

供氮水平对落叶松幼苗光合作用的影响

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摘要:为探讨落叶松光合作用对外界供氮环境变化的响应规律,采用砂培方法在温室内设置了 4 种供氮浓度(1、4、8 mmol/L 和 16 mmol/L),对生长在不同供氮水平下落叶松(*Larix gmelinii*)1 年生幼苗的气体交换参数、叶绿素荧光参数以及一些生化指标进行了测定。结果显示,随供氮水平的提高,落叶松幼苗针叶氮含量、叶绿素含量、类胡萝卜素含量、可溶性蛋白(TSP)含量和光饱和净光合速率(P_{\max})均显著增加,同时伴随着叶磷含量和胞间与外界 CO_2 浓度之比(C_i/C_a)的降低。然而,当供氮水平超过 8 mmol/L 增至 16 mmol/L 时,TSP 含量及 P_{\max} 不再增加,反而略有下降。供氮不足显著降低了幼苗针叶光系统 II 最大光能转换效率(F_v/F_m)、光系统 II 量子效率(Φ_{PSII})和光化学猝灭系数(qP),却增加了非光化学猝灭系数(NPQ)。而增加供氮可使 F_v/F_m 和 Φ_{PSII} 回升,同时 qP 升高, NPQ 下降,但当供氮水平超过 8 mmol/L 后,各叶绿素荧光参数变化幅度较小。结果表明,增加供氮可显著提高落叶松幼苗的光合能力,增加光系统 II 天线色素捕获的光能用于光化学电子传递的份额,减缓光抑制。然而,16 mmol/L 已经超过落叶松幼苗最适的供氮水平,过量供氮引起的负面效应可能主要与过低的叶磷含量导致的营养失衡有关。

关键词:落叶松;供氮水平;净光合速率;叶绿素荧光参数;营养失衡

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Effects of nitrogen supply on photosynthesis in larch seedlings

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Abstract: Nitrogen (N) is the most important nutrients for plants. Detailed studies on the influence of N supply on photosynthesis have been reported in many plant species, but seldom in larch, which is a significant forestation species in Northeast China. In this paper, we report the characteristics of photosynthesis in larch seedlings that have been provided with different N supplies.

The experiment was conducted in greenhouse from April 2003 to September 2003. On April 5, one-year-old larch (*Larix gmelinii*) seedlings were transplanted into plastic pot (diameter 30 cm, height 27 cm) containing sterilized and washed quartz sand after extensive washing and sterilizing of the roots. The seedlings were supplied with a complete nutrient solution for 40 days: This solution contained 4 mmol/L of NH_4NO_3 , 1 mmol/L of KH_2PO_4 , 1 mmol/L of KCl, 1 mmol/L of CaCl_2 , 0.6 mmol/L of MgSO_4 , 0.02 mmol/L of FeCl_3 , 6 $\mu\text{mol/L}$ of MnCl_2 , 0.016 mmol/L of H_3BO_3 , 0.3 $\mu\text{mol/L}$ of ZnCl_2 , 0.3 $\mu\text{mol/L}$ of CuCl_2 , 0.3 $\mu\text{mol/L}$ of NaMoO_4 . On the May 15, the seedlings were treated with four different N concentrations (1, 4, 8 and 16 mmol/L, respectively). After 15-weeks of treatment, gas exchange, chlorophyll fluorescence and some biochemical parameters were determined.

The results showed that with an increase in N supply, the levels of both N and chlorophyll in the needles were up significantly, while the phosphorus content declined. The light-saturated net photosynthetic rate (P_{\max}) of the needles showed a linear increase when N supply was increased form 1 mmol/L to 8 mmol/L. Meanwhile, total soluble protein (TSP) content and stomatal conductance (g_s) were also increased, whereas internal to ambient CO_2 concentration ratio (C_i/C_a) was

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decreased. When the N supply exceeded 8 mmol/L and reached 16 mmol/L, the P_{\max} and the TSP content exhibited a non-significant decrease. N deficiency caused a significant decline in the maximum quantum efficiency of photosystem II (PS II) photochemistry (F_v/F_m), quantum efficiency of PS II (Φ_{PSII}) and the photochemical quenching co-efficient (qP). These changes were accompanied by an increase in both the non-photochemical quenching co-efficient (NPQ) and the carotenoid/chlorophyll ratio (Car/Chl). Although increasing the N supply increased F_v/F_m , Φ_{PSII} and qP , the chlorophyll fluorescence parameters showed little change when the N level exceeded 8 mmol/L. These results suggested that when plants grow in a N deficiency condition, increasing the N supply can enhance their photosynthetic capability by improving photochemistry quantum efficiency of PS II and alleviating photoinhibition. Regarding the results of 16 mmol/L condition, although this condition may have exceeded the optimum N level for larch seedlings, the negative effect of excess N supply might be mainly due to nutrient imbalance.

