Korean J. Ecol. 19(4) : 341~351, 1996

Response of Old-field Plant Community to an Experimental Nitrogen Gradient

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질소 시비 구배에 따른 묵밭의 식물 군집 반응

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ABSTRACT

In order to elucidate the differences in early successional development among similarly aged old-fields having different soil nitrogen (N), caused by the land use history before the abandonment, the response of plant community along an experimental nitrogen gradient (control plot (*N0*), plot *N1* with 5.8g N/m², plot *N2* with 11.7g N/m² and plot *N3* with 23.3g N/m²) was investigated in a five-year-old abandoned field. Although the N content in soil among treatments was similar at the end of the growing season, N concentrations in plant tissue increased with the amount of N supplied. These results suggest that almost all the N contained in N-enriched soil might be absorbed by plants during the growing season after N supply. Vegetation tended to grow vigorously by nitrogen supply, and the standing biomass increased significantly in plots *N1* and *N2*. Species richness of plants, especially of annuals and perennials, was more reduced than the control plot, and the species diversity was also reduced by N supply. The importance value (*IV*) of species by N supply differed in each species along the position on the successional sere: *Artemisia princeps* var. *orientalis* as the dominant species in this old-field decreased slightly; annuals as the earlier successional species decreased clearly along nitrogen gradients; *Erigeron annuus* as the earlier successional species and as a strong competitor with *Artemisia princeps* var. *orientalis* had the highest *IV* by small N supply; *Miscanthus sinensis* and *Rubus crataegifolius* as the later successional species increased by large N supply. These results suggest that old-fields with high soil N might show the structural and functional characteristics of the earlier successional stages, but community composition in those old-fields might be changed more quickly from the earlier successional species than the later successional species.

Key words: Nitrogen gradient, Old-field, Productivity, Species diversity, Succession, *Artemisia, Erigeron, Miscanthus, Rubus*

INTRODUCTION

Many studies on the responses of old-field plant community to nutrient enrichment have been carried out because nutrient enrichment experiments in old-field communities provide an opportunity to test several ecological theories for early plant community development (Carson and Barrett 1988, Bakelaar and Odum 1978, Maly and Barrett 1984, Parrish and Bazzaz 1982, Tilman 1984, Tilman 1993, Song 1994). Nitrogen content in soil varies temporally and spatially in early successional old-field plant communities (Lee and Kim 1995, Robertson *et al.* 1988), and competition for nitrogen appears to play an important role in the replacement and persistence of dominant species during succession (Tilman 1985). Recent studies have focused on the response of old-field plant communities to fertilization gradients (Tilman 1987, Wilson and Tilman 1991). By and large, nutrient enrichment appears to invoke high net productivity, strong dominance and low plant species diversity (Maly and Barret 1984, Bakelaar and Odum 1978, Tilman 1993). According to Odum (1969), these structural and functional responses should be characteristics of early successional stages of community development. However, there are some disputes about the response of plant community to nutrient enrichment: some researchers have insisted upon the progressive succession (Mellinger and McNaughton 1975, Bakelaar and Odum 1978, Tilman 1990), but others upon retrogressive one (Hyder and Barrett 1986, Maly and Barrett 1984, Carson and Barrett 1988). Tilman (1987) reported that through a fertilization gradient experiment the early successional species reached peak abundance by low nutrient supply, whereas the later successional species gained dominance by high nutrient supply. These studies raised the questions to the effect of nutrient enrichment on plant community and to the relationship between nutrient enrichment and rate of succession.

This study addresses the following questions in order to elucidate the difference of early successional development among old-fields with similar ages having the different soil N content, caused by the land use history before the abandonment: 1) Does nitrogen enrichment affect the structural and functional characteristics of plant commnunity? 2) Does nitrogen enrichment alter the dominance of the earlier or later successional species? 3) Does nitrogen enrichment affect the rate of succession?

METHODS

This study was conducted in a five-year-old abandoned field, located in Chinbu-myon, Pyongchang-gun, Kangwon-do, Korea. This field had not been cultivated since 1989 (the last crop was corn), and was dominated by *Artemisia princeps* var. *orientalis*, *Erigeron annuus*, *Oenothera odorata*, *Miscanthus sinensis* and *Rubus crataegifolius*. The local climate is cold-temperate as described by Lee (1995). The top soil properties at 5 cm layer of the field were shown as 7.6% organic matter, 2.32mg/g total nitrogen (T-N) and pH 5.0.

