落叶松幼苗碳素和氮素的获取与分配对供氮水平的响应

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摘要 落叶松(*Larix gmelinii*)是中国东北林区最重要的工业用材树种,而且在北温带森林中具有重要的生态学意义。落叶松的种植区域内气温低、冬季长,氮素矿化速度低,供氮不足常常成为落叶松生长的限制因素。为揭示落叶松生长与氮素营养的关系,采用沙培法设置了 1、4、8 和 16 mmol·L⁻¹ 4 个供氮水平,研究了不同供氮条件下落叶松一年生幼苗对碳和氮的获取与分配的规律。结果显示,落叶松幼苗的生物量、全株氮浓度、氮含量、比氮吸收速率均随供氮水平的增加而升高,叶重比(*LWR*)、茎重比(*SWR*)及叶氮比(*LNR*)、茎氮比(*SNR*)亦随供氮水平的增加而增加,而根重比(*RWR*)和根氮比(*RNR*)则随供氮水平的增加而降低。当供氮水平从 1 mmol·L⁻¹ 增加至 8 mmol·L⁻¹ 时,落叶松幼苗相对生长速率呈线性增加,而全株氮生产力几乎未受供氮水平的影响;当供氮水平从 8 mmol·L⁻¹ 增加至 16 mmol·L⁻¹ 时,全株相对生长速率不再增加,全株氮生产力则显著下降。与全株氮生产力的变化不同,落叶松幼苗的叶氮生产力与供氮水平呈负相关。

关键词 落叶松 供氮水平 获取与分配 氮生产力

CARBON AND NITROGEN ACQUISITION AND ALLOCATION IN LARCH SEEDLINGS IN RESPONSE TO DIFFERENT N SUPPLY RATES

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Abstract Larch (*Larix gmelinii*) is the most important industrial timber species in northeastern China, and is ecological significant in boreal forest ecosystems. However, the growth of larch is often limited by nitrogen (N) availability because of slow litter decomposition rates due to low temperatures and the long winter in these northern forests. To explore the relationship between growth and soil N availability in larch, we treated one-year old larch seedlings to four different N supply levels (1, 4, 8 and 16 mmol·L⁻¹, respectively) and measured acquisition and allocation of carbon and N. The results showed that the biomass, whole plant N concentration, whole plant N content and special N absorption rate of larch seedlings were enhanced with N supply levels. With the increase in N supply, needle and stem weight ratios and needle and stem N weight ratios increased, whereas the root weight ratio and root N weight ratio decreased. As N supply levels increased from 1 mmol·L⁻¹ to 8 mmol·L⁻¹, whole plant relative growth rate (*RGR*) increased linearly, whereas whole plant N productivity (*NP_p*) remained constant. At the highest N treatment (16 mmol·L⁻¹), whole plant *RGR* was the same as in the 8 mmol·L⁻¹ N treatment, but *NP_p* decreased significantly compared with the 8 mmol·L⁻¹ treatment. In contrast, needle N productivity of larch seedlings exhibited a negative relationship with N supply level.

Key words Larch, N supply level, Acquisition, Allocation, Nitrogen productivity

Nitrogen (N) is an important ecological factor that affects plant growth and development, for it is not only a main part of the plant structure, but also the major component of the most active proteins, enzyme in plant physiological metabolism. N is the mineral nutrient most fre-

quently limiting to plant growth, even to forest ecosystems. Previous researches have been proven soil N availability basically limiting forest productivity in boreal forests (Su *et al.*, 2002). To improve forest productivity, many works on the relationship between N nutrient

