each of the study areas are shown in Tables 1-a and 1-b.

Soils of the CPER are representative of dark brown and brown soils (Mollisols) of the cool and semiarid grasslands of the Central Plains Region (USDA 1948). Approximately 85% are loams ranging from clay loams to sandy loams. Soils of Mt. Azuma, the OPAHR on Mt. Kuju and Mt. Aso are characterized by dark and black color, and known as Andsol which is generally of volcanic origin. Although this soil contains a high proportion of humus, the above-ground productivity is quite low because of high acidity (Yoshinaga and Aomine 1962; Yamane 1978). Regarding the soil type of Nara Park and Miyajima Island, it was in an immature stage of Forest Brown Soil.

Climate diagrams (Walter and Lieth 1967) at the station in or near the study areas were constructed for the

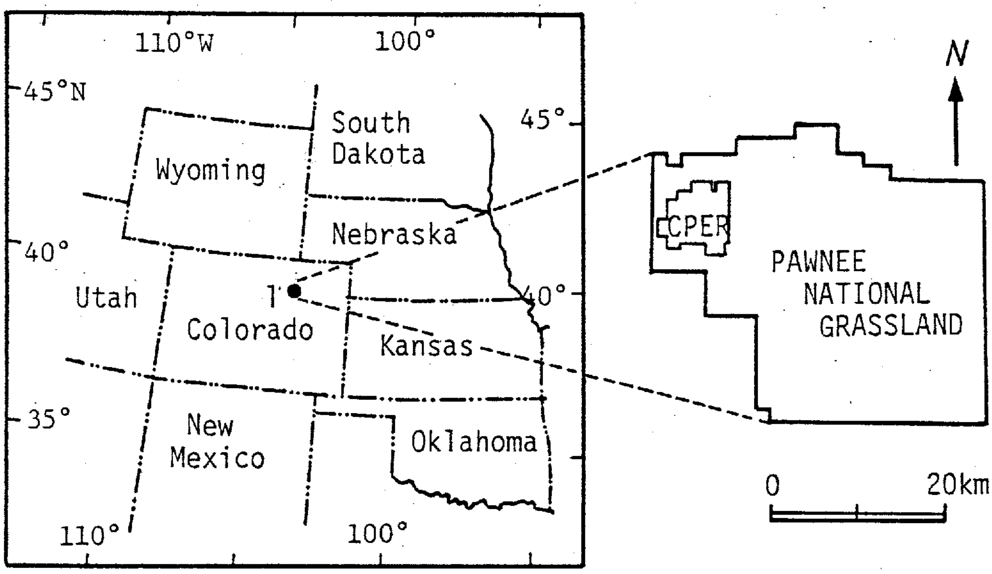

Fig. 1-a. Location of the study area of the Central Plains Experimental Range (CPER) at Pawnee National Grassland (Location No. 1).

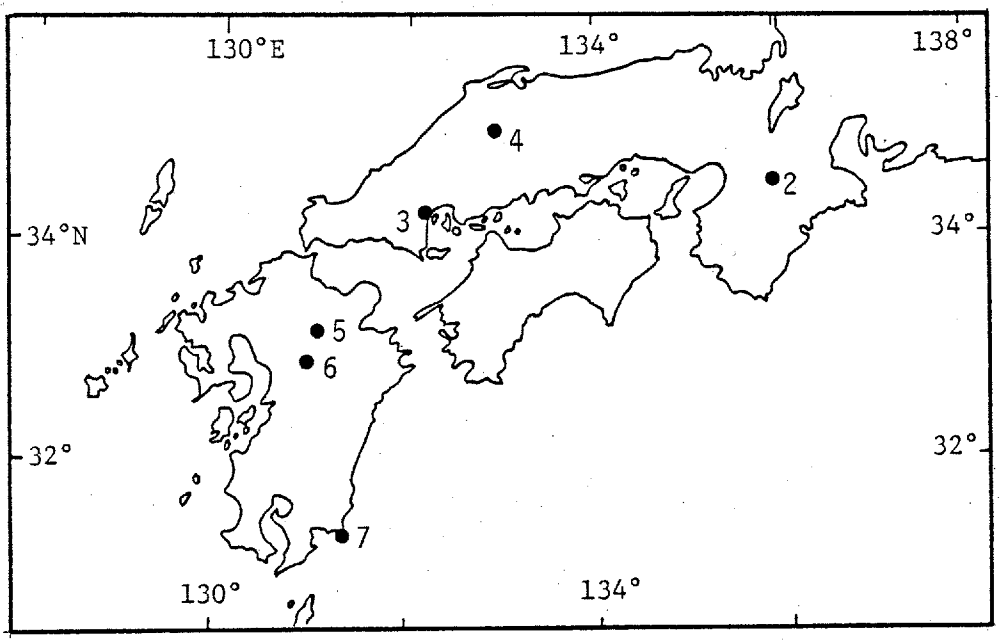

Fig. 1-b. Location of the study areas in semi-natural grasslands of southwestern Japan. 2: Nara Park; 3: Miyajima Island; 4: Mt. Azuma; 5: Oita Prefecture Animal Husbandry Range (OPAHR) on Mt. Kuju; 6: Mt. Aso; 7: Toi Misaki Point.

Table 1-a. Lacalities, soil type, herbivore type, and climate of the study areas

No. Study area	Lat.	Long.	Soil type	Herbivore	Climate
1. CPER	40°45'N	104°47'W	Mollisols	Livestock	Semiarid
2. Nara Park	34°41'N	135°50'E	Brown forest soils	Deer	Warm temperate
4. Miyajima Isl.	34°17'N	132°20'E	Immature soils	Deer	Warm temperate
3. Mt. Azuma	35°03'N	133°00'E	Andosol	Livestock	Cool temperate
5. OPAHR	33°02'N	131°17'E	Andosol	Livestock	Cool temperate
6. Mt. Aso	32°53'N	131°05'E	Andosol	Livestock	Cool temperate
7. Toi Misaki Pt.	31°20'N	131°20'E	Brown forest soils	Livestock	Warm temperate

CPER: Central Plains Experimental Range at Pawnee National Grassland, Colorado
OPAHR: Oita Prefecture Animal Husbandry Range on Mt. Kuju

Table 1-b. Vegetation type of the study areas

No.	Study area	Vegetation type
1.	CPER	Short grass steppe dominated by *Bouteloua gracilis*
2.	Nara Park	*Hydrocotylo-Zoysietum japonicae* (Suganuma & Kawai 1977) *Andropogoni-Miscanthetum sinensis* v. *gracillimus* (Haga & Suganuma 1983)
3.	Miyajima Isl.	*Hydrocotyle sibthorpioides*, *Poa annua* and *Zoysia japonica* community
4	Mt. Azuma	*Geranio-Zoysietum japonicae* (Suganuma 1966)
5.	OPAHR	*Arundinario-Miscanthetum sinensis* (Itow 1974)
6.	Mt. Aso	*Geranio-Zoysietum japonicae* (Suganuma 1966)
7.	Toi Misaki Pt.	*Centello-Zoysietum japonicae* (Itow 1970)

explanation of major climatic differences (Fig. 2a-b). The diagram of the CPER of Pawnee National Grassland shows a typical type of semiarid condition in the cool temperate zone while the areas in Japan exhibit an aspect of cool and warm temperate climate with high precipitation.

All of the study areas have long history of grazing, namely, by cattle at the CPER of Pawnee National Grassland, Mt. Azuma, the OPAHR on Mt. Kuju and Mt. Aso, by horses at Toi Misaki Point, and by sika deer (Cervus nippon) at Nara Park and Miyajima Island. The pastures have been subjected to heavy, moderate and light grazing by cattle since 1939 at the CPER and since 1979 at the OPAHR on Mt. Kuju. The treatments at the CPER were regulated so that approximately 200 Lb/acre of forage was left by the end of the summer growing season on heavy use pasture, 325Lb/acre on moderate use pasture and 450Lb/acre on light use pasture (from personal communication with Dr.M.C. Shoop, USDA Agricultural Research Service Crops Research Lab.). The grazing intensity at the OPAHR refers to pasturage that was grazed five times a year in heavily, three to four times a year in moderately, and two times a year in lightly grazed pasture (from personal communication with Mr. Kanatsuka, the Oita Prefecture Animal Husbandry Range Station). The above-ground biomass left at the end of the growing season is 265 to 677 g/m^2 in heavy grazing and 1707 to 3457g/m^2 in light grazing pasture (Hirotsu et al. 1980). The data were not available for

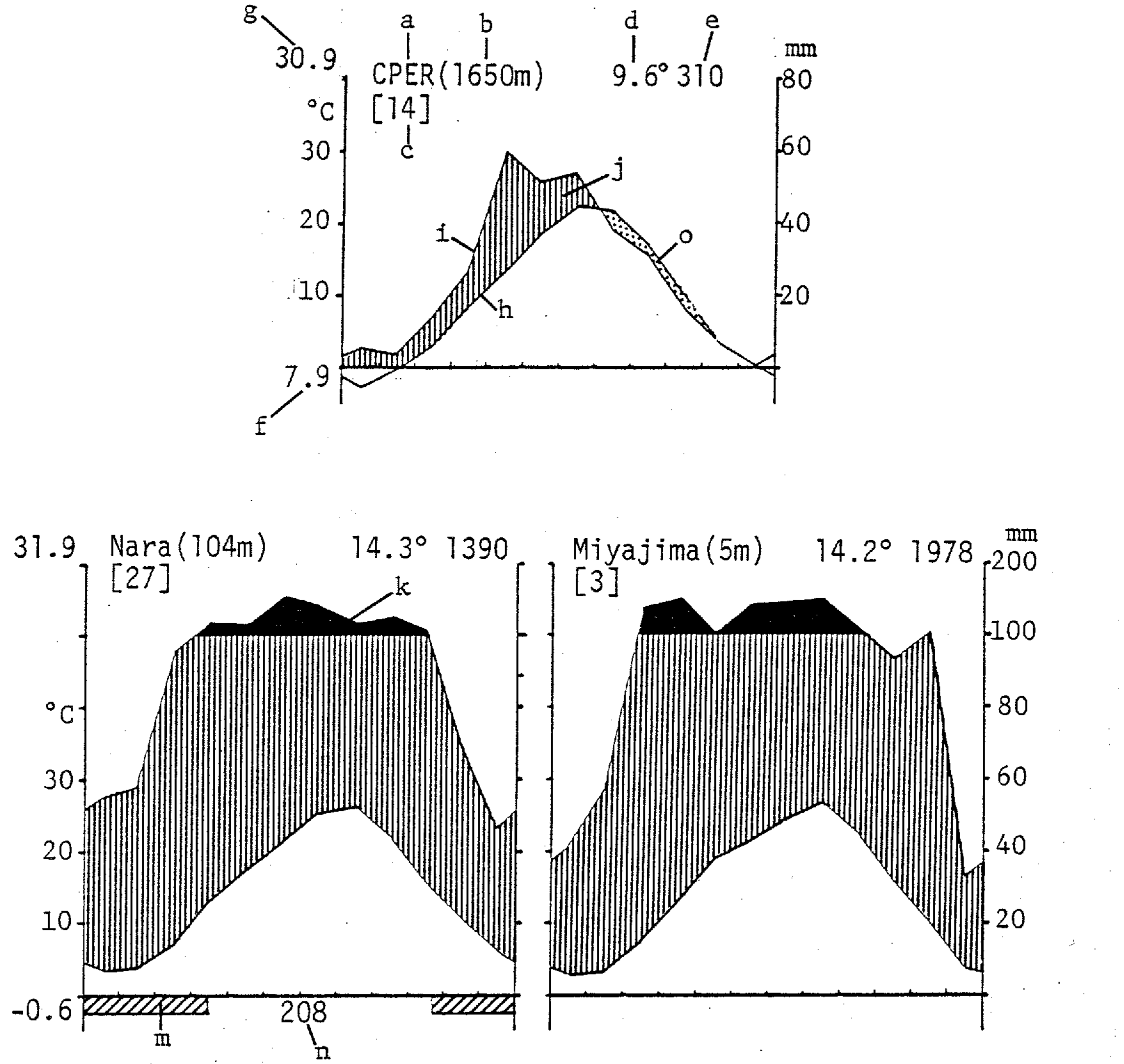

Fig. 2-a. Climatic diagrams of the CPER of Pawnee National Grassland, Nara Park and Miyajima Island. Abscissa: Month from January to December; Ordinate:1 division=10°C or 20mm rain. a: station, b: height above sea level, c: duration of observations in years, d: mean annual temperature in °C, e: mean annual precipitation in mm, f: mean daily temperature minimum of coldest month, g: mean daily temperature maximum of the warmest month, h: curve of mean monthly temperature, i: curve of mean monthly precipitation, j: relative humid season (vertical shading), k: mean rain over 100mm (black scale reduced to 1/10), m: months with absolute minimum below 0°C (diagonal shading), n: mean duration of frost-free period in days, o: relative period of drought (dotted). Not all of the above were available for every station. Where data are missing, the relevant places in the diagrams are left empty.

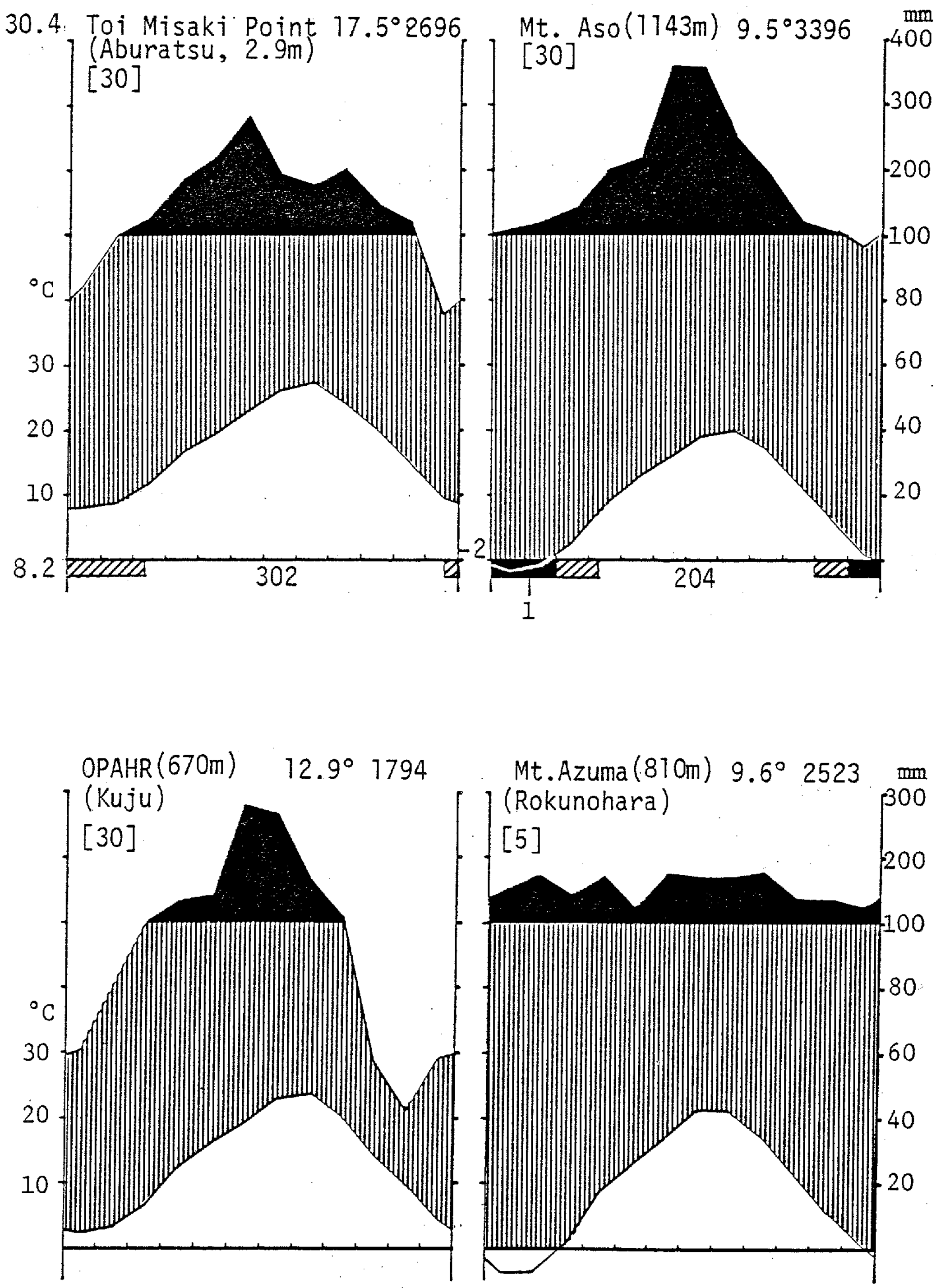

Fig. 2-b. Climatic diagrams of Toi Misaki Point, Mt. Aso, the OPAHR on Mt. Kuju and Mt. Azuma. Notations are same as those in Fig. 2-a. 1: months with mean minimum below 0°C (black).

moderate grazing.

The slopes of Mt. Azuma and the hillside of Mt. Aso have been pastured by domestic livestock and have been maintained as a short grass ecosystem. However, the population numbers of the livestock for every year are not stable and hence the pastures have not been maintained in different grazing intensities. For over 300 years, Toi Misaki has been used as pasturage for horses. Misaki horses totaled 73 including 8 stallions and 26 adult mares (above 3 years old) in 1979, 81 including 8 stallions and 24 adult mares in 1980 and 80 including 6 stallions and 34 adult mares in 1981 (Kaseda 1983).

Presently, the deer population of Nara Park is estimated over 1000 head (from personal communication with the Deer Protection Society at Nara Park) and 550 on Miyajima Island (Hayashi 1980). The vegetation of the deer-inhabited areas has been extensively affected by deer grazing and most of it has been maintained as short grass community of *Zoysia japonica*, *Hydrocotyle maritima* or *Poa annua* community. Due to the shortage of deer forage and abundance of unpalatable plants on Miyajima Island (Okuda 1984a) and unhabitable condition for deer over the entire area of island (Okuda 1984b), the dependency of deer foraging on the herbacious plant community is definitely high, and their influence on the ecosystem is much more extreme than in any other of the study areas.

IV. METHODS

1. Vegetation Data

For the research conducted at livestock pastures in semi-natural grasslands of southwestern Japan, at Nara Park and on Miyajima Island, sampling was repeated three times a year: April to May, June to July and September to October in 1983. Research at the CPER of Pawnee National Grassland was conducted during late July to early August in 1982 when most of the species were in a mature stage of development (French and Sauer 1974; Dickinson and Dodd 1976).

For the vegetation data, several transects were placed on three different positions of the hillslope (upland, mid-slope and lowland) in horizontal lines along the contour. Hillslopes chosen for sampling were generally inclined 15° to 25°, ranging in length from 50 m to 100 m at the study areas in Japan and 200-300 m at the CPER of Pawnee National Grassland. A transect contained 5-10 quadrats (50 x 50 cm) with 5 m intervals. For the community dominated by _Miscanthus sinensis_, quadrats of 1 m x 1 m size were used. The species/area curve was drawn to determine the appropriate quadrat size which was considered as 10% of the minimal area (Numata and Yoda 1955).

The total number of transects and quadrats at each study area was: 51 transects with 506 quadrats at the CPER, 14 transects with 71 qauadrats at Nara Park, 12 transects with 60 quadrats on Miyajima Island, 3 transects with 15 quadrats on Mt.Azuma, 11 transects with 55 quatrats at the OPAHR, 4 transects with 20 quadrats on Mt. Aso and 4 transects with 20 quadrats at Toi Misaki Point.

In the area of the CPER and the OPAHR, transects were placed at three or four different grazing intensities: heavy, moderate, light and none. Regarding the research at Nara Park and Miyajima Island, sampling was undertaken both outside the exclosure where the vegetation had been subjected to deer grazing and inside the exclosure where deer pressure on vegetation was eliminated. Exclosures were located in either an open condition without an overstory or a closed condition with a tree canopy. For the remaining areas, Mt. Azuma, Mt. Aso, Toi Misaki Point, there were no regimes to determine the grazing intensities. Therefore, the stands for sampling were only placed along the three different hillslope positions, among which the difference of grazing pressure was still expected due to the discriminative use by herbivores on the hillslope.

To evaluate the dominance of plant species, the importance value known as the Summed Dominance Ratio (SDR) and the relative importance value SDR' were used (Numata 1966). Coverage(C), plant height(H) and frequency(F) of a species were each made relative, C', F' and H'(%) respectively and the average of the sum of the three was taken as the importance value for each transect, namely:

$$SDR=(C'+H'+F')/3\ (\%) \qquad (1)$$

The tallest individual appearing in a quadrat represented the height of the species. The SDR value is highly correlated with the biomass of the plant species (Numata 1966). The relative importance value SDR' which is the ratio of the SDR to the total SDR within a transect was also determined:

$$SDR'=SDRsp/\Sigma SDRsp \times 100\ (\%) \qquad (2)$$

where SDRsp indicates the SDR determined by the equation (1) for each species and ΣSDRsp is the sum of SDRsp in a transect.

Since most of the C4 plants observed in the study areas of Japan consisted of graminoids, the analysis of C3 and C4 plant distribution was made restricted to the graminoids. The graminoids observed were classified into two physiologically differing groups, plants possessing C3 and those with C4 photosynthetic pathways, according to the results of the study by Waller and Lewis (1979), Kanai (1979), Hesla et al. (1982), Downton (1975), Krenzer et al. (1975), Smith and Epstein (1971), Teeri and Stowe (1976) and Mulroy and Rundel (1977).

To show the abundance of C3 and C4 graminoids in terms of variation of two groups as a whole, SDR' values (equation 2) of species were summed according to the discrimination of C3 and C4 species and expressed using formula (3) and (4).

$$\text{C3-SDR}' = \Sigma(\text{SDR}' \text{ of C3 graminoid}) \ (\%) \qquad (3)$$

$$\text{C4-SDR}' = \Sigma(\text{SDR}' \text{ of C4 graminoid}) \ (\%) \qquad (4)$$

Another way to express the variation of C3 and C4 graminoids, was derived from C3 and C4 indices which are the products of C3- or C4-SDR' (equation 3,4) and the total number of C3, C4 graminoid species respectively at each transect, namely,

$$\text{C3 Index} = \text{C3-SDR}' \times (\text{number of C3 graminoid species}) \qquad (5)$$

$$\text{C4 Index} = \text{C4-SDR}' \times (\text{number of C4 graminoid species}) \qquad (6)$$

2. Sampling and Analysis of Soil Data

Soils were sampled near each quadrat where the vegetation data were recorded, during late May to early August to define space structure, moisture storage, and soil organic matter. The number of samplings for soil is equivalent to that of quadrats for vegetation data. This sampling was undertaken at Nara Park, Miyajima Island, Mt. Azuma, the OPAHR on Mt. Kuju, Mt. Aso and Toi Misaki Point.

Soil data at the CPER of Pawnee National Grassland were not collected during the courses of the vegetation research. But results of the researches conducted by Schimel (1983) and Van Haveren (1983) at the CPER were cited for the discussion of vegetation and soil aspects.

A tubular core with 50 mm in diameter and 50 mm in length (100 cc) was used to extract soil samples at a depth of 10cm below the ground surface. This permited determination of the bulk density, pore space, maximum water holding capacity (MWHC), moisture percentage (MP), water content ratio (WCR), root mass, sand mass, carbon and nitrogen content, and of the C/N ratio.

The maximum water holding capacity (MWHC) of the soils was measured by allowing the soil core to absorb water for 24 hours. Moisture percentages (MP) were determined gravimetrically after drying the soil cores at 80 °C for 3 days (Dry weight) and were expressed as the percentage of grams of water to grams of soil (equation (7)). The water content ratio (WCR) was computed with the formula (8):

$$MP = (\text{Fresh weight} - \text{Dry weight}) / \text{Dry weight} \times 100(\%) \qquad (7)$$

$$WCR = (\text{Fresh weight} - \text{Dry weight}) / MWHC \times 100(\%) \qquad (8)$$

where fresh weight refers to the soil core weight at the time of sampling. The percentage of pore space in a given volume of soil was calculated from the formula:

Pore space=100-(BD/PD x 100) (%) (9)

where BD and PD represnt bulk density and particle density respectively. The specific gravity of dominant soil minerals - quarts, feldspars, micas and clay minerals - was approximately 2.65g/cc (Danahue et al. 1977) and was used as the standard value of particle density. Soil organic matter was determined by using the C-N coda (Yanagimoto Mt500) and expressed as the content of carbon and nitrogen in a soil volume of 100cc soil. Hardness of soils was also determined at depth of 10cm from the surface with using hardness meter.

