スギ苗の窒素利用過程とそれに対する土壌水分の影響

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論　文

Nitrogen Utilization by Sugi (*Cryptomeria japonica* D. DON) Seedlings and the Influences of Soil Moisture

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AKAMA, Akio: **Nitrogen utilization by sugi (*Cryptomeria japonica* D. DON) seedlings and the influences of soil moisture J. Jpn. For. Soc. 73: 128～134, 1991** One-year-old sugi (*Cryptomeria japonica* D. DON) seedlings were potted in April, ammonium (NH_4 series) and nitrate nitrogen (NO_3 series) were applied separately in July. Soil moisture was controlled under dry or wet conditions. Contents of inorganic nitrogen and free amino-acids were determined for three weeks after the application of nitrogen. Ammonium was not found in the roots with neither series. Ammonium might be assimilated immediately to amino-acids in roots. Nitrate was found in roots with the NO_3 series. A little nitrate nitrogen might be translocated from roots to shoots when nitrate was accumulated in the roots, but most of nitrate was reduced in roots. Large amounts of free amino-acids were found in the roots with the NH_4 series rather than in those with the NO_3 series. In shoots, free amino-acids increased soon after the nitrogen applications in the wet conditions of both series. The increments of amino-acids in shoots continued until the end of the experiment with the NH_4-wet series. Nitrate accumulation in roots with the NO_3 series might show that nitrate reduction is the rate-limiting factor in the process of nitrate utilization. The influences of soil moisture on nitrate reduction rarely were observed under the condition of −0.035 MPa. However, this soil moisture deficit was considered as influencing nitrate absorption, and ammonium absorption or amino-acids translocations from roots to shoots also might be influenced.

赤間亮夫：**スギ苗の窒素利用過程とそれに対する土壌水分の影響　日林誌 73：128～134, 1991**　4月に，1年生のスギ苗をポットに植栽し，7月にアンモニア態（NH_4区）と硝酸態（NO_3区）の窒素を施用し，同時に土壌水分を乾と湿の2区に調整した。窒素施用後，3週間にわたって樹体内の無機態窒素と遊離アミノ酸の濃度を測定した。いずれの処理区においても根の中にはアンモニア態の窒素は検出されず，アンモニア態窒素は吸収と同時にアミノ酸に同化されたと考えられた。NO_3区の根には多くの硝酸態窒素が検出されたが，地上部への移動はわずかであり，大部分は根で還元されると考えられた。地上部の遊離アミノ酸は湿潤区において，窒素施用後速やかに増加し，NH_4-湿潤区ではそれが試験終了まで続いた。根の遊離アミノ酸はNO_3区よりもNH_4区に多く検出された。NO_3区において，根に硝酸態窒素が集積していたことなどから，窒素源が硝酸態の場合，その利用過程においては硝酸還元が律速因子となっていた可能性が考えられる。土壌水分の硝酸還元に対する影響としての，乾燥区における硝酸態窒素の集積は，今回は認められなかった。−0.035 MPa程度の土壌水分状態でも，スギの窒素の吸収は制限されるようであり，さらに根から地上部へのアミノ酸の移動に影響する可能性も考えられた。

I. Introduction

The growth of sugi (*Cryptomeria japonica* D. DON), one of the most important species for reforestation in Japan, is very sensitive to soil moisture and is planted in areas of wet, well-drained conditions. The soil moisture of sugi plantations is approximately between −0.005 MPa and −0.02 MPa (IBARAGI *et al.*, 1956; MASHIMO, 1957).

Soil moisture is considered as influencing the process of nitrogen utilization. There are, however, few studies on the relationship between soil moisture and the nitrogen utilization of trees. MORI *et al.* (1971) studied the influence of soil moisture on the nitrogen metabolism of sugi seedlings, and demonstrated that

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amino-acids' concentrations, especially proline, increased in seedlings transplanted on a dry soil. This increment of proline might not be a primary response of nitrogen metabolism but a protective response in the body of a plant that was transferred into a severely dry condition.

