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On Relationship between Maximum Standing Crop and Species Density in the Herbaceous Vegetation of West Central Korea

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韓半島 中西部 草本植生에 있어서의 最大現存量과 種密度와의 관계에 대하여

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ABSTRACT

To test whether the Grime's model on relationship between maximum standing crop plus litter (350~750 g/m²) and species density (10~30/0.25 m²) fit well or not, a total of 52 samples, with 4 replicate plots (0.5 m x 0.5 m each) per sample, was collected from various forests, grass lands and coastal salt marshes in midwestern part of central Korean peninsula from September to October in 1982.

The result agrees well with the model for grass lands and salt marshes, that is, shape of curve for the maximum standing crop (minus litter) against species density indicates normal distribution. The number of species was 11 for the grassland and 7 for the salt marshes within the range of 300 g to 700 g per square meter for the maximum standing crop.

In forest stands, however, as the maximum standing crop of herbs increased the species density decreased. The Grime's model does not seem to fit with the results on forest stands of this study. It is examined further the relationships among the maximum standing crop, species density and eleven soil properties, and the possible cause of this discrepancy was disscussed.

INTRODUCTION

To elucidate phenomena of distribution and abundance of herbaceous vascular plant populations on terrestrial habitat, various quantitative studies such as association between and/or among species and horizontal distributional pattern of individual plant species,

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physiological studies on the range of tolerance of plant species and manipulative field plot studies as well as multivariate analysis of plant communities have been carried out by ecologists (Grieg-Smith, 1964; Etherington, 1975; Banister, 1976; Gauch, 1982).

Grime (1979) presented his unifying concept on the subject in terms of competition, stress and disturbance as a fundamental planning and direction of operation governing the distribution of plant species. With this assumption Al-Mufti, Sydes, Furness, Grime and Band (1977) suggested a general quantitative model on the relationship between maximum standing crop plus litter and species-density of herbs, which is based on the data from fourteen sites in England.

It is quite reasonable that dominance, stress and disturbance of plant species may act singly or together to restrict in one way or another for some species to establish in areas dominated by competitor, stress tolerant or ruderal according to Grime (1979). In the general model a corridor of high species density with about 10~30 herb species was observed from the range of 350~750 g of maximum standing crop plus litter per square meter. In the range, maximum niche-differentiation may be expected, thus maximum species density may be observed provided that there exist enough opportunities of ingress of suitable species. In other words, to predict the herbaceous species number, all one has to do are to determine the maximum standing crop plus litter and to assess the opportunity of ingress of plant species. The amount of maximum standing crop plus litter is dependent upon interaction among three processes: dominance, stress and disturbance provided that there exist opportunities of ingress of plant species and enough time for niche differentiation. Therefore, operative definitions of the three processes are necessary prerequisite for further understanding on the fundamental aspect of plant micro-distribution.

The dominance and stress are expected from the sites with high fertility and with low fertility respectively. Disturbance is far more difficult to define than fertility. Because to define disturbance it is required to have long term careful observation and elaboration of objective scheme of description in terms of integrative and quantitative means on the observed results.

With this in view, it is tentatively aimed firstly to test whether the model fits the herbaceous vegetation or not, secondly to correlate between maximum standing crop and physical environmental properties, and thirdly to correlate between species density and physical environmental factors in the central Korean peninsula.

MATERIALS AND METHODS

General procedure. Within west central part of Korean peninsula, attempt was made to collect vascular plant samples from habitats, which are as diverse as possible. At each habitat, sampling sites were selected from fairly uniform topography, physiognomy and disturbance. Extremely isolated areas from major vegetation by highway, large human settlement, and big city were excluded from this sampling. Amounts of litters among sites were highly variable because mowing, grazing, trampling and artificial fire-