V. RESULTS AND ANALYSIS

1. Vegetation Aspects

The C3 and C4 graminoid species which appeared in the study areas are listed with cliamte zone of their distribution in Tables 2-a, 2-b and 2-c. The total numbers of C3 and C4 species were 6 and 9 at the CPER, and 22 and 24 respectively in the semi-natural grasslands of southwestern Japan. Most of the species were widely distributed from cool to warm temperate zones, i.e., they were not endemic to certain areas. The study areas in Japan were located within a area where climatic conditions optimizes the growth of most speices.

1) Individual Response of C3 and C4 Species to the Grazing Intensity

Importance values (SDR and SDR') for some dominant species as a function of grazing intensity at three hilslope positions at the CPER of Pawnee National Grassland are shown in Fig. 3-a and 3-b.

Bouteloua gracilis (Fig.3-a), a C4 graminoid, had a high SDR value in all sample stands. In both the upland and the mid-slope position, its values were nearly 100%. No other grasses approached such high values. However, in the lowland

Tab. 2-a. List of C3 and C4 graminoid species at the CPER of Pawnee National Grassland

Species name	Distribution (climate zone)
C3 graminoids	
Agropyron smithii	cool temperate - subtropical zone
Carex eleocharis	cool temperate - subtropical zone
C. filifolia	subarctic - subtropical zone
Festuca octoflora	cool temperate - subtropical zone
Sitanion hystrix	cool temperate - subtropical zone
Stipa comata	subarctic - subtropical zone
C4 graminoids	
Aristida longiseta	cool temperate - subtropical zone
Bouteloua curtipendula	cool temperate - subtropical zone
B. hirsuta	cool temperate - subtropical zone
B. gracilis	cool temperate - subtropical zone
Buchloe dactyloides	cool temperate - subtropical zone
Distichlis stricta	cool temperate - subtropical zone
Muhlenbergia torreyi	cool temperate - subtropical zone
Munroa squarrosa	cool temperate - subtropical zone
Schedonnardus paniculatus	cool temperate - subtropical zone
Sporobolus cryptandrus	cool temperate - subtropical zone

Table 2-b. List of C3 graminoid species in semi-natural grasslands of southwestern Japan, Nara Park, Miyajima Island, Mt. Azuma, the OPAHR on Mt. Kuju, Mt. Aso and Toi Misaki Point

Species name	Distribution (climate zone)
C3 graminoids	
Agropyron ciliare	cool and warm temperate zone
Agrostis alba	cool temperate zone
A. clavata v. nukabo	arctic - warm temperate zone
Anthoxanthum odoratum	cool and warm temperate zone
Calamagrostis arundinacea	cool temperate zone
Carex breviculmis	cool and warm temperate zone
C. breviculmis v. discoidea	cool and warm temperate zone
C. gibba	cool and warm temperate zone
C. lanceolata	cool temperate zone
C. nervata	cool and warm temperate zone
Festuca parvigluma	cool and warm temperate zone
Glyceria acutiflora	cool and warm temperate zone
Isachne nipponensis	cool and warm temperate zone
Juncus effusus v. decipiens	cool and warm temperate zone
J. tenuis	cool and warm temperate zone
Luzula capitata	cool and warm temperate zone
L. multiflora	cool and warm temperate zone
Oplismenus undulatifolius	cool temperate - subtropical zone
Pleioblastus distichus	warm temperate zone
Poa annua	cool and warm temperate zone
P. sphondylodes	cool and warm temperate zone
Trisetum bifidum	cool and warm temperate zone

Table 2-c. List of C4 graminoid species in semi-natural grasslands of southwestern Japan, Nara Park, Miyajima Island, Mt. Azuma, the OPAHR on Mt. Kuju, Mt. Aso and Toi Misaki Point

Species name	Distribution (climate zone)
C4 graminoids	
Andropogon brevifolius	cool temperate - subtropical zone
A. virginicus	naturalized from north America
Arundinella hirta	cool and warm temperate zone
Cymbopogon tortilis	cool and warm temperate zone
Digitaria sanguinalis	cool temperate - tropical zone
D. violascens	cool temperate - tropical zone
Eleusine indica	warm temperate - tropical zone
Eragrostis ferruginea	cool and warm temperate zone
E. multicaulis	cool temperate - tropical zone
Fimbristylis complanata	cool temperate - tropical zone
F. dichotoma	cool temperate - tropical zone
Imperata cylindrica	cool temperate - tropical zone
Kyllinga brevifolia v. leiolepis	cool and warm temperate zone
Miscanthus sinensis	cool and warm temperate zone
M. sinensis v. gracillimus	cool and warm temperate zone
Muhlenbergia japonica	cool and warm temperate zone
Paspalum thumbergii	cool and warm temperate zone
Pennisetum alopecuroides	cool temperate - subtropical zone
Setaria glauca	cool temperate - tropical zone
S. pallide-fusca	cool temperate - tropical zone
S. viridis	cool and warm temperate zone
Sporobolus fertilis	cool and warm temperate zone
Zoysia japonica	cool and warm temperate zone
Z. tenuifolia	warm temperate - tropical zone

under heavily grazed pasture, it decreased to less than 25%. Although its SDR in the mid-slope was also quite high, ranging from 95 to 100%, the value of SDR' was smaller than in the upland due to high biomass and the variety of species.

An abundance of Agropyron smithii (Fig. 3-a), a C3 graminoid, generally declined with increase of grazing intensity at all three slope positions. The values of SDR at the non-grazed pasture were significantly higher than that at the heavily grazed pasture ($P<0.01$). The values of both SDR and SDR' were greatest at the lowland sites and least at the upland. The SDR' was relatively stable at the lowland position.

Buchloe dactyloides (Fig. 3-a), a C4 graminoid, exhibited the opposite pattern of that of Agropyron smithii; ie., relative covergage, C' (in equation (1)) of this species was significantly correlated negatively to that of Agropyron smithii ($R=0.880$, $P<0.01$. Figure was not shown) at the lowland. However, no significant correlation was obtained at the mid-slope and the upland areas. This species appeared to be highly competitive in the heavily grazed pasture where its SDR value was greater than any other grazing intensity ($P<0.01$) except at the mid-slope.

Carex eleocharis (Fig. 3-a), a C3 graminoid and the most abundant sedge at the CPER, was not strongly correlated with grazing intensity and/or slope position. However, the values of SDR and those of SDR' on average were slightly

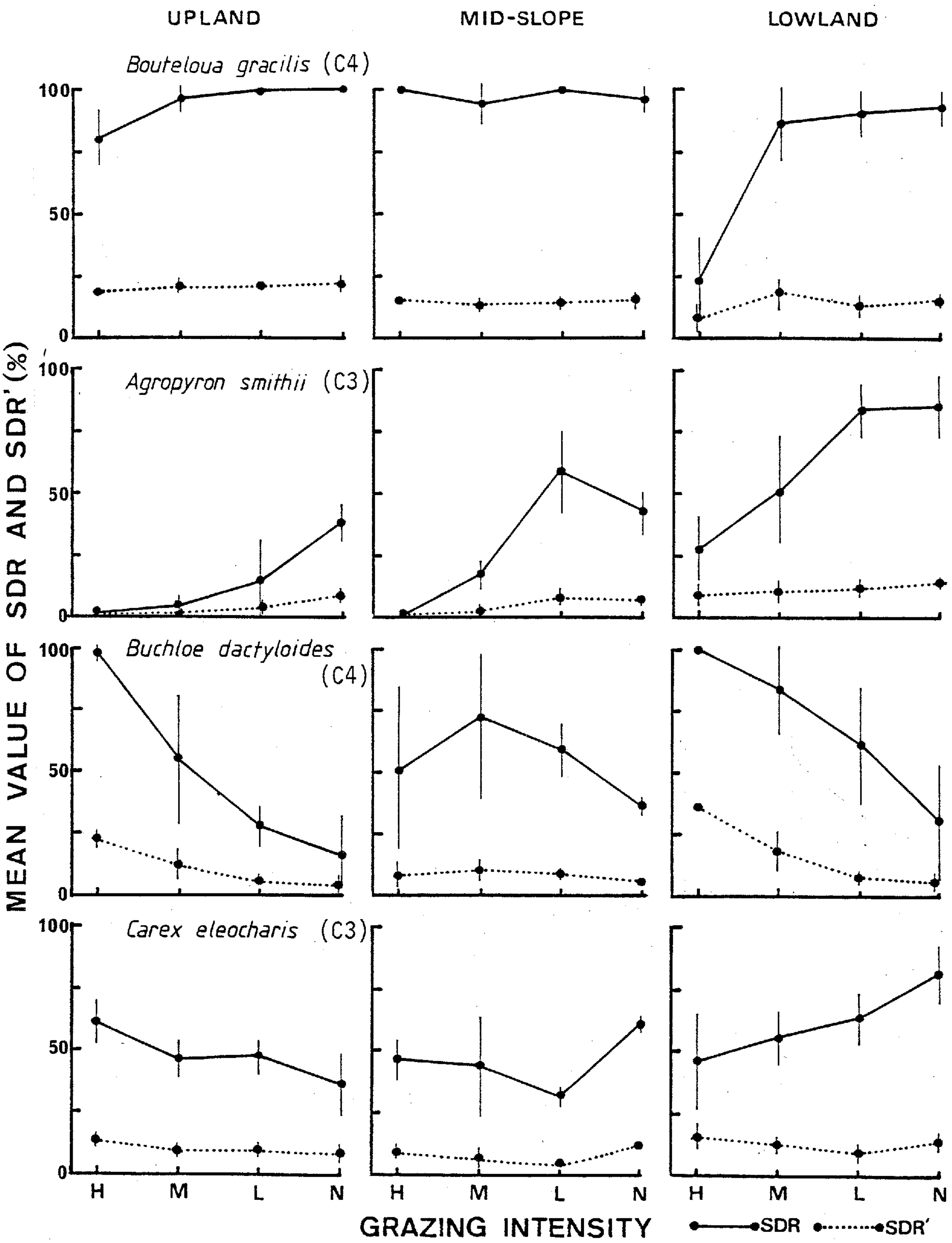

Fig. 3-a. Variations of SDR and SDR' values of diminant species in different grazing intensities at three hillslope positions in the CPER of Pawnee National Grassland. H: Heavy, M: Moderate, L: Light and N: Non-grazing. Vertical bars represent ±1 SD.

higher in the lowland, and the SDR' in the mid-slope were lower than in the other parts of the hillslope.

Aristida longiseta (Fig.3-b), a C4 grass and Stipa comata (Fig. 3-b), a C3 grass, both had relatively lower SDR and SDR' values at the upland and the lowland sites and higher values in the mid-slope areas, regardless of grazing intensity.

Sitanion hystrix (Fig. 3-b), a C3 graminoid, showed another type of pattern relative to the grazing intensity, i.e., the value was lowest at either moderately or lightly grazed but increased in heavily and non-grazed areas. The variation of the values among the four grazing intensities were not statistically different.

The SDR and SDR' values of Muhlenbergia torreyi (Fig. 3-b), a C4 grass, are significantly higher ($P<0.01$) in moderately and lightly grazed pastures than in either heavily or non-grazed pastures. This trend was consistent over every hillslope position, but most distinct in the mid-slope area where the SDR was higher than in the other slope positions.

The variation of SDR and SDR' of some representative species of C3 and C4 graminoids at the OPAHR on Mt. Kuju for three periods of growing season, May, July and October are illustrated in Figs. 3-c to 3-h.

Zoysia japonica (Fig. 3-c), a short and stoloniferous grass possesing the C4 photosynthetic pathway, showed an

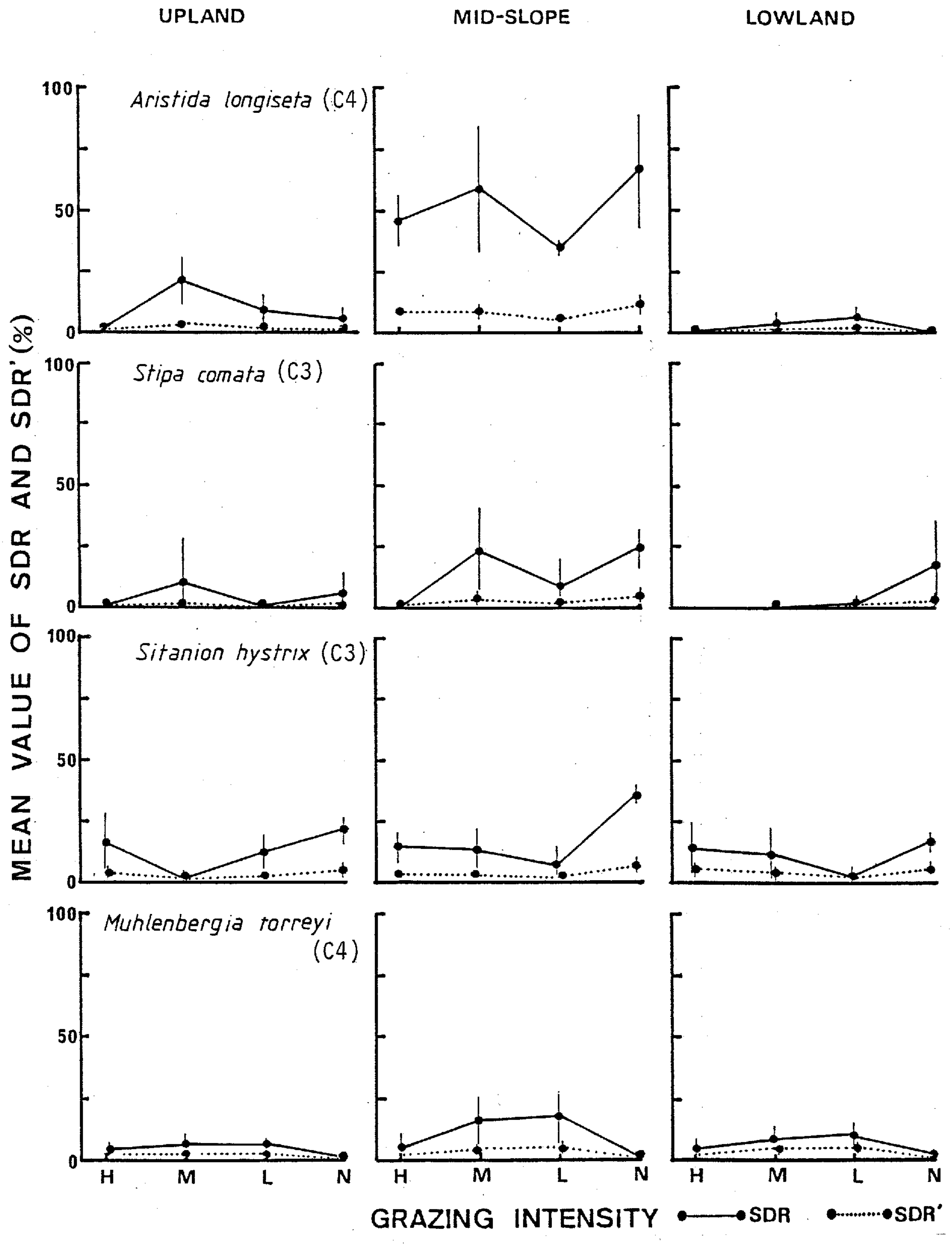

Fig. 3-b. Variations of SDR and SDR' values of diminant species in different grazing intensities at three hillslope positions in the CPER of Pawnee National Grassland. H: Heavy, M: Moderate, L: Light and N: Non-grazing. Vertical bars represent ±1 SD.

increasing trend as grazing increased. However, at the upland, it was not observed in any grazing pasture through the growing season and neither absolute (SDR) nor relative importance (SDR') values were recorded. The reduction from the heavily used to the lightly used pasture at the lowland position was approximately 60-70% in SDR and more than 15-20% in SDR' which were both statistically significant. This species is highly competitive and suppressive to the growth of other species in heavily used pastures.

The variations of SDR and SDR' in Imperata cylindrica (C4, Fig 3-d), and Arundinella hirta (C4, Fig. 3-e) showed about the similar pattern relative to the grazing intensities, i.e., their values exhibited to increase markedly with grazing. These trends were more obvious in May. However, the difference between the heavily and lightly used areas was not significant in the following situations: in both species at the lowland position in October, and in Arundinella hirta at every position of the hillslope in July. The variation of SDR values in Arundinella hirta in July was relatively stable as compared with that in May and October.

The mean SDR of Agrostis alba (C3, Fig. 3-f) generally showed the tendency to be highest in moderately and least in heavily or lightly grazed pastures at the mid-slope position in May and at every position of the hillslope in July. This implies that moderate grazing optimized the growth and

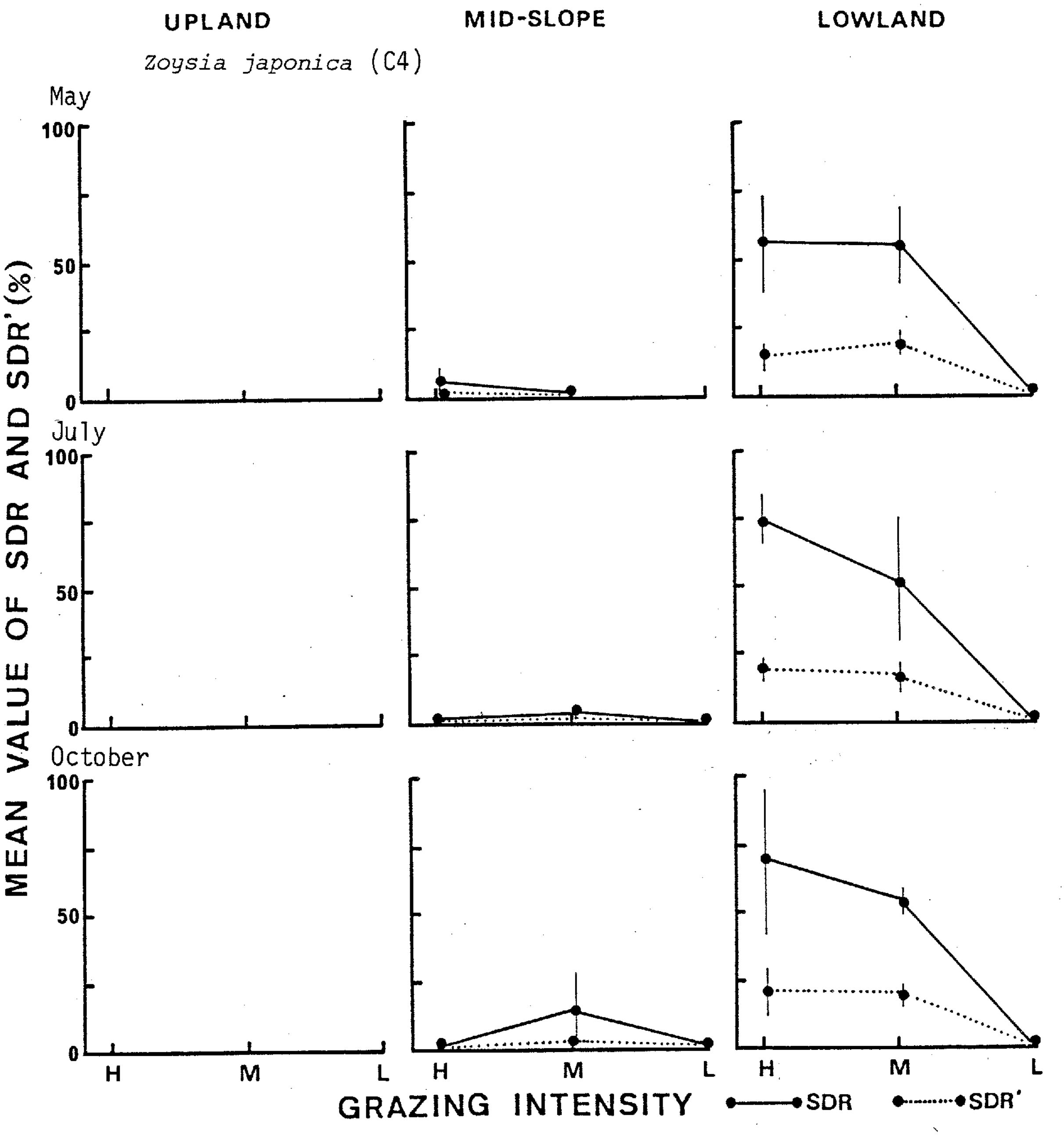

Fig. 3-c. Variations of SDR and SDR' values of Zoysia japonica (C4) in different grazing intensities at three hillslope positions in the OPAHR on Mt. Kuju in May, July and October. H: Heavy, M: Moderate and L: Light grazing. Vertical bars represent ±1 SD.

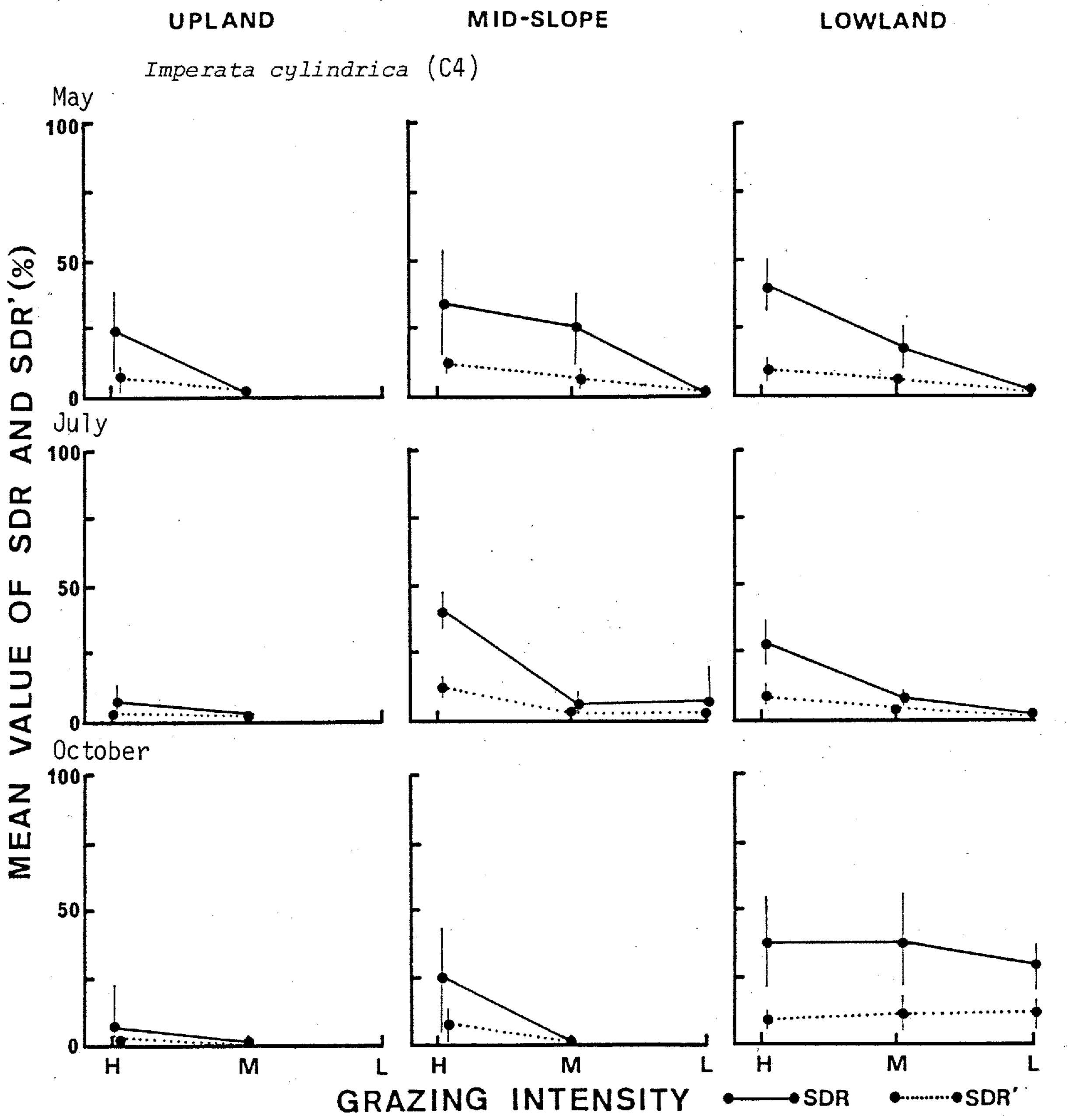

Fig. 3-d. Variations of SDR and SDR' values of Imperata cylindrica (C4) in different grazing intensities at three hillslope positions in the OPAHR on Mt. Kuju in May, July and October. H: Heavy, M: Moderate and L: Light grazing. Vertical bars represent ±1 SD.