and tree growth have been conducted in boreal forests (Ingstad & Kahr, 1985; Valinger, 1993; Seith *et al.*, 1996; Vejre *et al.*, 2001; Saarsalmi & Malkonen, 2001), and the effects of N supply on photosynthesis processes have been discussed from the point of physiological mechanism (Evans, 1989; Tan & Hogan, 1995; Warren *et al.*, 2003). Recently, the combined effects of N with other ecological factors such as CO₂ or O₃ were analyzed widely (Laitinen *et al.*, 2000; Grassi & Minotta, 2000; Utriainen & Holopainen, 2001a, 2001b). These works were mostly focused on Norway spruce (*Picea abies*) (Seith *et al.*, 1996; Grassi & Minotta, 2000; Nilsen & Abrahamsen, 2003) and Scots pine (*Pinus sylvestris*) (Laitinen *et al.*, 2000; Malagoli *et al.*, 2000; Utriainen & Holopainen, 2001b; Nilsen & Abrahamsen, 2003) widely distributed in Europe, and loblolly pine (*Pinus taeda*) (Green *et al.*, 1994; Griffin *et al.*, 1995) and Jack pine (*Pinus banksiana*) (Tan & Hogan, 1995, 1998) mainly grown in North America. However, there was few relative research conducted to conifers that grow in boreal forest of Asia (Son *et al.*, 2000; Qu *et al.*, 2003). As for China, much less work has been done in these aspects.

Larch (*Larix gmelinii*) is the most important industrial timber species in northeastern China and considered to have an important ecological significance in boreal forest ecosystems. In northeastern China, larch forest of plantations has reached 2 million hm², which accounts for 55% of plantations forest in northeastern China. However, the growth of larch is often limited by nitrogen (N) shortage because of slow decomposition rate of litter due to low temperatures and the long winter in boreal forest. In this study, we selected one-year-old larch seedlings as experimental materials, controlled N supply levels, growth and nutrition acquisition of larch seedling were determined; the response of carbon (C) and N acquisition and allocation to N supply level in larch seedling was reported. The aim of the study is to explore the relationships between larch growth and soil N availability, and provide a theoretic or practical basis to grow seedlings and fertilizer management for larch.

1 Materials and methods

1.1 Plant materials and growth conditions

Experiments were performed in a greenhouse with natural light from April to September, 2003, in Northeast Forestry University, Harbin. On April 12, after roots washing and sterilizing, one-year-old larch seedlings were transplanted to plastic pots (diameter 30 cm, height 27

cm) containing sterilized and washed quartz sand, two seedlings per pot. Seedlings were fed with the following complete nutrient solution modified from Utriainen and Holopainen (2001a) for 40 days: 4 mmol · L⁻¹ of NH₄NO₃, 1 mmol · L⁻¹ of KH₂PO₄, 1 mmol · L⁻¹ of KCl, 1 mmol · L⁻¹ of CaCl₂ · 6H₂O, 0.6 mmol · L⁻¹ of MgSO₄ · 7H₂O, 0.02 mmol · L⁻¹ of FeCl₃ · 6H₂O, 6 μmol · L⁻¹ of MnCl₂ · 4H₂O, 0.016 mmol · L⁻¹ of H₃BO₃, 0.3 μmol · L⁻¹ of ZnCl₂, 0.3 μmol · L⁻¹ of CuCl₂ · 2H₂O, 0.3 μmol · L⁻¹ of NaMoO₄ · 2H₂O. On May 15, seedlings were treated with 4 different N supply levels of 16, 8, 4 and 1 mmol · L⁻¹ respectively, 10 pots per treatment. Except NH₄NO₃, the other nutrient elements were fertilized same as above complete nutrient solution. The pH was adjusted to 5.5–6.0 using Ca(OH)₂ or H₂SO₄ as required. 200 ml of the nutrient solution per pot were supplied three times a week, and the plants were provided with sufficient water during the whole growing period.

1.2 Harvest and chemical analysis

Two destructive harvests were made at 40 and 110 days after treatments (DAT), respectively. Ten seedlings (5 pots) per treatment were harvested in each time. Each seedling was washed with deionized water, and grouped into needles, stems and roots separately. All the plant materials were dried at 70 °C for 72 h and weighed respectively, and then needles, stems and roots of seedlings grown in the same pot were mixed and grounded respectively for N concentration determination. Total N concentration (mg N · g⁻¹ DW) of needle, stem and root dry samples was determined by Kjeldahl method (Horneck & Miller, 1998).

