

不同供硼水平对绿豆植株形态及其叶片生长特征的影响

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摘要: 利用水培以绿豆为材料, 研究不同供硼水平对绿豆植株形态和叶片生长特征的影响。结果表明缺硼抑制绿豆生长, 但对根的影响较对冠的影响更大, 表现在缺硼导致冠根比增大; 缺硼明显抑制叶面积; 降低特定叶面积 (*SLA*), 这可能是由于缺硼影响细胞伸展的缘故, 造成叶片密度增加; 缺硼也提高叶片重量比 (*LWR*) 并导致叶脉间失绿, 说明缺硼叶片可能过量碳水化合物积累, 引起叶绿素降解。与适量供硼比较, 过量供硼也影响绿豆的生长, 但对冠根比没有影响, 表明过量供硼对根和冠具有相同的抑制作用; 硼中毒导致成熟叶片脱落, 从而影响叶面积, 但对特定叶面积 (*SLA*) 和叶片重量比 (*LWR*) 没有影响。

关键词: 硼; 植物形态; 叶片生长特征; *SLA*; *LWR*; 绿豆 (*Phaseolus aureus* Roxb)

Effects of different boron concentrations on the morphology and foliar generalities of mung bean

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Abstract: The effects of boron deficiency and toxicity on the morphology and foliar generalities of mung bean (*Phaseolus aureus* Roxb) were investigated in hydroponic culture. Reduced biomass production in response to limited supply of boron was accompanied by an increased shoot to root ratio. Foliar generalities were also altered by boron deficiency: leaf expansion was inhibited together with specific leaf area (*SLA*), implying that there was a high leaf cell density due to restricted cell expansion. An increased leaf weight ratio (*LWR*) and inter-veinal chlorosis evidenced in boron deficient leaves may indicate excessive carbohydrate accumulation, leading to a decline in chlorophyll content. Compared with shoot to root ratio when optimum boron was supplied, high levels of boron did not induce significant changes in shoot to root ratio, suggesting that supra-optimum boron has similar effects on shoot and root growth. Boron toxicity

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万方数据

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At all harvests, plants were divided into leaves, stem and root. Leaf area was determined with a leaf area meter (Leaf Area Services Ltd, Cambridge, UK). Harvested plant material was then dried at 80 °C for 48 h. Growth parameters were calculated according to Hunt^[11]. The leaf area ratio (*LAR*) is the ratio of

total leaf area to whole plant biomass. The leaf weight ratio (*LWR*) is the ratio of total leaf biomass per plant to the total biomass per plant. The specific leaf area (*SLA*) is the ratio of total leaf area per plant to total leaf biomass per plant. Relative growth rate (*RGR*) is calculated from the following formula:

$$RGR = (\log_e W_2 - \log_e W_1) / (t_2 - t_1)$$

Where, W_2 = total biomass per plant from the final harvest; W_1 = total biomass per plant from the initial harvest. $t_2 - t_1$ = time between harvest (days).

The data were subjected to 2-sample *t*-tests or one-way analyses of variance (ANOVAs) using the statistical package Minitab 11. Where required, Tukey multiple comparison tests were used following ANOVAs to identify significant differences between individual treatments.

2 RESULTS

2.1 Effects of boron on plant morphology and growth parameters

Symptoms of B deficiency were visible in roots after only two days of growth in the absence of B. Root tips were brown and there was a thickening of the apex. Root elongation stopped after two days of B deficiency. After ten days, expansion of the first trifoliate leaf was markedly reduced and growth of the second trifoliate leaf had ceased. No new leaf initials developed thereafter. At the first harvest the primary leaves were dark green, but after twenty days without B the first trifoliate leaves showed inter-veinal chlorosis and at the second harvest, the primary leaves also showed inter-veinal chlorosis

Visible signs of B toxicity first appeared in the primary leaves of plants grown in solution containing 500 μM B after eight days' treatment, by way of marginal chlorosis. Inhibition of root growth with high concentrations of B was seen after a further two days. After fourteen days of treatment the second trifoliate leaf also showed marginal chlorosis. Primary leaves had abscised by the first harvest. After a similar length of treatment the first trifoliate leaves of plants raised in 250 μM B showed similar toxicity symptoms. At the second harvest, marginal chlorosis had spread to all but the newest leaf when 500 μM B was supplied. Plants grown in 50 μM B solution showed no symptoms of deficiency or toxicity during the experiment.