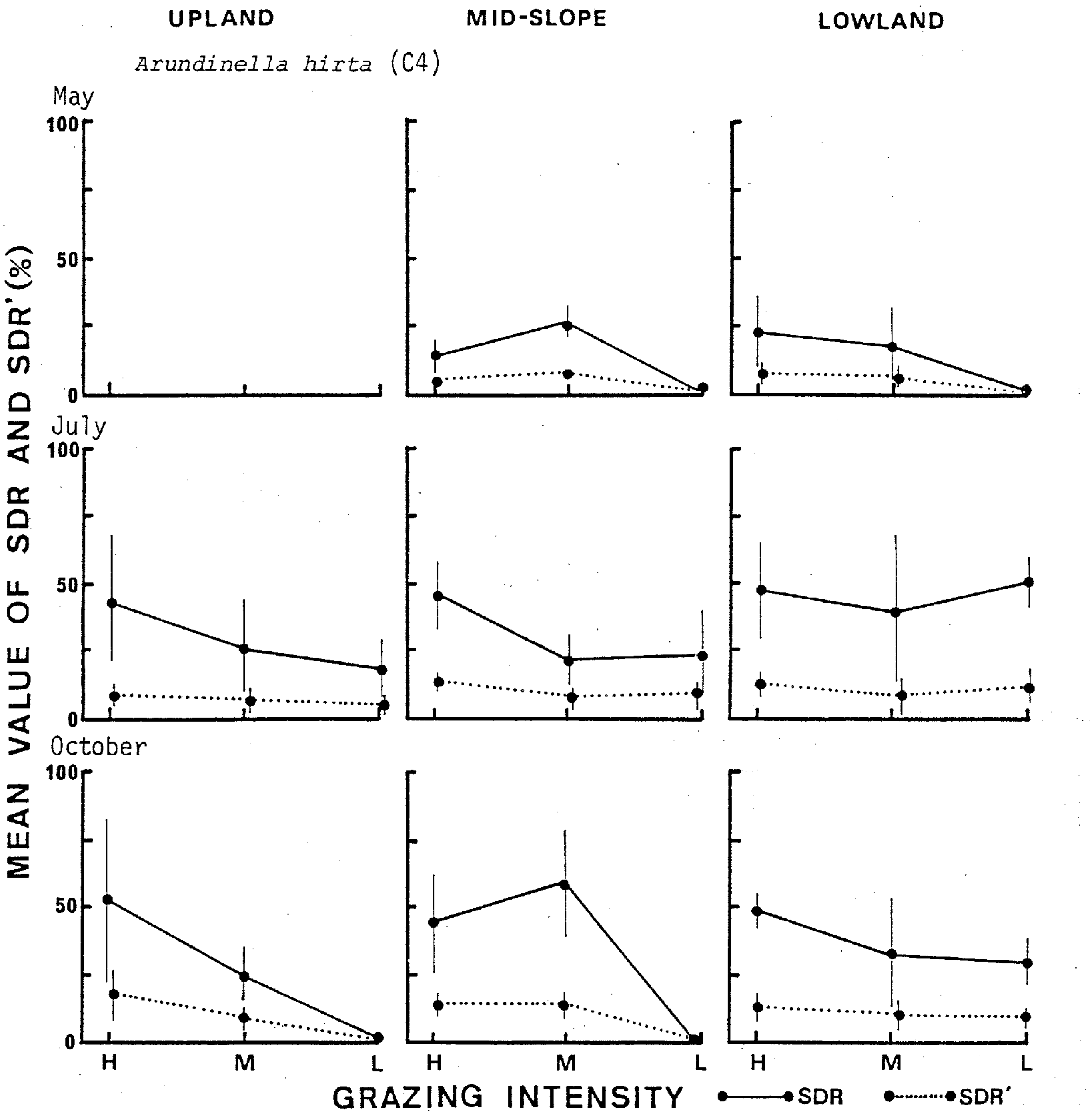

Fig. 3-e. Variations of SDR and SDR' values of Arundinella hirta (C4) in different grazing intensities at three hillslope positions in the OPAHR on Mt. Kuju in May, July and October. H: Heavy, M: Moderate and L: Light grazing. Vertical bars represent ±1 SD.

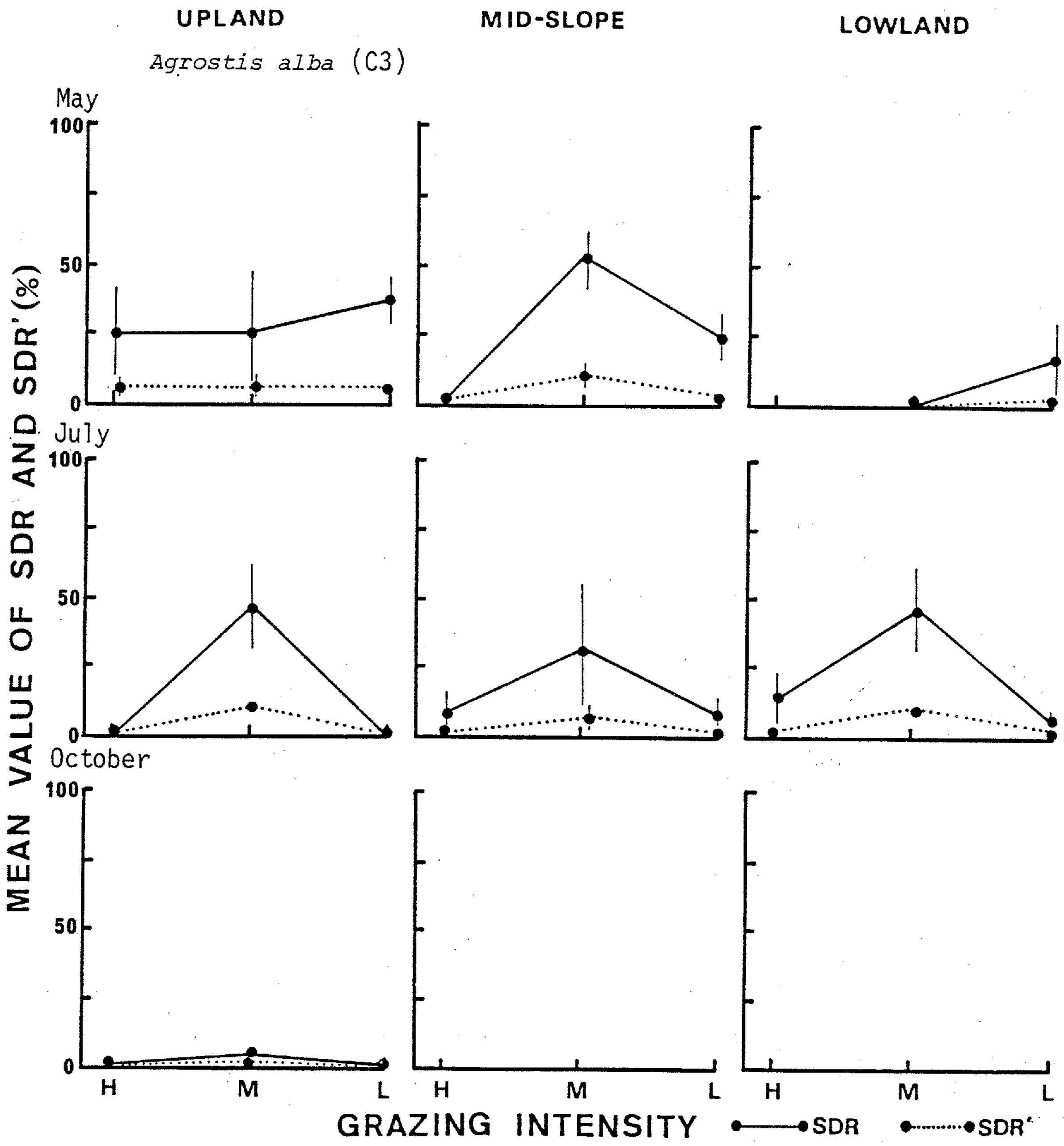

Fig. 3-f. Variations of SDR and SDR' values of Agrostis alba (C3) in different grazing intensities at three hillslope positions in the OPAHR on Mt. Kuju in May, July and October. H: Heavy, M: Moderate and L: Light grazing. Vertical bars represent ±1 SD.

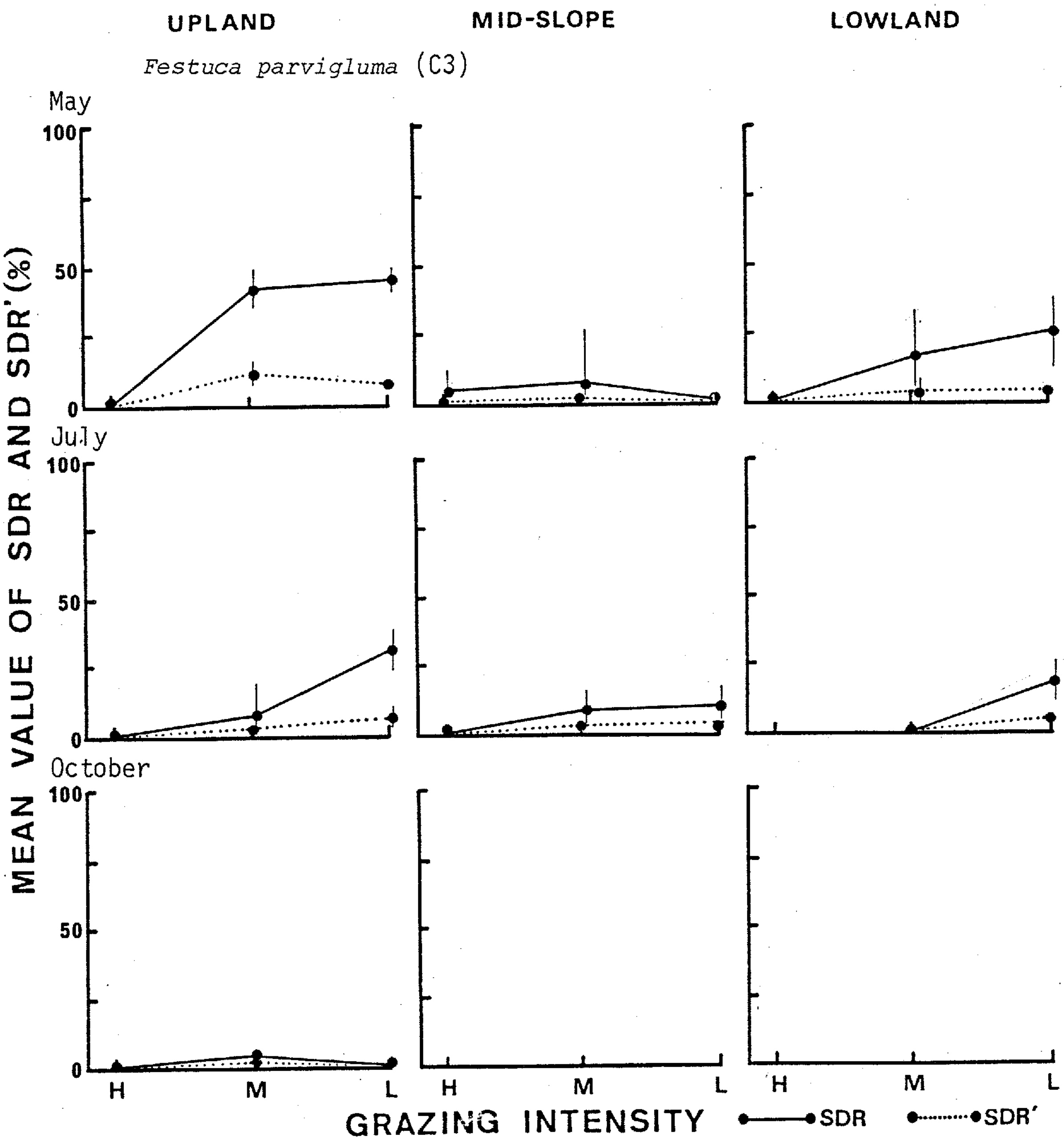

Fig. 3-g. Variations of SDR and SDR' values of Festuca parvigluma (C3) in different grazing intensities at three hillslope positions in the OPAHR on Mt. Kuju in May, July and October. H: Heavy, M: Moderate and L: Light grazing. Vertical bars represent ±1 SD.

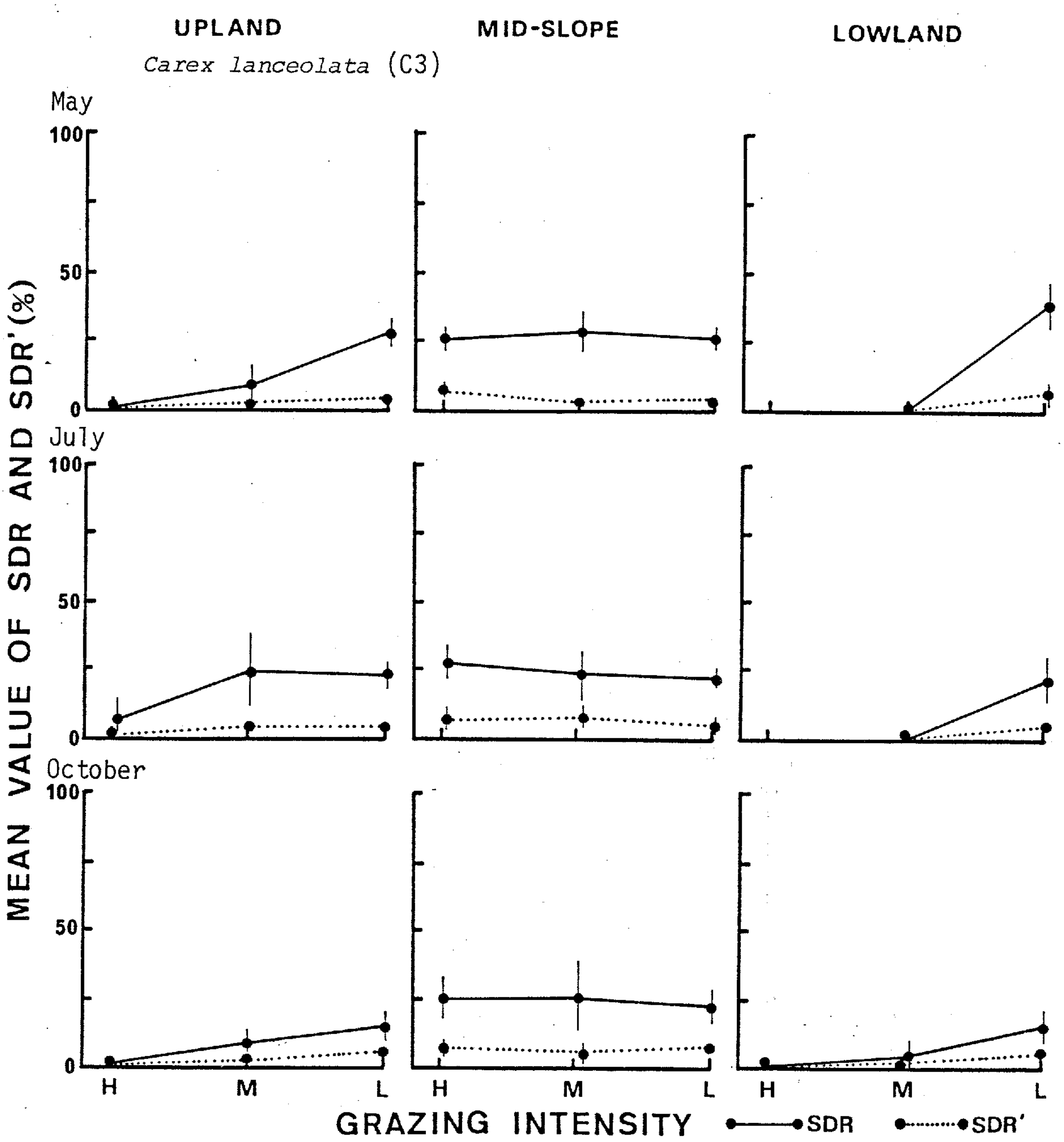

Fig. 3-h. Variations of SDR and SDR' values of Carex lanceolata (C3) in different grazing intensities at three hillslope positions in the OPAHR on Mt. Kuju in May, July and October. H: Heavy, M: Moderate and L: Light grazing. Vertical bars represent ±1 SD.

regrowth of this species. Agrostis alba appears to be most vigorous at the beginning of the growing season and depressed at the end of the growing season.

Festuca parvigluma (C3, Fig. 3-g) and Carex lanceolata (C3, Fig. 3-h) had the least values in the heavily grazed pasture and greatest in lightly grazed pasture in the upland and the lowland, but not in the mid-slope area. The difference between the two grazing regimes was statistically significant at least the 5% level. This trend expresses well that grazing performs a suppressive influence to some extent as far as the two species are concerned.

2) Variation of C3- and C4-SDR' (Figs. 4-a - 4-d)

The changes in C3- and C4-SDR' which are the sum of the relative importance values, SDR' at each transect (equation (3) and (4)), are illustrated in Figs. 4-a to 4-d and Tables 5 and 6. It should be kept in mind that the C3- and C4-SDR' were conserned with only graminoid species (perennial and annual). Thus, the sum of C3 and C4-SDR' does not reach to 100% because of the values for other life forms. The results are explained for the CPER of Pawnee National Grassland, the OPAHR on Mt. Kuju, Nara Park and Miyajima Island.

a. CPER of Pawnee National Grassland (Fig. 4-a)

The sum of C3-SDR' and C4-SDR' was decreased from 60% in heavily grazed areas to 43% in lightly grazed pastures in the upland and from 78% to 52% in the lowland. However, the value of the sum increased in the non-grazed pasture. This trend was not repeated in the mid-slope where the value showed little fluctuation relative to the grazing intensity.

C4-SDR' reduced its value with decreased grazing intensity at every position of the hillslope while C3-SDR' kept its value relatively constant between the heavily and lightly grazed areas, but sharply increased in the non-grazed areas. The C4-SDR' in heavily or moderately grazed pastures had a significantly ($P<0.01$) higher SDR'value than those in lightly or non-grazed areas at every hillslope position. On the other hand, the difference in the C3-SDR' relative to the grazing intensity was not significant except the difference betweeen the heavy and non-grazing at the mid-slope position.

C4 graminoids had higher values than C3 graminoids at all hillslope positions. However, in the lowland of non-grazed pasture, the C3-SDR' surpassed the C4-SDR' and was significantly higher than that of C4 graminoids. This trend was most distinctive at the lowland position. This fact suggests that the C3 graminoids were competitive and suppressive to the C4 graminoids in the non-grazed pasture especially at the lowland in non-grazing.

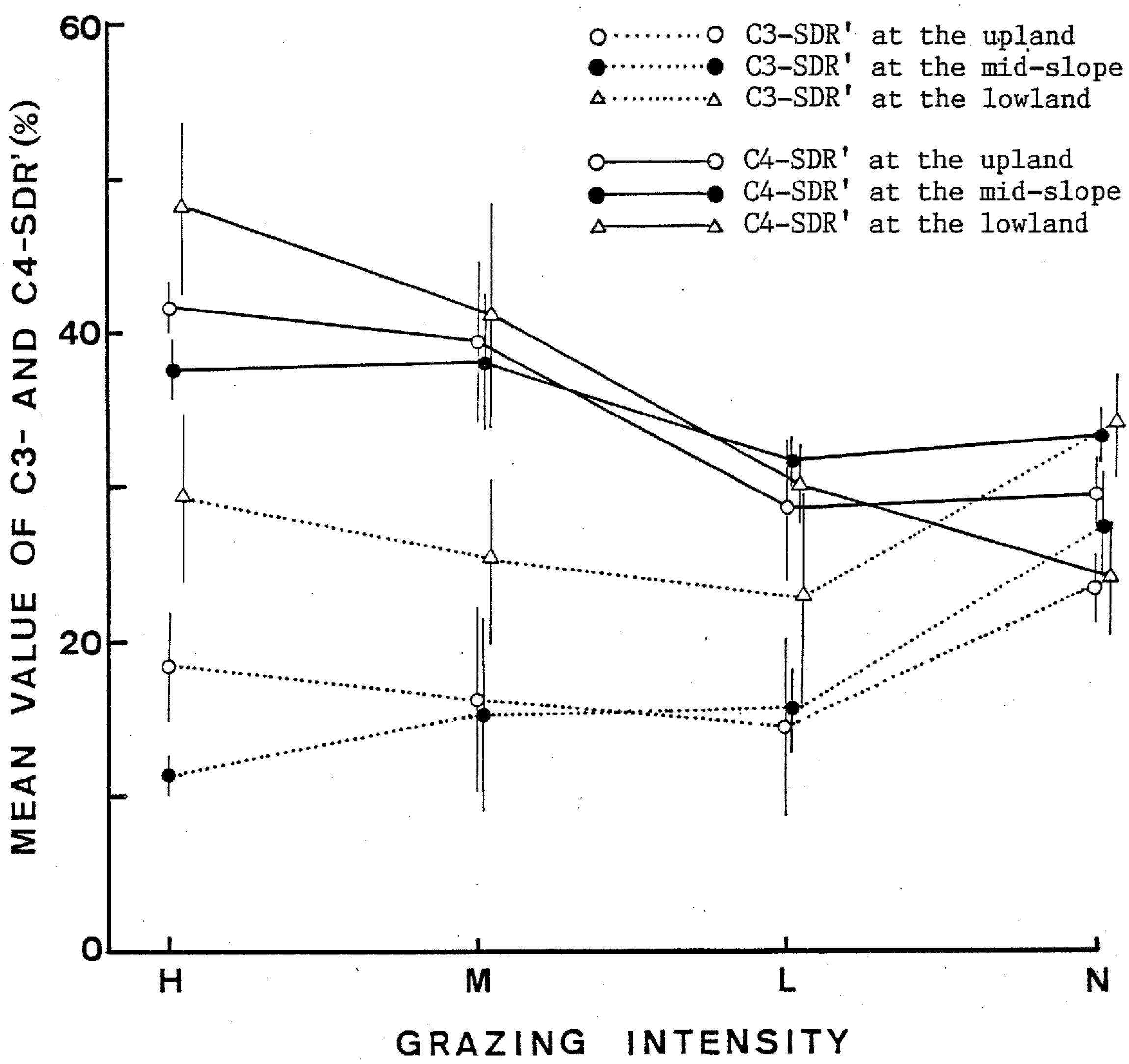

Fig. 4-a. Variations of C3- and C4-SDR' along four different grazing intensities at three hillslope positions in the CPER of Pawnee National Grassland. H: Heavy, M: Moderate, L: Light and N: Non-grazing. Vertical bars represent ±1 SD.

b. OPAHR on Mt. Kuju (Figs. 4-b - 4-d)

The general trends of the C3- and C4-SDR' were similar to those shown at the CPER, i.e., the C4-SDR' declined as the grazing pressure decreased and the C3-SDR' did not show so marked a difference relative to the grazing intensity (Fig. 4-b to 4-d). However, the difference in C3 and C4-SDR' among the three different hillslope positions, did correspond well with the results of the CPER. The mean C4-SDR' in the lowland was usually higher than those of the mid-slope and the upland, and the value in the upland was usually least among the three. This is because the cattle at the OPAHR also intensively frequented the lowland position. The reduction of C4-SDR' values from heavy to light was 100% at the upland, 100% at the mid-slope, and 71.8% at the lowland in May, 63.6% at the upland, 65.7% at mid-slope and 72.1% at the lowland in July, and 100% at the upland, 88.8% at the mid-slope and 61.4% at the lowland in October (The SDR' value of <u>Miscanthus</u> <u>sinensis</u> was excluded). These differences were all significant at the 1% level.