TSUTSUMI (1962) revealed in a hydroponic experiment that sugi grew well at a neutral pH on ammonium nitrogen, grew well at a lower pH on nitrate nitrogen, and that ammonium nitrate was the best as a nitrogen source for sugi. SANADA, and TSUTSUMI (1978), and AKAMA (1986, 1989) revealed that sugi absorbed both ammonium and nitrate nitrogen, although akamatsu (*Pinus densiflora* SIEB. et ZUCC.) absorbed mainly ammonium nitrogen. Hydroponic conditions are different from soil, but these results are considered to be related to the interspecific differences for site adaptabilities that sugi prefers more wet conditions as compared with akamatsu. The fact that soils on the lower parts of slopes contain large amounts of nitrate nitrogen (KATO, 1984 a,b) suggest the relationship between the nitrogen utilization process and the soil-moisture conditions. However, the process of nitrogen utilization in sugi has not been clear to date.

The nitrogen utilization process is considered to be divided into three parts, that is, absorption, assimilation, and translocation. Nitrate reduction is added when the nitrogen source is nitrate. This report covers the process of nitrogen utilization as studied by experiments using the application of different nitrogen forms on sugi seedlings with treatments of different soil-moisture conditions.

II. Materials and Methods

Seedlings (one-year-old) of sugi were transplanted into 1/2,000 a Wagner pots April, in 1985. The soil used was collected from the B-layer of a Light Colored Black Soil (Forest soils division, 1975), which was equivalent to Andosols of the Food and Agriculture Organization's classification. It contained 1.8 % of carbon and 0.15 % of nitrogen including 13 ppm of NH_4-N and 17 ppm of NO_3-N. CEC (cation exchange capacity) was 27 meq/100 g dry soil. Potassium phosphate, monobasic (KH_2PO_4, 2 g/pot), was applied to the soil before transplantation. The experiment was conducted in a greenhouse of our Institute. In the middle of July, the soil conditions of a NH_4 series and a NO_3 series were established by the addition of ammonium sulfate ($(NH_4)_2SO_4$, 4.72 g/pot) and calcium nitrate ($Ca(NO_3)_2 \cdot 4H_2O$, 8.43 g/pot), respectively. Next, the pots were subjected to two different soil-moisture conditions. Grouping was made by the formal differences of inorganic nitrogens and moisture conditions as follows: NH_4-dry, NH_4-wet, NO_3-dry, and NO_3-wet. Six pots with three seedlings per pot were prepared for each series. The relationship between the soil-water potential and the weight of pot was measured with a tensiometer in a preparatory experiment, and the soil-moisture of this study was controlled daily to −0.035 MPa and −0.006 MPa through the weighing of each pot. Weekly samplings were made with six seedlings (two pots) of each series for three weeks after the applications of nitrogen. After samplings, plants were divided into roots and shoots. Each part of six seedlings was mixed well separately. They were immediately freeze-dried and finely ground using a ball mill. Chemical analyses were made of the samples. An extract was prepared by suspending 0.1 g of sample powder in 10 ml of water. The suspensions were left standing for 30 min with occasional stirring. Then they were filtrated with Toyo filter paper (No.6). Ammonium and nitrate nitrogens of the extract were determined by ion chromatography. Another extract was prepared by suspending 0.5 g of sample powder in 10 ml of 80 % ethanol. The suspensions were left standing for 24 h in a refrigerator, and then they were filtrated with Toyo filter paper (No.6). Free amino-acids of the shoots and roots of the extracts were determined by an amino-acid analyzer (JLC-6 AH, JEOL). A combustion method with a CN corder (MT-600, Yanaco) was used for the analysis of total nitrogen. A nitric acid and perchloric acid mixture was used for the digestion of the samples, and the solutions were used for the analyses of metallic elements and phosphorus. Potassium and sodium were determined by flame photometry. Calcium and magnesium were analyzed by atomic absorption spectrophotometry. The molybdenum blue method (MURPHY, and RILEY, 1962) was used for the determination of phosphorus.