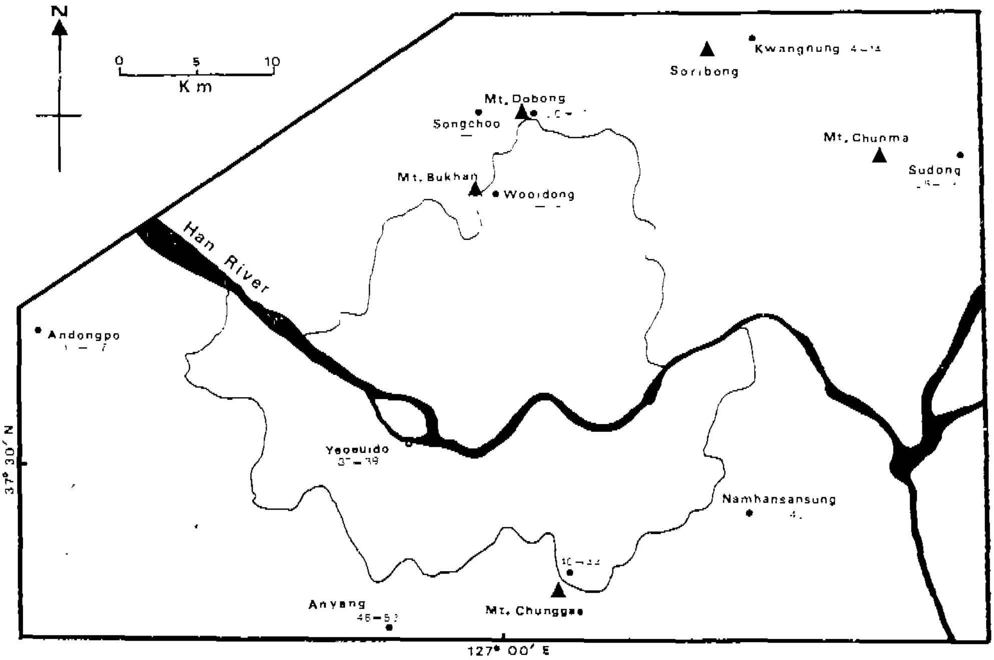

Fig. 1. Schematic map indicating the location of sampling sites.

setting are very extensive, frequent and variable. Therefore, the amount of litters was excluded from this sampling to minimize possible large errors derived from the variation. To obtatin maximum standing crop, samples were collected from the end of September to the end of October in 1982. Mosses were excluded from this study because they were very minor and very variable contributor to the vegetation around the study sites.

Sites. The fifty two sites are located within mid-western part of Korean peninsula (Fig. 1). This region originally belongs to summer green forest (broad leaved deciduous forest). Except well conserved areas, most parts of the region are occupied by secondary forests, mainly *Pinus densiflora* stand. The fifty two sites are located at the edges, insides, and outsides of summer green forests (mainly oaks), of coniferous stands (pines and larch), various grass lands, waste disposal areas from household, river sides, and salt marshes. In selecting the sites vegetation of recent origin was not necessarily excluded (Table 1).

Climate. The climate of Kwangnug, the eastern area of the region has the following characteristics: mean January temperature, 2.0 °C; mean August temperature, 15.9 °C; mean annual precipitation, 1245 mm (Oh, 1959), and the climate of Inchon, the western area of the region has the following characteristics: −3.7 °C; 25.0 °C; and 1127 mm respectively (Oh, 1979).

Sampling and laboratory procedure. At each site four 0.25 m^2 quadrats were set, and herbaceous plants were clipped at the soil surface to obtain replicated samples within rather small areas of vegetation (Grime, 1973). With each sample, number of species was