At the first harvest, all B-containing treatments had significantly greater biomass production compared to the no B treatment (Fig. 1a). An absence of B led to diminished RGRs (Fig. 1b) and at the second harvest, the biomass of seedlings grown in the absence of B was only 13% of that when B was supplied at 50 μM . Even when B supply was supra-optimum for growth, at 250 and 500 μM , the biomass of seedlings was significantly higher than that of seedlings which lacked B. Compared with that when B was present, biomass allocation between shoot and root was also altered by the absence of B at both harvests (Fig. 1c). B-deficient seedlings had significantly higher shoot to root ratios; however, at both harvests 500 and 250 μM B did not induce significant changes in shoot to root ratio compared with plants raised in 50 μM B. This may reflect that supra-optimum B concentrations exert similar effects on both shoot and root growth.

B-deprived plants grew the lowest number of leaves at both harvests. At the first harvest, 250 and 500 μM B produced similar numbers of leaves per plant to plants grown in 5 and 50 μM B concentrations. Due to abscission of the old leaves of plants supplied with 500 μM B there were fewer leaves at the second harvest than at the first harvest (Fig. 2a). Total leaf area per plant was also influenced by the supply of B (Fig. 2b). At both harvests plants grown in the absence of B had a significantly smaller total leaf area than those plants supplied with B at 5 and 50 μM . Although 250 and 500 μM concentrations of B were supra-optimal, plants also had a significantly higher leaf area compared to plants which received no B. At the first harvest, B treatment had no significant effect on the mean value of area per leaf (derived

from total leaf area and number of leaves per plant). However, at the second harvest, an absence of B resulted in a significantly lower mean value of area per leaf compared to B-supplied treatments. This probably reflects a B deficiency-related inhibition of leaf expansion of individual leaves. There were no significant differences in mean value of area per leaf between the different B concentrations (Fig. 2c).

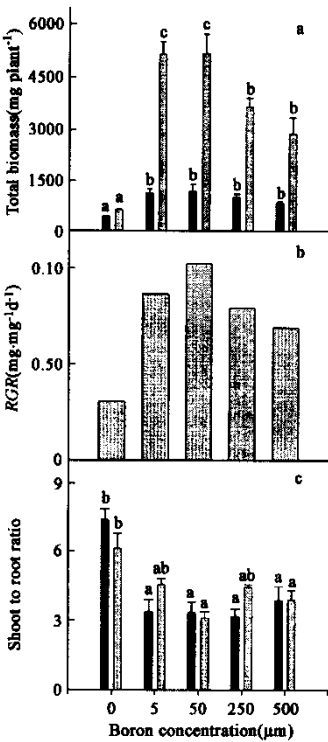


Fig. 1 Effects of boron on total biomass (a), relative growth rate (b) and shoot to root ratio (c)

Data presented are means ± SE of five replicates (except Fig. 1b). For each harvest, means with the same letter are not significantly different ($p < 0.05$). First harvest (■); second harvest (□)

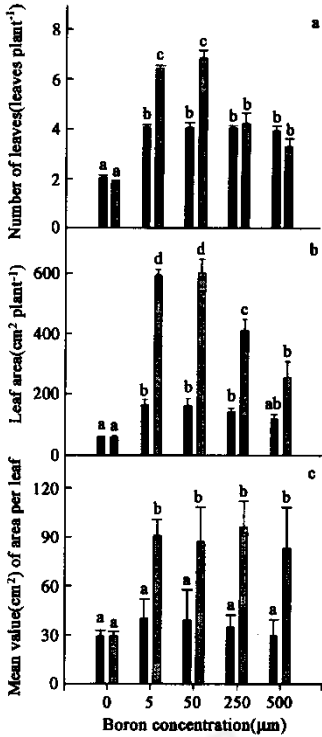


Fig. 2 Effects of boron on number of leaves (a), leaf area (b) and mean value of area per leaf (c)

Data presented are means ± SE of five replicates. For each harvest, means with the same letter are not significantly different ($p < 0.05$). The first harvest (■); second harvest (□)

Similar LARs were measured at the first harvest for all B treatments (Fig. 3a). At the second harvest, however, plants grown in the absence of B and at 500 μM B had significantly smaller LARs than for the other treatments B. An absence of B resulted in an increase in LWR (Fig. 3b). B deficiency also had a marked influence on SLA (Fig. 3c). Although there were no significant differences in SLA between any of the B concentrations for either harvest, the absence of B reduced SLA by about 30% at the first harvest and 50% at the second harvest.