Key words: larch; nitrogen supply; net photosynthetic rate; chlorophyll fluorescence; nutrient imbalance

氮素是影响植物生长发育的重要营养因子。植物叶片大约 75% 的氮素存在于叶绿体中^[1,2], 这其中的 30%~50% 被碳同化的关键酶——核酮糖-1,5-二磷酸羧化酶(Rubisco)所占据, 还有一部分被用于光捕获和电子传递等相关蛋白的合成^[3]。许多研究表明, 植物的叶氮含量与其净光合速率有着很强的相关性^[2~5], 供氮水平可通过影响叶氮含量而直接影响植物的光合能力。此外, 氮素供给对植物叶片的气孔导度^[6~8]、光合色素^[9,10]以及叶绿素荧光参数^[9,11,12]也都有很大的影响。然而, 这些研究工作多集中于农作物^[6~8,11~13], 关于供氮水平与造林树种光合作用关系的研究相对较少^[10]。

落叶松是我国东北地区重要的人工造林树种, 在温带森林生态系统中也具有非常重要的生态学意义。在东北林区, 由于气温低、冬季时间长, 凋落物的分解及有机物的矿化过程较为缓慢, 林地氮含量常常成为落叶松生长的限制因子。另一方面, 近年来对大气氮沉降的研究显示, 由于人类活动引发氮化物在大气中累积并向陆地和水域生态系统沉降, 导致林地氮含量有增加的趋势^[14~16]。然而, 人们对外界供氮环境发生改变时落叶松光合作用的变化规律还知之甚少。为此, 采用沙培方法设置供氮梯度, 观察了不同供氮水平下落叶松幼苗的气体交换及叶绿素荧光参数, 旨在探讨落叶松幼苗的光合作用及生产力形成对氮素供给变化的响应规律和机制, 并为落叶松的育苗及肥料管理提供理论依据和实践指导。

1 材料与方法

1.1 植物材料培养与处理

实验于 2003 年 4 月至 9 月在温室内进行, 供试苗木为同一批 1 年生兴安落叶松 (*Larix gmelinii*) 幼苗。4 月初, 将幼苗根系洗净、消毒后栽植于盛有石英砂(经 0.5% 盐酸浸泡 24 h 并用自来水洗至中性)并在底部打孔的塑料桶(直径 30 cm, 高 27 cm)中, 每桶植苗 2 株。5 月初开始, 开启温室两侧的通风窗, 使温室内、外的温度、湿度基本一致, 直至实验结束。

4 月初至 5 月 22 日之间, 浇灌氮素浓度为 8 mmol/L 的正常营养液, 以使幼苗生长健壮。

完全营养液按 Utriainen 和 Holopainen^[17]方法配制, 略加修改: NH_4NO_3 , 4 mmol/L; KH_2PO_4 , 1 mmol/L; KCl, 1 mmol/L; CaCl_2 , 1 mmol/L; MgSO_4 , 0.6 mmol/L; FeCl_3 , 0.02 mmol/L; MnCl_2 , 6 $\mu\text{mol/L}$; H_3BO_3 , 0.016 mmol/L; ZnCl_2 , 0.3 $\mu\text{mol/L}$; CuCl_2 , 0.3 $\mu\text{mol/L}$; NaMoO_4 , 0.3 $\mu\text{mol/L}$ 。

5 月 22 日开始进行供氮浓度的处理。选取大小一致、长势良好的幼苗随机分成 4 个组(每组 5 桶), 分别浇灌氮素浓度为 1 mmol/L、4 mmol/L、8 mmol/L 和 16 mmol/L 的营养液(通过调节 NH_4NO_3 的浓度实现, 其他营养成分浓度与完全营养液相同), 其中 8 mmol/L 相当于正常氮供给浓度。