Although the mean of C3-SDR' decreased from heavy to moderate grazing at the mid-slope area in May (Fig. 4-b), variations were not statistically significant. The difference relative to the grazing intensity for the other hillslopes were not also obvious.

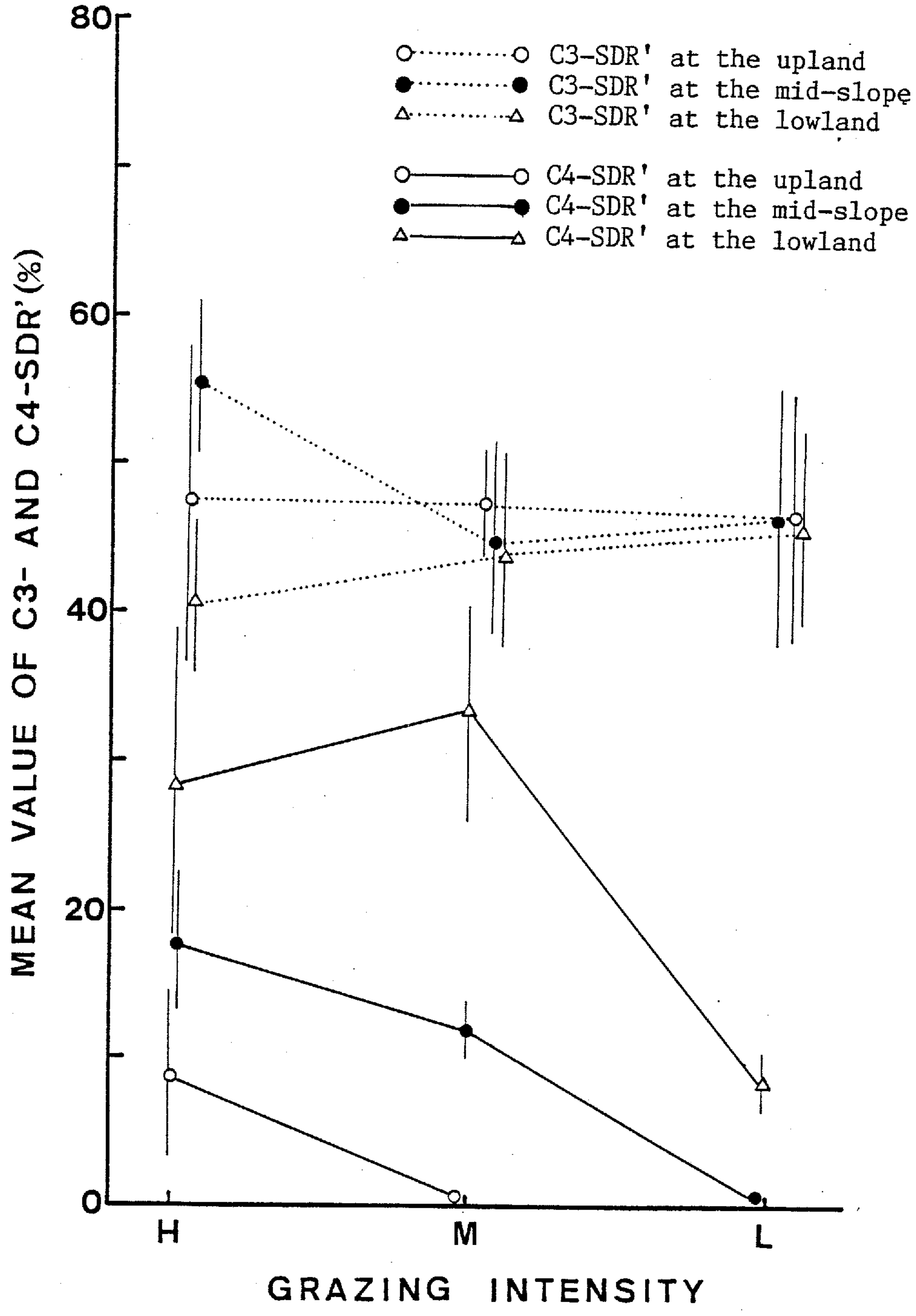

Fig. 4-b. Variations of C3- and C4-SDR' along three different grazing intensities at three hillslope positions in the OPAHR on Mt. Kuju in May. H: Heavy, M: Moderate, L: Light grazing. Vertical bars represent ±1 SD.

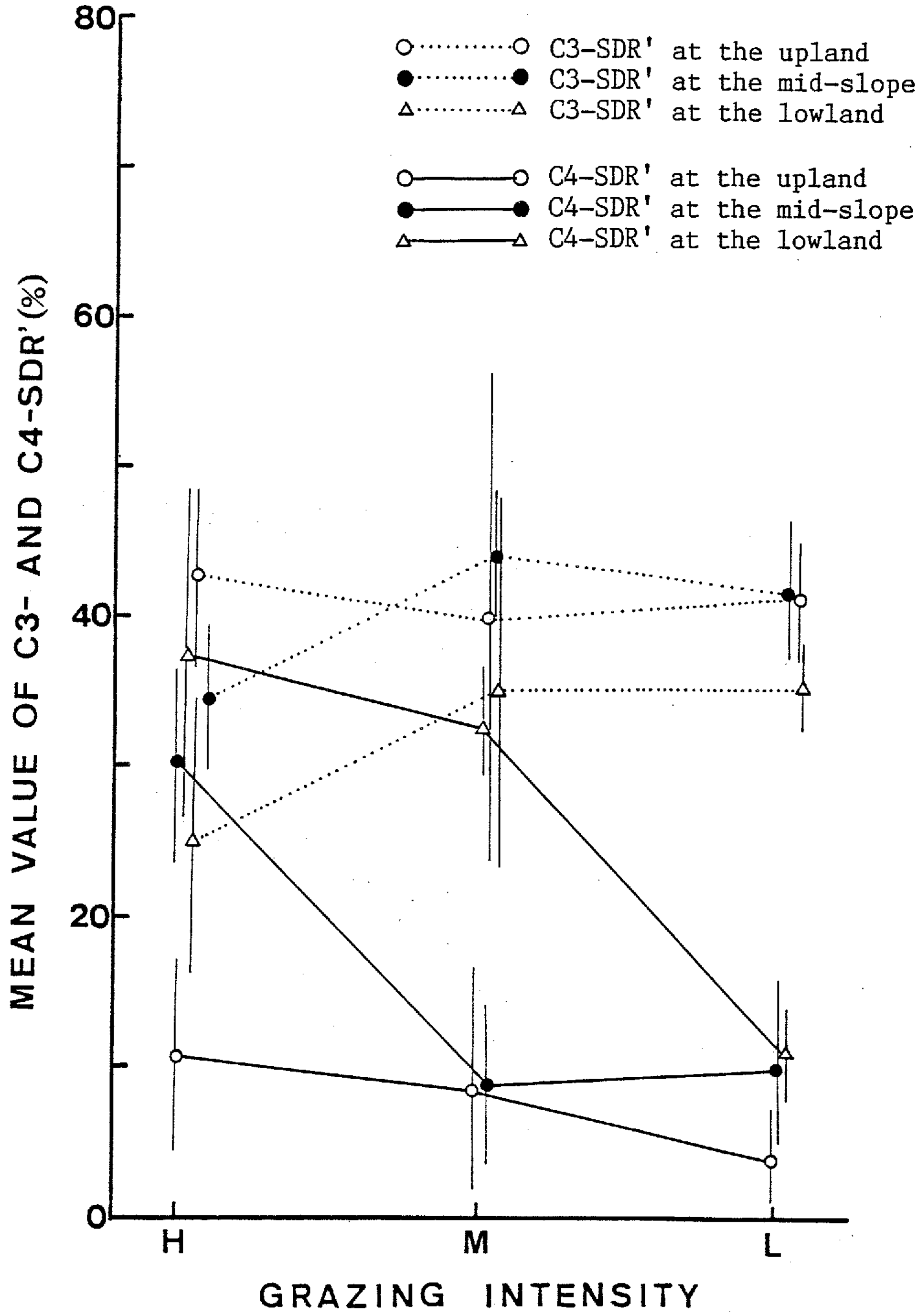

Fig. 4-c. Variations of C3- and C4-SDR' along three different grazing intensities at three hillslope positions in the OPAHR on Mt. Kuju in July. H: Heavy, M: Moderate, L: Light grazing. Vertical bars represent ±1 SD.

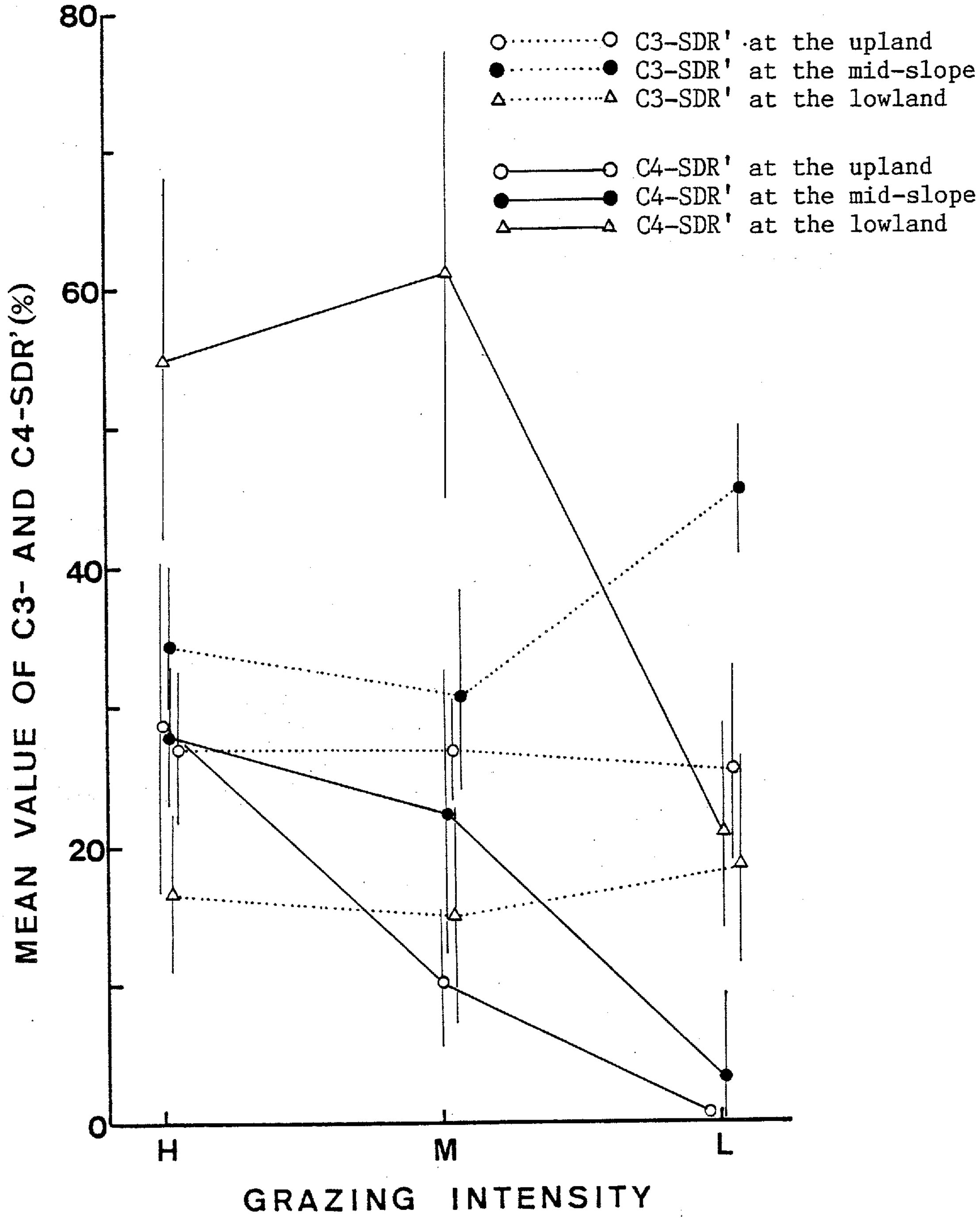

Fig. 4-d. Variations of C3- and C4-SDR' along three different grazing intensities at three hillslope positions in the OPAHR on Mt. Kuju in October. H: Heavy, M: Moderate, L: Light grazing. Vertical bars represent ±1 SD.

In Fig. 4-c which illustrates the same comparison between C3-SDR' and C4-SDR' in July, one can see that the some linear lines of the C3-SDR' and C4-SDR' were merged, although they were rather separated from one another in May. The values of C3-SDR' in the heavily used pasture completely overlapped those of C4-SDR' except in the case of the upland. C4-SDR' decreased from 38% to 15% in the lowland and from 32% to 10% in the mid-slope as grazing decreased. Those differences were significant at the 1% level. The variations of the C4-SDR' in the upland and the C3-SDR' at every position of hillslope, however, were not statistically different.

The linear lines of the C3-SDR' in October almost overlapped those of C4-SDR', except in a few cases. The variations of the C3-SDR' as a function of grazing intensity were still rather stable. However, at the mid-slope position, the C3-SDR' increased significantly ($P<0.05$) from 32% to 44%.

The trend of increased C4-SDR' as grazing declined similarly occurred in October as well as in May and July. It declined from approximately 28% (heavy) to 5% (light) at the mid-slope and from 27% to 2% in the upland. C4-SDR' in heavily and moderately grazed pastures at the mid-slope position ranged from 55% to 62% and were significantly higher ($P<0.01$) than any other values of C3-SDR' while its value in other months was lower than C3-SDR'. In general, C3 graminoids were dominant and competitive to the opponent, C4 graminoids, at the beginning of growing season. This competitive ability of C3 graminoids appeared to be depressed as the season progressed, and finally it was overtaken by C4 graminoids at the end of growing season.

c. Exclosures at Nara Park (Table 5) and Miyajima Island (Table 6)

Regarding the exclosure regime at Nara Park and Miyajima Island, the variation of C3 and C4-SDR' are illustrated in Tables 5 and 6. Stands 7 and 9 were located inside the exclosure and stands 6 and 8 were located outside the exclosure at Nara Park. The pair of stands 6 and 7 named as a Exclosure 6-7 (Ex. 6-7) were in a closed condition covered with a forest canopy which provided some shade. The stands of 8 and 9 (Ex. 8-9) were in relatively open and sunny conditions. The stands of 17,18,23,24,25 and 26 were from Miyajima Island where 17,23 and 25 were inside the exclosure and remainders were outside.

C4-SDR' at Ex. 6-7 under the closed condition exhibited an increase with grazing through the growing season; there were high values outside the exclosure and low or almost zero values inside the exclosure (Table 5). The differences were again statistically significant at 0.01 level. However, the C4-SDR' in the exclosure of open condition (Ex. 8-9) did not show any significant differences between outside and inside the exclosure. This is because light interception in the closed condition maximized the differences between the inside and the outside, or a sufficient irradiation supply in the open condition may have caused a minimization of the differences.

C3-SDR', on the other hand, generally exhibited smaller values outside the exclosures. Although the difference of C3-SDR' between inside and outside was expected to be greater in open stands because of its vulnerability under an irradiated condition, actually the difference of inside and outside between open and closed conditions was not so remarkable. However, the values at closed stands were greater than at open stands regardless of grazing (both for inside and outside). Both C3 and C4-SDR' showed a seasonal fluctuation; the former declined as the season progressed while the latter increased.

On Miyajima Island, there was no marked difference and no fixed trend in terms of variation in C3 and C4-SDR' between outside and inside the exclosures. The relations between the inside and outside, in terms of variation of the C3- and C4-SDR', conflicted from one stand to another, and most of the differences between the inside and the outside were not statistically significant (Table 6).

3) Variation of the Average Number of Species and Index Values of C3 and C4 Graminoids

a. CPER of Pawnee National Grassland (Table 3)

The variation of the average number of C3 and C4 species and index values (C3 and C4 Index) at the CPER are listed in Table 3. Since the index value was the product of a number of species and C3- and C4-SDR (equation (5) and (6)), the fluctuation of these values(C3 and C4 Index) were expected to be enlarged compared to the value of the C3- and C4-SDR'.

The number of C4 species at the CPER was usually greatest at the mid-slope area for all grazing regimes. There was little fluctuation among heavily, moderately and lightly grazed pastures except in the relation between the non-grazed and remaining three pastures. The average number of C4 species on non-grazed pasture was significantly lower than the remaining three pastures at the 0.05 level. However, this difference was rather indistinct at the upland; the value at the non-grazed pasture was not so markedly reduced. In contrast, the average number of C3 graminoid species was usually highest on non-grazed pastures regardless of the position of hillslope. The difference due to the position of hillslope was not so obvious as shown in the number of C4 graminoids.

The fluctuation pattern of the C4 Index was different

Table 3. Variations of importance value (number of C3 and C4 graminoid species; C3 and C4 Index) relative to four different grazing intensities at three hillslope positions in the CPER of Pawnee National Grassland

	Grazing Intensity			
	Heavy	Moderate	Light	Non
Upland				
No. of C3 species	2.3	3.0	2.5	4.0
No. of C4 species	3.0	3.6	3.3	3.0
C3 Index	17.1	27.2	18.0	22.0
C4 Index	125.5	142.4	96.4	88.9
Mid-slope				
No. of C3 species	2.5	4.0	3.3	4.0
No. of C4 species	4.5	4.8	4.5	3.3
C3 Index	28.6	65.7	49.9	110.6
C4 Index	168.0	186.6	145.2	108.3
Lowland				
No. of C3 species	2.8	2.5	2.5	4.0
No. of C4 species	3.3	4.0	4.8	2.5
C3 Index	83.7	54.6	59.2	139.3
C4 Index	157.3	161.6	147.1	59.2

from what was found in C4-SDR'. Although the C4-SDR' was always highest at heavily used pasture areas, C4 Index showed a maximum value at moderately grazed pasutre and a minimum value at non-grazed. The average C4 Index at moderate grazing was 161.6 in the lowland, 186.6 in the mid-slope and 142.2 in the upland. The values at the non-grazed pasture were significantly lower than those of the rest of three pastures at the 5% level over all hillslope positions. Hence the values of C4 Index were relatively low at the lowland as those found in C4-SDR'. On the other hand, the C3 Index was significantly higher ($P<0.05$) at the non-grazed pasture, although the variation from heavy to light conflicts depending upon the hillslope position.

b. OPAHR on Mt. Kuju (Tables 4-a - 4-c)

The trends of number of C3 and C4 species and Index values at the OPAHR were similar to those of the CPER. The average number of C4 species was greatest at either heavy or moderate grazing and least at light grazing. This was consistent over all the hillslope positions and seasons. The reduction of this value from heavy to light grazing was statistically significant at the 5% level except in the case of the upland in July and the mid-slope in October. The fluctuation of the number of C3 species was rather stable or showed relatively higher values at light grazing. Statistical analysis proved

Table 4-a. Variations of importance value (number of C3 and C4 graminoid species; C3 and C4 Index) relative to three different grazing intensities at three hillslope positions in the OPAHR on Mt. Kuju in May

	Grazing intensity		
	Heavy	Moderate	Light
Upland			
No. of C3 species	4.2	3.8	5.6
No. of C4 species	2.0	0	0
C3 Index	218.1	180.6	273.0
C4 Index	11.5	0	0
Mid-slope			
No. of C3 species	3.8	4.2	3.6
No. of C4 species	3.6	3.2	0
C3 Index	208.4	190.8	182.5
C4 Index	49.5	27.5	0
Lowland			
No. of C3 species	3.8	3.4	5.2
No. of C4 species	3.8	3.2	2.0
C3 Index	155.6	162.1	231.1
C4 Index	80.8	104.3	8.0

Table 4-b. Variations of importance value (number of C3 and C4 graminoid species; C3 and C4 Index) relative to three different grazing intensities at three hillslope positions in the OPAHR on Mt. Kuju in July

	Grazing intensity		
	Heavy	Moderate	Light
Upland			
No. of C3 species	3.0	3.8	4.0
No. of C4 species	2.2	1.6	1.8
C3 Index	130.2	173.8	185.5
C4 Index	14.9	8.4	3.9
Mid-slope			
No. of C3 species	2.6	4.0	2.6
No. of C4 species	3.6	2.2	1.8
C3 Index	90.4	167.5	108.5
C4 Index	80.6	14.6	10.3
Lowland			
No. of C3 species	2.2	2.0	3.6
No. of C4 species	3.4	2.8	2.0
C3 Index	77.3	74.4	141.3
C4 Index	100.6	73.7	10.4

Table 4-c. Variations of importance value (number of C3 and C4 graminoid species; C3 and C4 Index) relative to three different grazing intensities at three hillslope positions in the OPAHR on Mt. Kuju in October

	Grazing intensity		
	Heavy	Moderate	Light
Upland			
No. of C3 species	2.2	2.0	2.4
No. of C4 species	3.0	2.4	0
C3 Index	57.1	62.3	65.2
C4 Index	54.7	12.9	0
Mid-slope			
No. of C3 species	3.0	2.6	2.0
No. of C4 species	2.0	3.0	1.4
C3 Index	68.8	81.3	90.8
C4 Index	55.2	53.8	6.1
Lowland			
No. of C3 species	2.0	1.0	1.8
No. of C4 species	4.4	4.4	2.8
C3 Index	38.8	30.1	35.2
C4 Index	199.3	266.5	42.7

that the values were not different from one to another relative to the grazing in July and October. Plants of C3 species were generally replaced by C4 species as grazing intensity increased and the season progressed.

The C4 Index behaved as did the number of C4 species and C4-SDR', namely, it was reduced as grazing lessened. Moreover, the difference between the heavy and light grazing or between moderate and light grazing was statistically significant ($P<0.01$) for all hillslope positions in May, in the lowland and the mid-slope in July and the upland and the lowland in October. Changes between heavy and moderate were not so obvious. The C4 Index usually kept the highest value at the lowland and at the end of the growing season.

Contrary to this, the C3 Index showed stability relative to grazing at the mid-slope in May and at the upland and the lowland in October, exhibiting increasing trends for the remaining area and season. The values were much higher than those of the C4 Index at the beginning of the growing season, but were replaced and overtaken by the C4 Index at the end of the growing season.

c. Exclosures at Nara Park (Table 5) and Miyajima Island (Table 6)

Regarding the exclosure system at Nara Park, the variation of species number and index values of C3 and C4 graminoids exhibited the same trends as they were found with grazing intensity at the CPER and the OPAHR (Table 5).

The number of C4 species counted in both closed and open conditions showed a reducing pattern as grazing was excluded. The reducing rate at the open stand was not so great as that of the closed site. The latter ranged approximately from 80 to 100% while the former reducing rate ranged from 28 to 69%. This implies that the C4 gramioind species loses its occupational space completely in a closed condition if grazing pressure is not introduced. Differences between the outside and the inside exclosures were significant over all the months except in the case of closed sites (Ex. 8-9) in April. The number of C3 species showed an opposite response to that of the C4 graminoids; higher inside and lower outside the exclosures regardless of whether the exclosure was located in a closed or in an open condition. Most of the differences, however, were not statistically significant.