Forty 2m×2m square plots were placed permanently according to Latin square design for nitrogen fertilization. Urea with 46% N (commercial fertilizer) was sprayed by hand on the field on May 1st, 1993 with 4 different levels as follows: Control plot (N_0) without urea, plot N_1 with 5.8g N/m², plot N_2 with 11.7g N/m², plot N_3 with 23.3g N/m². Each plot had 10 replicates.

Soil samples were collected at the top soil, of which moisture content was determined by fresh weight basis (%) and T-N content by micro-Kjeldahl method (Jackson 1967). Relative light intensity was measured at 0.1 and 1.0m above ground with a quantum sensor (Cat. No. 550) of quantum meter (Ramsden 550).

Floristic composition, species density, height of vegetation, coverage and frequency of plant species were recorded within 1m×1m quadrat in the center of the plot to minimize edge effect on Sept. 15th, 1993. All plants were clipped at the ground level, brought to the laboratory, and then dried at 80℃ until constant weight. From the vegetation data, relative coverage (*RC*), relative frequency (*RF*), relative biomass (*RB*) and importance value ($IV = RC + RF + RB$) were calculated. Species richness and diversity indices of community were calculated based on the *IV* obtained from ten replicate plots. Dominance − diversity curve was drawn after Whittaker (1965, 1972). Indices of dominance, diversity and evenness were expressed by Simpson's (C), Shannon-Wiener's (H') and Pielou's (J'), as follows:

$$C = (n_i / N)^2,\ H' = -\Sigma(n_i / N)(ln\ (n_i / N)),\ \text{and}\ J' = H' / ln\ S$$

where n_i is the *IV* of species i, N is the sum of the *IV* for all species and S is the number of species.

ANOVA and Duncan's Multiple Range Test were used to determine significant differences in all components.

RESULTS

Abiotic environment

Soil moisture content during the growing season (Jul. − Aug.) ranged from 16% to 20% in all the plots and showed the lowest of 16% in $N1$ plot, which might be enough for plant growth (Fig. 1). Content of T-N in soil ranged from 2.9 to 3.1 mg N/g soil and they were not significantly different among the plots (Fig. 1). Relative light intensity (RLI) was significantly less in plots $N1$, $N2$ and $N3$ than that in plot $N0$ both at 0.1 and 1.0 m height above the ground, and those in plots $N1$ and $N2$ were less than that in plot $N3$ at 1.0 m height (Fig. 1).

Nitrogen concentration in tissue of major plant species

Mean N concentrations in tissue of five major species were significantly enhanced as N treatment increased (Table 1). Stem N concentrations in plots $N1$, $N2$ and $N3$ were as much as 1.9, 3.6 and 3.4 folds of that of plot $N0$ for *Erigeron annuus*, and as much as 1.3, 1.6 and 2.1 folds for *Artemisia princeps* var. *orientalis*, respectively.

Leaf N concentration in plot $N0$ was the highest in *Rubus crataegifolius* and the lowest in

