Classification of Calcicoles and Calcifuges on the Basis of the Ratio of Soluble to Insoluble Ca²⁺ and Mg²⁺ in the Leaves

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可溶性・不溶性 Ca²⁺과 Mg²⁺ 比에 의한 好石灰 및 嫌石灰植物의 分類

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ABSTRACT

In order to classify calcicoles and calcifuges within plant communities occurring on limestone and granite soils in Chungbuk Province, Korea, soil properties, constancy for all species by presence or absence, and ratios of soluble to insoluble Ca²⁺ and Mg²⁺ were investigated. In the limestone soils, soil pH values and Ca²⁺ and Mg²⁺ content, ranging 7.26~7.48, 5.32~7.37 mg Ca²⁺/g and $0.42 \sim 0.62$ mg Mg²⁺/g, respectively, were higher than those in the granite soil with pH 5.76, 1.03 mg Ca²⁺/g and 0.24 mg Mg²⁺/g. Species with high constancy in the 5 communities were classified into three groups; species group A (29~36% of total number of species) was composed of species occurring preferably on the limestone soil but not on the granite soil; group B (6%) chiefly occurring on the granite soil; group C (16-24%) is commonly distributed throughout both soils. Ratios of soluble to insoluble Ca2+ and Mg2+ ranged from 0.1 to 81.3 in the group A, 0.2 to 0.8 in the group B and 0.2 to 8.7 in the group C. Species within each group can be divided into two groups based on the values of the ratio, below or above 1.0. Consequently, each of the group A and C was classified again into two groups; the group A1 and C1 with the ratio of above 1.0 and the group A2 and C2 with below 1.0 but the ratio could not further subdivide the group B. From these results it was proposed that plants of the group A1 were termed as obligate calcicoles, the group B as obligate calcifuges, the group C1 as facultative calcicoles, the group C2 as facultative calcifuges and the group A2 as avoiding calcifuges.

INTRODUCTION

Limestone soils are higher in pH and in Ca2+ content and once known to occur in drier

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and warmer than nonlimestone ones (Salisbury, 1920; Rorison and Robinson, 1984; Jeffrey, 1987). The vegetation of the limestone and the surrounding nonlimestone areas exhibit a striking contrast in the abundance of common species and also in the occurrence of other species (Whittaker and Niering, 1968; Lee and Oh, 1970; Marrs and Proctor, 1978; Gauld and Robertson, 1985; Rzedowski, 1986; Druce and Wiliams, 1989). Lee and Oh (1970) reported be 33 taxa of calcicoles (15%) out of 227 taxa of the limestone flora of Todam, which is located close to this study area.

Calcicoles growing on limestone soil are considerably so more selective in the uptake of ions that they may contain a low net amount of Ca²⁺ in their tissue than calcifuges do (Jefferies and Willis, 1964). Calcicoles contain high content of water soluble Ca²⁺ existing as intracellular Ca²⁺ and malate form, whereas calcifuges normally contain low content of water insoluble Ca²⁺ existing as calcium-precipitating compounds, mainly Ca oxalate. Ratio of soluble cations to insoluble divalent cations in the tissue, therefore, has been used as a criterion to classify calcicoles and calcifuges (Horak and Kinzel, 1971; Kinzel, 1983).

In addition, whereas calcicoles tolerate high Ca content, calcifuges reveal poor performance and chlorosis owing to Ca-toxicity (Jefferies and Willis, 1964; Cooper, 1976; Marrs and Bannister, 1978a; Chang and Mok, 1981; Anderson, 1982; Hanson, 1984).

The purpose of this study is to elucidate chemical properties of the soil of limestone and granite and to classify species into calcicoles and calcifuges, on the basis of the ratios of water soluble to insoluble divalent cations by means of foliar analysis, within plant communities occurring on the limestone and the granite soils formed broadly in Chungbuk Province, Korea,

MATERIALS AND METHODS

Study Area

Materials used for the analyses of vegetation, soils and leaves were obtained from limestone area at Maepo-myun, Tanyang-gun as well as from granite area at Gumseung-myun, Chewon-gun, Chungbuk Province, where both areas were 7.5Km apart from each other towards north-east (Fig. 1). Samplings for communities of *Quercus variabilis*, *Q. dentata*, *Thuja orientalis* and *Pinus densiflora* were carried out in the limestone area.

Sampling and Grouping of Species

Plant communities, on the basis of dominant species of tree layer, were subjectively selected from the stand with a relatively homogeneous physiognomy. Presence or absence for all species were tallied within $10 \,\mathrm{m} \times 10 \,\mathrm{m}$ quadrat in each stand. Samplings were carried out on June to July, 1989. Constancy of species was calculated from the species table and constancy classes were sorted out on the intervals of 20%; species with constancy of

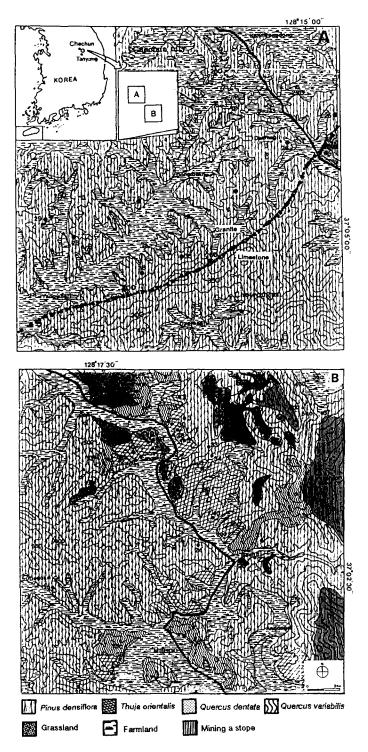


Fig. 1. Vegetation maps showing the study sites selected to investigate the structure of communities A; granite area, B; limestone area, Points nearby numerals indicate sampling sites.