每周浇 3 次营养液, 每次 200 ml, 并适当根据情况补充水分。幼苗处理 15 周后采样、测定。

1.2 针叶气体交换及叶绿素荧光参数的测定

用 LI-6400P 光合仪(LI-Cor, Inc, 美国)测定落叶松幼苗针叶在饱和光强 1600 $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$ 下的净光合速率(P_{\max})、气孔导度(g_s)和胞间 CO_2 浓度(C_i)。

测定时使用开放气路, 空气流速为 0.5 L/min, 叶温 25 $^{\circ}\text{C}$, 相对湿度 60%, 外界 CO_2 浓度(C_a)为 360 $\mu\text{mol}/\text{mol}$ 。

P_{\max} 以单位干重针叶的 CO_2 同化量表示, 以叶室内针叶的干重代替光合仪中的叶面积计算而得。

用 FMS-2.02 脉冲调制荧光仪(Hansatech, Inc, 英国)测定落叶松幼苗的叶绿素荧光。参照冯玉龙等^[18]的方法, 针叶暗适应 30 min 后, 用弱测量光测定初始荧光(F_o), 随后给以强闪光(5000 $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$, 脉冲时间 0.7 s)测得最大荧光(F_m), 当荧光产量从 F_m 快降回到 F_o 时, 打开作用光(800 $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$), 当荧光恒定时, 测得稳态荧光(F_s); 再加上一个强闪光(5000 $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$, 脉冲时间 0.7 s)后, 测得能化类囊体最大荧光(F'_m)。

计算得到可变荧光(F_v)= $F_m - F_o$; 光系统 II (PS II) 最大光能转换效率(F_v/F_m); PS II 量子效率(Φ_{PSII})= $(F'_m - F_s)/F'_m$;

光化学猝灭系数 (qP) = $(F'_m - F_s)/(F'_m - F_o)^{[19]}$; 非光化学猝灭系数 (NPQ) = $(F_m - F'_m)/F'_m^{[20]}$ 。

气体交换及叶绿素荧光参数均选用上层侧枝上无遮荫的成熟针叶进行测定。为尽量减小日变化对测量结果产生的影响,以增强可比性,测定均在 9:30~11:00 进行,此期间室内光线充足且变化不大。所有参数的测定均 5 次重复。

1.3 针叶氮、磷含量的测定

将每桶 2 株幼苗针叶全部取下作为 1 个样品,于 80℃ 烘至恒重后粉碎,参照崔晓阳^[21]的方法,采用自动凯氏定氮仪测定全氮含量,采用硫酸-高氯酸溶-钼锑抗比色法测定全磷含量。

1.4 针叶叶绿素、类胡萝卜素及可溶性蛋白含量的测定

按照 Wellburn^[22]推荐的二甲基甲酰胺方法测定叶绿素和类胡萝卜素含量。按照 Bradford^[23]的方法测定可溶性蛋白(TSP)的含量。

所有数据采用 DPS Data Processing System Ver. 3.01^[24]进行统计分析。

2 结果

2.1 供氮水平对落叶松幼苗针叶氮、磷含量的影响

供氮水平的差异显著影响了落叶松幼苗针叶的氮含量。随供氮水平从 1 mmol/L 增加至 16 mmol/L,落叶松幼苗针叶的氮含量几乎呈线性增加(图 1a)。供氮水平也显著影响了针叶的磷含量,但与氮含量的变化趋势不同,随着供氮水平的增加,针叶的磷含量逐渐下降(图 1b)。

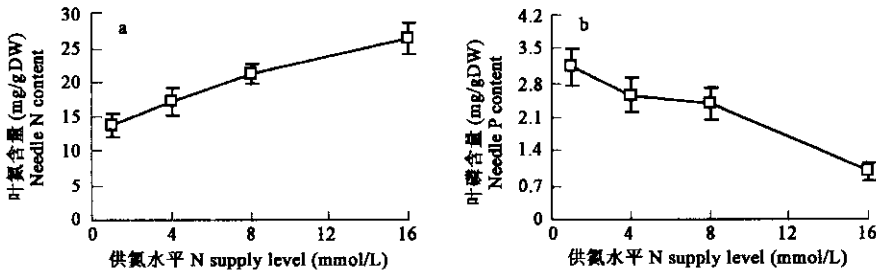


图 1 供氮水平对落叶松幼苗针叶氮含量和磷含量的影响

Fig.1 Effects of nitrogen supply level on nitrogen and phosphorus content in needles of larch seedling