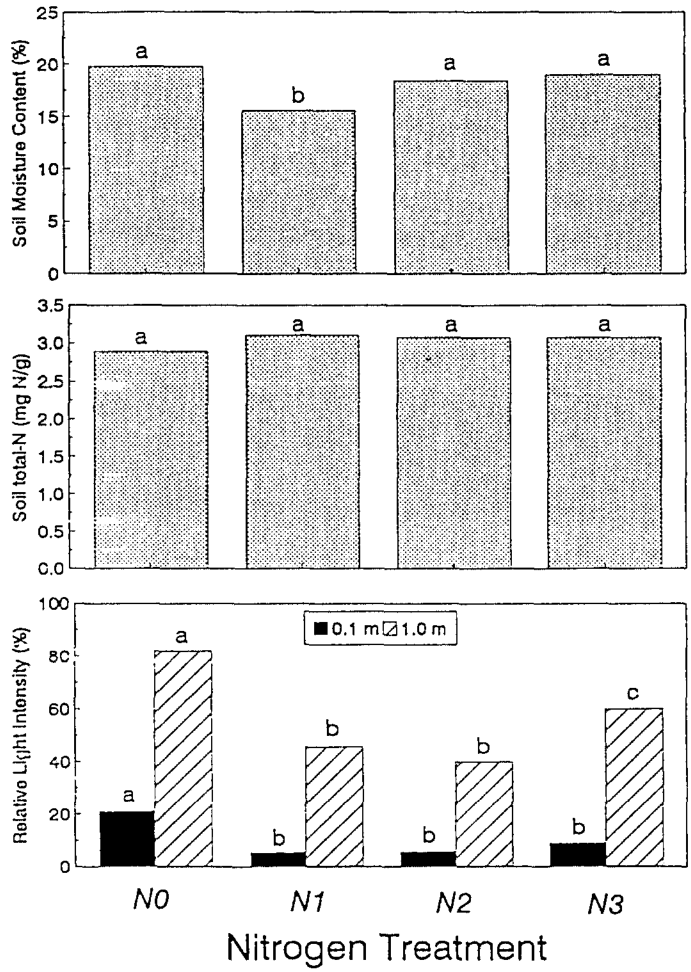

Fig. 1. Responses of soil moisture content, soil nitrogen and relative light intensity (10cm and 1m above ground level) to an experimental nitrogen gradient. Mean values with the same small letter on the same shaped bar are not significantly different (Duncan's Multiple Range Test, $P > 0.05$).

Miscanthus sinensis. Leaf N concentrations in *Artemisia princeps* var. *orientalis* and *Oenothera odorata* as forb were higher than that in *Miscanthus sinensis* as grass. Increasing effect of N in leaf tissue by N supply was more conspicuous in *Oenothera odorata* and *Miscanthus sinensis* than in *Artemisia princeps* var. *orientalis*. Ratio of N concentration of leaf to stem in *Artemisia* decreased with increasing N treatment, *i.e.* 2.9, 2.7, 2.7 and 2.3 in plots N_0, N_1, N_2 and N_3, respectively (Table 1).

Standing biomass, coverage and height of vegetation

Coverage and height of vegetation increased significantly by nitrogen supply, though

Table 1. Mean N concentration (mg N / g DM) in tissue of major species grown at different levels of N supply

Species	Organ	Nitrogen treatment			
		N0	*N1*	*N2*	*N3*
Erigeron annuus	stems	4.0[a]	7.7[b]	14.3[c]	13.5[c]
Artemisia princeps	stems	6.5[a]	8.7[a]	10.4[a]	13.9[b]
var. *orientalis*	leaves	19.1[a]	23.1[a]	28.5[b]	31.3[b]
Oenothera odorata	leaves	17.4[a]	26.1[b]	33.9[c]	33.3[c]
Miscanthus sinensis	leaves	8.6[a]	14.8[b]	19.8[c]	18.5[c]
Rubus crataegifolius	leaves	22.6[a]	24.1[a]	31.2[b]	34.9[c]

N0: control, *N1*: 5.8g N / m^2, *N2*: 11.7g N / m^2, *N3*: 23.3g N / m^2.
Mean values with the same letter within the organs of each species are not significantly different (Duncan's multiple test, P>.05).

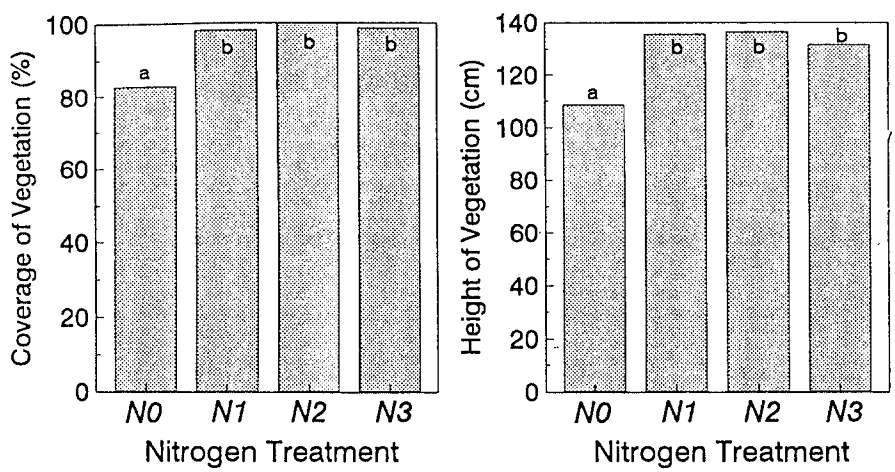

Fig. 2. Responses of ground coverage and height of vegetation to an experimental nitrogen gradient. Mean bar values with the same small letter are not significantly different (Duncan's Multiple Range Test, P>.05).

they was not significantly different among N treatment levels (Fig. 2).