Table 1. Some characteristics of the sites investigated

Site and the numbers	Average species density/ 0.25m²	Maximm standing crop (gr·dry wt./m²)	Representative species
1. Songchoo; Under deciduous forest	6.75	21.16	*Carex siderosticta, Smilax oldhami, Disporum smilacinum* var. *album*
2. Ditto; Open grass land	9.25	394.48	*Calamagrostis arundinacea, Festuca ovina* var. *vulgaris, Miscanthus sinensis* var. *pupurascens*
3. Ditto; Riverside bank	4.25	293.83	*Persicaria Hydropiper* var. *vulgaris, Persicaria Thumbergii* var. *coreana, Artemisia asiatica*
4. Kwangnung; Under *Abies holophylla* forest	7.50	26.88	*Carex siderosticta, Disporum smilacinum* var. *album, Polygonatum japonicum*
5. Ditto; Edge of *Abies holophylla* forest	8.25	46.13	*Potentilla fragarioides* var. *typica, Impatiens Textori, Commelina communis*
6. Ditto; Under deciduous forest	5.75	16.35	*Syneilesis palmata, Disporum smilacinum* var. *album, Polygonatum japonicum*
7. Ditto; Edge of deciduous forest	6.25	44.84	*Carex lanceolata, Disporum smilacinum* var. *album, Polygonatum japonicum*
8. Ditto; Under deciduous forest	8.00	33.26	*Viola mandshurica, Carex siderosticta, Polygonatum japonicum*
9. Ditto; Edge of deciduous forest	9.00	24.59	*Potentilla fragarioides* var. *typica, Disporum similacinum* var. *album, Polygonatum japonicum*
10. Ditto; Under *Pinus koraiensis* forest	7.00	52.58	*Ligularia ·Fischeri, Carex siderosticta, Smilax nipponica*
11. Ditto; Edge of *Pinus koraiensis* forest	10.25	52.34	*Manispermum dahuricum, Potentilla fragarioides* var. *typica, Oplismenus undulatifolius*
12. Ditto; Under *Larix Kaempferi* forest	9.75	30.06	*Manispermum dahuricum, Potentilla Freyniana, Carex siderosticta*
13. Ditto; Edge of *Larix Kaempferi* forest	7.25	101.67	*Persicaria Hydropiper* var. *vulgaris, Viola mandshurica, Adenocaulon adhaerescens*
14. Ditto; Under *Pinus densiflora* forest	6.25	151.60	*Potentilla, fragarioides* var. *typica, Carex lanceolata Miscanthus sinensis* var. *purpurascens*
15. Andongpo; Mixed grass land	5	250	*Salicornia herbacea, Suaeda japonica, Plantago yezomaritima*
16. Ditto; *Phragmites longivalvis* community	2	1147	*Phragmites longivalvis*
17. Ditto; Mixed grass land	7	656	*Carex scabrifolia, Phragmites longivalvis, Zoysia sinica*
18. Ditto; Ditto	4	76	*Salicornia herbacea, Suaeda japonica, Plantago yezomaritina*
19. Ditto; *Suaeda japonica* community	1	260.64	*Suaeda japonica*
20. Ditto; *Salicornia herbacea* community	5	273.76	*Salicornia herbacea, Artemisia scogaria, Aster Trioplium*
21. Ditto; *Triglochin maritimum* community	1	817.7	*Triglochin maritimum*