III. Results

The pH of the soil changed from 5.7 to 5.9 in the NH_4 series and to 5.6 in the NO_3 series during three weeks of the experimental period. In the soil of each pot of the NH_4 series, approximately 200 ppm of NH_4-N and under 20 ppm of NO_3-N were found, and in the soil of each pot of the NO_3 series, under 20 ppm of NH_4-N and approximately 200 ppm of NO_3-N were found after the nitrogen applications until the end of the experiment. The growth of the seedlings did not show clear differences among the applications of different nitrogen forms and soil moisture conditions. The water potential in the seedling was not measured, but water ratios ((fresh weight−dry weight)/dry weight) of shoots were 2.6 in the dry conditions and 3.0 in the wet conditions on the average at the end of the experiment.

The concentrations of total nitrogen in shoots was larger in wet groups than in dry ones (Fig. 1), and their increments were the greatest in the NH_4-wet series. In roots, the differences of total nitrogen concentrations among the treatments were less than those in shoots (Fig. 2).

Ammonium nitrogen was found more in shoots of the NH_4 series than in those of the NO_3 series (Fig. 3), but it was not found at all in the roots of both series.

The differences of nitrate nitrogen concentrations in shoots among the treatments were not clear, although there was a small increase of the

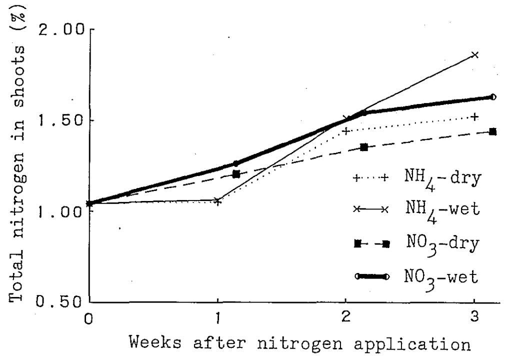

Fig. 1. Changes of total nitrogen concentrations in shoots of NH_4-dry, NH_4-wet, NO_3-dry, and NO_3-wet series

Notes : Concentrations are shown on a dry bases. Weekly samplings were made with six seedlings of each series, but first samplings of the NO_3 series were made on the eighth day after the nitrogen applications.

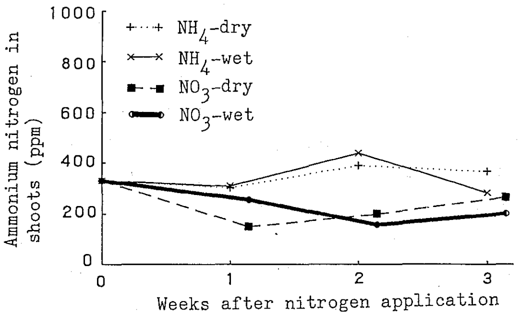

Fig. 3. Changes of ammonium nitrogen concentrations in shoots of NH_4-dry, NH_4-wet, NO_3-dry, and NO_3-wet series

Note : Same as in Fig. 1.

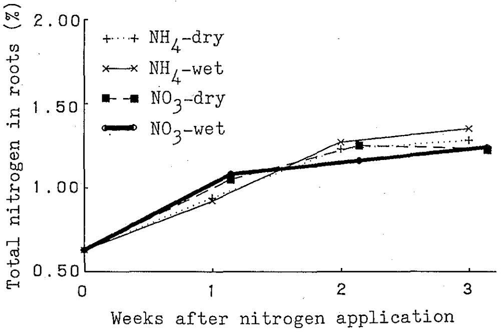

Fig. 2. Changes of total nitrogen concentrations in roots of NH_4-dry, NH_4-wet, NO_3-dry, and NO_3-wet series

Note : Same as in Fig. 1.

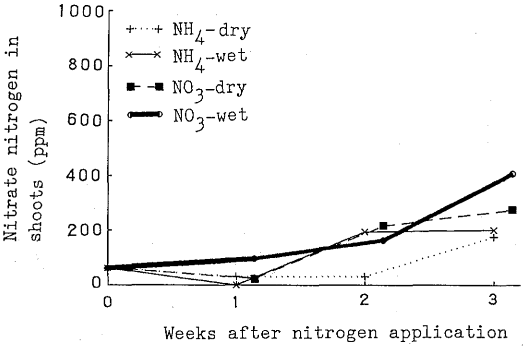

Fig. 4. Changes of nitrate nitrogen concentrations in shoots of NH_4-dry, NH_4-wet, NO_3-dry, and NO_3-wet series

Note : Same as in Fig. 1.

concentrations of the NO_3-wet series (Fig. 4). Nitrate nitrogen in roots of the NO_3 series increased remarkably after the nitrogen applications, and its increments were greater in the wet conditions than in the dry (Fig. 5).