Standing biomass of each species did not differ significantly among N treatment levels due to the spatial variation among samples of the same treatment (Table 2). Standing biomass of *Erigeron annuus, Artemisia princeps* var. *orientalis* and *Oenothera odorata,* the earlier successional species, were the largest in plot *N1* with small N supply, while those of *Rubus crataegifolius* and *Miscanthus sinensis,* the later successional species in this early old-field succession were the largest in plots *N2* and *N3* with medium and large N supplies (Table 2). The sum of standing biomass for all the species was significantly higher in plots *N1* and *N2* than that in plot *N0*, and those in plots *N0*, *N1*, *N2* and *N3* were 349, 541, 530 and 393 g DM / m^2 (100 : 155 : 152 : 112), respectively (Table 2).

Table 2. Mean standing biomass (g DM /m^2) of major species in relation to nitrogen supply

Species	Nitrogen treatment			
	N0	*N1*	*N2*	*N3*
Erigeron annuus	42.7^a	111.7^a	65.1^a	28.5^a
Artemisia princeps var. *orientalis*	227.5^a	283.7^a	246.7^a	180.3^a
Oenothera odorata	29.9^a	77.9^a	56.3^a	56.3^a
Miscanthus sinensis	25.4^a	31.2^a	35.0^a	41.1^a
Rubus crataegifolius	20.7^a	26.4^a	115.3^a	71.3^a
Others	2.8^a	9.8^a	11.8^a	15.1^a
Total	349.0^a	540.7^b	530.2^b	392.6^{ab}

N0: control, *N1*: 5.8g N /m^2, *N2*: 11.7g N /m^2, *N3*: 23.3g N /m^2.
Mean values with the same letter within the organs of each species are not significantly different (Duncan's multiple test, $P>0.05$).

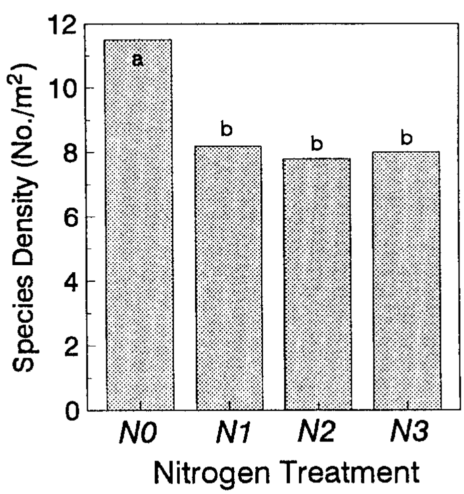

Fig. 3. Responses of species density to an experimental nitrogen gradient. Mean bar values with the same small letter are not significantly different (Duncan's Multiple Range Test, $P>0.05$).

Species diversity

Species density (No. /m^2) was dramatically reduced by N supply, and those were 11.5, 8.2, 7.8 and 8.0 species /m^2 (100:73:68:71) in plots *N0*, *N1*, *N2* and *N3*, respectively (Fig. 3).

Species richness of annuals and perennials gradually decreased, but that of woody species increased slightly as N treatment increased (Table 3). Species richness decreased clearly as N treatment increased (Table 3). Simpson's dominance (C) and Shannon-Wiener's diversity (H') indices decreased slightly, while Pielou's evenness (J') index increased slightly as N treatment increased (Table 3).

The dominance-diversity curves along N supply levels was shown in Fig. 4. Although percentage of *IV* of *Artemisia princeps* var. *orientalis*, the dominant species in this old-field, decreased slightly by N supply, the upper portions of the curve appeared to be in similar shape in all the plots. The lower portion of the curve, however, tended to be considerably steep as N treatment increased, and it may be due to the extinction of many annuals and perennials (Fig. 4).

Table 3. Species richness and diversity indices in relation to nitrogen treatment

	Nitrogen treatment			
	N0	*N1*	*N2*	*N3*
Species richness				
annuals	14	10	7	5
biennials	2	2	2	2
perennials	14	11	9	8
shrubs	7	6	8	8
total	37	29	26	23
Simpson's dominance (*C*)	0.20	0.20	0.19	0.18
Pielou's evenness (*J'*)	0.64	0.64	0.65	0.68
Shannon-Wiener's diversity (*H'*)	2.32	2.15	2.14	2.15

N0: control, *N1*: 5.8g N/m^2, *N2*: 11.7g N/m^2, *N3*: 23.3g N/m^2.