1.3 Calculations

Dry weight ratios (g · g⁻¹) of needles (*LWR*), stems (*SWR*) and roots (*RWR*) or N weight ratios (g N · g N⁻¹) of needles (*LNR*), stems (*SNR*) and roots (*RNR*) were calculated as ratios of component dry, or N, weight to total dry, or N, weight in each seedling. Nitrogen concentration of the whole plant was determined from needle, stem and root component dry weights and N concentrations. Relative growth rate (*RGR*) was calculated as described by de Groot *et al.* (2001). Specific nitrogen absorption rate (*SNAR*) was calculated from the equations given in Nielsen *et al.* (2001).

$$SNAR = [M(t_{110DAT}) - M(t_{40DAT})] / [t_{110DAT} - t_{40DAT}] \times [\ln R(t_{110DAT}) - \ln R(t_{40DAT})] / [R(t_{110DAT}) - R(t_{40DAT})]$$

where *M* is the N content per plant, and *R* is root dry weight (g). *SNAR* is a measure of the net N absorption rate per unit root dry weight (mg · g⁻¹ root DW · d⁻¹),

over the interval $t_{40\text{DAT}}$ to $t_{110\text{DAT}}$.

Plant nitrogen productivity (NP_p) and needle nitrogen productivity (NP_L) were calculated from the equations given in Eckstein and Karlsson (2001) as between harvest averages from each replicate.

$$NP = [W(t_{110\text{DAT}}) - W(t_{40\text{DAT}})] / [t_{110\text{DAT}} - t_{40\text{DAT}}] \times [\ln M(t_{110\text{DAT}}) - \ln M(t_{40\text{DAT}})] / [M(t_{110\text{DAT}}) - M(t_{40\text{DAT}})]$$

Where M is the N content per plant (when calculate NP_p) or needle N content per plant (when calculate NP_L), and W is plant dry weight (g). NP is a measure of dry weight return for N absorption (the productive efficiency), it expressed plant dry weight increase rate per unit of N content ($\text{g DW} \cdot \text{g}^{-1} \text{N} \cdot \text{d}^{-1}$), over the interval $t_{40\text{DAT}}$ to $t_{110\text{DAT}}$.

1.4 Statistical analysis

Standard error, variance, regression and correlation coefficients were calculated by standard methods with the DPS Data Processing System Ver. 3.01 (Tang & Feng, 2002).

2 Results

2.1 Larch seedling biomass

Plant biomass reflects plant growth status and directly relates to C acquisition. After 40-day-treatment, needle biomass increased in a small scale with the increase of N supply level, whereas stem biomass decreased and root biomass increased slightly at severe shortage of N supply ($1 \text{ mmol} \cdot \text{L}^{-1}$), and they were stable at other N supply levels. There are no significant differences were shown be-

tween different treatments ($p > 0.05$). After 110-day-treatment, needle and stem biomasses remarkably enhanced with the increment of N supply level at $1 - 8 \text{ mmol} \cdot \text{L}^{-1}$, while biomasses enhancement shrunk with the excessive N supply level of $16 \text{ mmol} \cdot \text{L}^{-1}$. The maximum needle and stem biomasses at $16 \text{ mmol} \cdot \text{L}^{-1}$ N supply level were 3.3 and 3.4 times to those at $1 \text{ mmol} \cdot \text{L}^{-1}$ N supply level, respectively. At the same time, variation in root biomass was not significant ($p > 0.05$) though a light enhancement was found when N supply level rose from $1 \text{ mmol} \cdot \text{L}^{-1}$ to $8 \text{ mmol} \cdot \text{L}^{-1}$ and a light shrinkage did at $16 \text{ mmol} \cdot \text{L}^{-1}$ N supply level. Similar as needle and stem, the whole plant biomass rose with the increase of N supply level, but excessive N supply ($16 \text{ mmol} \cdot \text{L}^{-1}$) led to a less increment of whole plant biomass (Fig. 1).