The concentrations of free amino-acids' nitrogen in shoots (Fig. 6) increased soon after the nitrogen applications in the wet conditions of both series. However, the increments of the NO_3-wet series declined through the following two weeks. In the NH_4-wet series, the increments continued until the end of the experiment. These increments in the dry series were less than those in the wet series. Glutamine, proline, and citrulline increased especially in the shoots of the NH_4-wet series (Table 1).

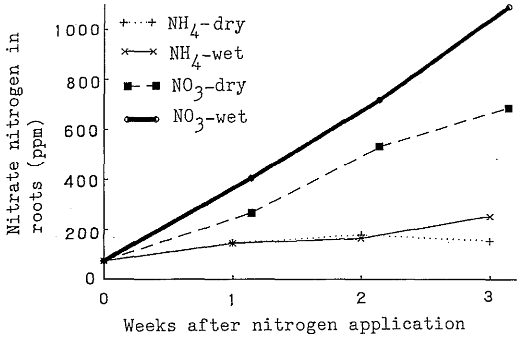

Fig. 5. Changes of nitrate nitrogen concentrations in roots of NH_4-dry, NH_4-wet, NO_3-dry, and NO_3-wet series

Note : Same as in Fig. 1.

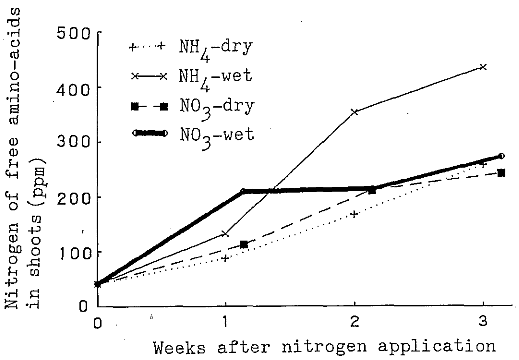

Fig. 6. Changes of nitrogen concentrations of free amino-acids in shoots of NH_4-dry, NH_4-wet, NO_3-dry, and NO_3-wet series

Note : Same as in Fig. 1.

Table 1. Changes of free amino-acids in shoots (μmol/g on a dry basis)

Series		NH_4-dry			NH_4-wet			NO_3-dry			NO_3-wet		
Weeks	0	1	2	3	1	2	3	1	2	3	1	2	3
Amino-acids													
Aspartic acid	0.18	0.30	0.10	0.24	0.30	0.12	0.30	0.19	0.04	0.26	0.27	0.04	0.22
Threonine	0.16	0.18	0.22	0.34	0.25	0.37	0.45	0.23	0.24	0.38	0.35	0.21	0.32
Serine	0.23	0.47	1.03	1.16	0.68	1.34	1.58	0.48	1.04	1.57	0.77	0.76	0.86
Asparagine	0.00	0.06	0.08	0.08	0.05	0.12	0.11	0.04	0.07	0.10	0.06	0.07	0.06
Glutamic acid	0.88	1.29	1.68	1.44	1.92	2.27	1.85	1.48	1.88	1.51	2.04	1.74	1.70
Glutamine	0.11	0.60	0.91	0.82	0.58	2.18	1.32	0.56	0.85	0.71	1.14	0.74	0.55
Proline	0.08	0.36	0.92	1.86	0.72	2.06	3.17	0.61	1.52	1.48	1.53	1.33	1.51
Glycine	0.03	0.05	0.12	0.25	0.06	0.22	0.50	0.05	0.09	0.12	0.13	0.14	0.17
Citrulline	0.04	0.27	1.08	1.83	0.67	2.61	3.95	0.58	1.61	2.11	1.30	2.14	2.98
Alanine	0.25	0.46	0.70	0.66	0.77	0.84	1.30	0.59	0.95	0.70	0.88	0.57	0.55
Valine	0.08	0.10	0.12	0.14	0.12	0.16	0.22	0.11	0.14	0.18	0.16	0.16	0.17
Isoleucine	0.05	0.03	0.05	0.05	0.05	0.06	0.08	0.04	0.05	0.07	0.05	0.04	0.07
Leucine	0.04	0.04	0.06	0.05	0.05	0.05	0.08	0.05	0.07	0.07	0.06	0.05	0.07
Tyrosine	0.03	0.03	0.04	0.06	0.05	0.06	0.08	0.05	0.06	0.09	0.05	0.05	0.07
Phenylalanine	0.09	0.11	0.12	0.11	0.11	0.13	0.13	0.12	0.17	0.19	0.14	0.13	0.13
GABA*	0.17	0.36	0.83	0.72	0.63	1.11	0.88	0.58	0.91	0.98	0.80	0.79	0.93
Ornithine	0.01	0.02	0.04	0.08	0.02	0.07	0.08	0.01	0.03	0.03	0.02	0.03	0.03
Lysine	0.05	0.02	0.05	0.14	0.04	0.17	0.19	0.03	0.05	0.06	0.04	0.04	0.09
Histidine	0.02	0.01	0.03	0.09	0.02	0.08	0.12	0.02	0.04	0.05	0.04	0.04	0.07
Arginine	0.03	0.05	0.11	0.83	0.07	0.81	1.19	0.08	0.25	0.35	0.28	0.23	0.51
Total	2.52	4.82	8.29	10.93	7.14	14.81	17.58	5.92	10.07	11.01	10.11	9.29	11.06