数据为平均值±标准差($n=5$),Data are mean ±SE($n=5$) 标准差线上具有相同字母标记的表示处理间无显著差异 The bars followed by the same letter are not significantly different ($p>0.05$, t -test)

2.2 供氮水平对落叶松幼苗叶绿素、类胡萝卜素及可溶性蛋白含量的影响

从表 1 可看出,随供氮水平的升高,落叶松幼苗针叶的总叶绿素(Chl)含量及类胡萝卜素(Car)含量随之增加,各供氮水平间均达到了显著水平($p<0.05$),但叶绿素 a 与叶绿素 b 之比(Chl a/Chl b)却没有显著差异($p<0.05$)。类胡萝卜素含量与叶绿素含量的比值(Car/Chl)在各供氮水平间有差异,随供氮水平的增加 Car / Chl 呈逐渐下降的趋势。

表 1 供氮水平对落叶松幼苗针叶叶绿素(Chl)含量、类胡萝卜素(Car)含量、叶绿素 a 与叶绿素 b 之比(Chla/Chlb)和类胡萝卜素与叶绿素之比(Car/Chl)的影响

Table 1 Effects of nitrogen supply level on chlorophyll (Chl) content, carotenoid (Car) content, chlorophyll a/chlorophyll b ratio (Chla/Chlb) and carotenoid / chlorophyll ratio (Car/Chl) in needles of larch seedling

供氮水平 N supply level (mmol/L)	叶绿素含量 Chl content(mg/g DW)	类胡萝卜素含量 Car content(mg/g DW)	叶绿素 a/叶绿素 b Chl a/Chl b	类胡萝卜素/叶绿素 Car/Chl
1	3.853±0.422 a	0.755±0.088 a	2.680±0.186 a	0.196±0.004 a
4	5.363±0.821 b	0.937±0.113 b	2.745±0.024 a	0.176±0.007 b
8	7.215±0.475 c	1.217±0.061 c	2.689±0.067 a	0.169±0.008 bc
16	9.467±1.482 d	1.531±0.192 d	2.649±0.153 a	0.162±0.010 c

数据为平均值±标准差($n=5$),Data are mean ±SE($n=5$) 同列具有相同字母标记的数字间无显著差异. The mean within the same column sharing the same letters are not significantly different ($p>0.05$, t -test)

落叶松幼苗针叶的可溶性蛋白(TSP)含量在供氮水平从 1 mmol/L 增加至 8 mmol/L 时呈线性增加,而当供氮水平增加至

16 mmol/L 时, TSP 含量却略有降低。

2.3 供氮水平对落叶松幼苗气体交换参数的影响

饱和和光强下的净光合速率(P_{\max})是最能反映植株光合能力的参数。供氮水平的差异显著影响了落叶松幼苗的光合能力(图 3)。供氮严重不足时(1 mmol/L), 落叶松幼苗的 P_{\max} 最小, 当供氮水平增至 8 mmol/L 时达到最大, 而当供氮水平继续增加至 16 mmol/L 时, P_{\max} 反而有所下降, 但与供氮水平为 8 mmol/L 时的差异未达到显著水平($p < 0.05$)。

图 4 呈现的是不同供氮水平下落叶松幼苗针叶的气孔导度(g_s)和胞间与外界 CO_2 浓度之比(C_i/C_a)的情况。随供氮水平的提高, g_s 逐渐增加, 供氮水平为 8 mmol/L 时达最大, 继续增加供氮, g_s 不再变化(图 4a)。但是除供氮为 1 mmol/L 和 8 mmol/L 之间的 g_s 差异达显著水平外, 其余各处理间差异均不显著。与 g_s 的变化不同, 在供氮严重缺乏(1 mmol/L)时, C_i/C_a 最高, 随供氮水平的提高, C_i/C_a 逐渐下降, 在供氮为 8 mmol/L 时达到稳定状态, 继续增加供氮 C_i/C_a 不再变化(图 4b)。

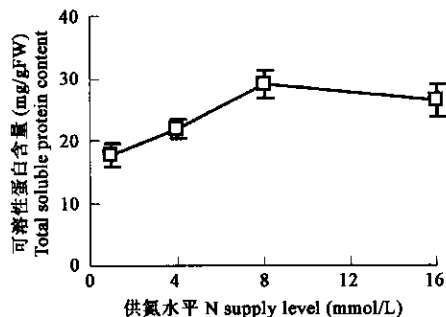


图 2 供氮水平对落叶松幼苗针叶可溶性蛋白含量的影响

Fig. 2 Effects of nitrogen supply level on total soluble protein in needles of larch seedling