2.2 Allocation of biomass among organs

The variations in biomass of different organs in larch seedlings induced by different N supply levels resulted in the difference of biomass allocation among different organs. LWR , SWR and RWR are important indexes to reflect the biomass allocation pattern among plant organs. LWR rose with the promotion of N supply, and LWR under short-term treatment (40 days) was higher than that under long-term treatment (110 days). After 40-day-treatment, SWR at $4 \text{ mmol} \cdot \text{L}^{-1}$ N supply level was the highest, but no significant difference was shown between various treatments. During the seedling development (110-day-treatment), SWR showed a similar trend to LWR . Whereas comparing with LWR and SWR , an inverse trend of RWR was observed. RWR apparently

Fig.1 Relationships between N supply level and biomass in larch seedlings
Vertical bars indicate standard errors of means ($n = 10$) ○: 40 days after treatment ●: 110 days after treatment

improved with the lack of N supply and prolongation of treatment. After 40-day-treatments, *RWR* were 0.33 $\text{g}\cdot\text{g}^{-1}$ DW at 1 $\text{mmol}\cdot\text{L}^{-1}$ N supply level and 0.22 $\text{g}\cdot\text{g}^{-1}$ DW at 16 $\text{mmol}\cdot\text{L}^{-1}$ N supply level respectively, while After 110-day-treatments, *RWR* were 0.53 $\text{g}\cdot\text{g}^{-1}$ DW at 1 $\text{mmol}\cdot\text{L}^{-1}$ N supply level and 0.26 $\text{g}\cdot\text{g}^{-1}$ DW at 16 $\text{mmol}\cdot\text{L}^{-1}$ N supply level respectively, which implied that the seedlings exhibited a kind of adaptation to long-term N nutrient shortage (Fig. 2).

2.3 N concentration and N content

After 40-day-treatment, N concentration of whole seedling was 9.15 $\text{mg}\cdot\text{g}^{-1}$ DW at 1 $\text{mmol}\cdot\text{L}^{-1}$ N supply level and that increased to 14.68 $\text{mg}\cdot\text{g}^{-1}$ DW at 16 $\text{mmol}\cdot\text{L}^{-1}$ N supply level, and that did from 9.19 $\text{mg}\cdot\text{g}^{-1}$ DW at 1 $\text{mmol}\cdot\text{L}^{-1}$ N supply level to 18.51 $\text{mg}\cdot\text{g}^{-1}$ DW at 16 $\text{mmol}\cdot\text{L}^{-1}$ N supply level after 110-day-treatment, which reflected that N concentration of whole seedling improved with the N availability. In addition, under the condition of severe shortage of N supply, treatment term didn't influence N concentration of whole seedling (Fig. 3A).

The product of N concentration and biomass of whole seedling is N content of whole seedling. After 40-day-treatment, N content of whole seedling increased with N supply level in a small scale, while after 110-day-treatment, an obvious increment was induced by the co-reac-

tion of biomass and N concentration to the N nutrient availability. A positive linear relationship was showed between N supply level and N content at 1 – 8 $\text{mmol}\cdot\text{L}^{-1}$ of N supply level, then at 16 $\text{mmol}\cdot\text{L}^{-1}$ N supply level the N accumulation rate reduced after 110-day-treatment. N content at 16 $\text{mmol}\cdot\text{L}^{-1}$ of N supply level was 4.4 times than that at 1 $\text{mmol}\cdot\text{L}^{-1}$ N supply level (Fig. 3B).

2.4 Allocation of N among organs

LNR, *SNR*, and *RNR* are important indexes in the determination of N allocation among plant organs. There was a positive relationship between N supply and *LNR*, but a negative correlation between treatment time and *LNR*, which suggested plant N allocation in needles declined though needle N content quantitatively rose with plant development. After 40 days treatment, the maximum *SNR* was 0.13 $\text{g}\cdot\text{g}^{-1}$ N DW at 4 $\text{mmol}\cdot\text{L}^{-1}$ N supply level, and stable at 0.11 $\text{g}\cdot\text{g}^{-1}$ N DW at 8 – 16 $\text{mmol}\cdot\text{L}^{-1}$ of N supply level. After 110 days treatment, *SNR* was positively related to N supply level when N supply level was 1 – 8 $\text{mmol}\cdot\text{L}^{-1}$. Similar to *RWR*, *RNR* declined with increase of N availability and plant age (Fig. 4).