* GABA, γ amino butyric acid.

Nitrogen of free amino-acids in roots increased remarkably in the NH_4 series as compared with the NO_3 series (Fig. 7). The increase in the NH_4 series mainly resulted in increases of glutamine and asparagine. Citrulline also increased in roots of the NH_4-wet series (Table 2).

Concentrations of minerals are shown in Tables 3, and 4. Phosphorus in roots continuously increased except in the NO_3-wet series. Phosphorus in shoots decreased in the NO_3 series. In shoots of the NH_4 series, phosphorus increased in dry conditions and decreased in wet conditions after the nitrogen applications, but at the end of the experiments the phosphorus concentrations returned to their original values. Potassium and calcium in shoots of the NO_3 series increased, but changes of them in the NH_4 series were similar to those of phosphorus. Potassium, sodium, calcium, and magnesium in roots decreased one week after the nitrogen applications in the NH_4 series. All through the experiment period, the concentrations of metallic elements in shoots and roots of the NO_3 series were rather large compared with those of the NH_4 series.

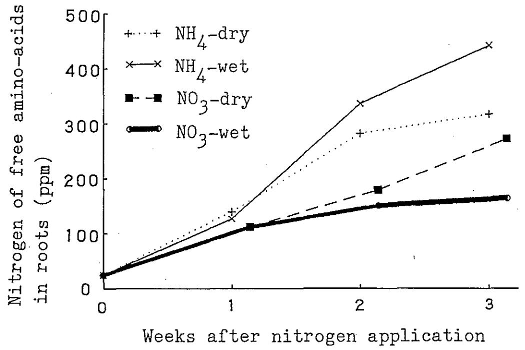

Fig. 7. Changes of nitrogen concentrations of free amino-acids in roots of NH_4-dry, NH_4-wet, NO_3-dry, and NO_3-wet series

Note : Same as in Fig. 1.

IV. Discussion

The fact that in this study, concentrations of metallic elements, which are cations, of the NO_3 series were rather large compared with those of the NH_4 series, suggests that exchanging absorp-

Table 2. Changes of free amino-acids in roots (μmol/g on a dry basis)