数据为平均值 \pm 标准差 ($n=5$), Data are mean \pm SE ($n=5$) 标准差线上具有相同字母标记的表示处理间无显著差异 The bars followed by the same letter are not significantly different ($p > 0.05$, t -test)

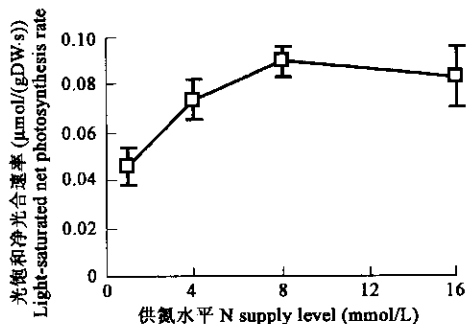


图 3 供氮水平对落叶松幼苗光饱和和净光合速率(P_{\max})的影响

Fig. 3 Effects of nitrogen supply level on light-saturated net photosynthetic rate (P_{\max}) of larch seedling

数据为平均值 \pm 标准差 ($n=5$), Data are mean \pm SE ($n=5$) 标准差线上具有相同字母标记的表示处理间无显著差异 The bars followed by the same letter are not significantly different ($p > 0.05$, t -test)

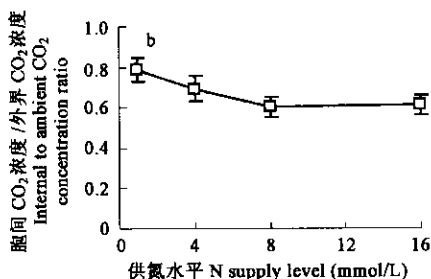
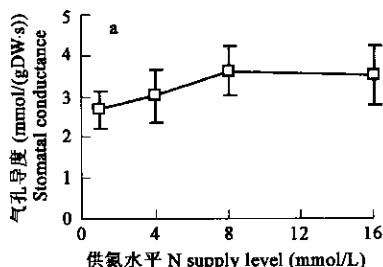


图 4 供氮水平对落叶松幼苗针叶气孔导度(g_s)和胞间与外界 CO_2 浓度之比(C_i/C_a)的影响

Fig. 4 Effects of nitrogen supply level on stomatal conductance (g_s) and internal to ambient CO_2 concentration ratio (C_i/C_a) in needles of larch seedling

数据为平均值 \pm 标准差 ($n=5$), Data are mean \pm SE ($n=5$) 标准差线上具有相同字母标记的表示处理间无显著差异 The bars followed by the same letter are not significantly different ($p > 0.05$, t -test)

2.4 供氮水平对落叶松幼苗叶绿素荧光参数的影响

随供氮水平的提高, 针叶初始荧光(F_0)随之下降, 而最大荧光(F_m)显著升高(图 5)。 F_v/F_m 反映 PS II 反应中心最大光能转换效率, F_v/F_m 的降低是光合作用光抑制的显著特征, 常被作为判断是否发生光抑制的标准^[25], Φ_{PSI} 是指非循环电子传递量子效率, 它可反映 PS II 反应中心实际的光化学活性^[26]。从图 5 也看出, 供氮不足时显著降低 F_v/F_m 和 Φ_{PSI} , 增加供氮可使 F_v/F_m 和 Φ_{PSI} 回升, 但当供氮水平超过 8 mmol/L 后, F_v/F_m 和 Φ_{PSI} 的变化不大。另外, 供氮不足也显著减小了落叶松幼苗针叶的光化学猝灭系数(qP)。然而, 落叶松幼苗非光化学猝灭系数(NPQ)却在供氮严重不足时(1 mmol/L)最高, 供氮水平为 16 mmol/L 时最低, 与供氮水平呈负相关。