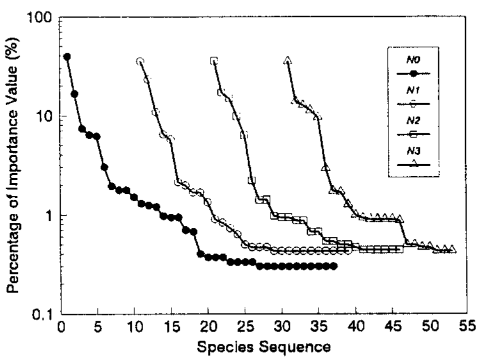

Fig. 4. Responses of dominance-diversity curve to an experimental nitrogen gradient.

Importance values of the major species

Importance values (*IV*) of annuals were reduced dramatically and those of perennials slightly. *IV* of biennials, however, was enhanced considerably by small N supply and those of shrubs by large N supply (Table 4). The *IV* of *Persicaria* spp. and *Artemisia* spp. were reduced, while that of *Oenothera odorata* was enhanced by N supply. The *IV* of *Erigeron annuus* showed the greatest value in plot *N1*, while those of *Miscanthus sinensis* and *Rubus crataegifolius* in plots *N2* or *N3* (Table 4).

DISCUSSION

Although nitrogen content in soil did not increase, N concentrations in tissues of major species increased with the amount of N supplied (Fig. 1, Table 1). These results suggest that almost all the N supplied onto soil might be absorbed by plants during the growing season after N supply. Parrish and Bazzaz (1982) reported that the earlier successional species had not only higher N concentration per unit dry matter but also more marked elevations in tissue N concentration along soil nitrogen gradients than the later successional species did. As N supply increased, N uptake by stem was more enhanced in *Erigeron annuus,* the earlier successional species, than in *Artemisia princeps* var. *orientalis,* the later successional species, and N uptake by leaf was more enhanced in *Artemisia princeps* var. *orientalis* and *Oenothera odorata,* the earlier successional species, than in *Rubus*

Table 4. Importance value (*IV*) of selected species[a] in relation to nitrogen treatment

Life-form	Nitrogen treatment			
	N0	*N1*	*N2*	*N3*
Annuals	31.6	23.2	13.3	15.7
Persicaria fauriei	5.3	5.0	1.3	2.7
Persicaria blumei	5.3	5.0	4.2	2.7
Pinellia ternata	0.9	2.7	1.3	5.2
Other annuals	20.1	10.5	6.5	5.1
Biennials	71.5	102.0	80.2	75.7
Erigeron annuus	49.4	69.3	50.8	41.7
Oenothera odorata	22.1	32.7	29.4	34.0
Perennials	162.8	140.2	142.5	151.7
Artemisia princeps var. *orientalis*	118.1	105.7	106.7	105.7
Artemisia feddei	9.0	6.4	6.6	8.8
Miscanthus sinensis	18.5	17.3	18.9	29.0
Other perennials	17.2	10.8	10.3	8.2
Shrubs	34.3	33.3	61.4	57.0
Rubus crataegifolius	19.2	19.4	44.7	38.2
Boehmeria spicata	5.8	1.3	1.5	1.4
Spiraea prunifolia var. *simpliciflora*	3.9	5.9	2.8	2.8
Salix hulteni		4.0	2.6	5.1
Other woody species	5.4	6.7	12.4	14.6

[a] Selected species having the *IV*>5 for at least one treatment plot.

crataegifolius, the later successional species (Table 1). Leaf N concentration of forbs such as *Artemisia princeps* var. *orientalis* and *Oenothera odorata* was much higher than that of grass such as *Miscanthus sinensis*, while N uptake effect by N supply was more remarkable in grasses than in forbs (Table 1).

Odum (1969) postulated that as a community develops, net primary productivity should decline but species diversity should increase, and suggested that community with soil nutrient supply represent the characteristics of the earlier successional stages, *i.e.* low species diversity as structural characteristic and high net primary productivity as functional characteristic, because internal stabilizing mechanism of community be disturbed by soil nutrient supply. Many researchers reported that by soil nutrient supply net primary productivity was enhanced and species diversity was reduced (Bakelaar and odum 1978, Carson and Barrett 1988, Hyder and Barrett 1986, Wilson and Tilman 1991).

Vegetation grew vigorously by soil N supply (Fig. 2). The standing biomass increased significantly both in plots *N1* and *N2*, but not in plot *N3*, which would be explained as the unbalance among essential ions by surplus N supply (Table 2). Species richness and species diversity were less in N supplied plots than in plot N_0, especially in annuals and perennials (Figs. 3-4, Table 3). These results were fairly in accordance with the Odum (1969)'s hypothesis. The decrease of species diversity by N supply may be explained both by decreasing gain of new species and by increasing loss of existing species (Tilman 1993). The loss of species along N gradient may result from failure of recruitment after the death of existing individuals. The low availability of light for subcanopy plants in N supply plots might increase mortality and decrease species diversity by excluding slow-growing and/or shade-intolerant species (Goldberg and Miller 1990) (Fig. 1, Table 3).