 $1 \sim 20\%$, $21 \sim 40\%$, $41 \sim 60\%$, $61 \sim 80\%$ and $81 \sim 100\%$ were designated as class I, II, III, IV and V, respectively (Mueller-Dombois and Ellenberg, 1974). A species group included species with constancy class of above IV. Particularly, species which reported as the limestone indicators by Lee and Oh (1970) such as *Neillia uyekii* and *Diarthron linifolium* even if constancy class of species was below IV in the limestone communities, were also included in the species group.

Chemical Analyses

For foliar analyses, recently matured leaves of limestone plants and the granite plants were collected from the corresponding limestone and granite communities at the end of May, 1990, dried at 80°C for 48 h. and then ground to powder to pass through a 1 mm sieve with a micromill (Janke and Kunkel, model MFCS1). To determine soluble cations K⁺, Mg²⁺, and Ca²⁺, extract was prepared by the following procedure: the powder of 0.2 g DM was soaked into 20 ml of dist. water for 24 h, stirred for 30 min. and then filtered through Watmann No. 44 paper (Kinzel, 1969; Horak and Kinzel, 1971). To determine total cations, another extract was prepared by acidic digestion with 0.2 g DM of the same material after the procedure of Allen *et al.* (1986). Content of various cations were determined from these extracts by atomic absorption spectrophotometer (Model-901). Difference between content of the total cations and of the soluble cations was to regard as water insoluble cations. For soil physico-chemical analyses, soils were collected from the corresponding plant communities and the analyses were carried out by the procedures of Kim *et al.* (1990).

RESULTS

Soil Properties

Soil pH values ranging $7.26 \sim 7.48$ in the limestone soils were higher than that in the granite soil with pH 5.76. Ca²⁺ content of the limestone soil with $5.32 \sim 7$. $37 \, \text{mg Ca}^{2+} / \text{g}$ soil, was $5 \sim 7$ folds of that of the granite soil with $1.03 \, \text{mg Ca}^{2+} / \text{g}$ (Table 1). Content of Mg²⁺ or K⁺ in the limestone soil ranging $0.42 \sim 0.61 \, \text{mg Mg}^{2+} / \text{g}$ or $0.39 \sim 0.62 \, \text{mg K}^+ / \text{g}$, also was larger than that in the granite soil with $0.24 \, \text{mg Mg}^{2+} / \text{g}$ or $0.28 \, \text{mg K}^+ / \text{g}$. The largest amount of total cations was contained in Q. variabilis community soil compared with the soil of the other three limestone communities, but only one fourth or one sixth of them in the limestone soils were contained in P. densiflora community of the granite soil. Ratios of monovalent K to divalents Ca plus Mg were $0.07 \sim 0.09$ in the limestone soils and 0.22 in the granite soil, and therefore, the difference between the two was $2 \sim 3 \, \text{folds}$.

Species Group by Constancy Class

Species with high constancy in the 5 communities investigated were classified into three groups; species group A was composed of species occurring preferably on the lime-

	Co		Granite				
Soil factors	Community -	Quercus variabilis	Quercus dentata	Thuja orientalis	Pinus densiflora	Pinus densiflora	
pН		7.48	7.48	7.48	7.48	5.76	
		± 0.34	± 0.26	± 0.40	± 0.50	± 0.35	
Calcium(mg/g)		7.37	5.32	5.36	5.57	1.03	
		± 0.18	± 0.57	± 0.23	± 0.33	± 0.12	
Magnesium(mg/g)		0.61	0.43	0.50	0.42	0.24	
		± 0.08	± 0.12	± 0.07	± 0.10	± 0.05	
Potassium(mg/g)		0.62	0.39	0.51	0.49	0.28	
		± 0.03	± 0.02	± 0.05	± 0.07	± 0.04	
Total cation		8.60	6.14	6.37	6.48	1.55	
K/Ca+Mg		0.08	0.07	0.09	0.08	0.22	

Table 1. Physicochemical properties of soil of different communities on the limestone and granite areas.

stone soil but not on the granite soil; species group B occurring only on the granite soil with the exception for several rare species on limestone one; species of the group C were commonly distributed throughout on both soils (Table 2). The group A was consisted of 29 species (26%) out of 110 species in Q. variabilis community, 30 species (30%) of 101 species in Q. dentata community, 31 species (36%) of 87 species in T. orientalis community, 29 species (23%) of 128 species in P. densiflora community of the limestone soils. In contrast, group A was composed of only 6 rare species (6%) of 94 species in P. densiflora community of the granite soil.

The group B was made up of 6 species (6%) with high constancy out of 94 speciess in P. densiflora community in the granite soil but in the limestone soil only 2 rare species (2%) out of 128 species in the same community as well as none or 2 species (1%) in the other three communities. The group C was composed of 21 species (16~24%) out of 87-128 species for the five communities both in the limestone and granite soils.

Calcicoles and Calcifuges Classified by the Ratio of Divalent Cations.

In comparisons between content of water soluble cations, Ca²⁺ and Mg²⁺, and insoluble cations, Ca²⁺ and Mg²⁺, in the leaves of the species group A such as *Abelia coreana* and *Scabiosa mansenensis* and of the species such as *Rhododendron mucronulatum* and *Melampyrum roseum*, the former contained much more soluble cations than insoluble ones, especially in Ca²⁺ content, but the reverse was true in the latter (Fig. 2). Such experimental data for many species accumulated in our lab showed similar tendency.