2.2 Effects of boron on foliar generalities

The influence of B deprivation on leaf development was manifest in different ways, depending on the particular leaf in question. Leaf area of the primary leaves was not affected by B treatment at first harvest (Fig. 4b). However, biomass of the primary leaves was significantly greater when supply of B was limited

to 0.05 μM or withheld completely, compared to when B was supplied at 0.5 or 50 μM (Fig. 4a). SLA was therefore lower when B supply was either very limited or absent (Fig. 4c).

Other leaves did not show the same responses to B. The first trifoliate leaf developed most rapidly when B was supplied at 0.05 μM , whereas 50 μM B was optimum for growth of the second, third, fourth and fifth true leaves. The second and subsequent trifoliate leaves did not develop at all in the absence of B, and only two trifoliate leaves developed when B was limited to 0.05 μM . The biomass of the first trifoliate leaf was greatest when B was supplied at 0.05 μM (Fig. 4d). However, leaf area was significantly greater when B was supplied than when it was not, and all concentrations of supplied B produced about the same expansion (Fig. 4e). These trends were observed for both harvests. SLA was, therefore, least at 0.05 μM and greatest for the highest concentration of B employed, 50 μM (Fig. 4f). The second trifoliate leaf responded differently to B (Figs. 4g, h & i). Leaf biomass and area both increased with increasing concentrations of B, but such that SLA was again greatest at 50 μM B. When B was supplied at 0.05 μM , development of the second trifoliate leaf was severely limited compared with the same leaf of plants supplied with 50 μM B (Figs. 4g & h). Foliar development beyond the second trifoliate leaf was limited to plants that were supplied with B at 0.5 and

50 μM B. By the first harvest, the third true leaf had developed in both those treatments while the fourth leaf was only evident at 50 μM B. The fifth leaf was only evident at the time of the second harvest (Figs. 4p & q). Comparisons between the third, fourth and fifth trifoliate leaves at the second harvest showed that 50 μM B resulted in greater leaf biomass and leaf area than did 0.5 μM (Figs. 4j~r).

It was generally noticed that when B was deficient, the leaves were more fragile and had developed inter-veinal chlorosis. At the first harvest, for example, the first trifoliate leaves of plants raised in the absence of B showed chlorosis. So did the second trifoliate leaves of plants grown in 0.05 μM B at the second harvest

3 DISCUSSION

The experiments reported above have demonstrated symptoms of B deficiency and toxicity in plants where a wide range of concentrations of B has been employed. Since the entire focus of this project is concerned with the role of B in plant development, the comments that follow are almost exclusively restricted to deficiency and deficiency of B. Toxicity effects of B will not be discussed here.

The current work has demonstrated that biomass production is depressed when B supply is absent or

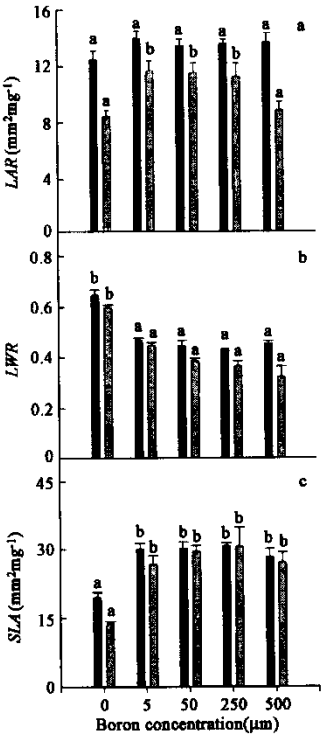


Fig. 3 Effects of boron on leaf area ratio (a), leaf weight ratio (b) and specific leaf area (c). Data presented are means \pm SE of five replicates. For each harvest, means with the same letter are not significantly different ($p < 0.05$). The first harvest (■); second harvest (▨)