2.5 Relative growth rate

A positive linear correlation between N supply and *RGR* of whole plant was found at 1 – 8 $\text{mmol}\cdot\text{L}^{-1}$ N supply level during the time interval from 40 days to 110

Fig.2 Relationships between N supply level and needle weight ratio (*LWR*), stem weight ratio (*SWR*), root weight ratio (*RWR*) of larch seedlings
Vertical bars indicate standard errors of means ($n = 10$) ○: 40 days after treatment ●: 110 days after treatment

Fig.3 Relationships between N supply level and N concentration (A) and N content (B) in whole plant of larch seedling
Vertical bars indicate standard errors of means ($n = 5$) ○: 40 days after treatment ●: 110 days after treatment

Fig.4 Correlations between N supply level and needle N weight ratio (*LNR*), stem N weight ratio (*SNR*), root N weight ratio (*RNR*) of larch seedlings
Vertical bars indicate standard errors of means ($n = 10$) ○: 40 days after treatment ●: 110 days after treatment

days (Fig. 5). When N supply level reached $16 \text{ mmol} \cdot \text{L}^{-1}$, *RGR* of whole plant was similar to that at $8 \text{ mmol} \cdot \text{L}^{-1}$ N supply level, and similar changes were found in needle *RGR*. Variation in stem *RGR* was similar to that in *RGR* of whole plant at $1 - 8 \text{ mmol} \cdot \text{L}^{-1}$ N supply level, whereas there was a little increase in stem *RGR* at $16 \text{ mmol} \cdot \text{L}^{-1}$ N supply level compared with that at $8 \text{ mmol} \cdot \text{L}^{-1}$ N supply level. At the same time, except for the condition of severe N shortage, stem *RGR* was higher than *RGR* of whole plant; while needle *RGR* was always lower than *RGR* of whole plant. Root *RGR* was higher than *RGR* of whole plant (Fig. 5).

Fig.5 Effects of N supply level on relative growth rate in larch seedlings

2.6 N productivity and special N absorption rate

Whole plant N productivity (NP_P) shows plant biomass accumulation rate per unit plant N content. NP_P remain stable at $1 - 4 \text{ mmol} \cdot \text{L}^{-1}$ N supply level, then rose a little at $8 \text{ mmol} \cdot \text{L}^{-1}$ N supply level, and declined at $16 \text{ mmol} \cdot \text{L}^{-1}$ N supply level. Needle N productivity (NP_L) shows plant biomass accumulation rate per unit needle N content. NP_L inversely related to N supply level. The maximum NP_L was $2.52 \text{ g DW} \cdot \text{g}^{-1} \text{N} \cdot \text{d}^{-1}$ at $1 \text{ mmol} \cdot \text{L}^{-1}$ N supply level, and NP_L was only 65.5 % of the maximum at $16 \text{ mmol} \cdot \text{L}^{-1}$ N supply level, which revealed the higher N supply level, the lower N productive efficiency of larch needle was (Fig. 6).

SNAR linearly increased from $0.22 \text{ mg} \cdot \text{g}^{-1} \text{root DW} \cdot \text{d}^{-1}$ at $1 \text{ mmol} \cdot \text{L}^{-1}$ N supply level to $1.43 \text{ mg} \cdot \text{g}^{-1} \text{root DW} \cdot \text{d}^{-1}$ at $16 \text{ mmol} \cdot \text{L}^{-1}$ N supply level, which explored

the positive relationship between N supply and *SNAR* (Fig. 7).

Fig.6 Correlations between N supply level and N productivity of larch seedlings

Fig.7 Correlations between N supply level and special N absorption rate of larch seedlings

3 Discussion

3.1 Plant growth

Biomass is the most important index to reflect the plant growth status. Increased N supply usually enhances plant growth, as a consequence, the biomass of shoot or whole plant may increase with the increase of N supply (Green *et al.*, 1994; Seith *et al.*, 1996; Paponov *et al.*, 2000). Our data of one-year-old larch seedlings are consistent with these observations (Fig. 1). The effect of N supply, however, on root growth in absolute terms is more variable than that on shoot growth. Additional N