Reduction of the C4 Index from outside to inside in closed sites was almost 100% and the difference was significant at the P=0.01 level, while relatively little difference was derived from April to September. Regarding the C3 graminoids, the trend of being greater inside and less outside the exclosure was also true in the case of the C3 Index. However, few differences were derived from open stands in June and September. Maximum values of C3 Index

Table 5. Variations of importance value (C3- and C4-SDR'; number of C3 and C4 graminoid species; C3 and C4 Index) for inside and outside the exclosures in open and closed conditions and for three periods of the growing season, April, June and September at Nara Park

	Closed(Ex.6-7*)		Open(Ex.8-9)	
	out	in	out	in
April				
C3-SDR'(%)	48.1	60.8	29.1	45.2
C4-SDR'(%)	8.9	0	19.0	21.3
No. of C3 species	3.0	3.4	1.4	3.0
No. of C4 species	0.9	0	1.4	1.0
C3 Index	144.4	255.3	54.8	137.3
C4 Index	12.3	0	43.4	37.2
June				
C3-SDR'(%)	43.0	59.9	32.1	46.8
C4-SDR'(%)	24.6	1.2	28.5	25.8
No. of C3 species	2.0	3.4	2.4	3.0
No. of C4 species	2.2	0.2	2.6	0.8
C3 Index	91.1	212.1	118.4	139.5
C4 Index	59.0	1.2	29.9	30.7
September				
C3-SDR'(%)	28.4	53.6	25.1	26.9
C4-SDR'(%)	45.3	4.5	44.5	33.4
No. of C3 species	1.6	3.6	1.8	1.6
No. of C4 species	2.0	0.4	2.5	0.4
C3 Index	69.6	192.2	49.8	53.3
C4 Index	97.0	4.5	109.2	41.3

*Exclosure 6-7

Table 6. Variations of importance value (C3- and C4-SDR'; number of C3 and C4 graminoid species; C3 and C4 Index) for inside and outside the exclosures and for three periods of the growing season, April, July and October on Miyajima Island

	Ex. 17-18*		Ex. 23-24		Ex. 25-26	
	out	in	out	in	out	in
April						
C3-SDR'(%)	9.0	3.9	21.8	14.8	7.9	0
C4-SDR'(%)	32.7	30.5	37.9	61.6	64.4	44.0
No. of C3 species	0.8	0.2	1.8	0.6	0.4	0
No. of C4 species	1.0	1.4	1.0	1.0	1.0	1.0
C3 Index	9.4	3.9	48.6	14.8	7.1	0
C4 Index	32.7	43.1	37.9	61.6	64.4	44.0
July						
C3-SDR'(%)	1.3	0	0	33.2	0	0
C4-SDR'(%)	32.9	46.9	69.1	58.2	68.2	49.9
No. of C3 species	0.2	0	0	0.8	0	0
No. of C4 species	1.8	1.0	2.8	1.0	1.0	1.6
C3 Index	1.3	0	0	33.2	0	0
C4 Index	60.4	46.9	192.6	58.2	68.3	83.7
October						
C3-SDR'(%)	0	0	6.0	0	0	1.1
C4-SDR'(%)	35.1	39.0	46.3	67.5	56.6	68.3
No. of C3 species	0	0	0.4	0	0	0.2
No. of C4 species	1.0	1.0	2.2	1.4	1.0	1.6
C3 Index	0	0	6.0	0	0	1.1
C4 Index	35.1	39.0	113.0	98.6	56.6	119.4

*Exclosure 17-18

were recorded inside the exclosure of closed condition in April.

The number of C3 and C4 species on Miyajima Island did not show any uniform trends and showed conflicting differences depending on the month (Table 6). That is, the general trends of C3 and C4 graminoids, namely, high values of C3 for inside and of C4 for outside and low values of C3 for outside and of C4 for inside the exclosures, were not consistent for every exclosure and month. Furthermore, due to a fewer number of species counted as either C3 or C4 graminoids, it was difficult to evaluate the replacement from C3 to C4 graminoids by using number of species and Index value. The exclosure which showed significant differences between the outside and inside was Ex. 23-24 in July where the number of C4 species was reduced from 2.8 to 1.0 and C3 species increased from 0 to 0.8. The index value of C3 and C4 graminoids also conflicted depending on the exclosures and season.

2. Soil Aspects

Herbivore pressure in terms of the frequency of trampling and resting has a possible effect on altering primarily the soil's physical condition which then induces the secondary alternation of the soil's chemical aspects. Physical and chemical aspects of the soils such as bulk density, pore space, maximum water holding capcity (MWHC), moisture percentage (MP), water content ratio (WCR) and soil organic matter (carbon and nitrogen) content, were the factors to be examined here. The variation of those aspects relative to the grazing intensity are shown in Table 7-a to 7-c.

a. OPAHR on Mt. Kuju (Table 7-a)

Both bulk density and pore space did not exhibit any significant changes in the upland with reduced grazing. This trend was also repeated in the mid-slope. The bulk density ranged approximately from 33g/100cc to 37g/100cc and the pore space was around 86% for those two hillslope positions regardless of grazing intensity. However, in the lowland position, the results were different. Bulk density showed a significant increase as grazing increased. While it varies from 39.9g/100cc in light to 56.2g/100cc in heavy with significant difference ($P<0.01$), the pore space decreased from 84.9%(light) to 78.8%(heavy).

The same trends were found in MWHC, MP and WCR; namely, little difference in the upland and the mid-slope and an outstanding difference in the lowland. MWHC and MP, in the lowland, were both reduced from 74.5g/100cc (light) to around 70g/100cc (moderate and heavy) from 153.3% (light) to 89.9% and 99.4% (heavy and moderate), respectively. The

Table 7-a. Soil property means for three grazing intensities and three hillslope positions at the OPAHR on Mt. Kuju.

	Grazing Intensity		
	Heavy	Moderate	Light
Upland			
Bulk density(g/100cc)	33.3	32.6	36.2
Pore space(%)	87.4	87.7	86.2
MWHC(g/100cc)	78.7	78.7	77.3
MP(%)	175.0	205.8	186.1
WCR(%)	74.0	84.8	87.8
Hardness	19.1	16.1	15.8
Root mass(g/100cc)	1.5	1.3	1.2
Sand mass(g/100cc)	0.1	0.1	0
Silt mass(g/100cc)	33.0	33.3	37.0
C-content(mg/100cc)	7403.2	7068.4	7620.0
N-content(mg/100cc)	436.3	408.4	425.1
C/N ratio	17.0	17.3	17.9
Mid-slope			
Bulk density(g/100cc)	37.4	37.3	36.0
Pore space(%)	85.9	85.9	86.4
MWHC(g/100cc)	78.2	78.8	77.5
MP(%)	174.8	188.9	191.6
WCR(%)	83.3	89.2	89.0
Hardness	20.1	16.0	16.0
Root mass(g/100cc)	2.8	1.6	1.3
Sand mass(g/100cc)	0	0	0
Silt mass(g/100cc)	36.4	37.4	36.3
C-content(mg/100cc)	7749.8	7561.4	7747.7
N-content(mg/100cc)	450.2	462.1	406.3
C/N ratio	17.3	16.4	19.1
Lowland			
Bulk density(g/100cc)	56.2	70.3	39.9
Pore space(%)	78.8	73.5	84.9
MWHC(g/100cc)	70.9	68.0	74.5
MP(%)	99.4	89.9	153.3
WCR(%)	77.6	90.0	81.9
Hardness	21.0	20.0	17.5
Root mass(g/100cc)	1.4	1.5	2.8
Sand mass(g/100cc)	0	0.4	0.1
Silt mass(g/100cc)	56.6	66.5	38.6
C-content(mg/100cc)	5621.3	6330.7	5758.9
N-content(mg/100cc)	309.4	355.7	323.1
C/N ratio	18.4	17.8	17.9

MWHC: Maximum Water Holding Capacity, MP: Moisture Percentage, WCR: Water Content Ratio.

differences were statistically significant at the 0.05 level for MWHC and at the 0.01 level for moisture percentage (MP).

Contrary to these findings, soil hardness exhibited distinct differences for all hillslope positions. With decreasing grazing pressure, the value declined significantly ($P<0.05$), from 19.1 (heavy) to 15.8 (light) in the upland, from 20.1 (heavy) to 16 (light) in the mid-slope and from 21 (heavy) to 17.5 in the lowland. These differences between the heavy and light grazing were all significant at least at the 0.05 level.

Root mass and sand mass per 100cc were not strongly correlated with grazing. The former, however, showed a slightly higher value at the mid-slope for each grazing pasture. The silt mass was the value obtained by subtracting the sand mass from dry weight of core. Therefore, the trends of this factor were basically the same as those of bulk density.

Although the total carbon content in volume bases declined from the top to the bottom of the hillslope for every grazing intensity, it did not show any striking fluctuation as a function of grazing. Nitrogen content did not show any change with grazing as well. Maximum and minimum values of carbon and nitrogen content exhibited some divergence among the different positions of hillslope.

Concerning the C/N ratio, it showed a sequential decline from the lowland to the upland in the heavily grazed pasture, but not in the remaining pastures. Statistical analysis showed that those variations were not significant and were rather stable relative to both the hillslope positions and grazing intensity.

b. Exclosures at Nara Park (Table 7-b) and Miyajima Island (Table 7-c)

Most of the soil's physical and chemical aspects at Nara Park showed little variation between the two regimes, inside and outside the exclosure, or conflicted with one another. Bulk density, however, did show a distinctive difference between the open and closed conditions, but not in the exclosure regime.

MWHC in the closed condition showed a slightly higher value inside the exclosure and this relationship was reversed in the open condition. Similarly, the responses of MP and WCR to grazing pressure were dependent upon whether exclosures were located in open or closed conditions. Soil hardness in the open condition significantly declined ($P<0.01$) inside the exclosure, but not in the closed condition.

In contrast, the carbon and nitrogen content in volume bases appeared to respond to the grazing pressure regardless of whether the exclosure had been placed in open or closed sites. Both carbon and nitrogen content declined when grazing was excluded. The difference between the two regimes

Table 7-b. Soil property means for inside and outside exclosures in closed and open conditions at Nara Park

	Closed(Ex.6-7)		Open(Ex.8-9)	
	out	in	out	in
Bulk density(g/100cc)	113.1	119.1	123.6	124.4
Pore space(%)	57.3	55.1	53.4	53.1
MWHC(g/100cc)	43.8	46.8	46.2	42.0
MP(%)	27.4	30.4	25.9	18.9
WCR(%)	69.8	73.1	68.4	56.6
Hardness	18.2	18.6	18.2	15.8
Root mass(g/100cc)	0.1	0.1	0.1	0.2
Sand mass(g/100cc)	6.2	13.8	30.0	12.9
Silt mass(g/100cc)	107.9	106.1	112.1	111.8
C-content(mg/100cc)	4801.4	3946.5	3769.9	2863.7
N-content(mg/100cc)	312.8	262.2	269.9	205.2
C/N ratio	15.4	14.7	13.9	14.0

MWHC: Maximum Water Holding Capacity, MP: Moisture Percentage, WCR: Water Content Ratio.

was significant at the 0.01 level. C/N ratio correlated with the fluctuation of nitrogen content. However, no significant difference of C/N ratio was found between the inside and outside exclosures.

The data from Miyamjima island exhibited distinct relaionships in some foctors relative to the grazing intensity (Table 7-c). Bulk density generally showed a slight increase with grazing included, although this difference did not reach a significant level. The variation in value of pore space was exactly opposite to that of bulk density. No difference was found in MWHC as a function of grazing. MP were slightly higher inside the exclosure except in Exclosure 17-18. The difference in soil hardness between inside and outside the exclosure was statistically significant at the 0.01 level for all exclosures. It declined remarkably when grazing was excluded from 28.7 (out) to 21.0 (in) on the average. Silt mass also responded similarly as did soil hardness with high values outside and low values inside.

For all of the three exclosures, 17-18, 23-24 and 25-26, carbon and nitrogen content correlated markedly with grazing. Total carbon content was significantly reduced when grazing was excluded. The mean of the values ranged from 3281.6 to 4448.3 mg/100cc outside whereas it varies from 2741.8 to 3141.2 mg/100cc inside the exclosure. Total nitrogen content outside was also greater than that inside

Table 7-c. Soil property means for inside and outside exclosures on Miyajima Island

	Ex.17-18		Ex.23-24		Ex.25-26	
	Out	In	Out	In	Out	In
Bulk density(g/100cc)	133.6	128.1	130.8	124.4	121.1	114.4
Pore space(%)	49.6	51.7	50.6	53.1	54.3	56.8
MWHC(g/100cc)	37.2	36.6	39.5	40.7	40.4	40.8
MP(%)	15.4	14.4	16.2	20.6	15.5	17.8
WCR(%)	54.9	49.1	53.2	61.5	46.5	49.7
Hardness	27.8	24.0	27.5	21.6	29.9	17.6
Root mass(g/100cc)	0.4	0.6	0.6	1.0	1.3	0.9
Sand mass(g/100cc)	65.3	62.9	50.6	61.6	49.2	50.6
Silt mass(g/100cc)	69.3	66.7	81.7	64.5	72.7	63.3
C-content(mg/100cc)	3281.6	2741.8	4222.3	3141.2	4448.3	2779.1
N-content(mg/100cc)	172.7	145.0	196.2	190.1	241.3	151.0
C/N ratio	18.7	18.5	21.8	16.6	18.5	18.4

MWHC: Maximum Water Holding Capacity, MP: Moisture Percentage,
WCR: Water Content Ratio.

the exclosure. The exception to this was Exclosure 23-24 where the difference was slight. C/N ratio was generally stable between inside and outside, although it was remarkably higher outside than inside at Exclosure 23-24.

3. Variations of C3- and C4 Importance Relative to Biotic and Abiotic Factors

1) Relationship between the Importance of C3 and C4 Graminoids and That of the Dominant Species, *Miscanthus sinensis* and *Zoysia japonica* (Table 8)

Simple regression analyses were applied to analyze the coefficency between the C3, C4-SDR' and the abundance expressed as Summed Dominance Ratio (SDR) of *Miscanthus sinensis* and *Zoysia japonica*. Similar analyses were done concerning C3 and C4 Indices. The objective of this part of the study was to examine to what extent the abundance of C3 and C4 graminoids was regulated by the dominance of *Miscanthus sinensis* and *Zoysia japonica*. Thereby, both of the relative importance values (SDR') of *Miscanthus sinensis* (C4) and *Zoysia japonica* (C4) were subtracted from the total value of C4-SDR'.

Miscanthus sinensis and *Zoysia japonica* have been recognized as two extremes of a succession in the

Table 8. Effects of two dominant grasses, Miscanthus sinensis and Zoysia japonica on the importance value (C3- and C4-SDR'; C3 and C4 Index) at the OPAHR on Mt. Kuju for three periods of growing season, May, July and October. Figures are correlation coefficients with analysis of variance

	SDR of Miscanthus sinensis	SDR of Zoysia japonica
May		
C3-SDR'	0.43** (+)	.
C4-SDR'	0.72** (-)	0.49** (+)
C3 Index	.	.
C4 Index	0.65** (-)	0.42** (+)
July		
C3-SDR'	.	.
C4-SDR'	0.50** (-)	.
C3 Index	.	.
C4 Index	0.44** (-)	.
October		
C3-SDR'	.	0.44** (-)
C4-SDR'	0.72** (-)	0.33** (+)
C3 Index	0.33* (+)	0.42** (-)
C4 Index	0.64** (-)	0.34* (+)

(+): positive relation, (-): negative relation, **$P<0.01$, *$P<0.05$

semi-natural grassland, that is, the succession retrogresses from the community of Miscanthus sinensis type to that of Zoysia japonica type with increased grazing pressure. Thus, the results of analysis demonstrated the idea of how the C3 and C4 graminoids were affected by scale of the sequential changes in grazing pressure rather than by discrete nominal scale: heavy, moderate, light and non-grazing, or outside and inside the excloure and so on.

The results at the OPAHR on Mt. Kuju agree well with what was found in section 1-(2) and (3) of this chapter. Both the C4-SDR' and C4 Index showed significant correlations with the relative abundance of Miscanthus sinensis ($P<0.01$) in all three periods of the growing season (Table 8). The regression coefficients were all negative and the correlation coefficients with C4-SDR' varied from 0.50 for July to 0.72 for May and October. The regression equation were: $Y=17.78-0.16X$ for May, $Y=42.73-0.34X$ for October. The relatively lower coefficient for July implies that the abundance and growth of C4 graminoids were not regulated by Miscanthus sinensis so strictly in this season of year. The same trends were observed in the C4 Index which exhibited slightly lower correlation coefficients than C4-SDR'. Positive correlations were derived from the relationship between C4-SDR' and the SDR of Zoysia japonica with statistical significance at the 0.01 level for May and at the 0.05 level for October. Again, both of C4-SDR' and C4

Index for July were independent from the abundance of Zoysia japonica.

Regarding C3 graminoids, both C3-SDR' and C3 Index were not so strongly correlated with abundance of Miscanthus sinensis and Zoysia japonica. However, the response of C3-SDR' to the independent variables, Miscanthus sinensis and Zoysia japonica, appeared to be opposite from what was found in C4-SDR' and C4 Index. Regression coefficients with Miscanthus sinensis were positive in C3-SDR' for May and C3 Index for October, while the coefficients were negative with Zoysia japonica.

Due to the relatively low abundance of Miscanthus sinensis and no sequential change from the Zoysia to the Miscanthus type in the remainig study areas (Toi Misaki Point, Mt. Aso, Mt Azuma, Nara Park and Miyajima Island) the C3-, C4-SDR'and C3, C4 Index were not strongly correlated with the two dominant species, Miscanthus sinensis and Zoysia japonica (data were not shown). Thus these two species could not represent the sequence of successional development in these study areas. C3 Index at Nara Park for July was the only one which showed a positive relationship to Miscanthus sinensis ($R=0.70$, $P<0.01$). SDR values of Zoysia japonica were, contrary to the results from the OPAHR, negatively correlated with both C3 and C4 importance values in these five remaining areas with a few exceptional cases. This implies that Zoysia japonica was so suppressive to any other graminoid species and that there was a little room available even for other C4 graminoids.

2) Variation of C3- and C4 Importance Values related to the Topography (Tables 9-a - 9-d)

Assuming that the habitat use of herbivores of all types depends on the topographic features, then certain hillslope positions were less frequented and others were more utilized. According to this assumption, which is to be discussed later and supported by much previously published literature, the vegetation of each hillslope position is subjected to different grazing intensities by herbivores. Consequently, the importance values of C4 and C3 graminoids are altered along the hillslope positions and are attributed to the discriminative use on hillside by herbivore, although this variation of vegetation is also attributed to the alternation of soil factors along the hillslope, which is discussed later.

The variation of C3 and C4 importance values (C3-, C4-SDR' and Index value) related to the topographic features in terms of hillslope position at the CPER and the OPAHR have already been shown with grazing intensity in Fig. 4-a to 4-d and Tables 3, 4-a, 4-b and 4-c. At the heavily grazed pasture of the CPER, both C3 and C4-SDR' of the mid-slope were significantly lower ($P<0.01$) than in either the upland or the lowland. As grazing pressure was decreased, the difference of C4-SDR' among the three hillslope positions became indistinct (Fig. 4-a). C3-SDR', on the other hand, kept a high value at the lowland position regardless of grazing intensity.

The trends of C4-SDR' at the OPAHR slightly agreed with what was found at the CPER (Figs.4-b - 4-d). However, the most frequented area was the lowland and least utilized was the upland. Therefore, the grazing condition of the mid-slope appeared to be an intermediate one between the upland and the lowland. C3-SDR' of the mid-slope at the heavily grazed area was generally higher than that of the other parts of the hillslope except in July.

For the remaining study areas, the variation of importance values along the hillslope positions exhibited mostly similar trends compared with that of the CPER and of the OPAHR (Tables 9-a to 9-d). At Toi Misaki, both the C4-SDR' and C4 Index were significantly($P<0.05$) reduced at the mid-slope compared with those at the upland and the lowland positions, although the reduction in May was not distinct. The importance values of C3 graminoids (C3-SDR' and C3 Index) were greatest at the lowland in May and July and at the mid-slope in October (Table 9-a). The mean importance values of C3 and C4 graminoids at Mt. Aso present a similar pattern to some extent (Table 9-b). The C4-SDR' generally declined as the hillslope position became lower,

Table 9-a. Variations of importance values (C3- and C4-SDR'; number of C3 and C4 graminoid species; C3 and C4 Index) at three hillslope positions for three periods of the growing season, May, July and October at Toi Misaki Point

	Hillslope position		
	Upland	Mid-slope	Lowland
May			
C3-SDR'(%)	23.6	18.9	23.9
C4-SDR'(%)	26.0	15.7	23.1
No. of C3 species	3.2	3.8	3.0
No. of C4 species	2.6	2.6	2.6
C3 Index	75.6	74.0	77.8
C4 Index	68.2	46.7	61.5
July			
C3-SDR'(%)	6.3	4.7	13.6
C4-SDR'(%)	45.5	19.0	42.5
No. of C3 species	1.0	1.0	1.4
No. of C4 species	4.6	3.4	4.0
C3 Index	9.0	6.9	20.1
C4 Index	197.9	62.9	178.6
October			
C3-SDR'(%)	6.8	14.9	1.8
C4-SDR'(%)	68.0	38.0	62.4
No. of C3 species	1.8	1.4	0.4
No. of C4 species	6.2	3.8	5.6
C3 Index	13.9	21.2	3.6
C4 Index	437.3	163.0	348.7

Table 9-b. Variations of importance values (C3- and C4-SDR'; number of C3 and C4 graminoid species; C3 and C4 Index) at three hillslope positions for three periods of the growing season, May, July and October on Mt. Aso

	Hillslope position		
	Upland	Mid-slope	Lowland
May			
C3-SDR'(%)	35.9	30.9	52.6
C4-SDR'(%)	16.0	13.6	11.5
No. of C3 species	3.8	3.6	4.8
No. of C4 species	2.0	1.4	1.4
C3 Index	135.1	109.7	251.1
C4 Index	33.6	17.5	16.1
July			
C3-SDR'(%)	32.0	33.6	28.4
C4-SDR'(%)	38.0	34.7	31.5
No. of C3 species	3.2	3.8	2.8
No. of C4 species	3.8	3.4	3.2
C3 Index	123.7	128.5	86.4
C4 Index	143.9	101.3	102.1
October			
C3-SDR'(%)	13.7	15.1	19.1
C4-SDR'(%)	42.5	39.6	36.0
No. of C3 species	1.6	2.4	1.8
No. of C4 species	3.6	2.0	2.4
C3 Index	22.8	39.8	36.0
C4 Index	146.5	86.1	87.4

whereas the C3-SDR' was usually highest at the lowland position.

On Mt. Azuma, C4-SDR' of the upland was significantly higher than the others at least at the 5% level (Table 9-c). Moreover, the value of the mid-slope in July was significantly ($P<0.01$) lowest among the three. Contrary to this, C3-SDR' and C3 Index were highest at the lowland position. The differences between the lowland and the other positions were statistically significant in May and July at the 5% level. Similarly, the trends of C4 importance on the hillside of Wakakusayama at Nara Park showed the least value at the mid-slope and the highest at the upland or the lowland (Table 9-d). The importance of the C3 graminoids behaved oppositely to that of the C4 graminoids. It decreased at the lowland and the upland.

Apparently, the C3 and C4 graminoids' distribution correlated with topographic features. In general, the importance of C4 graminoids exhibited smaller values at the mid-slope position at least. Response of C4 Index similar to the C4-SDR' suggests that the variety of C4 graminoids at the mid-slope was less than at the remaining hillslope positions. The importance values of C3 graminoids, on the other hand, were generally greatest at the lowland or the mid-slope areas where the C4 graminoids were less vigorous.