Water soluble K^+ content in the leaves ranged $3.8 \sim 43.6 \,\mathrm{mg} \; K^+ / \mathrm{g} \; \mathrm{DM}$ in all the species groups (Table 3). Particularly large K^+ content, above $30 \,\mathrm{mg} \; K^+ / \mathrm{g} \; \mathrm{DM}$, were found in *Thalictrum filamentosum*, *Dioscorea batatas* and *Viola variegata* growing on the limestone soil.

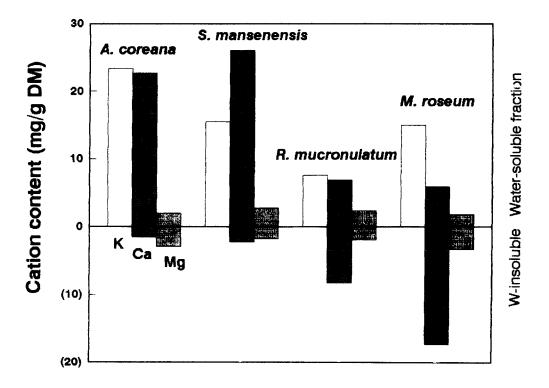


Fig. 2. Comparison of cation content (mg/g DM) in the leaves of species group A such as *Abelia coreana* and *Scabiosa mansenensis* with in those of species group B such as *Rhododendron mucronulatum* and *Melampyrum roserm*. Species group A contains more water soluble Ca than water insoluble one but species group B contains large content of insoluble Ca.

These plants, known as potasium plants (Horak and Kinzel, 1971), belonged to the group A and C though they occurred on the limestone soils. Specifically low K^+ content, approximately $3.8 \sim 9.2 \, \text{mg} \ K^+ / \text{g} \ DM$, was found in dominant species of the limestone communities such as $Q.\ variabilis,\ Q.\ dentata,\ T.\ orientalis$ and $P.\ densiflora$.

Jefferies and Willis (1964) found that K⁺ content of the leaves of a typical calcifuges was less than that of typical calcicoles

Water soluble Ca²⁺ content in the leaves ranged 1.2~32.6 mg Ca²⁺/g DM in the whole species (Table 3). The soluble Ca²⁺ content was larger in the groups A1 and C1 than in the group B. Large soluble Ca²⁺ content, above 20 mg Ca²⁺/g DM, was found in species associated closely with the limestone communities such as A. coreana, S. mansenensis (see Fig. 2) and Lithospermum arvense belonging to the group A and Dictamnus dasycarpus, Clematis mandshurica, Rubia cordifolia var. pratensis, Indigofera kirilowii belonging to the group C. Water soluble Mg²⁺ content in the leaves ranged 0.5~7.7 mg Mg²⁺/g DM (Table 3). As described above the status of each soluble cation varied independently of the other cations in the different species, Ratios of soluble monovalent, K⁺ to soluble divalents,

Table 2. Constancy table of different communities on the limestone area and the granite area

		Li ————	mestone		Granite
	Quercus variabilis	Quercus dentata	Thuja orientalis	Pinus densiflora	Pinus densiflord
Group A					
Spiraea chinensis	V	V	V	V	
Isodon inflexus	V	V	V.	N	
Rhamnus davurica	I IV	V	V	V	I
Lonicera japonica Dioscorea batatas	V	V V	V M	IV V	
Euonymus alatus	ľ	v	II	Ϋ́	
Ulmus macrocarpa	l v	Ň	Ÿ	Ň	
Securinega suffruticosa	. IV	V	II	V	
Patrinia rupestris	III	V	V	II	
Thalictrum filamentosum		V	<u>v</u> ,	V	Ι
Euphorbia pekinensis		V	11	N	
Isachne globosa	N T	11	V	II	
Lithospermum arvense	I I	V V	II II	IV I	
Pyrus ussuriensis Thuja orientalis	I	Ī	w V	İ	
Rhapontica uniflora	I II	П	Ň	v	
Asparagus oligoclonos	lπ	IV	II	Ϋ́	I
Quercus variabilis	Ϊ́	Ï	Ï	,	Î
Galium kinuta	ľ	Ñ	Ī	IV	*
Sophora flavescens	IV	П	I	īV	I
taackia amurensis	į IV	II	IV	I	
Abelia taihyoni	ĺ	IV	IV	II Ì	
Rhus chinensis	Ш	I	${f N}$	11	I
Themeda triandra	_	_			
var. japonica	Į II	I	I V	I	
Buxaus microphylla		W	*		
var. coreana	IV T	II	Ι	Į	
Platycarya strobilacea	I II	IV IV	II II	I	
Scabiosa mansenensis Abelia coreana	1 11	IV IV	I I	I	
Viburnum carlesii	I	14	Ī	N	
Diarthron linifolium	Î	I	Ī	.,	
Neillia uyekii	Ī	Ī	Ī	I	
Group B				······································	
Rhododendron mucronulat	um				V
Melampyrum roseum					V
Quercus mongolica		I		I	V
Quercus serrata			I	I	V
Pulsatilla koreana					IV
Rhus trichocarpa		•			IV .
Group C					
Carex lanceolata	V	V	V	V	V
Clematis mandshurica	j V	V	V	V	m j
Quercus dentata	V	V	V	V	IV
Cocculus trilobus) V	V	V	V	Ш
Spodiopogon cotulifer	V	V	V	V.	IV
Arundinella hirta	I	V	V	IV	V
Viola variegata	IV T	V V	V	I	I
Lespedeza cyrtobotrya Miscanthus sinensis		V	N V	V M	N N
Pinus densiflora	I I	Ī	<u>V</u>	W V	V
Juniperus rigida	<u> </u>	V V	I	ľ	v I
Smilax sieboldii	IV	Ň	IV	V	N N
Indigofera kirilowii	Ï	I	Ï	Ĭ	v
Leibnitzia anandria	İÏ	I	Ň	Ň	ν̈́
Pueraria thunbergiana	ĺv	Ī	Ï	Ï	ň
Atractylodes japonica	Ň	Ī	Ï	Ň	ıı i
Celastrus orbiculatus	īV		Ī	īV	Ī
Rubia cordifolia					Í
var. pratensis	l N	IV	I	II	I
Dictamnus dasycarpus	IV.	I	<u>IV</u>	II	II j
Fraximus rhynchophylla	Į ĮV	N	Ī	I	П
Zanthoxylum pipericum	I	I	I	N	V
Total number of species	110	101	87	128	94