supply to low-N soil enhances shoot growth, but that may increased, unaffected, or decreased root growth. In the present study, after 110 days treatment, root biomass was almost unaffected with increasing N availability (Fig. 1). Differently, very high N supply decreased the root/shoot ratio of young coniferous trees in other pot experiments due to both enhanced shoot growth and slightly decreased root growth (van Dijk *et al.*, 1990; Olsthoorn *et al.*, 1991). In a Swedish field experiment, the amount of healthy looking small roots was decreased after N fertilization (Clemensson-Lindell & Asp, 1995), In other cases, however, not only shoot growth but also root growth of trees was enhanced by increasing N supply, both in pot experiments (Mackie-Dawson *et al.*, 1994) and in the field (Ahlström *et al.*, 1988; Rosengren-Brinck *et al.*, 1995). The effect of N supply to soil on root biomass production will depends not only on the previous N supply and the amount of N added, but also on the plant species (Griffin *et al.*, 1995) and the simultaneous supply of other mineral nutrients.

Whole plant biomass of larch seedling always increased when concentration of N supplied from $1\text{ mmol}\cdot\text{L}^{-1}$ up to $16\text{ mmol}\cdot\text{L}^{-1}$, but in the $16\text{ mmol}\cdot\text{L}^{-1}$ N treatment, the increment of the total dry weight decreased (Fig. 1), and the whole plant *RGR* was the same as that in the $8\text{ mmol}\cdot\text{L}^{-1}$ N supply treatment (Fig. 5). Similar results have been found in Jack pine (Tan & Hogan, 1995) and Norway spruce (Seith *et al.*, 1996). These suggest that plant may have an inherent maximal *RGR* in a given period, excessive N supply can't enhance plant growth unlimitedly. In addition, the data indicate that $16\text{ mmol}\cdot\text{L}^{-1}$ N supply might have reached the N concentration which made larch seedling obtain the maximal *RGR*, and further N supply might decrease *RGR*, even inhibit growth of larch seedlings, because previous research has found excessive N supply could decrease accumulation of whole plant biomass (Nakaji *et al.*, 2001).

3.2 Nitrogen concentration and nitrogen absorption

Plants absorb nutrients from soil by root system, and transport them to organs of plant for plant growth and other life activities. Thereby, N supply level would inevitably affect N uptake and N status in plants. In our study, whole plant N concentration of larch seedling was elevated with the increase N supply level (Fig. 3A), which was consisted with the response of other conifers to N availability (Ingestad & Kahr, 1985; Brown *et al.*, 1996b; Tan & Hogan, 1998). In addition, needle, stem and root N concentrations increased linearly with increasing whole plant N concentration after 110 days treatment (Fig. 8). However, the slope for needles was greater than unity (1.308) whereas that for stems and roots were less than unity (0.551 and 0.937 5, respectively). That meant, needles N concentration increased faster whereas

stems and roots N concentration increased slower than whole plant N concentration, this may indicate that needles N concentration is more sensitive to N supply than N concentrations of stem and root.

SNAR of larch seedling showed a strongly positive relationship with N supply level (Fig. 7), similar results have been reported in *Picea sitchensis* and *Tsuga heterophylla* seedlings (Brown *et al.*, 1996b), the relationship between *SNAR* and N supply level may mainly due to the enhancement of sink strength (Fig. 3B) which arise from rapid growth at high N supply level.

3.3 Allocation of biomass and nitrogen

The core of the "functional equilibrium" hypothesis (Brouwer, 1962; 1983) is that plants shift their allocation towards shoots if the carbon gain of the shoot is impaired by a low level of above-ground resources, such as light and CO_2 . Similarly, plants shift allocation towards roots at a low level of below-ground resource, such as nutrients and water. These shifts could be seen as adaptive, as that enable the plant to capture more of those resources that most strongly limit plant growth. In present study, both biomass and N allocation pattern at two harvest times all support this hypothesis. When N supply level declined from $16\text{ mmol}\cdot\text{L}^{-1}$ to $1\text{ mmol}\cdot\text{L}^{-1}$, the *LWR*, *LNR*, *SWR* and *SNR* decreased whereas *RWR* and *RNR*