The *IV* of *Artemisia princeps* var. *orientalis*, the dominant species in this old-field, was slightly reduced by N supply (Table 4). Bakelaar and Odum (1978) observed that relative dominance of *Solidago* sp., the dominant species in eight year-old abandoned field, increased by fertilization, while Song (1994) found that relative dominance of *Miscanthus sinensis*, the dominant species in sixteen year-old abandoned field, decreased but that of *Artemisia princeps* increased by fertilization. *IV* of annuals, which is the earlier successional species, decreased prominently as N supply increased, but that of *Erigeron annuus*, which is the earlier successional species as a biennial and a strong competitor with *Artemisia princeps* var. *orientalis*, increased in plot N_1. Those of *Miscanthus sinensis* and *Rubus crataegifolius*, the later successional species, increased in plots N_2 and/or N_3 (Table 4). Some workers observed that relative dominance of the earlier successional species was enhanced and the rate of old-field succession retarded by continuous nutrient supply (Hyder and Barrett 1986, Maly and Barrett 1984, Carson and Barrett 1988). Other workers, however, found that relative dominance of the later successional species was enhanced by short-term nutrient supply (Mellinger and McNaughton 1975, Bakelaar and Odum 1978). Tilman (1987) found that through a fertilization gradient experiment annuals and short-lived perennials, the earlier successional species, reached the highest abundance by low N supply, whereas long-lived herbaceous and woody species, the later successional species, dominated by high N supply as presented in our results.

It can be concluded that old-fields having high N content in soil among similarly aged old-fields might show lower species diversity and higher productivity, the characteristics of the earlier successinal stages, and faster exchange in species composition from the earlier successional species to the later species through the sere than old-fields having low N in soil.

ACKNOWLEDGMENTS

We thank Mr. I.Y. Choi., Y.B. Ku, K.B. Kim, K.D. Kim and Dr. J.W. Kim working in the Plant Ecology Laboratory of S.N.U. for their helps in field and laboratory throughout this study.

요 약

비슷한 연령의 묵밭간에 방기 전의 질소 시비 전력의 차이가 초기 식생 발달에 미치는 영향을 밝히기 위하여 5년차 묵밭에 질소무처리구 (*N0*), 질소 5.8g N/m^2 처리구 (*N1*), 질소 11.7g N/m^2 처리구 (*N2*) 및 질소 23.3g N/m^2 처리구 (*N3*)의 질소 시비 구배를 처리하여 식물 군집의 반응을 조사하였다. 생육기 말의 토양내 질소함량은 처리구간에 차가 없었으나, 주요 우점식물의 질소 흡수량은 질소 시비 구배에 따라 현저하게 증가하였다. 이 사실은 처리한 대부분의 질소를 식물체가 바로 흡수하였음을 시사한다. 질소 시비에 의해 식생의 식피율, 키 및 식물량은 현저히 증가하였는데, 특히 식물량은 *N1*과 *N2*에서 크게 증가하였다. 종풍부도와 종다양도는 질소시비에 의하여 현저하게 감소하였는데, 특히 1년생식물과 다년생초본의 종수가 더욱 감소하였다. 질소처리에 의한 중요치는 우점종인 쑥에서 질소처리에 의해 약간 낮아졌고, 천이초기종인 1년생식물에서 서서히 낮아졌는데 그 이유는 질소시비가 식물량을 증가시키고 식물량의 증가가 수광량을 감소시키는데 있었다. 천이초기종이며 쑥의 경쟁자인 개망초는 소량의 질소를 시비한 *N1*구에서 최대값을 나타내었고, 천이후기종인 참억새와 산딸기는 다량의 질소를 시비한 *N2*와 *N3*구에서 증가하였다. 이상의 결과는 비슷한 연령의 묵밭중에서 질소함량이 많은 묵밭은 질소함량이 적은 곳보다 종다양도가 낮고 생산성이 높은 천이 초기의 군집 속성을 나타내지만, 군집의 종조성이 천이초기종에서 후기종으로 보다 빠르게 이행하고 있음을 시사한다.

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(*Received May 15, 1996*)