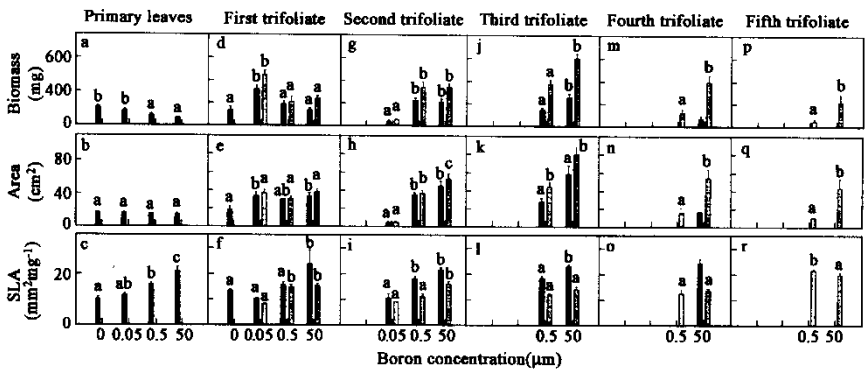


Fig. 4 Effects of boron on foliar generativities

Data presented are means \pm SE of five replicates. For each harvest, means with the same letter are not significantly different ($p < 0.05$). The first harvest (■); second harvest (□).

limited. Such an effect might be predicted on the basis of much previous work which has established and confirmed that B is an essential micronutrient^[4, 12]. Reduced biomass production by mung bean in response to limited B was accompanied by an increased shoot to root ratio (Figs. 1a & c). While both root and shoot growth were diminished when B was in limited supply, the former was more severely restricted than the latter, at least for the duration of the experiments. The increased shoot to root ratio resulting from B deficiency is consistent with the view of Marschner *et al.* (1996)^[13] that only those nutrients which are mobile in the phloem show favoured partitioning to the roots.

Notwithstanding an early influence on root growth, B deficiency had significant influences on leaf development. These have been the focus of the current study. In overall terms, when there was no supply of B to the seedlings only one trifoliate leaf developed (Fig. 4d & e). This could imply that B is necessary for the early stages of leaf development and particularly leaf initiation. Such a proposition would be consistent with the general observation that B is necessary for cell division as in the growth of roots^[7]. Not only were leaf number and area per plant increased when B was supplied at 5 or 50 μM , other leaf characteristics, such as the mean area per leaf, also differed from those of B-deficient plants. Further study of specific or individual leaves in the current report has highlighted several salient points, representing novel observations.

Primary leaves were influenced by limited B supply in that leaf biomass was enhanced, whereas subsequent trifoliate leaves were dependent on B for their expansion as well as their biomass accumulation. Expansion of the primary leaves was not influenced by a lack of exogenously supplied B (Fig. 4b). The development of the first trifoliate leaf of mung bean was enhanced by supply of B at 0.05 μM that, relative to the same leaf on plants deprived of B, enhanced both biomass (Fig. 4d) and expansion (Fig. 4e). At 0.5 μM , however, B was supra-optimal for biomass production but not expansion at the second harvest. Leaf expansion and biomass production of subsequent trifoliate leaves, however, increased with increasing concentrations of supplied B. Collectively, these observations indicate that seed B can sustain primary leaves and only limited development of the first trifoliate leaves. Further leaf development necessitates a supply of B even during the early stages of development of subsequent trifoliate leaves. The requirement of B for leaf expansion as presented here, is consistent with previous reports^[14~16].

Leaf biomass and leaf area did not change in the same proportions with B deficiency. Correspondingly, *SLA* was decreased with B deficiency (Figs. 3c & 4) and *LWR* increased with B deficiency (Fig. 3b). The decrease in *SLA* reflects either increased leaf density or thickness, or both, of leaves when plants were raised under conditions of B deficiency, since *SLA* is a reflection of both leaf density and thickness as indicated by Witkowski and Lamont^[17].

The low *SLA* and greater biomass of primary leaves when B supply was absent may relate to source-sink relationships. The limited growth evidenced in both roots and new leaves under deficient conditions would, presumably, place a lesser demand on the resources of the primary leaves. The decrease in *SLA* in primary leaves may correspond with the accumulation of total non-structural carbohydrate. This could reflect a direct influence of B within the functional leaves themselves or an indirect influence of B exerted elsewhere and influencing source-sink relationships within the plant. Therefore, further investigation of the effect of B on photosynthesis and the carbohydrate status of leaves is necessary.

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