Table 3. Cation concentrations (mg/g DM) of the species selected from each community

	S	Water coluble	:	Soluble K+	Wat insol	er uble	Divalent w-sol		Total cation
Species	K+	Ca ²⁺	Mg2+	Ca ²⁺ +Mg ²	+ Ca2+	Mg2+	Insol	Insol-C	Ca ²⁺
Obligate Calcicole	s	(Gr	oup	A1)					
Galium kinuta	10.2	21.1	3.3	0.4	0.1	0.3	81.3	211.0	34.7
Isachne globosa	17.6	7.3	1.9	1.9	0.4	0.5	10.2	18.3	27.7
Euphorbia pekinensis	•	11.0	2.8	1.2	1.2	0.8	6.9	9.2	31.9
Scabiosa mansenensis	1	26.0	2.7	0.5	2.3	1.8	6.8	11.3	48.3
Abelia coreana	7	22.6	1.9	1.0	1.6	3.0	5.3	14.1	52.4
Sophora flavescens	1	16.3	1.9	0.4	1.2	2.5	4.9 4.3	13.6	28.7 48.9
Thalictrum filamentosum Patrinia rupestris	19.5	3.1 3.1	2.8 1.9	1.9 1.8	1.4 1.7	1.1 1.5	4.3 3.4	9.4 5.4	33.7
Lithospermum arvense	1	32.6	2.6	1.0	12.7	2.4	2.3	2.7	85.6
Securinega suffruticosa	1	12.1	3.1	1.3	4.3	2.2	2.3	2.8	40.8
Euonymus alatus		10.1	2.4	0.9	4.4	1.2	2.2	2.3	32.4
Maackia amurensis	12.5	16.9	7.7	0.5	10.7	0.4	2.2	1.6	48.1
Asparagus oligoclonos	20.8	12.3	2.4	1.4	4.3	2.6	2.1	2.9	42.4
Pyrus ussuriensis	15.3		2.1	2.1	3.0	0.6	2.0	1.8	26.3
Lonicera japonica	1	10.9	4.1	1.0	4.1	3.5	1.7	2.7	30.6
Diarthron linifolium	l .	11.4	2.4	1.3	6.0	2.8	1.6	1.9	39.9
Themeda triandra var. japonica	9.3		1.9	1.3	2.8	1.7	1.5	1.8	20.7
Viburnum carlesii	13.4 19.0		2.1 2.6	1.2 1.8	5.8 5.5	1.4 1.7	1.5 1.5	1.5 1.5	31.4 37.0
Abelia taihyoni Buxus microphylla var. coreana	5.5		2.0	0.6	7.6	0.9	1.3	1.0	23.9
Rhamnus davurica	13.6		1.7	1.6	6.6	0.9	1.1	1.0	29.4
Avoiding calcifuge									
Quercus variabilis	3.8		1.0	0.4	11.5	3.1	0.6	0.7	27.3
Thuja orientalis	7.4		1.8	1.2	9.1	3.5	0.5	0.5	26.4
Platycarya strobilacea	8.3		1.2	1.1	12.8	1.9	0.5	0.5	30.4
Ulmus macrocarpa	19.1		1.9	3,3	17.8	3.0	0.3	0.2	45.7
Spiraea chinensis	14.1	2.0	1.4	4.1	8.0	1.9	0.3	0.3	27.4
Neillia uyekii	15.1		2.7	1.8	23.8	3.1	0.3	0.2	50.5
Rhapontica uniflora	26.6		1.9	4.2	23.1	1.8	0.3	0.2	53.8
Rhus chinensis	10.7		2.7	2.7	14.3	2.3	0.2	0.1	31.3
Dioscorea batatas	30.5 22.2			6.4	19.7		0.2	0.1 0.1	57.8 48.3
Isodon inflexus Obligate calcifuge			1.1	7.4 B)	17.3	3.0	0.1	0.1	40.3
	11.6			1.2	9,5	1 77	0.0		32.2
Rhus trichocarpa Rhododendron mucronulatum	7.5		0.9	0.8	8.3	1.7 2.0	0.8 0.7	0.9 0.8	26.9
Melampyrum roseum	14.9		1.8	2.0	17.4	3.4	0.4	0.3	43.3
Pulsatilla koreana	21.0		1.5	5.1	9,2	3.0	0.3	0.3	37.3
Quercus serrata	9.0		1.7	1.4	15.1	1.9	0.3	0.3	32.4
Quercus mongolica	6.2		1.2	2.6	10.6	2.4	0.2	0.1	21.4
Facultative calcic	ole	es ((Gr	oup (C1)				
Dictamnus dasycarpus	17.3	22.4	2.0	0.7	0.6	2.2	8.7	37.3	44.5
Clematis mandshurica		23.1	0.8	0.6	1.9	1.0	8.4	12.1	40.3
Arundinella hirta		14.3	2.2	0.6	0.8	1.4	7.5	17.9	27.1
Rubia cordifolia var. pratensis		29.1	2.1	0.3	2.2	2.5	6.7	13.2	44.3
Indigofera kirilowii		21.2	2.4	0.3	1.0	3.8	4.9	21.2	34.7
Carex lanceolata		13.3	0.5	0.8	4.4	0.4	2.9	3.0	29.7
Lespedeza cyrtobotrya		17.2	2.5	0.6	9.3	1.5	1.8	1.8	41.5
Smilax sieboldii Zanthoxylum pipericum		13.9 13.4	1.2	1.2	6.9	1.4	1.8	2.0	41.7
	·			1.0	6.6	1.7	1.8	2.0	37.0
Facultative calcif				oup (1 ^	~ ^		FA ^
Atracylodes japonica Pinus densiflora	9.2	10.9 2.0	1.3	2.1	11.0	1.6	0.9	1.0	50.2
Spodiopogon cotulifer	13.7		1.5	1.0 1.6	2.0 8.0	0.9 1.6	0.9 0.9	1.0 0.9	14.9 32.1
Leibnitzia anandria	24.0		1.0	3.0	8.1	2.5	0.8	0.9	32.1 42.8
Celastrus orbiculatus		11.8	2.8	0.6	17.3	1.5	0.8	0.9	42.6
Pueraria thunbergiana		10.8	1.8	0.8	15.9	2.4	0.8	0.7	41.4
Cocculus trilobus	17.0		0.5	2.3	9.7	1.4	0.6	0.6	34.8
Miscanthus sinensis	20.8		0.5	2.6	12.8	1.0	0.6	0.6	42.8
Fraxinus rhynchophylla	14.9		0.6	2.9	12.3	2.5	0.4	0.4	34.8
Juniperus rigida	6.8		0.8	1.2	14.8	1.4	0.4	0.3	28.9
Quercus dentata	4.1		2.6	0.8	16.6	2.1	0.3	0.2	28.2
Viola variegata	43.6	1.5	2.5	10.9	16.7	3.0	0.2	0.1	67.3