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22. Andongpo; *Carex scabrifolia community*	5.25	244.8	*Plantago yezomaritina, Artemisia scogaria, Carex scabrifolia*
23. Ditto; Ditto	3.5	778.9	*Artemisia scogaria, Carex scabrifolia, Phragmites longivalvis*
24. Ditto; *Suaeda glauca* community	2.75	1094.31	*Suaeda glauca, Suaeda japonica, Plantago yezomaritima*
25. Ditto; *Eragrostis ferrugainea* community	4.25	515.32	*Calamargostis Epigeios, Eragrostis ferrugainea, Setaria lutescens*
26. Ditto; Mixed grass land	5.00	309.98	*Salicornia herbacea, Plantago yezomaritima, Aster Tripolium*
27. Ditto; Ditto	4.50	527.32	*Salicornia herbacea, Suaeda japonica, Plantago yezomaritima*
28. Sudong; Under *Larix Kaempferi* forest	7.75	40.78	*Potentilla fragarioides* var. *typica, Ligularia Fischeri, Calamagrostis arundinacea* var. *sciurioides*
29. Ditto; Open grass land	11.75	216.09	*Astilbe chinensis* var. *typica, Impatiens Textori, Atractylodes lyrata*
30. Mt. Dobong; Open grass land	4.00	373.04	*Carex lanceolata, Miscanthus sinensis* var. *purpurascens, Spodiopogen sibiricus*
31. Ditto; Under deciduous forest	5.25	30.74	*Ainsliaea acerifolia, Smilax nipponica, Disporum smilacinum* var. *album*
32. Ditto; Ditto	6.50	51.25	*Thalictrum aquilegifolium* var. *japonica, Carex lanceolata, Smilax nipponica*
33. Wooidong; Open grass land (road side)	8.50	769.36	*Kochia scoparia. Digitaria sanguinalis* var. *cilialis, Arundinella* spp.
34. Ditto; Waste disposal area (house hold)	7.50	684.52	*Kochia scoparia, Arundinella* spp., *Digitaria sanguinalis, Setaria Viridis*
35. Ditto; Open grass land (trench side)	8.50	394.72	*Persicaria Hydropiper* var. *vulgaris, Amaranthus mangostanus, Solanum vulgare*
36. Ditto; Open grass land	11.25	489.51	*Viola mandshuria, Oenothera odorata, Setaria viridis*
37. Yeoeuido; Along river side	7.25	581.45	*Phragmites longivalvis. Acorus asiaticus*
38. Ditto; Ditto	6.75	674.69	*Plantago asiatica, Acorus asiaticus, Phragmites longivalvis*
39. Ditto; Ditto	9.50	347.37	*Atriplex* spp., *Trifolium repens, Plantago asiatica*
40. Mt. Chunggae; Rice paddy (fallow)	8.25	554.45	*Cyperus* spp., *Arundinella* spp.
41. Ditto; Open grass land	1.00	2982.92	*Miscanthus sinensis* var. *purpurascens*
42. Ditto; Along crop land	5.50	371.09	*Artemisia keiskeana, Arundinella* spp., *Setarica viridis*
43. Ditto; Under black locust-*Pinus densiflora* forest	4.75	83.50	*Thalictrum aquilegifolium* var. *japonica, Aster scaber, Carex lanceolata*
44. Ditto; Edge of black locust-*Pinus densiflora* forest	5.00	282.67	*Lysimachia barystachys, Potentilla fragarioides* var. *typica, Carex lanceolata*
45. Namhansansung; Under oak forest	5.25	116.07	*Sanguisorba cornea, Carex lanceolata, Festuca ovina* var. *vulgaris*
46. Anyang; Under pine and oak mixed forest	5.50	148.72	*Carex lanceolata, Festuca ovina* var. *vulgaris, Miscanthus sinensis* var. *purpurascens*
47. Ditto; Edge of tomb (mound)	4.00	306.20	*Carex lanceolata, Miscanthus sinensis* var. *purpurascens*

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48. Anyang; Under pine and oak mixed	5.00	320.70	*Potentilla fragarioides* var. *typica*, *Porphyroscias decursiva*, *Miscanthus sinensis* var. *purpurascens*
49. Ditto; River side	4.67	902.23	*Peucedanum terebinthaceum*, *Miscanthus sinensis* var. *purpurascens*
50. Ditto; Under oak forest	3.75	120.73	*Carex lanceolata*, *Festuca ovina* var. *vulgaris*, *Miscanthus sinensis* var. *purpurascens*
51. Ditto; Rail-way bank	5.25	466.80	*Artemisia asiatica*, *Digitaria sanguinalis* var. *ciliatis*, *Setaria viridis*
52. Ditto; Open grass land	7.50	269.85	*Trifolium repens*, *Erigeron canadensis*, *Setaria viridis*

determined and the material was dried in a oven at 80 °C for 72 hr prior to weighing.