Table 9-c. Variations of importance values (C3- and C4-SDR'; number of C3 and C4 graminoid species; C3 and C4 Index) at three hillslope positions for three periods of the growing season, May, July and October on Mt. Azuma

	Hillslope position		
	Upland	Mid-slope	Lowland
May			
C3-SDR'(%)	45.1	32.1	60.7
C4-SDR'(%)	30.3	16.0	13.7
No. of C3 species	2.4	3.0	5.0
No. of C4 species	1.2	1.4	1.2
C3 Index	110.3	96.2	300.3
C4 Index	39.1	18.0	23.5
July			
C3-SDR'(%)	24.1	29.3	39.0
C4-SDR'(%)	43.8	25.0	34.8
No. of C3 species	1.2	2.6	3.0
No. of C4 species	1.2	1.2	1.8
C3 Index	30.7	78.67	127.0
C4 Index	53.8	30.3	68.1
October			
C3-SDR'(%)	22.2	30.5	31.4
C4-SDR'(%)	44.1	28.2	36.7
No. of C3 species	2.2	2.8	3.0
No. of C4 species	1.2	1.4	2.2
C3 Index	55.6	86.7	102.1
C4 Index	56.7	41.1	86.0

Table 9-d. Variations of importance values (C3- and C4-SDR'; number of C3 and C4 graminoid species; C3 and C4 Index) at three hillslope positions for three periods of the growing season, April, June and September at Wakakusayama of Nara Park

	Hillslope position				
	Upland	Mid-slope		Lowland	
April					
C3-SDR'(%)	45.3	30.2	16.8	17.6	35.5
C4-SDR'(%)	50.4	14.5	20.5	64.3	64.5
No. of C3 species	1.0	2.8	1.8	1.2	1.2
No. of C4 species	1.0	0.8	1.0	1.4	1.0
C3 Index	45.3	87.2	34.1	33.8	45.5
C4 Index	50.4	14.5	20.5	64.3	64.5
June					
C3-SDR'(%)	16.5	24.8	29.7	20.0	23.7
C4-SDR'(%)	76.2	18.0	13.4	72.7	66.4
No. of C3 species	0.6	3.4	3.6	1.4	1.4
No. of C4 species	1.0	2.2	1.2	1.6	1.6
C3 Index	23.5	85.8	120.5	29.1	36.3
C4 Index	76.2	51.2	35.4	117.3	104.5
September					
C3-SDR'(%)	0	6.2	6.2	1.1	4.0
C4-SDR'(%)	92.7	28.3	23.1	86.8	86.7
No. of C3 species	0	1.0	1.0	0.2	0.4
No. of C4 species	1.2	2.8	1.8	2.4	2.2
C3 Index	0	6.2	9.5	1.1	4.0
C4 Index	112.7	80.7	50.7	189.4	193.5

3) Correlation of C3- and C4 Importance Values and Soil Factors (Figs. 5-a - 5-g)

The C3 and C4 importance values (C3-, C4-SDR' and Index value) were each regressed to the soil factors. Figs. 5-a to 5-g illustrate the regression analyses in which the data of vegetation and soil were congregated into two major groups of the study area: one from the pasture for the livestock and the other from the areas inhabited by sika deer (Cervus nippon). The former includes the data of Toi Misaki, the OPAHR on Mt. Kuju, Mt. Aso and Mt. Azuma (Figs. 5-a to 5-d). The latter was from Nara Park and Miyajima Island (Figs. 5-e to 5-g). This separation was done due to the concern that the correlations between the vegetation and soil depend on the herbivore type (livestock or wild animal), and on the major soil or rock type. The hypothesis is that the correlations between vegetational aspects (abundance of C3 and C4 graminoids) and their external attributes (biotic and abiotic factors) do not vary with the type of herbivore, soil or rock on the study areas.

Soil factors treated as independent variables were: bulk density, pore space, maximum water holding capacity (MWHC), moisture percentage (MP), water content ratio (WCR), soil hardness, carbon and nitrogen content in volume bases and C/N ratio. With using F-test, each correlation coefficient was examined. The correlations which did not show any statistical significance (P>0.05) are not shown in the Figures.

As far as the livestock pasture was concerned, the importance value of C4 graminoids (C4-SDR' and C4 Index) was enhanced as bulk density and soil hardness increased, and declined as a function of MWHC, MP, carbon content and C/N ratio. Contrary to these findings , C3 importance values increased with MWHC, MP, carbon and nitrogen content and C/N ratio and declined as bulk density increased (Figs. 5-a to 5-d).

The trends at the deer-inhabited areas were nearly the same as those at the livestock pasture, except for C/N ratio. C4 importance values were related to the soil factors once or twice out of the 3 periods of the growing season while C3 importance values exhibited a significant correlation with its attributes three times during the entire growing season. The repressive soil factors upon the C4 importance were: MP, WCR and nitrogen content, and inducing factors were: soil hardness and C/N ratio. C3 importance values overcame the C4 importance as the above factors altered in the opposite direction. It increased as a function of MP, MWHC and nitrogen content, and declined as the soil hardness and C/N ratio increased. Bulk density and carbon contents were not significant enough to be allocated to the vegetation aspects.

In comparison of the two areas, the livestock pasture and the deer inhabited areas, the conflicting relationship was only with C/N ratio. The relationships with the other

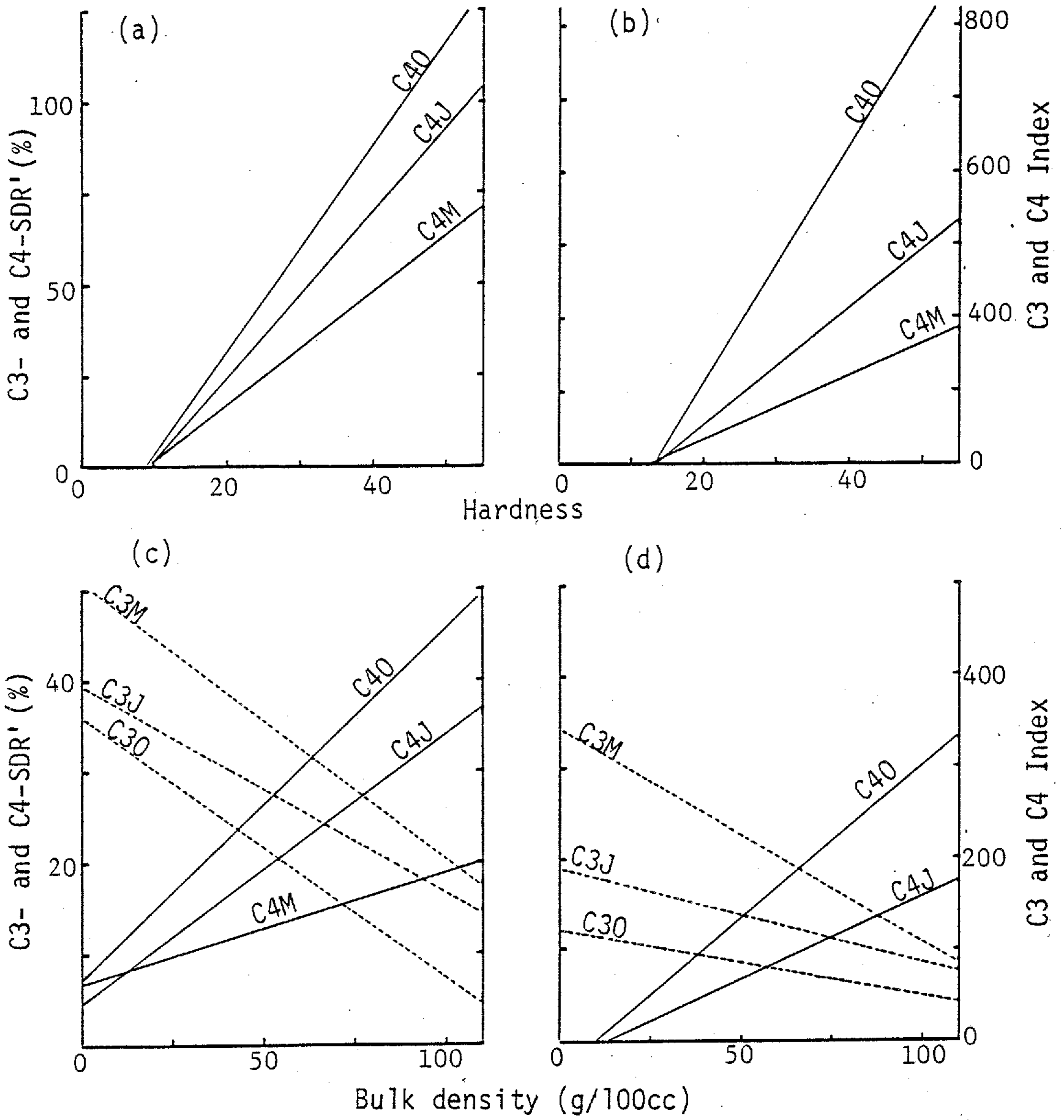

Fig. 5-a. Relationships between the importance value (C3-SDR', C4-SDR', C3 Index and C4 Index) and soil properties at livestock pastures. C3M, C3J, C3O indicate the importance value of C3 graminoids in May, July and October respectively. C4M, C4J, C4O are the notations for C4 graminoids same as for C3 graminoids. (a) and (b): relations of importance values and soil hardness (n=22). (c) and (d): relations of importance values and bulk density (n=22). Regression line was only illustrated when the probability level was less than 0.05.

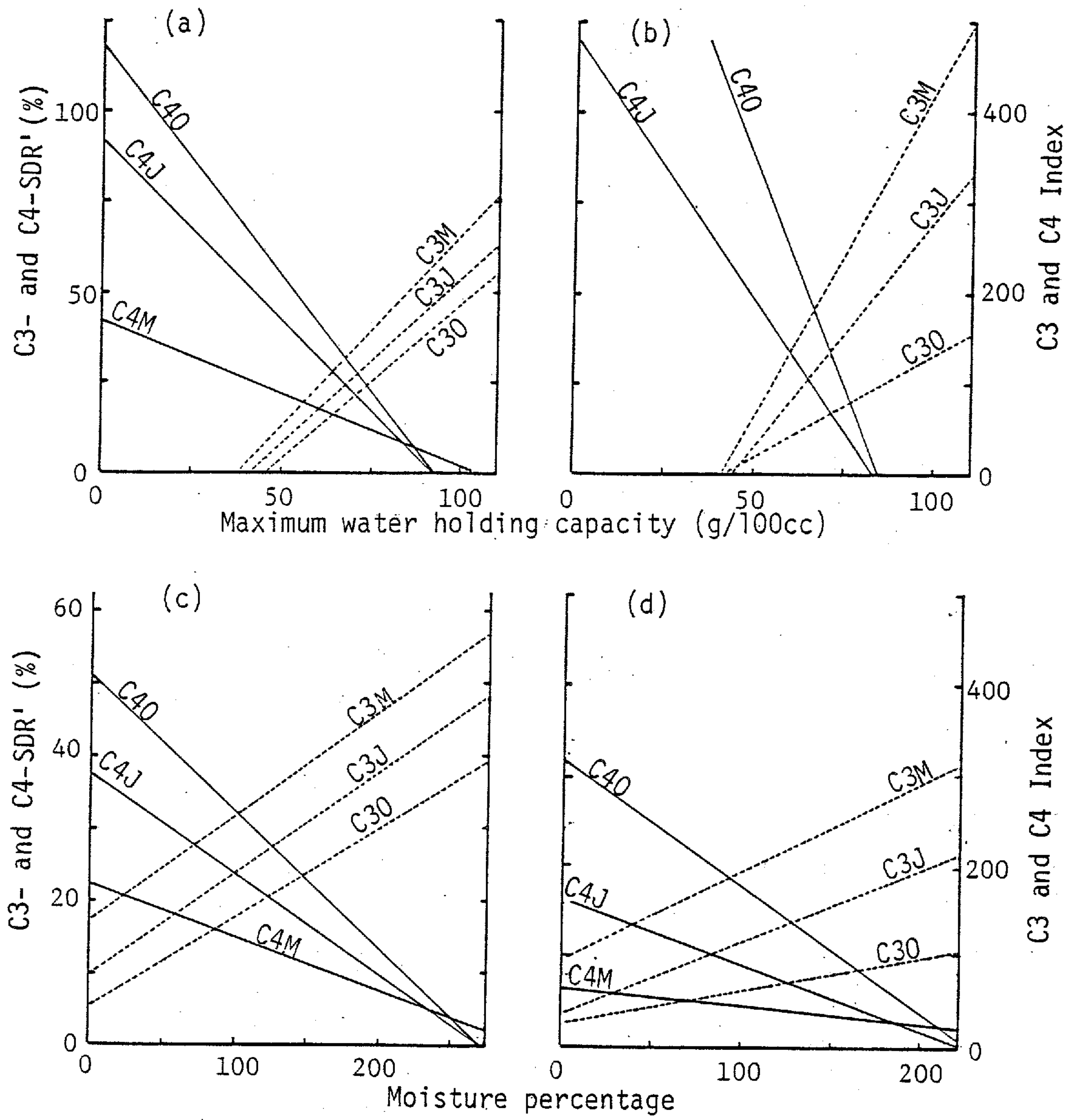

Fig. 5-b. Relationships between the importance values (C3-SDR', C4-SDR', C3 Index and C4 Index) and soil properties at livestock pastures. Notations and sample sizes are same as in Fig. 5-a. (a) and (b): relations of importance values and maximum water holding capacity (MWHC). (c) and (d): relations of importance values and moisture percentage (MP).

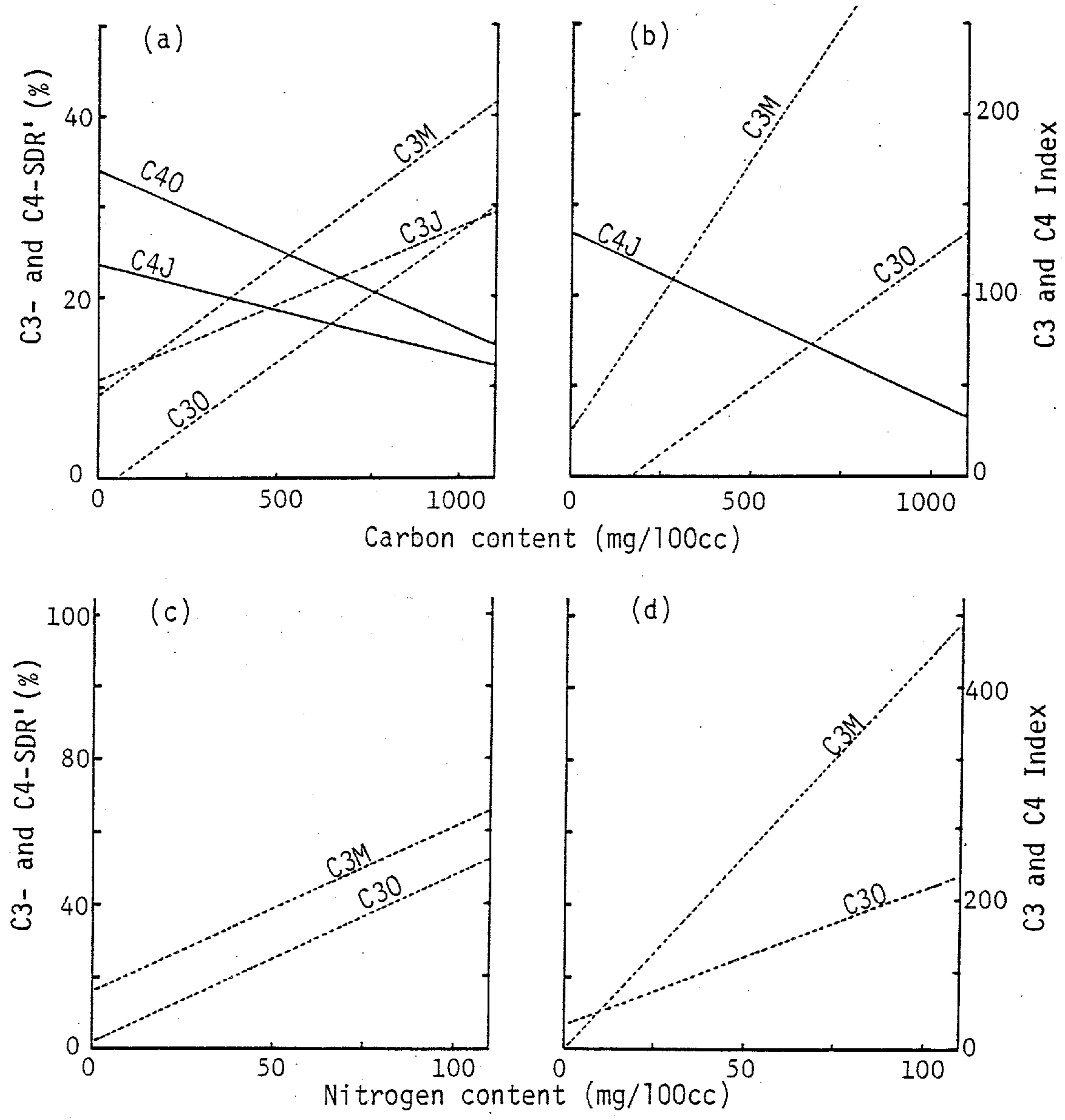

Fig. 5-c. Relationships between the importance values (C3-SDR', C4-SDR', C3 Index and C4 Index) and soil properties at livestock pastures. Notations and sample sizes are same as in Fig. 5-a. (a) and (b): relations of importance values and carbon content. (c) and (d): relations of importance values and nitrogen content.

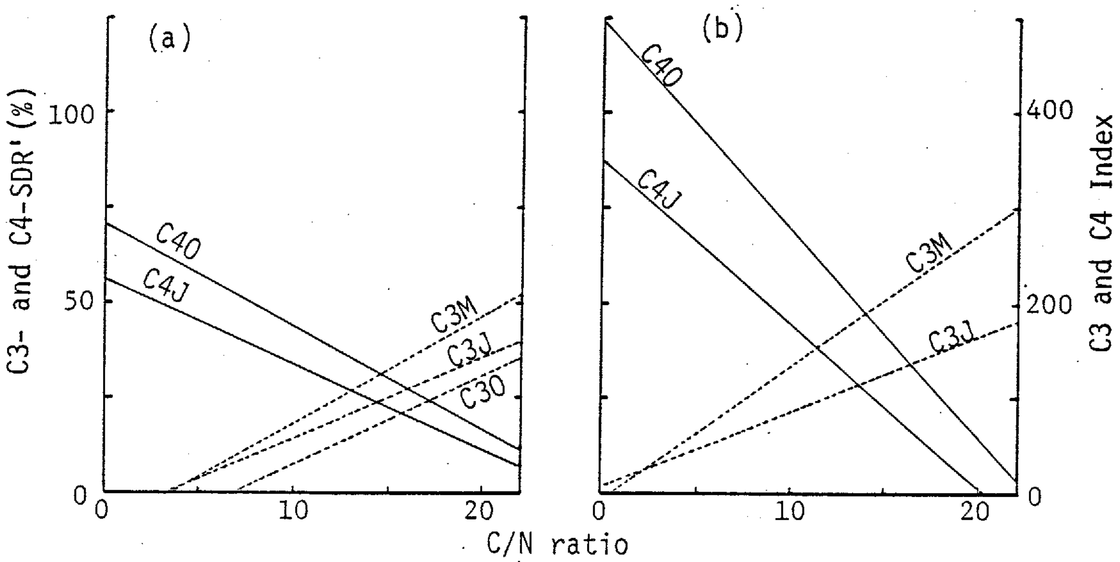

Fig. 5-d. Relationships between the importance values (C3-SDR', C4-SDR', C3 Index and C4 Index) and soil properties at livestock pastures. Notations and sample sizes are same as in Fig. 5-a. (a) and (b): relations of importance values and C/N ratio.

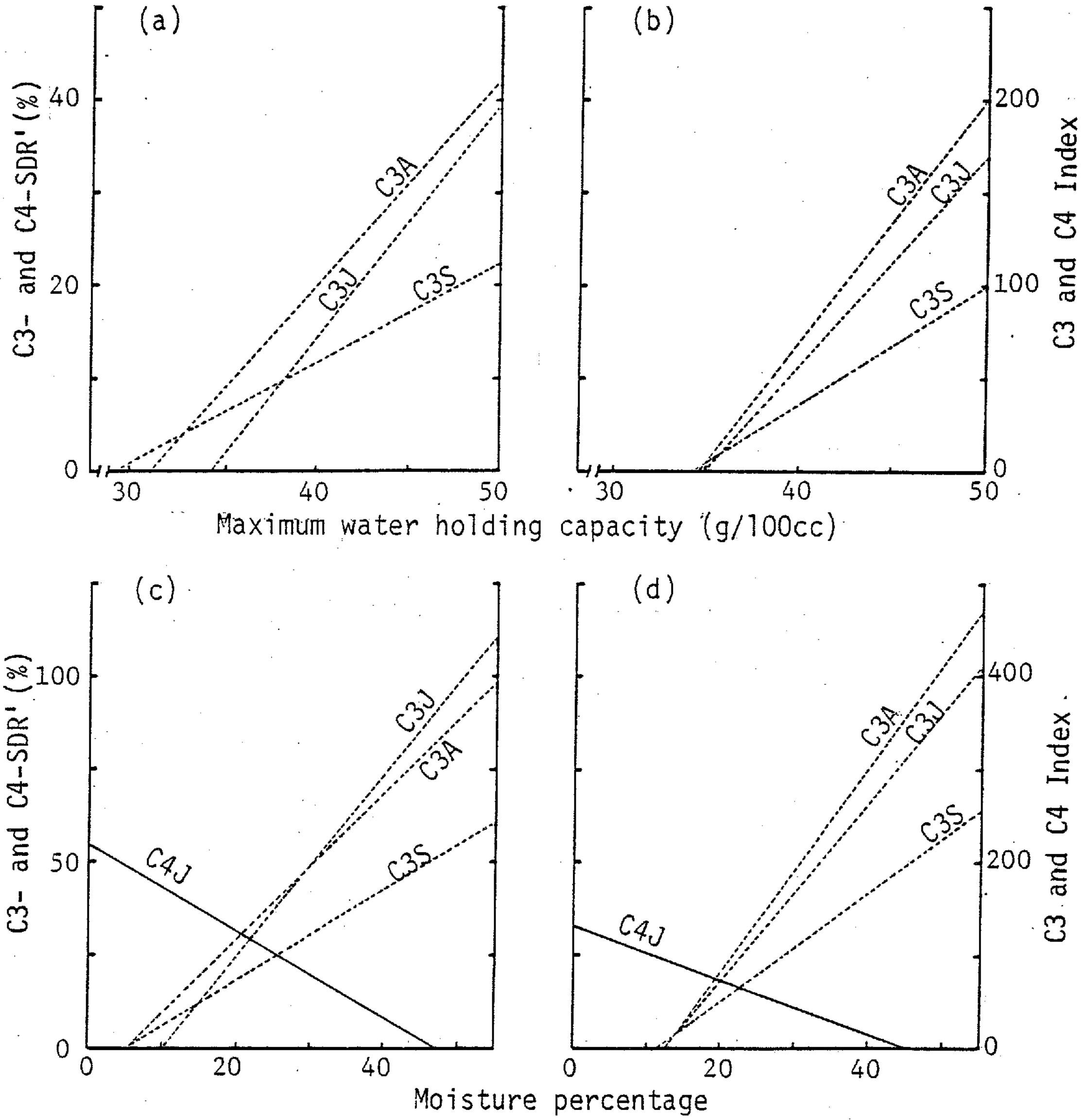

Fig. 5-e. Relationships between the importance values (C3-SDR', C4-SDR', C3 Index and C4 Index) and soil properties at Nara Park and on Miyajima Island inhabited by sika deer (<u>Cervus nippon</u>). C3A, C3J, C3S indicate the importance values of C3 graminoids in April, June (July on Miyajima Island) and September (October on Miyajima Island) respectively. C4A, C4J, C4S are the notation for C4 graminoids same as for C3 graminoids. (a) and (b): relations of importance values and maximum water holding capacity (MWHC) (n=24). (c) and (d): relations of importance values and moisture percentage (MP) (n=24).