 Ca^{2+} and Mg^{2+} , ranged $0.4 \sim 7.4$ in the group A, $0.8 \sim 5.1$ in the group B and $0.3 \sim 10.9$ in the group C (Table 3). These ratios revealed a wide range between 8 and 55 folds in the different species.

Water insoluble Ca^{2+} content in the leaves ranged $0.1 \sim 23.8 \,\mathrm{mg}$ Ca^{2+}/g DM (Table 3). Less insoluble Ca^{2+} content below $1.0 \,\mathrm{mg}$ Ca^{2+}/g DM were found in *Galium kinuta* and *Isachne globosa* belonging to the group A which were specifically associated with the limestone communities, and *D. dasycarpus* and *Arundinella hirta* belonging to the group C which consisted of common species in both limestone and granite communities. The plants belonging to the group B contained the large amount, above $8.3 \,\mathrm{mg}$ Ca^{2+}/g DM, of insoluble Ca^{2+} compared with soluble Ca^{2+} . The plants listed as indicators by Lee and Oh (1970), such as *A. coreana*, *A. taihyoni*, *S. mansenensis*, *P. rupestris* and *D. linifolium* belonging to the group A, also contained a fairly small amount of insoluble Ca^{2+} . Insoluble Mg^{2+} content in the leaves ranged $0.3 \sim 5.8 \,\mathrm{mg}$ Mg^{2+}/g DM, which range was fairly narrow.

Total content of cations, including soluble and insoluble, ranged from $15.0 \,\mathrm{mg/g}$ DM for P. densiflora to $85.6 \,\mathrm{mg/g}$ DM for L. arvense. Total content of cations in the leaves from the limestone communities was specifically large in some species such as A. hirta, Q. dentata etc., but rather small in other species such as R. cordifolia var. pratensis, I. kirilowii, P. densiflora etc. (Table 3). These content showed marked variations in different species growing whether on the same soil or on the different soils. Furthermore, in terms of cation content of the group C growing on the limestone or the granite soil, soluble K^+ content of the leaves from the granite soil tended to be larger than those from the limestone soil but the reverse was true in soluble Ca^{2+} (Table 4). Content of insoluble Ca^{2+} tended to increase in the leaves from the limestone soil with the exception of R. cordifolia var. pratensis and I. kirilowii. Criterion for the classification of the species group could be neither the ratio of soluble monovalent to divalent nor the content of total cations because of no specificity in the different species groups.

Finally, ratios of soluble to insoluble divalent cations, $Ca^{2+} + Mg^{2+} / Ca^{2+} + Mg^{2+}$, ranged from 0.1 to 81.3 in the group A, 0.2 to 0.8 in the group B and 0.2 to 8.7 in the group C (Table 3). Intuitively, values of the ratio, either below or above 1.0, sorted out two groups from each species group. Species with ratio of above 1.0 were implied to contain larger content of soluble cations than insoluble ones, and *vice versa*. Species listed in Table 2, therefore, could be distinguished with ratios of above or below 1.0 and then rearranged in the order of the value from large ratio to small one within each species group, as arranged in Table 3.

Consequently, each of the species group A or C was classified again into two groups; the group A1 and C1 with the ratio of above 1.0 and the group A2 and C2 with below 1.0 but never the group B was distinguished with the value of the ratio. In terms of the ratio of soluble Ca^{2+} to insoluble Ca^{2+} , high ratios were also found in the group A1 and C1 but the reverse was true in the groups A2 and C2 as well as in the group B (Table 3).