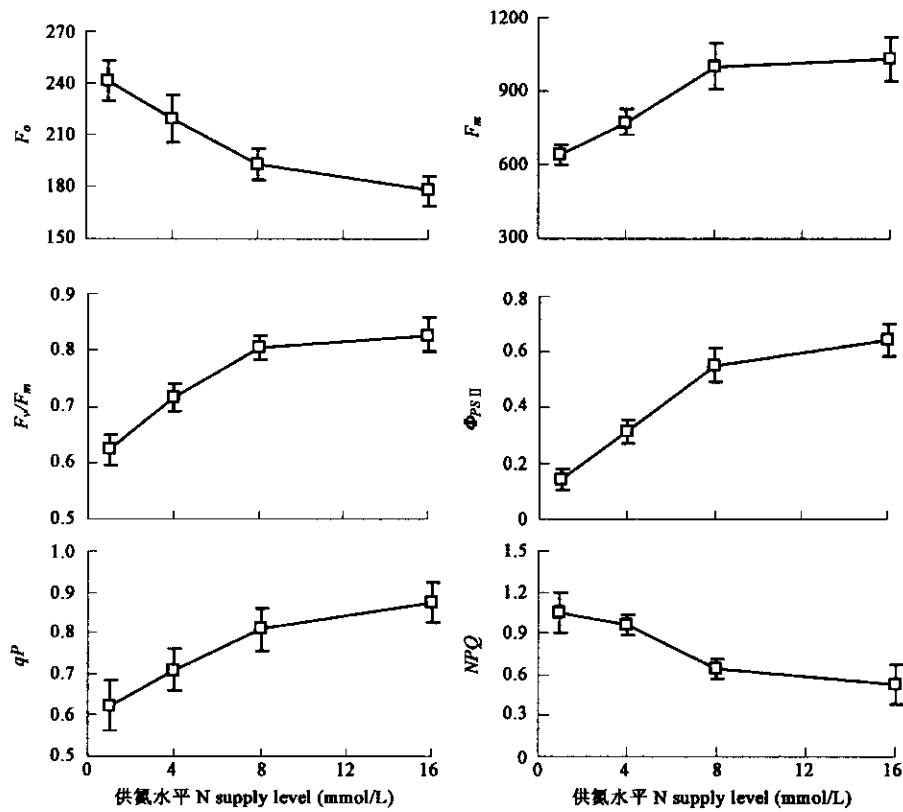


图 5 供氮水平对落叶松幼苗叶绿素荧光参数的影响

Fig. 5 Effects of nitrogen supply level on chlorophyll fluorescence parameters of larch seedling

F_0 初始荧光 Origin fluorescence; F_m 最大荧光 Maximum fluorescence; F_v/F_m 光系统 II 最大光能转换效率 Maximum quantum efficiency of PS II photochemistry; Φ_{PSII} 光系统 II 量子效率 Quantum efficiency of PS II ; qP 光化学猝灭系数 Photochemical quenching co-efficient; NPQ 非光化学猝灭系数 Non-photochemical quenching co-efficient

数据为平均值±标准差 ($n=5$), Data are mean ± SE ($n=5$) 标准差线上具有相同字母标记的表示处理间无显著差异 The bars followed by the same letter are not significantly different ($p>0.05$, t -test)

3 讨论

多数研究表明,植物叶片的氮含量随外界环境中氮有效性的增加而增加^[27~29],即使当供氮过量并限制植物生长时依然如此^[30]。不过,对于当年生水曲柳(*Fraxinus mandshurica*)幼苗,当供氮水平超过 8 mmol/L 时,叶总氮含量开始下降^[10]。落叶松幼苗针叶的氮含量是随着供氮水平的升高而呈线性增加的(图 1)。

许多研究表明植物叶片的氮含量与光合能力有很强的正相关性^[2,3,5]。本实验中,落叶松幼苗针叶的氮含量与其 P_{max} 呈曲线相关(图 6),当叶氮含量超过 24 mg/g 后 P_{max} 开始下降。在西加云杉(*Picea sitchensis*)、美西侧柏(*Thuja plicata*)和西部铁杉(*Tsuga heterophylla*)幼苗^[28]和油桃(*Prunus persica*)^[31]中也有相似的结果。通常而言, P_{max} 随叶氮含量或供氮水平的增加而增加应该是由 g_s 的增加和/或羧化能力的提高的结果。随供氮水平的提高,落叶松幼苗针叶的可溶性蛋白(TSP)含量显著增加,这可能意味着核酮糖-1,5-二磷酸羧化酶(Rubisco)含量的增加及羧化能力的提高,因为 TSP 大部分是由 Rubisco 所组成的^[32]。落叶松幼苗的 g_s 与 P_{max} 呈显著正相关,但 C_i/C_a 在供氮严重不足时(1 mmol/L)最高并随供氮水平的增加而逐渐降低(图 4b),这意味着在低氮水平下低的 g_s 并不是 P_{max} 降低的主要原因,因为只有在 g_s 与 C_i/C_a 都降低时才能说明光合能力的下降是由气孔限制所引起^[33]。由此推断,随供氮水平的提高, g_s 的增加对于