Fig.8 Relationships between whole plant N concentration and N concentrations of needle, stem and root in larch seedlings after 110-day-treatment
Each point represents the mean of two seedlings

increased significantly (Fig. 2, 4), this suggests that at low N supply, larch seedling allocates less biomass and N to shoot whereas does more biomass and N to root to alleviate stress induced by N deficiency, similar results have been reported both in trees (Griffin *et al.*, 1995; Ibrahim *et al.*, 1998; Tan & Hogan, 1998) and herbs (Boot *et al.*, 1992; Lutze & Gifford, 1998; Paponov *et al.*, 2000). For instance, in a study on loblolly pine and ponderosa pine (*Pinus ponderosa*) by Griffin *et al.* (1995), decreased N supply significantly increases root/shoot biomass ratio, and also shifts N to root, but this only companies with a decrease of *SNR*, whereas *LNR* was unaffected. However, in the same study, the responses of ponderosa pine to N supply far differ from loblolly pine, increased N supply neither influences biomass root/shoot ratio nor alters allocation patterns of N in needles, stems and roots. This may suggest allocation of biomass and N relates to not only N supply level but also tree species.

Larch seedling allocates their dry matter and N in needles, stems and roots largely on the basis of internal N status, as can be seen from the significant positive linear relationships between the *LWR*, *SWR*, *LNR*, *SNR* and whole plant N concentration, and negative linear relations between *RWR*, *RNR* and whole plant N concentration (Fig. 9). Similarly, Tan and Hogan (1998) have found whole plant N concentration of Jack pine seedling posi-

tively related to *LWR* and *LNR*, negatively related to *RWR* and *RNR*, but only weakly correlated to *SWR* and *SNR*. In addition, as internal N status declined, the variation in *LNR* and *RNR* were faster than that of *LWR* and *RWR* (i. e. The slopes of regression lines for N weight ratio were steeper), so they concluded that the co-ordination of N distribution within plants may be an active process, independent of, and/or in association with, dry matter partitioning. In our study, however, as whole plant N concentration decreased, variation in *LNR* was faster than that of *LWR*, but the slopes of the lines for *SNR* (0.005 2) and *RNR*(-0.020 4) were gentler than those for *SWR* (0.010 1) and *RWR* (-0.023 0) respectively, which is consistent with the reports of Abrahamson and Caswell (1982), Pavlik (1983), and Boot *et al.* (1992). Thereby, N distribution within larch seedlings may be mainly triggered by biomass allocation in this study, and no so called "active process" was present.

3.4 Nitrogen productivity

As N supply elevated from 1 mmol • L⁻¹ to 8 mmol•L⁻¹, total biomass and *RGR* linearly increased (Fig. 5), whereas *NP_P* was steady (Fig. 6), these displayed N productive efficiency of larch seedling was unaffected in this scope of N supply level. When N supply arrived at 16 mmol•L⁻¹, however, the larch seedling

Fig.9 Correlations between whole plant N concentration and needle, stem and root weight ratios or N weight ratios in larch seedlings after 110-day-treatment
Each point represents the mean of two seedlings

showed a tendency to accumulate nitrogen at luxury levels with no corresponding increase of growth, as can be seen from the significant decline of NP_P (Fig. 6). Such a tendency has previously been noticed in *Alnus* (Ingstad, 1981), *Populus* or *Paulownia* (Jia & Ingstad, 1984) and other conifers (Ingstad & Kahr, 1985). Decreasing of NP_P at high N supply may be due to the depression of photosynthesis induced by nutrients imbalance (Nakaji *et al.*, 2001, 2002) or self-shading (Brown *et al.*, 1996a). Alternatively, strong respiration caused by high tissue N concentration in high N plant (Lambers *et al.*, 1990; Ryan, 1991) may be another possible reason.

When increasing rate of biomass was measured in needle N content (NP_L), negative relationships were found between NP_L and N supply level (Fig. 6) and needle N concentration, which is consistent with the results of Brown *et al.* (1996b), Lutze and Gifford (1998). Inverse changes of NP_L with elevation of N concentration may indicate that an increasing proportion of needle N is accumulating in soluble, non-photosynthetic compounds, e.g. free amino acids (Gezelius & Näsholm, 1993).

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