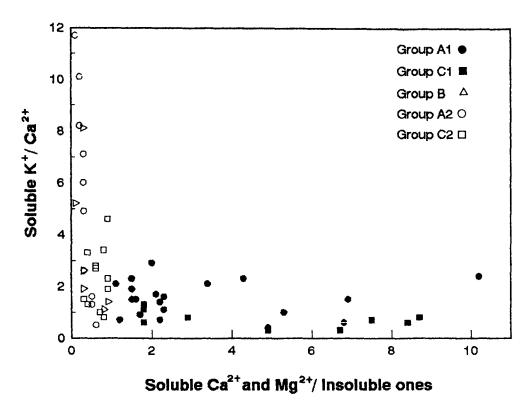


Fig. 3. Relationships between ratios of content of soluble Ca^{2+} and Mg^{2+} to insoluble ones and ratios of content of soluble K^+ to Ca^{2+}

Relationships between ratios of the content of soluble to insoluble Ca²⁺ and Mg²⁺ and ratios of the content of soluble K⁺ to soluble Ca²⁺ were shown in Fig. 3. The species groups were clearly divided into two groups; one was consisted of the groups A1 and C1 which possesed above 1.0 in ratio of soluble to insoluble divalent cations, and the other was consisted of the groups A2, B and C2 with ratios of below 1.0. Furthermore, the latter was divided again on the basis of above or below 4.0 in the ratios of soluble K⁺ to soluble Ca²⁺; species with ratio above 4.0 was designated as potassium plants and those with below 4.0 as oxalate type plants termed by Horak and Kinzel (1971).

In conclusion, from these results it was proposed that the plants of the species group A1 were termed as obligate calcicoles, the group B as obligate calcifuges, the group C1 as facultative calcicoles, the group C2 as facultative calcifuges, and the group A2 as avoiding calcifuges. The reason for designating the group A2 as avoiding calcifuges was that the plants belonging to this group could avoid physiologically converting a large amount of imported external Ca^{2+} to soluble Ca^{2+} and adjusting internal osmotic potential in spite that they always occurred on the limestone soil.

DISCUSSION

Foregoing data on soil properties show that these are large differences in soil pH and Ca content between the soils of the limestone and the granite: in terms of soil pH the former has pH \geq 7 and the latter \leq 6; in terms of total cation content the former is more $5\sim$ 6 folds of the latter, especially large in Ca²⁺ content but not so in Mg²⁺ and K⁺ (Table 1). Grubb *et al.* (1969) pointed out that pH 5 of soil was a critical value above which calcicoles could grow well but below which they could not. Accepting their suggestion even in the granite soil with pH 5.76 in this study site, calcicoles could occur on the place where the soil pH changes with seasons (Kim *et al.*, 1990, 1991). In the limestone soils forming the different plant communities, uniformity of both the soil pH and the cation content is surprising. There are, however, marked variations in cation content absorbed by different species growing on the limestone or the granite soils (Table 3).

The species can be clearly distinguished by means of constancy into three groups on both the limestone and the granite soils regardless of the type of plant communities. The species group A occurring in the limestone communities is composed of $23 \sim 36\%$ of specific species out of whole species but that in the granite community with only 6% of rare species, which percentage values may increase more if the number of study sites increases: the group B is made up of 6% of specific species in the granite community but none or 1% of rare species in the limestone ones: the group C is made up of $16 \sim 24\%$ of common species of both communities. Typical limestone flora are made up of 15% of calcicoles in Korea (Lee and Oh, 1970) and 5% in chalk range of South Irland (Druce and Wiliams, 1989).

These results suggest that plants on the soils of limestone and granite should have specifically evolved into the different species, namely calcicoles and calcifuges, as indicated early by Hope-Simpson (1938) and others (Iljin, 1940; Horak and Kinzel, 1971; Rattenböck, 1978; Kinzel, 1983). Species groups suggest that limestone soil have evolved to be changed the species composition to differ from the granite soil.

In the results of foliar analyses, ratios of soluble monovalent (K^+) to divalents (Ca^{2+} and Mg^{2+}) in the leaves tended to be small in the calcicoles, especially in the facultative calcicoles (group C1) but large in the avoiding (group A2), obligate (B) and facultative (C2) calcifuges, which means that the calcicoles growing on the limestone soil can accumulate much more soluble Ca^{2+} and Mg^{2+} than K^+ with exception of the potassium plants but the reverse is true in the calcifuges growing on the limestone soil because of allowing the maximum K^+ uptake under an optimal Ca^+ content in soil (Table 3 and 4) (Olsen, 1942; Viet, 1944; Jefferies and Willis, 1964; Kinzel, 1983). Probably it is assumed that low productivity of crops of calcifuges on the limestone soil is related to inhibiting metabolism by less K^+ uptake and high free Ca^{2+} in soil. Content of soluble monovalent

 (K^+) in both calcicoles and calcifuges growing on the limestone soil are less than those growing on the granite soil and the reverse is true in the content of soluble divalent (Table 4).

Table 4. The cation concentrations in mg/g DM as soluble, insoluble and total in the leaves of the group C grown on the limestone (L) or on the granite soils (G), and ratio (L/G) of limestone to granite leaves