Five replicate measurements for soil depth and soil compressibility were made, and 3 soil cores were also taken with soil sleeve at each site. The soils were dried at room temperature, and passed through 2 mm soil sieve for the determination of soil miosture, saturation capacity, pore space and soil pH. For pH determination the air dried soil and distilled water were mixed at the ratio of 1:2 by weight. Before the determination of exchangeable K, Ca, and Na, the soil was treated with pH 7.0 ammonium acetate, and the amounts were determined by flame-photometer. The amount of easily soluble P was determined by spectrophotometer (Bray, 1948). For the determination of loss on ignition and total nitrogen the air dried soil was passed through 0.5 mm soil sieve. The loss on ignition was measured after drying 4 hr period at 450 °C in electric muffle furnace. The amount of total nitrogen was determined by micro-Kjeldahl method.

RESULTS AND DISCUSSION

Relationship between maximum standing crop and species density

Forest community. An unexpected tendency was that as the amount of maximum standing crop (MSC) increased the member of species decreased in the forest community (Fig. 2). In a well protected summer green forest (sites 6 and 32) the MSC amounted to 50 g/m^2 and the species density was 5～6/0.25 m^2. In slightly disturbed site and well protected reforested areas (sites 1, 4, 8, 10, 12 and 28) the amount of MSC was similar to the protected summer green forest but the species densities were 7 to 11 per 0.25 m^2. In slightly disturbed areas (sites 43, 44, 45, 46, 48 and 50) the MSC was slightly greater than these areas, but the species density of the disturbed areas was only 5 per 0.25 m^2. Within the forest communities (sites 4, 6, 8, 10 and 43) the MSC and the species density were higher than those of the edge of the forest communities (sites 5, 7, 9, 11 and 44).

It was inferred that the relation between MSC and species density was significantly negative ($r=-0.585$, $p<0.01$) in the herbaceous layer under forest communities as a whole. As it appeares in Fig. 2, no positive relationship between MSC and species density was observed, that is, the curve of the MSC against species density for the forest community was not bell shaped but showed only a half of normal curve. It is

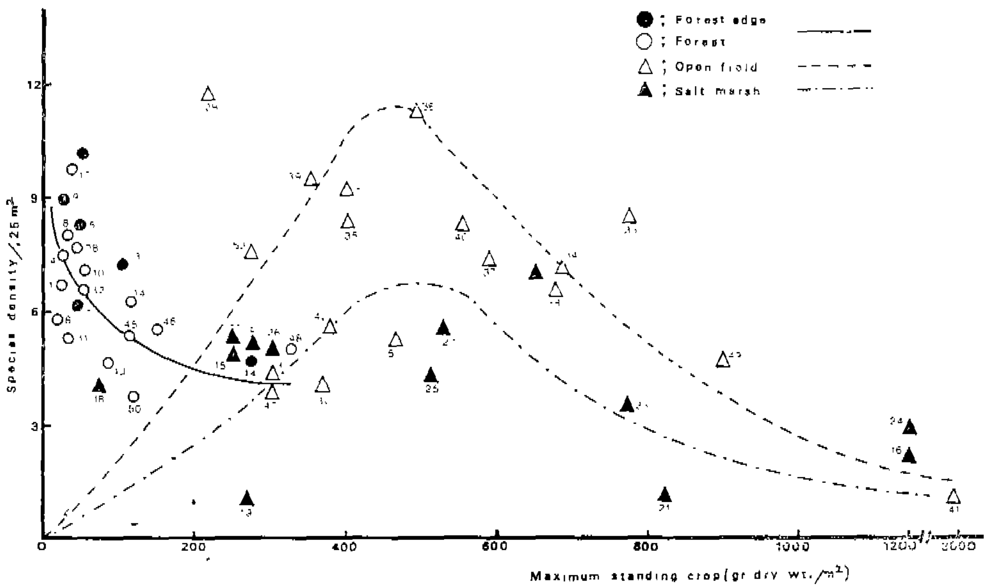

Fig. 2. The relationship between maximum standing crop and average species density of herb, at fifty-two sites.

surmised that the samples taken in this study probably did not include those from extremely disturbed and/or sterile sites or there might not exist really such extreme sites in forest community in this region. It is of interest to note again that apparently intensively disturbed sites (43, 44, 45, 46, 48 and 50) have higher MSC and lower species density than the less disturbed sites (1, 4, 8, 10, 11 and 12) while the latter had lower MSC and higher species density than the former.