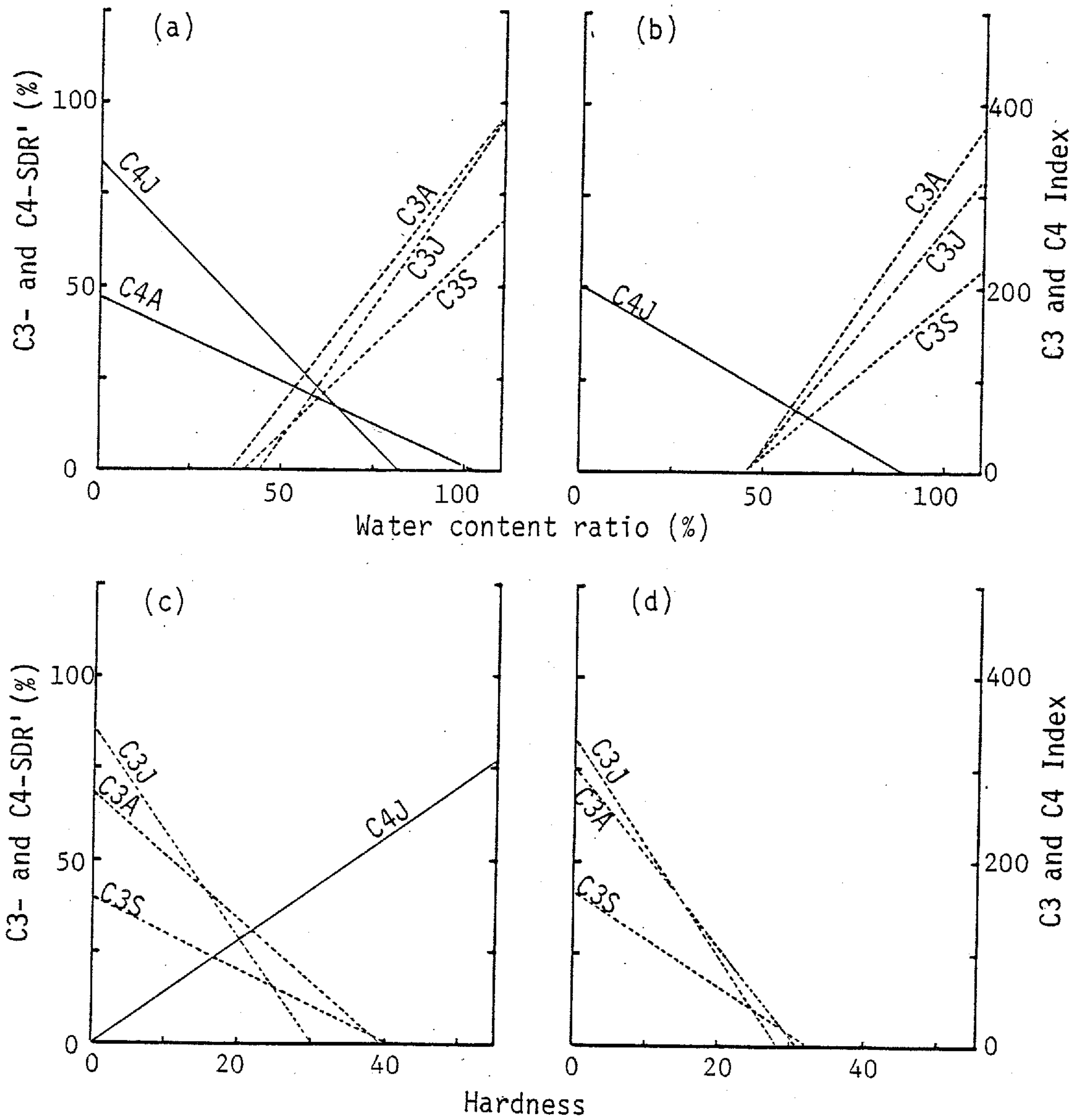

Fig. 5-f. Relationships between the importance values (C3-SDR', C4-SDR', C3 Index and C4 Index) and soil properties at Nara Park and Miyajima Island. Notations and sample sizes are same as in Fig. 5-e. (a) and (b): relations of importance values and water content ratio (WCR). (c) and (d): relations of importance values and hardness.

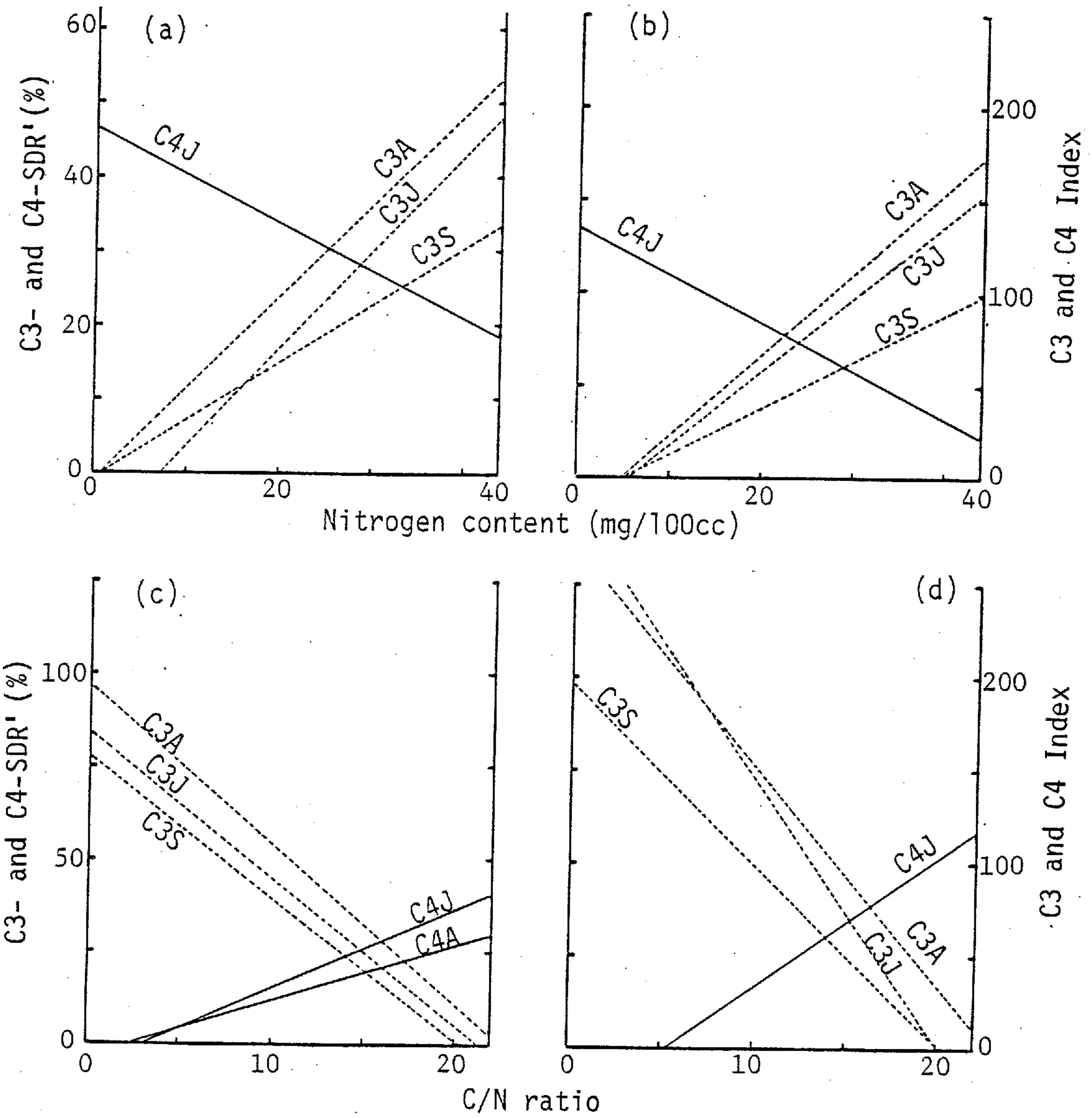

Fig. 5-g. Relationships between the importance values (C3-SDR', C4-SDR', C3 Index and C4 Index) and soil properties at Nara Park and Miyajima Island. Notations and sample sizes are same as in Fig. 5-e. (a) and (b): relations of importance values and nitrogen content. (c) and (d): relations of importance values and C/N ratio.

factors correspond well with one another. A general trend over all the study areas was found to be thus: the extent of the soil factor's effect varied from site to site (data were not shown). Although the physical soil factors like bulk density, MWHC and MP, exhibited consistent correlations with vegetation aspects all over the areas, carbon and nitrogen content did not appear to have a fixed influence upon the vegetation.

4) Correlation among Soil Factors

Based upon the hypothesis that herbivores influence the soil's physical structure, a further question arises: To what extent are those soil factors related to one another and how might one soil factor affect another which ultimately can modify the competitive relationships among plants? To settle this question, simple linear regression analyses among soil factors were done. Correlation coefficients with anaysis of variance (F-test) were listed in Table 10-a for the livestock pasture and in Table 10-b for deer-inhabited areas. Only the relationships with probability less than 5% were illustrated.

Bulk density related negatively with pore space, C/N ratio, carbon and nitrogen content, MP, MWHC, and positively with soil hardness. MWHC showed a positive correlation with pore space, carbon and nitrogen content, C/N ratio, MP, and

Table 10-a. Correlations between soil properties with analysis of variance at live stock pastures (n=22)

	Pore space	C/N ratio	N-cont.	C-cont.	Hard-ness	WCR	MP	MWHC
Bulkdensity	1.00** (-)	0.78** (-)	0.56* (-)	0.81** (-)	.	.	0.90** (-)	0.92** (-)
MWHC	0.92** (+)	0.80** (+)	.	0.68** (+)	.	.	0.97** (+)	
MP	0.90** (+)	0.75** (+)	.	0.67** (+)	.	.		
WCR	.	.	.	.	.			
Hardness	.	.	.	.				
C-content	0.81** (+)	0.61** (+)	0.89** (+)					
N-content	0.56** (+)	.						
C/N ratio	0.78** (+)							

MWHC: Maximum Water Holding Capacity, MP: Moisture Percentage, WCR: Water Content Ratio, (+): positive correlation, (-): negative correlation, **: $P<0.01$, *: $P<0.05$

Table 10-b. Correlations between soil properties with analysis of variance at Nara Park and Miyajima Island (deer inhabited area) (n=24)

	Pore space	C/N ratio	N-cont.	C-cont.	Hard-ness	WCR	MP	MWHC
Bulk density	1.00** (-)	.	.	0.44* (-)	0.68** (+)	.	0.62** (-)	0.53* (-)
MWHC	0.53* (+)	.	0.61** (+)	0.46* (+)	0.70** (-)	0.80** (+)	0.92** (+)	
MP	0.62** (+)	.	0.61** (+)	0.47** (+)	0.71** (-)	0.92** (+)		
WCR	.	0.51* (-)	0.58** (+)	.	0.56** (-)			
Hardness	0.68** (-)	.	.	.				
C-content	0.44* (+)	.	0.90** (+)					
N-content	.	.						
C/N ratio	.							

MWHC: Maximum Water Holding Capacity, MP: Moisture Percentage, WCR: Water Content Ratio, (+): positive correlation, (-): negative correlation, **: $P<0.01$, *: $P<0.05$

related negatively with soil hardness. Moisture percentage behaved similarly to MWHC; that is, there was a negative correlation with hardness and a positive correlation with carbon and nitrogen content. WCR was the one which showed the fewest relationships to the other factors. Hardness exhibited a positive correlation with bulk density and negative one with water-related factors. However, both WCR and hardness did not show any relationship with others in livestock pasture. The relationships between pore space and soil organic matter (C and N) were positive across all the places and hence, carbon content correlated positively with nitrogen content and vise versa. The C/N ratio at livestock pastures showed a positive relationship to pore space which was an alternative description of bulk density (see chapter III, equation (9)).

The implications of the results in this section represent some schematic ideas on sequential relationships among herbivores - soil - vegetation. Referring to the soil data shown in section 2, in this chapter, soil bulk density and hardness appear to be primary factors influenced by herbivores and have some potential to regulate the other factors. Recall that the significant differences for these two foctors were observed among the differently grazed pastures or between the inside and outside exclosures. With an increase in the grazing pressure, the bulk density and hardness of soil should be increased. This process seriously damages the space structure of soils: pore space and maximum water holding capacity. With a decrease in those capacities, the moisture percentage, nitrogen and carbon content are reduced. These alternations of soil condition, especially water-related factors, apparently influence the competition on C3 and C4 plants.

VI. DISCUSSION

1. Grazing Tolerant and Intolerant Traits in C3 and C4 Graminoids

With the following evidence, the results of the present study confirm the hypothesis that herbivores were a significant factor influencing the competition of C3 and C4 graminoids.

(1) As a function of grazing intensity, along a discrete nominal scale (non, light, moderate and heavy grazing), the importance of C4 graminoids increased and that of C3 graminoids declined with the C3 and C4-SDR', the number of species, and C3 and C4 Indices.

(2) The exclosure technique at Nara Park represented the same idea, i.e., the tolerance of C4 graminoids and vulnerability of C3 graminoids with grazing.

(3) Importance value of C3 and C4 graminoids exhibited definite trends as a function of a progressive and/or retrogressive succession which was expressed as a replacement series from a *Zoysia japonica* to a *Miscanthus sinensis* type community, and which was attributed to different grazing intensities.

(4) The abundance of C3 and C4 graminoids was closely related to topographic features which also strictly regulated habitat use of herbivores; that is, the distributional

difference of C3 and C4 graminoids along the hillslope position can be attributed to the discriminative grazing use by herbivores.

(5) The trends of replacement between the C3 and C4 graminoids relative to the different grazing intensities occurred regardless of climate, whether the ecosystem was in a semi-arid natural grassland or a semi-natural grassland with high precipitation. This suggests that grazing was one of the primary factors regulating the competition of C3 and C4 graminoids.

1) Measurement of Successional Stage Related to Grazing

Concerning the evidence (3), there are numerous field studies reporting that the semi-natural grassland succession progresses from a Zoysia japonica to a Miscanthus sinensis type with decreasing grazing intensity (Horikawa and Itow 1958; Kurosaki et al. 1958; Shiratsuki and Itow 1958; Itow 1962, 1963, 1967, 1974, 1975; Suganuma 1966, 1967). Since Miscanthus sinensis is categorized as a tall grass and Zoysia japonica is a short grass, succession in this sense can be categorized as a replacement from a short to a tall grass ecosystem. This idea also corresponds to that of a natural grassland of mixed grass prairie which is a floristic complex of tall and short grass prairie. When the mixed grass prairie is stressed by heavy grazing or drought, short grass species tend to increase in abundance (Barbour et al.1980). McNaughton (1983) also stated in his study of Serengetii National Park that short grasslands predominated below a 700mm mean annual rainfall and at heavily grazed sites, on hilltops at higher-rainfall locations.

2) Spatial Use of Herbivore along the Hillslope

Several authors have already shown that the pattern of cattle spacial use within a pasture is dependent on topography (evidence (4)). Senft et al. (1980,1982) at the CPER compared the predicted and observed seasonal patterns of cattle spacial use and found excellent correlation to pasture characteristics, the upland, the mid-slope and the lowland. Specifically during the growing season, cattle frequented the lowlands while they used the upland during the dormant season. Thus, the upland and the lowland vegetation may be affected more strongly by grazing than the vegetation of the mid-slope areas. Similarly, Kaseda (1983) studied seasonal changes in the home range of Misaki horses at Toi Misaki, and reported that the ridge tops were frequented by horses.

As a supplemental research during the course of the present study at Toi Misaki, cattle distribution on three topographical features, ridge (upland), the mid-slope and the lowland was also assessed (Table 11). Apparently, the

Table 11. Number of horses observed at three hill-slope positions of Toi Misaki Point

	Hillslope position		
	Upland	Mid-slope	Lowland
Time			
9:00	14	2	1
10:00	10	6	0
11:00	14	3	2
13:00	12	3	0
14:00	14	7	0
15:00	13	2	0
16:00	3	3	8
17:00	8	3	5

horses spent longer periods of time on ridge tops (the upland) than in any other area. Early in the evening, they moved down to the lowland of the hillslope.

Horikawa and Itow (1958) studied the developmental process of a stepped plant community which was caused by a lessened frequency on the trail pass by cattle. This community occurred more commonly at an inclined plane (the mid-slope) than on a flat plane (the upland and the lowland) where the cattle enjoyed ease of mobility; thus, the vegetation of the upland and the lowland was equally and strongly affected. As the cattle trail become wider, the area of the stepped community diminished as in the upland and the lowland. This community mainly consisted of tall and tread-intolerant plants, such as *Miscanthus sinensis* and *Ilex crenata*, while the trail pass was usually dominated by treading tolerant plants: *Arundinella hirta*, *Arundinaria pygmaea* var. *glabra* and *Zoysia japonica*.

3) Competition of C3 and C4 Plants

Since few studies have focused on the interrelationship of C3 and C4 plants with specific concerns related to herbivore interference, little information is available for a comparison with the evidence (1) and (2) from the present study. However, reviewing previous literature demonstrating floristics relative to the grazing intensity without studying the relationships of C3 and C4 plants, may provide a possible comparison.

At a site of the desert grasslands in Arizona, where the components of vegetation were predominantly C4 species, most of the C4 graminoids were decreased markedly in heavily grazed areas (Schmuts and Smith 1976). Moreover, Syvertsen et al.(1976) reported the low importance of C4 species (as determined by biomass) in several grazed lowlands of the Chihuahuan Desert Site, while Eickmeir (1978) showed a declining C4 cover (with replacement by CAM species) toward low elevation desert areas of Big Bend National Park, which is a part of the park most severely altered by overgrazing (Whitson 1974). Wentworth (1983) also stated in his study of southeastern Arizona that successful features of C4 graminoids with high temperature, high irradiance and low moisture were not so apparent on heavily grazed area.

The declining trends of C4 plants in desert grasslands were contrary to the present study. The interpretations of these conflicts between the results of previous studies and those of the present study are: (i) most of the graminoid species in those desert grasslands consisted of C4 graminoids and C3 plants were mainly shrubby species, (ii) cattle selectively removed the grasses, the predominant C4 species, thereby promoting an increase of C3 shrubby species (Hastings and Turner 1965; Humphrey 1958), i.e., the competitors of C4 graminoids were not C3 graminoids but C3 shrubby species.

(iii) competiton and replacement between C3 and C4 graminoids were not so obvious; i.e., C3 graminoids cannot be an aggressive counterpart to C4 graminoids in those arid grasslands. Thus, the situation of desert grasslands may not be readily comparable to that of the mixed or short grass prairie and semi-natural grassland where a fair amount of rainfall still makes room for the C3 graminoids.

Coppock et al. (1983) studied the effect of black tailed prairie dogs upon the vegetation of a mixed-grass prairie at the Wind Cave National Park in South Dakota. According to their report, the importance (above-ground biomass) of both C3 and C4 graminoids decreased as a function of time since the initiation of colonization. On the other hand, the proportion of shrubs and forbs increased on this scale. Seasonal fluctuation of C3 and C4 graminoids followed typical trends (Lauenroth and Whitman 1977; Ode et al. 1980; Kemp 1983) in the area with a short grazing history (0-2 year inhabitance), namely, cool season C3 graminoids formed a high proportion of the total number of graminoids at the beginning of the growing season and were overtaken by warm season C4 graminoids in the summer. However, in young dog towns inhabited for 3 to 8 years, the importance of C4 graminoids was always greater than that of C3 graminoids from the beginning to the end of the growing season and did not show any replacement trends between C3 and C4 graminoids. The implication of this is that C4 graminoids exposed to moderate grazing show a tolerance which is not so distinctive in the C3 graminoids.

Since the prairie dog is a heavy grazer, the plant cover around one population center exhibited a distinct concentric zonation (Osborn and Allen 1949). Population concentration of prairie dogs sometimes resulted in complete eradication of palatable food plants and finaly in denudation of the central area. Therefore, comparisons between the effects of prairie dogs and livestocks on vegetation may not be appropriate due to the difference in grazing pressure level. The situation of the prairie dog probably resembles the effect of deer at Nara Park and Miyajima Island in Japan.

At the CPER, Klipple and Costello (1960) studied vegetation responses to different grazing intensities. Although they did not focus on the physiological function system (C3 and C4 photosynthetic pathway), C4 graminoid's importance increased as grazing pressure increased. On the other hand, the importance value of C3 graminoids to the total graminoids was declined. This trend is the result of a research undertaken during 1952-53, 12 years after the experiment was initiated. The longer the duration of the experiment, the more apparent the difference in C3 and C4 graminoid distribution. This has also been shown in the present study at the CPER which was presented 42 years after the initiation of the original experiment.

4) Other Attributes of C3 and C4 Graminoids besides Photosynthetic Efficiency

The conclusion here, as far as the present observations are concerned, is that C4 graminoids exhibit more tolerant traits than C3 graminoids do in relation to grazing stress. Now the question arises: are those tolerances to grazing primarily correlated with the physiological function system (photosynthetic pathway) of C3 and C4 graminoids? The results of the present study affirm this question although there still ramain some negative aspects as follows:

The responses of C3 and C4 graminoids to the grazing might be attributed to the life forms or morphological advantages of each species rather than the plant's physiology. For example, sod formers are more resistent to grazing than bunch grasses because they have so many growing points (Barbour et al. 1980). Tomanek and Albertson (1957) reported differences in response to grazing intensity in mid-grasses, short-grasses and forbs. According to them, short-grasses were more tolerant to grazing than mid-grasses. Although there are variations in height within a species, Bouteloua gracilis, Buchloe dactyloides, and Carex eloeocharis are usually categorized as short graminoids while Agropyron smithii and Aristida longiseta are as mid-height grasses. Regarding the graminoid species in the semi-natural grasslands in Japan, Zoysia japonica is a short grass growing with rhizome elongation (Suganuma 1963; Itow 1967) while others are mostly bunch grasses with erected forms.

Plants which are resistant to grazing tend to increase with a decrease or delay in height and erectness of growth, growth rate, leaf elevation, shoot apex elevation, time of floral differentiation and proportion of reproductive shoots (Cooper 1951; Branson 1956; Neiland and Curtis 1956; Peterson 1962). Archer and Tieszen (1980) also reported that some graminoid species in tundra avoid the cessation of leaf production and death due to their apical meristems being typically positioned 10 to 15mm below the layer of moss and soil.

One type of regrowth is culmless or culmed vegetative and reproductive shoots (Cook and Stoddart 1953; Rechenthin 1956). By proper timing in the height of defoliation, culmed shoots can be stopped to force tillering from basal auxiliary buds (Hyder and Sneva 1963).

Another attribute is the defense mechanism of plants. Strongly awned grasses such as Sitanion hystrix and Stipa comata cause mechanical injuries to animals and confound the problem of grazing uniformity (Hyder 1972).

Although the graminoids in the present study may be categorized as having some of the attributes listed above, physiological functions of C3 and C4 graminoids can still possibly be correlated with herbivores by examining the following evidence.

First, not only C4-SDR' but also the number of C4 graminoid species responded positively to the grazing stress. This indicates that, despite a few C4 graminoids which show decreasing trends with grazing, many other C4 species compensate for the losses, which is due to the grazing-intolerant C4 specise, namely, most of the grazing tolerant species were categorized as C4 graminoids and many of the intorelant species were the representatives of C3 graminoids.

Second, in the results showing the response of some dominant species to the grazing (see the section 1-(1) of chapter V. RESULTS AND ANALYSIS), some C4 species such as Arundinella hirta and Imperata cylindrica also follow the general pattern of C4-SDR' in relation to grazing. That is, the variation of C3- or C4-SDR' was not largely accounted for by one or two C3 and C4 graminoids. Arundinella hirta and Imperata cylindrica were described as tolerant species (Horikawa and Itow 1958) in semi-natural grasslands in Japan.

The past literature and results of the present study suggest that as a principle of nature, C4 graminoids have some mechanical tolerance to grazing, or C3 and C4 graminoids respond physiologically to soil conditions and other abiotic factors could possibly be influenced by herbivore activity. The abiotic factors associated with C3 and C4 graminoids in relation to the herbivore are discussed in the next section.