Species		Water soluble			Water insoluble		Total cation
		K+	Ca ²⁺	Mg ²⁺	Ca ²⁺	Mg ²⁺	
Facultative calcicoles (Gr	oup C1)						
Indigofera kirilowii	L	6.2	21.2	2.4	1.0	3,8	34.7
	G	15.1	21.1	2.7	2.5	3.4	44.9
	L/G	0.4	1.0	0.9	0.4	1.1	0.8
Arundinella hirta	L	9.8	14.3	2.2	0,8	1.4	27.1
	G	11.9	6.5	0.8	0.4	1.1	20.7
	L/G	0.8	2.2	2.8	2.0	1.3	1.3
Rubia cordifolia var.	L	8.4	29.1	2.1	2.2	2.5	44.3
pratensis	G	29.4	5.4	1.2	13,6	2.5	52.1
	L/G	0.3	5.4	1.8	0.2	1.0	0.9
Carex lanceolata	L	11.1	13.3	0.5	4.4	0.4	29.7
	G	16.5	11.7	0.4	2.8	0.9	32.3
	L/G	0.7	1.1	1.3	1.6	0.4	0.9
Facultative calcifuges (Gr	coup C2)						
Pinus densiflora	L	9.2	2.0	0.8	2.0	0.9	14.9
	G	20,5	1.0	0.4	1.2	0.8	24.0
	L/G	0.4	2.0	2.0	1.7	1.1	0.0
Quercus dentata							0.6
Quercus dentata	L	4.1	2,8	2.6	16.6	2.1	28.2
Quercus dentata		4.1 8.7	2.8 2.7	2.6 0.6	16.6 10.4	2.1 1.3	
Quercus dentata	L						28.2
•	L G	8.7	2.7	0.6	10.4	1.3	28.2 23.3
•	L G L/G	8.7 0.5	2.7 1.0	0.6 4.3	10.4 1.6	1.3 1.6	28.2 23.3 1.2
•	L G L/G L	8.7 0.5 9.0	2.7 1.0 11.8	0.6 4.3 2.8	10.4 1.6 17.3	1.3 1.6 1.5	28.2 23.3 1.2 42.4
Celastrus orbiculatus	L G L/G L G	8.7 0.5 9.0 16.8	2.7 1.0 11.8 10.8	0.6 4.3 2.8 0.5	10.4 1.6 17.3 14.1	1.3 1.6 1.5 0.8	28.2 23.3 1.2 42.4 42.9
Celastrus orbiculatus	L G L/G L G L/G	8.7 0.5 9.0 16.8 0.5	2.7 1.0 11.8 10.8 1.1	0.6 4.3 2.8 0.5 5.6	10.4 1.6 17.3 14.1 1.2	1.3 1.6 1.5 0.8 1.9	28.2 23.3 1.2 42.4 42.9 1.0
Celastrus orbiculatus	L G L/G L G L/G L	8.7 0.5 9.0 16.8 0.5 6.8	2.7 1.0 11.8 10.8 1.1 5.1	0.6 4.3 2.8 0.5 5.6 0.8	10.4 1.6 17.3 14.1 1.2 14.8	1.3 1.6 1.5 0.8 1.9 1.4	28.2 23.3 1.2 42.4 42.9 1.0 28.9
Celastrus orbiculatus Iuniperus rigida	L G L/G L G L/G L	8.7 0.5 9.0 16.8 0.5 6.8 10.6	2.7 1.0 11.8 10.8 1.1 5.1 1.5	0.6 4.3 2.8 0.5 5.6 0.8 0.6	10.4 1.6 17.3 14.1 1.2 14.8 11.3	1.3 1.6 1.5 0.8 1.9 1.4	28.2 23.3 1.2 42.4 42.9 1.0 28.9 25.4
Celastrus orbiculatus Iuniperus rigida	L G L/G L G L/G L G	8.7 0.5 9.0 16.8 0.5 6.8 10.6 0.6	2.7 1.0 11.8 10.8 1.1 5.1 1.5 3.4	0.6 4.3 2.8 0.5 5.6 0.8 0.6 1.3	10.4 1.6 17.3 14.1 1.2 14.8 11.3 1.3	1.3 1.6 1.5 0.8 1.9 1.4 1.4	28.2 23.3 1.2 42.4 42.9 1.0 28.9 25.4 1.1
Celastrus orbiculatus Iuniperus rigida	L G L/G L G L/G L G L/G L	8.7 0.5 9.0 16.8 0.5 6.8 10.6 0.6 13.7	2.7 1.0 11.8 10.8 1.1 5.1 1.5 3.4 7.3	0.6 4.3 2.8 0.5 5.6 0.8 0.6 1.3 1.5	10.4 1.6 17.3 14.1 1.2 14.8 11.3 1.3 8.0	1.3 1.6 1.5 0.8 1.9 1.4 1.4 1.0	28.2 23.3 1.2 42.4 42.9 1.0 28.9 25.4 1.1 32.1
Quercus dentata Celastrus orbiculatus Juniperus rigida Spodiopogon cotulifer Miscanthus sinensis	L G L/G L G L/G L G L/G L	8.7 0.5 9.0 16.8 0.5 6.8 10.6 0.6 13.7 14.3	2.7 1.0 11.8 10.8 1.1 5.1 1.5 3.4 7.3 2.6	0.6 4.3 2.8 0.5 5.6 0.8 0.6 1.3 1.5	10.4 1.6 17.3 14.1 1.2 14.8 11.3 1.3 8.0 4.7	1.3 1.6 1.5 0.8 1.9 1.4 1.0 1.6	28.2 23.3 1.2 42.4 42.9 1.0 28.9 25.4 1.1 32.1 23.6
Celastrus orbiculatus Iuniperus rigida Spodiopogon cotulifer	L G L/G L G L/G L G L/G L	8.7 0.5 9.0 16.8 0.5 6.8 10.6 0.6 13.7 14.3 0.9	2.7 1.0 11.8 10.8 1.1 5.1 1.5 3.4 7.3 2.6 2.8	0.6 4.3 2.8 0.5 5.6 0.8 0.6 1.3 1.5 0.5 3.0	10.4 1.6 17.3 14.1 1.2 14.8 11.3 8.0 4.7 1.7	1.3 1.6 1.5 0.8 1.9 1.4 1.4 1.0 1.6 1.5	28.2 23.3 1.2 42.4 42.9 1.0 28.9 25.4 1.1 32.1 23.6 1.4

Insoluble divalents are much more accumulated in the calcifuges including the avoiding, obligate and facultative grown on the limestone soil than in those grown on the granite one, but none of the facultative calcicoles (C1) grown on the limestone soil follow such trends (Table 2 and 4).