The curve of species density against MSC for forest community (Fig. 2) does not agree with the model by Al-Mufti *et al.* (1977). This maybe due to the difference in estimation of MSC in this study with that of Al-Mufti's procedure, that is, in this study litter was not included during sampling of MSC.

Grassland and coastal salt marsh. In these sites it was observed the definite tendency that as the amount of MSC increased up to 400~600 g/m² species density also increased to 11~12/0.25 m² and further increase of MSC resulted in decrease of species density (Fig. 2). This agrees relatively well with the Grime's thesis, even though the shape of "corridor" was not quite similar with that of Grime's (1979). The sites 3, 42, 47 and 51 were from relatively recently reclaimed land, around crop field, near a tomb (every year being denuded), and shoulder of railway respectively, which were intensively disturbed every year. If this part of curve appeared to be on lower position, the shape of the curve probably more closely resembled with the left part of Grime's model. The same token applies to the right part of the curve.

In coastal salt marshes the curve appeared to be rather wider than the corridor shape of Grime. The lower species density of this community than that of grass land may be partly explained by the extremely stressfull environment of the sites in general: high salinity, low soil pore space, and low total nitrogen except the sites 16 and 21, where brackish water inundates regularly.

Relationship between MSC and soil properties

In herb layers under forest canopy, of the 11 soil properties studied maximum field capacity, pore space, loss on ignition and total nitrogen showed significant negative correlation with MSC, that is, as general fertility increased the MSC decreased. This might have occurred from the result of reduced light intensity over herb layer under forest canopy, and the reduced light probably indirectly limited mineral and water resource allocation to the herb layer species (Table 2).

Table 2. Correlation coefficients between maximum standing crop and soil properties and averages of soil properties at 49 sites in west-central region of Korea

	Forest, n=20		Grass land, n=18		Coastal salt marsh, n=11		Total, n=49	
	Average	*r*	Average	*r*	Average	*r*	Average	*r*
Depth of Soil (cm)	31.62	−.221	32.79	−.155	50.00		36.24	.036
Soil Compressibility (kg/cm^2)	.512	.211	.834	−.033				
Maximum Field Capacity (%)	77.95	−.418*	60.54	.234	56.25	.400	66.69	−.189
Pore Space (%)	68.88	−.401*	40.29	.173	53.82	.053	54.99	−.293**
Soil pH (Lab.)	5.24	−.183	6.01	−.352	7.11	.053	5.95	.122
Loss on Ignition (%)	13.61	−.557**	6.79	.215	5.31	.243	9.24	−.376***
Easily Soluble Phosphorus (ppm)	9.16	.359	27.15	−.078	72.01	−.320	29.88	.147
Exchangeable Potassium (ppm)	136.78	−.169	150.47	.062	601.82	.363	246.21	.231
Exchangeable Calcium (ppm)	350.04	−.261	396.54	−.158	485.66	.687**	397.57	.038
Exchangeable Sodium (ppm)	12.85	−.247	34.01	−.093	4920.24	−.236	1169.49	.123
Total Nitrogen (%)	.257	−.587***	.112	.318	.092	.278	.163	−.298

*$p<.05$, **$p<.01$, ***$p<.001$

In contrast to forest community, no significant correlation was observed between MSC of grass land and the soil properties. This might have resulted from more intensive and frequent impact of trampling, mowing, grazing and fire setting on the grass land than those on forest community. Because of the stronger diverse disruptive effect on grass land than to that on forest land, it was considered that the over all differences among soil properties could not possibly be detected. This gives some reasons which explains the different shape of the curves between the forest community and the grass land.