2. Adaptive Mechanism of C3 and C4 Graminoids to Grazing

The possible interpretation of how and why the C4 plants were more adaptive to grazing than C3 plants can be derived from two sources, direct and indirect adaptive significance. Direct adaptive significance referred to here includes: tolerance to the mechanical clipping or defoliation, other physically advantageous traits for the competition with C3 species and selective grazing or avoidance by herbivores of C4 plants. Indirect significance may be attributed to the adaptation of C3 and C4 plants to abiotic factors such as irradiance and water supply in soils which are primarily subjected to herbivore influence.

A. Direct Adaptive Significance

1) Time of Growth

Mechanical tolerance of plants has already been discussed in a previous section. However, very little previously published literature has ever demonstrated that C4 plants have defenses or protective mechanisms that may sustain injury from grazing. Even if most of the C4 species had exhibited those advantages in regrowth mechanisms after clipping or at the time of elongation of inflorescence or shoot apex, suspicions still remains as to whether the mechanisms were strictly correlated with and attributed to physiology.

Speculation on this point is as follows: since C3 plants optimize during the cool growing season (Hofstra and Hesketh 1969; Zeltch 1971) when most forages for wildlife and livestock are unavailable, C3 graminoids are easily and extensively damaged by herbivores looking eagerly for food. On the other hand, the time of elongation of the leaves and inflorescence on C4 graminoids generally occur during the warm season when a relatively greater amount of forage is available.

2) Growth and Regrowth Rate after Clipping

Since the growth rate of C4 plants is four times greater than that of C3 heliophytes (Black 1973; Kelly et al. 1976), the regrowth rate of C4 plants after defoliation is considered to be higher than that of C3 plants. Defoliation experiments in relation to competition provide some ideas as to what extent C3 or C4 graminoids show adaptive significance in terms of regrowth after clipping.

Archer and Detling (unpubl.) studied the effects of defoliation and competition on the regrowth of Andropogon gerardi (C4 graminoid) and Carex filifolia (C3 graminoid) during the season from June to August. According to this research, tillers of A. gerardi subjected to multiple defoliation with reduced competition produced significantly more leaves than did non defoliated tillers or tillers of multiple defoliation under full competition. No significant differences in numbers of the leaves generated were found among the Carex tillers. As they suggested, the time of defoliation and duration of experiment (July to August) might have optimized only the regrowth of C4 graminoid, *A. gerardi*, and not that of C3 graminoid, *Carex filifolia*, which exerted a full compliment of leaves prior to the innitiation of the clipping treatment.

Those findings, however, were based upon a simple experimental design with only two species. Thus, it many not be possible to support the overall trends of C3 and C4 plants in relation to defoliation or actual herbivore grazing.

3) Herbivore Preference

Other possible explanations can be derived from the different feeding preferences of herbivores on C3 and C4 plants (Caswell and Reed 1976; Boutton et al. 1978), or the precluding biochemical mechanisms of grazing avoidance (Archer and Tieszen 1980; Ryan 1978) or the specific enzymes found only in C4 plants (Black 1969; Hatch 1976) or other attributes related to the differences of photosynthetic pathways.

Caswell et al. (1973) hypothesized that for herbivores, C4 plants were generally less nutritious than C3 plants. Although herbivore preference for C4 and C3 plants largely depends on herbivore species (Tieszen et al. 1979a; Tieszen and Imbamba 1980), large amounts of potential nutrients in the bundle sheath of C4 plants may not be readily available due to the slow degradation of the bundle sheath cell wall by rumen bacteria (Akin and Burdick 1977) and insect herbivore (Caswell and Reed 1975).

Additionally, the effect of herbivore's saliva on regrowth (Bonner 1940; Readon et al. 1974; Dyer and Bokhari 1976; Detling et al. 1981) has to be kept in mind if a biochemical relationship between one herbivore species and one plant species exists.

B. Indirect Adaptive Significance

The result of this study demonstrated a strong correlation between C3 and C4 species' distribution and physical and chemical factors of the soil, topography, temperature, and light interception via a canopy, suggesting that the competitive ability of C3 and C4 graminoids largely depends on these factors. In addition to this, soil condition was altered among the differing grazing pastures. The discussion here is specifically focused on the sequential chain of relationships among herbivore - abiotic factors (soil and light) - vegetation.

1) Water Use Efficiency

Although the essential adaptive feature of C4 plants is that the system concentrates CO_2 in the parenchymatous bundlesheath cells (Bjorkman 1976), this creates a more favorable microenvironment for the functioning of Rudp carboxylase, and thereby is at an advantage under various environmental conditions, where intercelluar CO_2 may become limited (Tieszen and Imbamba 1980).

One advantage of C4 plants that has been well established is their greater water use efficiency; meaning that less water is necessary to fix a molecule of CO2 in C4 plants than in C3 plants. Black (1971) stated that C4 plants require about half as much water as C3 plants to produce one unit of dry matter.

The physiological feature of water use efficiency in C3 and C4 plants has been reviewed and demostrated by some authors in field studies (Tieszen et al. 1979b; Barnes and Harrison 1982; Archer 1984), and indoor experiment (Matsunaka and Saka 1977; Detling 1979; Fribourg et al. 1982; Kemp 1983). The consensus of these authors was that C4 species were more abundant and tolerant in water limited conditions such as in the upland or the ridges.

2) Temperature

Water is not the only factor related to advantageous traits of C4 species, and hence, the water use efficiency in C4 species does not usually mean that C4 species have a significant advantage over C3 species in some arid environments. Cold desert was not found to be a preferable condition for C4 shrub species (Caldwell et al. 1977). The results of the present study showed that C4 graminoids were not so competitive with C3 graminoids at the beginning of the growing season. These facts suggest that temperature is also a significant factor in C3-C4 species competition.

Replacement between C3 and C4 plants relative to the temperature fluctuation-dimension is due to the fact that most plants with photorespiration do not exhibit a pronounced temperature optima as do C4 plants (Hofstra and Hesketh 1969; Zeltch 1971). In C3 plants, increasing photorespiration at higher temperatures makes photosynthesis less rapid (Moore 1977).

Williams (1974) and Russel and Williams (1982) examined the adaptive significance of temperature by using one C3 and one C4 graminoid in an experimentally designed observation. Increasing pretreatment day temperatures by 20°, 30° and 40°C resulted in decreased photosynthesis in Agropyron smithii (C3) while in Bouteloua gracilis (C4) the net photosynthesis was increased. The former C3 species exhibited lower high temperature damage thresholds while the latter C4 species showed the highest tolerance to high temperature with threshold values beginnig at 44-49°C for cool-grown plants and at 53-55°C for warm-grown plants. The results of this experimental work agree well with broad geographical studies of C3 and C4 plant distribution. Teeri and Stowe (1976) stated that high minimum temperatures during the growing season have the strongest correlation with the abundance of C4 grasses in regional flora of the North American continent. Tieszen et al. (1979b) found altitudinal differnces in Kenya; the C4 tribes, Chlorideae, Eragrostideae, Sporoboleae, and Aristideae were abundant at low altitudes while the C3 tribes Aveneae, Festsuceae, and Agrostideae were found only at high altitudes.

3) Nitrogen Use Efficiency

Another characteristic difference between the C3 and C4 species, at least among the gramineae, is in the use of nitrogen. Although Brown (1978) cited much literature to support the hypothesis that C4 plants have a greater nitrogen use efficiency (biomass production per unit of nitrogen in plant) than C3 plants do, in an experiment by Christie and Detling (1982), little evidence was provided to support the postulate that the difference in nitorgen use efficiency between C3 and C4 pathways may be advantageous only for C4 plants. Christie and Detling (1982) concluded that the growth differential in C3 and C4 grasses at two temperatures (20/12 °C and 30/15°C for day/ night temperature) would result in an uneven utilization of the soil nitrogen resources on a seasonal basis.

In the present study, the responses of C3 and C4 graminoids to the nitrogen content of soil were obvious for the C3-SDR' but not for the C4-SDR' in both livestock pastures and deer habitats. Therefore, the competition of C3 and C4 plants for nitrogen resources in soils may not be so distinct as for the other soil factors

4) Irradiance and Light Intensity

Irradiance was also an important regulating factor upon C3 and C4 competition. Under the condition of maximum solar radiation (about 1.3 $cal/cm^2/min$), only about 0.6 $cal/cm^2/min$ is available in the 400 to 700 nm wave length region which is absorbed primarily by chlorophyll, and available for photosynthesis (Zeltch 1971). This level is generally saturating for C3 species but not for most C4 species (Moore 1977).

Dye et al. (1972) found similar high photosynthesis rates and lack of light-saturation at full sunlight in Bouteloua gracilis (C4) when it was under low soil moisture stress. As soil moisture stress developed, however, the maximum gas exchange rates were reduced and plants were light saturated at lower intensities. In a study of the C3 species Festuca rubra, Ruets (1973) found that variation in daily radiation in the mountain meadow accounted for most of the variation in daily photosynthesis. Thus, in their respective natural environments, both C3 and C4 species are commonly light-limited in their photosynthetic response.

The removal of the overstory vegetation by herbivore grazing and browsing obviously induces the irradiance of the understory with an increase in temperature, which then causes moisture to evaporate from the ground. Taking those additional changes of environment into account, light intensity can be a primary factor influencing C3 and C4 plant distribution. This agrees well with the fact that fluctuation of C4-SDR' and C4 Index largely depends on the dominance of a tall grass, Miscanthus sinensis at the OPAHR and on the crown density of the overstory at Nara Park.

The mechanisms of light saturation of C3 and C4 species related to abiotic factors are, however, rather complicated. Thus, recent experimental work was designed with coupled factors as combinations of water and temperature (Ozturk et al. 1981), temperature and nitrogen, and temperature and solar radiation (Vong and Murata 1978; Christie and Detling 1982). The overall trends of those combined factors were, as Wentworth (1983) stated in his study in southeastern Arizona, found in the relative successes of C4 species in habitats characterized by high temperature, high irradiance and low moisture.

5) Topographical Features

Topography is a good example for explaining a combination of several abiotic factors, and is also a regulating factor in determining the distribution of C3 and C4 plants. Besides the relationship between the frequency of herbivore use and the different positions of hillslope (the upland, the mid-slope and the lowland), which were discussed in a previous section, topography, itself, has a sequential gradient of various abiotic factors from the top of the hills to the bottom of the slope. That is, an ecological cline known as "catena" exists along the slope.

Then the problem arises: what the constituents of those ecological gradients are and to what extent each factor relates to the above ground competition of plants. The relationship between topography and vegetation has been studied by numerous researchers, and soil moisture gradients along hillsides are known to determine species composition in the Great Plains Grassland (Dix 1958; Hulett et al. 1968). The presence of such different plant coummunities under one climate must be attributed largely to the differences in geological materials from which the soil was derived, and primarily to those differences in soil moisture and temperature regimes related to the different materials (Branson et al. 1965).

Maximum available water was significantly higher in the fine textured surface soils of the lowland sites than in the coarse textured sands of the dune sites. Since surface runoff and the internal down slope flow of water in saturated and unsaturated states maintain relatively dry knolls and humid troughs (Jenny 1980), soil moisture may ultimately cause a gradient of salinity or nutrient content.

In southern Arizona, Nicholson and Bonham (1977) found that the distribution of Bouteloua species was influenced by organic matter, pH and lime. Hadley and Buccos (1967) also found that the plant community composition and the net primary production in a native tall grass prairie of North Dakota were correlated to the soil salinity and internal drainage.

White (1961) in South Dakota concluded that the distribution of grasses was related to soil fertility. He also stated, however, that the presence of Andropogon spp. and Bouteloua curtipendula on the soil microridges could not be attributed to a more favourable moisture regime than that found in the adjacent soil microvalleys which had Agropyron smithii as the dominant species.

Other factors which might influence grass distribution along soil catenas are textural variations of soil (Malo et al. 1974), bulk density and cation exchange capacity (Kleiss

1970). According to the study of Malo et al. (1974) in North Dakota, the soil properties increasing as a function of distance from summit to toeslope were: organic carbon(%) and depth to greater than 1.4g/cc bulk density. It was found that the geometric mean particle size of the A-horizon decreased for the same dimension, suggesting a process of particle sorting. An abrupt decrease in bulk density values was found at the lower landscape position caused by greater amounts of organic material and finer-textured materials.

The basic features of a study by Kleiss (1970) were identical to what was found by Malo et al. (1974), stating that hillslope sedimentary processes affecting particle size also influence the quantity of organic material that accumulates at various slope elevations.

Kayama (1975) studied some soil factors along the hillslope of Kawatabi, Japan, and reported that the solid-phase percentage varied with topography, namely, at the base of a gentle slope, the solid phase was extremely small in the surface soil 0-20cm in depth.

At the CPER, Schimel (1983) studied nutrient dynamics along a catena, and found that carbon, nitrogen, phosphorus and clay increased donwnslope, with the largest increase occurring from the mid-slope to swale positions. The moisture content of the soil was highest in swales. This topographic feature at the CPER supports the result of C3 and C4 plant distribution and is attributed to their physiological traits expressed as response to moisture and irradiance.

The implication of those factors along the hillslope supports the idea that the distribution of two types of grasses (C3 and C4 graminoids) respond to those ecological gradients which, however, are also subjected to herbivore pressure due to their discriminative utilization on a slope (see section 3-(2) of Chapter V. RESULT).

3. Conclusion (Relationships among Herbivore - Soil - C3 and C4 Graminoid Distribution)

As shown in the results, physical soil and water-related factors, such as soil hardness, bulk density, pore space and maximum water holding capacity did show a marked difference among the differently grazed pastures and exclosures.

Several reports in the literature have demonstrated the effects of the trampling and vegetation removal by grazing animals on soil compaction of range land (Galbraith 1971; Gifford and Hawkins 1976). Soil compaction has important hydrologic implications in terms of a reduced infiltration rate and increased run-off impacts and erosion potential on plant growth (Orr 1975; Gifford et al. 1977).

At the CPER, Van Haveren (1983) studied the soil bulk density in differently grazed pastures, heavy, moderate and light, and reported that regarding fine-textured soils, the average bulk density in the heavily grazed pasture was 13.4% and 11.8% higher than in the lightly grazed and moderately grazed pastures, respectively. However, regarding coarse-textured soils, the soil bulk density means of the three grazing treatments were not significantly different, indicating that soil compaction due to grazing occurred primarily on fine-textured soils at the CPER.

These reports and the results of the present study support the hypothesis that the herbivore is one of the significant factors altering the compaction and aerobic space of soils which causes a sequential change in other soil structures and water- and nutrient-related conditions. However, the soil type should be homogeneous when bulk density is used to compare the effect of grazing treatments on soil compaction (Laycock and Conrad 1967).

Herbivore feces and urine make nutrients more readily available for decomposition, thereby stimulate microbial activity and increase the turnover of nutrients (Barbour et al. 1980). The results at the OPAHR showed that there was no significant change in organic matter among the different grazing pastures, suggesting livestock did not contribute to the carbon and nitrogen cycle. However, in the exclosure regime at Nara Park and on Miyajima Island, both carbon and nitrogen content exhibited higher values outside the exclosure.

Gillard (1967) stated that 80% of the nitrogen from feces remaininig on the pasture surface is lost by volatilization, but when sufficient numbers of dung beetles are present for quick burial, the loss is reduced from 5 to 15%. In other studies, quick recycling of volatile nutrients in feces by the burying activity of dung beetles increased pasture yields as a result of the incorporation of organic matter into the soil, with a concomitant increase in soil friability, aeration, and water-holding capacity (Gillard 1967; Bornemisszа and Williams 1970; Macqeen and Beirne 1975). Microbial trophic structure and available soil pore space influence rates of decomposition and mineralization (Elliott et al. 1980).

According to the above findings, the difference in nitrogen content is due to the absence or lessened activity of dung beetles at the OPAHR, and to their presence and vigorous activity at Nara Park and on Miyajima Island. However, since the advantageous feature of C4 plants in terms of nutrient uptake was not obvious, it is not clear whether herbivores influenced the competition of C3 and C4 graminoids through the process of urination and fecal elimination.

The results of the present study and of a review of past literature, suggest the idea of a sequential relationship among herbivores, soil and vegetation aspects and indicate that herbivores indirectly regulate the C3 and C4 plant-competition; namely, herbivores modify soil and other abiotic conditions which fit or do not fit the physiological traits of C3 or C4 species. Direct influences have already been discussed in a previous section.

In conclusion, the mechanism of those interactions, herbivore - abiotic factors - C3 and C4 plant competition, are schematically illustrated in Fig. 6 (see chapter IV, section 3-(4) for detail). The sequential relationships among herbivores, soil and vegetation may not be readily applicable in a area where herbivores selectively graze C4 herbaceous plants due to the shortage of the food as in the shrubby desert community shown in previous studies in Arizona and in Chihuahuan Desert Sites or the extremely disturbed area due to the heavy grazer as seen in the present study on Miyajima Island. However the interrelationships among the three factors should be consistent in a area where habitat ranges of C3 and C4 graminoids are well overlapped and are in a central area of their distribution range rather than in a peripheral area.

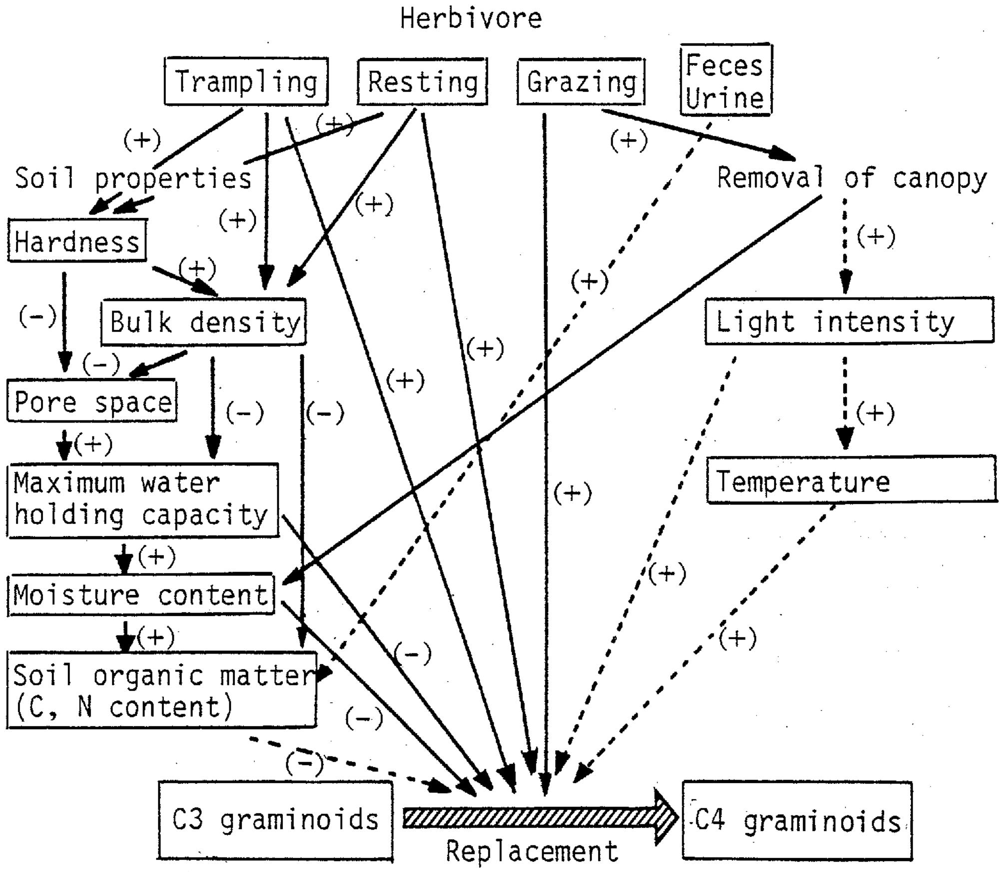

Fig. 6. Factors affecting the replacement of C3 graminoids by C4 graminoids and their interrelations. Solid line indicates the relation examined in the present study and ascertained to be either negative or positive. Dashed line refers to the relation predicted from the data of present study and of published literature.

VII. SUMMARY

1. A study was conducted to determine the effects of herbivores on the competition of C3 and C4 graminoids at the Central Plains Experimental Range (the CPER) in northern Colorado, USA., and several places in southwestern Japan: Nara Park, Miyajima Island, Mt. Azuma, the Oita Prefecture Animal Husbandry Range (the OPAHR) on Mt. Kuju, Mt. Aso, and Toi-Misaki Point. Herbivore effects were mainly derived from cattle at the CPER, Mt. Azuma, the OPAHR on Mt. Kuju and Mt. Aso, from horses at Toi Misaki Point, and from half-tamed deer (Cervus nippon) at Nara Park and Miyajima Island.

2. The main objective of the present study was to demonstrate to what extent herbivores correlate with two physiological function systems in C3 and C4 graminoids. The hypothesis investigated was: the abundance of C3 and C4 graminoids is dependent on direct herbivore influence, and also on indirect influences brought about by a process of micro-environmental modification caused by herbivores, such as that in water resources and irradiance, which are physiologically advantageous or disadvantageous to C3 and C4 plants.

3. The importance values of C3 and C4 graminoids were expressed as summed dominace ratio (SDR), relative importance value (SDR'), cumulative value for C3 and C4 graminoids (C3- and C4-SDR'), the number of C3 and C4 graminoid species, and

index value (C3- or C4-SDR' multiplied by the number of C3 or C4 graminoids species respectively).

4. To examine the indirect influence (in the relationship among herbivore - abiotic factors - vegetational aspects), the soil properties: bulk density, maximum water holding capacity (MWHC), moisture percentage (MP), water content ratio (WCR), soil organic matter (carbon and nitrogen content) and soil hardness were measured. Sampling for vegetation and soils was done along an ecological cline, from the upland to the lowland of the hillslope where those factors listed above exhibited sequential alternations. This procedure was repeated in differently grazed pastures (heavy, moderate, light and non-grazing) and different exclosure systems (inside and outside the fence).

5. The results were:

(1) As a function of grazing intensity, using discrete nominal variables (from heavy to non-grazing), the importance of C4 graminoids markedly increased and that of C3 graminoids generally declined.

(2) Studies in the exclosure regime excluding the intensive deer grazing in Nara Park also showed similar trends: tolerance of C4 graminoid and vulnerable traits of C3 graminoids. The extent of grazing effects depends on the exclosure condition - open or closed - with or without canopies. However, the results on Miyajima Island were not distinct in terms of responses of C3 and C4 graminoids to the

grazing.

(3) C3 and C4 importance values responded to the ecological gradient in progressive or retrogressive succession, which were expressed as a replacement of a *Zoysia japonica* and a *Miscanthus sinensis* type community, and were attributed to the different grazing intensities. This also suggests that the abrupt increase in light intensity and temperature caused by the removal of the canopy (*Miscanthus sinensis*) influenced the competitive relationship between C3 and C4 graminoids.

(4) There was a close relationship between the abundance of the C3, C4 graminoids and topographical features of the hillslope (the upland, the mid-slope and the lowland), which regulate the spatial use by herbivores, indicating that the distributional difference of C3 and C4 graminoids along the hillslope is largely due to the discriminative herbivore use of the pasture.

(5) Simple regression techniques were used to define the relationships between soil properties and C3, C4 graminoid distribution. The importance of C3 and C4 graminoids showed significant correlations mostly with soil properties, especially water-related factors and bulk density. This suggests that the physiological functions of those two types of graminoids responded to these soil factors.

(6) Herbivore activity, such as grazing, trampling and resting on the ground, altered the soil condition.

Differences in soil bulk density, hardness and space structure were distinct among the differently grazed areas.

6. The evidences listed above support the hypothesis that herbivores influence C3 and C4 graminoid competition: directly with grazing which stimulates tolerant and intolerant characteristics of C3 and C4 graminoids, and indirectly with modified soil condition and light intensity, which fit or do not fit the physiological traits of C3 and C4 species.

7. The fact that these trends occurred consistently over all the study areas regardless of major climate differences and herbivore type suggests that the herbivore is a primary regulator in the competition between the C3 and C4 graminoids. However, if the grazing pressure upon the vegetation is extremely high as seen in herbaceous communities on Miyajima Island, the relations of herbivores and C3 and C4 graminoid distribution are indistinctive.

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