Ratio of soluble to insoluble divalent cations can be used as a good criterion to classify the calcicoles and calcifuges in the community. It is surprising, however, that the total cation content in the leaves are similar with each other whichever the obligate and facultative calcicoles or calcifuges grow on either the limestone soil or the granite one (Table 3 and 4), in spite that total cation content of the limestone soils is $4\sim6$ fold larger than that of the granite soil (Table 1). Water insoluble Ca^{2+} content differ largely in the different species within a species group but the insoluble Mg^{2+} does not so. The insoluble Ca^{2+} as well as insoluble Mg^{2+} exists in the apoplast and the vacuoles.

Surplus soluble K⁺ absorbed, when the plants grow on the granite soil (see Table 4), contributes physiologically to the adjustment of the osmotic potential, neutralizes the soluble and macromolecular anions and performs other functions in cytoplasm (Clarkson and Hanson, 1980; Mengel and Kirkby, 1987). Surplus soluble Ca²⁺ taken up, when the calcicoles grow on the limestone soil (see Table 3 and 4), will be incorporated into Ca-malate as counter-ion in the vacuole and adjust themselves ecologically to reduce the osmotic potential to survive in dry limestone habitats (Iljin, 1940; Horak and Kinzel, 1971; Rattenböck, 1978; Clarkson and Hanson, 1980; Hanson, 1984). Surplus insoluble Ca²⁺ and Mg²⁺ absorbed when the calcifuges grow on limestone soil (see Table 3), will be incorporated into Ca or Mg -oxalate, -carbonate and -phosphate, and into various organelles, enzymes and cell walls (Mengel and Kirkby, 1987; Stow, 1989; Gilroy, 1987; Evans *et al.*, 1991).

It is probably assumed that low productivity of crops in the limestone areas is related to inhibiting metabolism by high Ca^{2+} content in the soil. They suggest that the ratios of soluble divalent to monovalent should be $0.28 \, ^{\sim} \, 0.47$ for calcifuges and $0.018 \, ^{\sim} \, 0.024$ for calcicoles.

Content of total cations in the limestone soils is $4\sim6$ fold larger (Table 1) than that in the granite. However, the amounts of total cations in the leaves grown on the limestone soil and on the granite one are almost similar each other with the ratio $0.6\sim1.4$ in the group C1 and group C2 (Table 3).

Horak and Kinzel (1971) have classified plants in respect of their K^+/Ca^{2+} ratio and termed potassium plants containing large amount K^+ but a little free Ca^{2+} . Jefferies and Willis (1964) emphasized that ratio of soluble divalents to monovalents was significant rather than soluble Ca^{2+} alone in influencing plant distribution.

The question is raised why different communities with the corresponding dominant species are formed on the same limestone soil. Practically, *Q. variabilis* belonging to the avoiding calcifuge (group A2) tends to occur at a east facing slope and thick soil, *Q.*

dentata belonging to the facultative calcifuge (group C2) on the a south facing slope and thin soil, *T. orientalis* beonging to the avoiding calcifuge (group A2) on the south-west facing cliff and thin soil and *P. densiflora* belonging to the facultative calcifuge (group C2) on the north facing slope and thick soil, which all dominant species have the attributes of calcifuges in spite that they grow on the limestone soil. The reasons should be sought for the moisture content rather than the Ca²⁺ content in the soils. Experimental evidences on the drought resistance elucidated that *Q. variabilis* withstands drought by covering themselves with dense trichomes, having sparse stomata on leaf abaxial surface and by decreasing leaf water potential slowly after water withdrawal, and *Q. dentata* and *T. orientalis* do with large root/shoot ratio and or small leaf area ratio (Kim, 1990; Kwak and Kim, 1991a, 1991b). Soil moisture in the limestone soil studied, however, is too high to suffer from drought damage (Kim *et al.*, 1990, 1991).

적 요

충북의 석회암토양과 그에 인접한 화강암토양에 분포하는 군락 내의 토양의 특성과 호석회식물 및 혐석회식물의 분류를 위하여 물리화학적 특성, 군락 구성종의 유무에 따른 종의 상재도 조사 및 식물체 잎속의 수용성ㆍ불용성 K⁺, Ca²⁺ 및 Mg²⁺ 합량을 측정하였다.

석회암토양의 pH, Ca²+ 및 Mg²+ 함량, 각각 7.26~7.48, 5.32~7.37 mg Ca²+ /g 및 0.42~0.62 mg Mg²+ /g은 화강암토양의 것, 각각 5.76, 1.03 mg Ca²+ /g 및 0.24 mg Mg²+ /g 보다 높았다. 조사된 5 군락의 종조성으로부터 고상재도의 종을 무리지음으로써 석회암군락에서 고상재도로 출현하는 종군 A (총출현종의 29~36%), 화강암군락에서 고상재도를 갖는 종군 B (6%) 그리고두 지역의 군락에서 공통으로 고상재도를 갖는 종군 C (16~24%)로 구분되었다. 각 종군의 잎속의 불용성 Ca²+과 Mg²+에 대한 수용성 비는 종군 A에서 0.1~81.3, 종군 B에서 0.2~0.8 그리고 종군 C 에서 0.2~8.7 이었다. 각 종의 2가 이온 비를 1 이상 또는 1 이하로 구분한 결과 종군 A 와 종군 C 는 각각 1 이상의 종군 A1과 종군 C1 그리고 1 이하의 종군 A2와 종군 C2로 구분되었고 종군 B는 모두 1.0 이하이었다. 이 결과로 부터 종군 A1에 속하는 식물을 절대호석회식물, 종군 A2를 기괴성협석회식물, 종군 B를 절대협석회식물, 종군 C1을 임의호석회식물 그리고 종군 C2를 임의협석회식물로 분류하게 되었다.

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