Series		NH_4-dry			NH_4-wet			NO_3-dry			NO_3-wet		
Weeks	0	1	2	3	1	2	3	1	2	3	1	2	3
Amino-acids													
Aspartic acid	0.00	0.04	0.10	0.08	0.04	0.09	0.08	0.05	0.09	0.04	0.05	0.08	0.04
Threonine	0.07	0.15	0.29	0.35	0.14	0.34	0.45	0.13	0.21	0.31	0.14	0.18	0.21
Serine	0.13	0.29	0.59	0.72	0.30	0.72	0.95	0.24	0.48	0.71	0.28	0.41	0.45
Asparagine	0.03	0.55	0.85	0.95	0.42	0.94	1.42	0.42	0.42	0.53	0.37	0.31	0.24
Glutamic acid	0.08	0.32	0.65	1.26	0.28	0.66	1.43	0.36	0.53	1.02	0.32	0.51	0.60
Glutamine	0.12	1.05	2.39	1.94	0.91	3.55	3.02	0.53	0.69	0.68	0.57	0.60	0.46
Proline	0.03	0.15	0.23	0.37	0.11	0.35	0.13	0.15	0.23	0.24	0.21	0.19	0.18
Glycine	0.04	0.11	0.35	0.48	0.12	0.48	0.72	0.07	0.17	0.28	0.08	0.15	0.18
Citrulline	0.11	0.37	1.29	1.63	0.38	1.79	2.86	0.44	1.40	2.72	0.39	0.98	1.38
Alanine	0.15	0.67	1.05	1.35	0.61	1.23	1.08	0.60	0.79	0.26	0.55	0.73	0.69
Valine	0.06	0.14	0.25	0.26	0.14	0.22	0.26	0.12	0.19	0.27	0.13	0.16	0.18
Isoleucine	0.05	0.07	0.13	0.13	0.07	0.12	0.13	0.06	0.10	0.12	0.05	0.08	0.08
Leucine	0.05	0.12	0.16	0.17	0.09	0.14	0.17	0.09	0.12	0.15	0.09	0.11	0.10
Tyrosine	0.02	0.06	0.07	0.06	0.04	0.09	0.06	0.05	0.07	0.09	0.05	0.06	0.06
Phenylalanine	0.03	0.07	0.09	0.10	0.06	0.10	0.14	0.06	0.07	0.10	0.07	0.08	0.08
GABA*	0.22	0.80	1.65	2.01	0.68	1.45	2.08	1.00	1.41	2.51	1.14	1.54	1.63
Ornithine	0.01	0.02	0.03	0.05	0.01	0.04	0.04	0.01	0.02	0.03	0.01	0.02	0.01
Lysine	0.01	0.02	0.05	0.06	0.01	0.04	0.06	0.02	0.03	0.04	0.02	0.03	0.03
Histidine	0.01	0.01	0.02	0.08	0.01	0.02	0.05	0.01	0.01	0.03	0.01	0.02	0.01
Arginine	0.02	0.63	0.98	1.03	0.62	0.86	1.51	0.42	0.45	0.62	0.41	0.38	0.39
Total	1.28	5.62	11.20	13.04	5.04	13.24	16.62	4.81	7.47	10.74	4.94	6.60	7.05

* GABA, γ amino butyric acid.

Table 3. Changes of nutrient concentrations in shoots (% on a dry basis)

Series		NH_4-dry			NH_4-wet			NO_3-dry			NO_3-wet		
Weeks	0	1	2	3	1	2	3	1	2	3	1	2	3
Nutrients													
P	0.15	0.16	0.17	0.14	0.12	0.11	0.15	0.13	0.12	0.14	0.14	0.13	0.13
K	1.46	1.80	1.63	1.39	1.23	1.29	1.47	1.59	1.71	1.87	1.55	1.61	1.78
Na	0.05	0.06	0.06	0.05	0.04	0.05	0.06	0.05	0.07	0.12	0.05	0.06	0.09
Ca	0.58	0.64	0.60	0.47	0.49	0.48	0.53	0.66	0.70	0.65	0.61	0.72	0.75
Mg	0.15	0.18	0.17	0.13	0.14	0.13	0.15	0.17	0.17	0.14	0.16	0.17	0.17

Table 4. Changes of nutrient concentrations in roots (% on a dry basis)

Series		NH_4-dry			NH_4-wet			NO_3-dry			NO_3-wet		
Weeks	0	1	2	3	1	2	3	1	2	3	1	2	3
Nutrients													
P	0.08	0.08	0.11	0.12	0.11	0.11	0.12	0.09	0.11	0.12	0.11	0.10	0.09
K	0.61	0.48	0.59	0.65	0.58	0.72	0.71	0.64	0.79	0.81	0.69	0.85	0.73
Na	0.23	0.19	0.19	0.24	0.21	0.26	0.23	0.22	0.28	0.28	0.30	0.25	0.25
Ca	0.34	0.29	0.32	0.29	0.31	0.37	0.35	0.35	0.41	0.42	0.42	0.41	0.42
Mg	0.23	0.16	0.18	0.20	0.20	0.22	0.22	0.19	0.26	0.28	0.24	0.24	0.24

tions of ammonium or nitrate absorption accompanied metallic elements (MARSCHNER, 1986) because ammonium is a cation and nitrate is an anion.