Table 3. Correlation coefficients between species density and soil properties and averages of soil properties at 49 sites in west-central region of Korea

	Forest, n=21		Grass land, n=17				Coastal salt marsh, n=11			
			Left side, n=9		Right side, n=8		Left side, n=5		Right side, n=6	
	Average	*r*	Average	*r*	Average	*r*	Average	*r*	Average	*r*
Depth of Soil (cm)	31.62	−.066	30.85	−.224	36.29	.522	50.00		50.00	
Soil Compressibility (kg/cm²)	.51	.169	1.00	.384	.58	.010				
Maximum Field Capacity (%)	77.95	.345	54.99	.156	69.28	.180	56.97	.538	55.84	−.351
Pore Space (%)	68.88	.375	36.61	.143	46.08	.198	53.90	.949*	53.77	.171
Soil pH (Lab.)	5.25	.349	6.11	.107	5.84	.475	7.16	−.962**	7.10	−.060
Loss on Ignition (%)	13.61	.187	6.57	−.043	7.13	−.134	5.22	.838	5.37	−.102
Easily Soluble Phosphorus (ppm)	9.16	.271	22.98	−.047	33.70	.446	81.89	−.788	66.37	−.379
Exchangeable Postassium (ppm)	136.78	.330	143.73	.083	161.07	.319	590.50	.735	608.29	−.659
Exchangeable Calcium (ppm)	350.04	.595***	360.75	.316	452.79	.274	371.00	.596	551.19	−.375
Exchangeable Sodium (ppm)	12.85	.132	29.64	.395	40.88	.361	5693.30	−.075	4276.1	−.678
Total Nitrogen (%)	.257	.640***	.096	−.154	.136	−.022	.100	.770	.087	−.131

$^*p<.05$, $^{**}p<.01$, $^{***}p<.001$

Relationship between species density and soil properties

Forest Community. Of the 11 soil properties studied, except soil depth, most of them seemed to show positive correlation with species density, expecially the amount of exchangeable Ca and total N showed significant positive correlation (Table 3). This seems to be contradictory with Grime's thesis that competitive site (fertile site) may not allow to establish many species, that is, not lead to high species density. It is a reasonable idea that the general increase of fertility may lead to favor the competitive species. It might have happened that my data were not sufficiently collected from the sites equivalent to left half of the corridor of the model, that is, from these sites with heavy stress and with intensive disturbance in forest community.

Grass land. As mentioned earlier for the grass land community as a whole the curve showing relationship between MSC and species density indicates normal distribution (Fig. 2). To examine statistically this tendency, the area of normal curve was divided into two equal parts by drawing perpendicular line from the peak to MSC axis (X-axis). Henceforth the equal parts be designated as left side and right side. Correlation analysis between the species density and the soil properties were made separately for each part. No general tendency was obtainable from the correlation analyses for the grass land. For the salt marsh community, however, the correlation analysis for lift side-sites appeared to be positive but for the right side it showed negative tendency in general with the exception of soil pH. Even though these were not significant statistically this tendency seems to indicate implicitly that the number of species increases as soil properties improves up to a certain stage, but beyond the stage the higher soil fertility rather acts adversely to the establishment of new species in the salt marsh.

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摘　　要

最大現存量이 350～750 g/m²일 때 種密度가 10～30/0.25 m²에 다다른다고 하는 Grime의 모델이 中西部韓半島草本植生에 대하여도 適用되는지를 알아보기 위하여 자종 森林草地, 일반 草地 및 海邊鹽濕地에서 1982年 9月에서 10月 사이에 總 52個의 最大 現存量標本을 수집하였다. 각 標本은 4개의 方形區(0.5×0.5 m)를 설치 刈取했다. 草地(非森林)와 海邊鹽濕地에서는 Grime의 model과 近似한 결과를 얻었다. 즉 最大 現存量 300～700 g에서 種密度의 最高値, 7～11을 얻었다. 그러나 森林內草地에서는 最大現存量이 增加함에 따라 種密度는 계속 減少하였다. 이는 Grime의 model과는 不合致된다. 이들 現象을 보다 살펴 보기 위하여 最大現存量, 種密度 및 11가지 土壤要因들 사이의 相互 관계를 分析하고 그러한 差異의 원인을 논의했다.

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