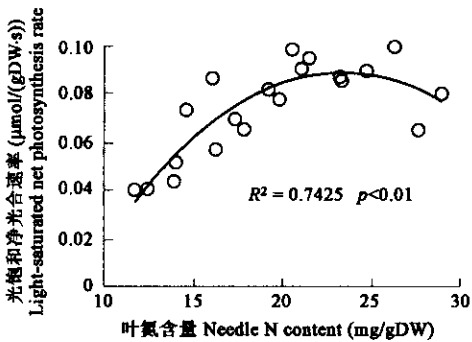


图 6 落叶松幼苗光饱和净光合速率与其叶氮含量的关系

Fig. 6 Relationship between the light-saturated net photosynthetic rate (P_{max}) and nitrogen contents in needles of larch seedling

光合能力的提高可能并不起主要作用。随着供氮水平的提高,叶绿素含量增加而导致的光捕获能力的提高可能是 P_{\max} 增加的另一原因。

供氮过高导致 P_{\max} 和 TSP 含量降低已在许多植物中报道过^[10,13,30]。本研究中过量供氮引发的负面效应可能主要与此时低的叶磷含量有关,低的叶磷含量常被解释为稀释效应^[34,35]或根对磷的吸收能力被抑制^[36,37]。叶片中磷相对于氮的营养失衡将抑制 Robisco 蛋白的合成而导致光合能力的降低^[30]。当供氮水平为 16 mmol/L 时,落叶松针叶的氮磷含量比(N/P)可以高达 28.02 g/g,这一比值已相当于导致花旗松(*Pseudotsuga menziesii*)幼苗生长下降 10%的 20~30 g/g 的域值^[38]。事实上,当供氮水平从 8 mmol/L 增加到 16 mmol/L,落叶松幼苗的 P_{\max} 和 TSP 均未再增加,反而略有下降,说明 16 mmol/L 已经超过落叶松幼苗最适的供氮水平。

与“表观性”的气体交换指标相比,叶绿素荧光参数更具有反映“内在性”的特点。供氮为 1 mmol/L 时,落叶松幼苗针叶的 F_o 升高,同时 F_m 下降(图 5a,b),这意味着 D1 蛋白或反应中心其他组分可能已失活或受到破坏^[39,40]。因为供氮不足通常导致蛋白合成能力的下降,以致光破坏的 PS II 反应中心不能有效的被修复,从而产生光抑制现象。 F_v/F_m 和 Φ_{PSII} 随供氮水平的降低而下降的这一变化(图 5c,d)也说明了在供氮不足时,落叶松幼苗更容易发生光合作用光抑制,而增施氮肥可有效的提高光化学效率,减缓光抑制。相似的结果在小麦^[12]、棉花^[11]、菜豆^[9]及玉米^[41]的研究中也有发现,但也有一些研究中并未发现外界供氮对植株的光化学效率(F_v/F_m)产生影响^[7,8,42]。这种氮依赖的 F_v/F_m 变化的分歧可能是源于植物体内氮有效循环机制的差异和叶内潜在的氮分配格局的不同^[9]。 qP 反映了 PS II 天线色素捕获的光能用于光化学电子传递的份额, NPQ 则反映 PS II 天线色素吸收的光能不能用于光化学电子传递而以热的形式耗散掉的部分。随着供氮水平的降低,落叶松幼苗的 qP 下降,同时伴随着 NPQ 的增加(图 5),这也进一步证明了供氮不足导致了落叶松幼苗的光化学效率降低,使得捕获的光能不能被有效利用,而以热的形式被耗散掉了。另一方面,热耗散也是一种光保护机制,可以防御过剩光能对光合机构造成伤害,热耗散的程度与类胡萝卜素(Car)的含量有关^[25]。为了解生长在不同供氮水平下的植株的光能吸收与光保护的关系,比较了各处理间 Car 含量与 Chl 含量的比值(Car/Chl),结果表明,Car/Chl 随供氮水平的降低而升高(表 1),保护功能增强。 NPQ 和 Car/Chl 的增加可能是落叶松幼苗为防御光破坏而对低的氮供给产生的一种适应性机制^[43]。

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