The first step in the assimilation of inorganic nitrogen is amino-acids synthesis from ammonium (MIFLIN, and LEA, 1976). The result that ammonium nitrogen was not found in the roots of this study suggests that the ammonium nitrogen was assimilated to amino-acids in the roots before the translocation to the shoots. This probably occurs to counteract the poisonous effects of ammonium.

It is generally accepted that nitrate nitrogen is reduced into ammonium before the assimilation into amino-acids. The capacity for nitrate reduction in the roots of woody species usually is very great (SMIRNOFF, and STEWART, 1985). The report that the translocation form of nitrogen in sugi is mainly citrulline (MORI, 1975) suggests that sugi also can reduce nitrate in roots. In this study, nitrate nitrogen remarkably increased in roots of the NO_3 series, especially of the NO_3-wet series, but a little nitrate nitrogen was found in shoots of the NO_3-wet series. Therefore, the results suggest that most of the nitrate nitrogen was reduced in the roots, although a little nitrate nitrogen was translocated to the shoots.

The facts that nitrate nitrogen accumulated and ammonium was not found in roots of the NO_3 series might show that nitrate reduction was the rate-limiting factor in the utilization process of nitrate.

KAUFMANN (1968) revealed that the growths of some coniferous species were reduced under soil-moisture conditions of -0.2 MPa or more. However, forest soils in Japan usually are rather moist. The water potentials of most forest soil in Japan are approximately between -0.005 MPa and -0.1 MPa (MASHIMO, 1957). Nevertheless, it is well-known that the growth of sugi is very sensitive to soil moisture conditions. In my study, the seedlings in the dry conditions (soil moisture of -0.035 MPa) had less water than the seedlings in the wet conditions (soil moisture of -0.006 MPa). The degree of the water deficit of the seedlings was not determined physiologically, but the soil moisture conditions affected the nitrogen-utilization process of the seedlings.

A considerable amount of nitrogen of free amino-acids was accumulated even in the roots of the NH_4-dry series, and concentrations of total nitrogen in roots showed little difference between the NH_4-dry and the NH_4-wet series. Therefore, the effects of soil moisture on the absorption of ammonium was not clear. However, the remarkable difference of the concentrations of total nitrogen and the nitrogen of free amino-acids in shoots between the NH_4-wet and the NH_4-dry series suggests that soil moisture affected the absorption of ammonium or the translocation of amino-acids from roots to shoots. The soil moisture also may affect the absorption of nitrate nitrogen because the seedlings of the NO_3-wet series accumulated more nitrate nitrogen than did those of the NO_3-dry series.

HANWAY, and ENGLEHORN (1958) showed that corn accumulated nitrate under drought conditions. PLAUT (1974) found that the accumulation of nitrate in wheat seedlings under drought conditions was associated with reduced nitrate reductase activity. In the soil moisture conditions of this study, however, the nitrate accumulation as a result of the inhibition of nitrate reduction by drought was not observed in the NO_3-dry series.

In conclusion, absorbed ammonium nitrogen was assimilated into amino-acids immediately in roots and subsequently was translocated to the shoots. Absorbed nitrate nitrogen also was assimilated into amino-acids mainly in the roots, but a little of it was translocated as nitrate and assimilated in the shoots. Nitrate reduction in roots might be the rate-limiting factor in the process of nitrate utilization. Nitrate absorption and ammonium absorption or translocation of amino-acids from roots to shoots was affected by the moderate soil moisture deficits (−0.035 MPa). However, inhibition of nitrate reduction and assimilation of nitrogen to amino-acids were not observed under this soil moisture condition.

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