

PLANT ARCHITECTURE OF *PASPALUM VAGINATUM* SCHWARTZ MODIFIED BY NITRATE AND AMMONIUM NUTRITION¹

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ABSTRACT - *Paspalum vaginatum* Schwartz plants were grown under greenhouse conditions in a continuous-flow hydroponic culture, containing NO_3^- or NH_4^+ or NH_4NO_3 as nitrogen source. After 30 days, the size of aerial biomass and root system decreased significantly when plants were supplied with NH_4^+ as exclusive nitrogen source. Compared to NO_3^- treatment, reducing and non-reducing sugars were decreasing together with a significant increase in amino acids content. NH_4^+ -nutrition caused tillers to grow toward an orthogravitropic position (average angle of 68° with respect to the horizontal), and with NO_3^- -nutrition, tillers tended to become diagravitropic (average angle of 23°). With NH_4NO_3 all the parameters measured had values in between those of the other two sources. Thus, the morphologic differences among plants growing in NO_3^- or NH_4^+ nutrition confirm the hypothesis that nitrogen source determines the growth habit of tillers in *P. vaginatum* by modulating the endogenous levels of reducing-non-reducing sugars.

Index terms: nitrogen source, orthogravitropism, diagravitropism, sucrose.

A ARQUITETURA DE *PASPALUM VAGINATUM* SCHWARTZ MODIFICADA PELA NUTRIÇÃO DE NITRATO E AMÔNIO

RESUMO - Plantas de *Paspalum vaginatum* Schwartz foram cultivadas em casa de vegetação, em cultura hidropônica de fluxo contínuo, contendo NO_3^- , NH_4^+ ou NH_4NO_3 como fontes exclusivas de nitrogênio. Após 30 dias, o peso da matéria seca da parte aérea e da raiz diminuiu significativamente quando as plantas receberam NH_4^+ . Comparando esse tratamento com NO_3^- , ocorreu decréscimo no teor de açúcares redutores e não-redutores e aumento significativo no conteúdo de aminoácidos. A aplicação de NH_4^+ causou crescimento das hastes na direção ortogravitrópica (ângulo médio de 68° em relação à horizontal), e nas plantas que receberam NO_3^- , as hastes tendiam a tornar-se diagravitrópicas (ângulo médio de 23°). Com NH_4NO_3 , todos os parâmetros medidos apresentaram valores entre os das outras duas fontes. As diferenças morfológicas entre as plantas nutridas com NO_3^- ou NH_4^+ confirmam a hipótese segundo a qual a fonte de nitrogênio determina o hábito de crescimento das hastes em *Paspalum vaginatum* ao regular os níveis endógenos dos açúcares redutores e não-redutores.

Termos para indexação: fonte de nitrogênio, ortogravitrópico, diagravitrópico, sucrose.

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INTRODUCTION

The growth habit of grasses such as *Cynodon dactylon*, *C. plectostachyum* and *Paspalum vaginatum* is determined by their endogenous sucrose content. This means that high concentrations of non-reducing sugars determine the diagravitropic growth of tillers; moreover plants

tested in environments that diminish their sucrose content, the growth habit of tillers tends to become orthotropics (Montaldi, 1969, 1970, 1973, 1974; Willemoës et al., 1988).

Gnanam et al. (1980) demonstrated that NH_4^+ completely inhibits light activation of two enzymes of photosynthesis, resulting in an accumulation of photosynthetic PGA which is metabolized via pyruvate and Krebs cycle. This leads to an increase in the availability of carbon skeletons for amino acid biosynthesis. Ammonium ions that enter the plant must be immediately assimilated to avoid toxic effects on plant metabolism.

In higher plants, NH_4^+ enrichment increases the flow of newly fixed carbon into TCA-cycle intermediates and amino acids while decreasing the carbon flux into sucrose and starch (Elrifí & Turpin, 1986). In seedling plants supplied with NH_4^+ , Goyal et al. (1982) and Mehrer & Mohr (1989) observed that the carbohydrate reserves quickly disappeared, so that proteins and lipids are used as respiratory substrates.

Different forms of inorganic nitrogen elicit distinct morphogenic effects on plants (Aspinall, 1961; McIntyre, 1971, 1972; Betria & Montaldi, 1976; Leakey et al., 1978; Montaldi et al., 1984) and also act as important regulators of photosynthetic carbon flow (Elrifí & Turpin, 1986).

McIntyre (1965) found in plants of *Agropiron repens* that, by varying the nitrogen supply, it was possible to control the behavior of rhizome buds. In this regard the buds ceased growth at low nitrogen concentration, whereas at high nitrogen concentration, the buds grew out as branches.

Nitrogen supplied as NH_4NO_3 to the rhizomes of *A. repens*, attached to the parent plant, caused the apical bud to develop as a tiller instead of rhizomes (McIntyre, 1972). Moreover, rhizomes growing with low nitrogen supply showed higher carbohydrate content than those growing in a high supply. Montaldi (1970) has shown that NH_4^+ or urea opposed the morphogenic effect of sucrose on diagravitropism of *C. dactylon*.

In this work was tested the hypothesis that nitrogen nutrition determines the growth habit of tillers in *P. vaginatum* by modulating the endogenous concentrations of reducing-non-reducing sugars.

MATERIAL AND METHODS

Plant material and growth condition

Plants of *P. vaginatum* were obtained from phytomers (node with attached leaf, the subtending internode and the axillary bud) rooted on moist vermiculite in a growth chamber at $22 \pm 2^\circ\text{C}$. During 10 days pretreatment period, seedlings were grown into continuously aerated hydroponic culture units that received a half-strength nutrient solution containing 1.0 mM NO_3^- , 0.25 mM H_2PO_4^- , 1.25 mM K^+ , 0.5 mM SO_4^{2-} , 0.25 mM Ca^{2+} , 0.25 mM Mg^{2+} , 19 mM B, 7.2 mM Cl, 3.7 mM Zn, 0.13 mM Cu, 0.05 mM Mo and 10 mM Fe as Fe-Sequestrene (Chaillou et al., 1994) (complete nutrient solution) until the start of the treatments. Seedlings with roots between 5 and 10 cm long were transferred into 200 mL tubes with continuously-flow hydroponic culture (1 plant per tube) and placed in opaque boxes to avoid the effect of light on roots.

The experiment consisted of four treatments on 12 plants each, arranged in a completely random design; the treatments were as follows: (a) Complete nutrient solution; (b) Complete nutrient solution (without NO_3^-) containing 1.0 mM NH_4^+ , as NH_4Cl ; (c) Complete nutrient solution (without NO_3^-) containing 1.0 mol m^{-3} NH_4^+ , as $(\text{NH}_4)_2\text{SO}_4$; (d) Complete nutrient solution containing 0.5 mM NH_4^+ plus 0.5 mM NO_3^- , as NO_3NH_4 . Except for SO_4^{2-} , which was used as the variable ion, concentrations of other nutrients were the same for treatments solutions as for the pretreatment solution, and the pH was adjusted to 6.4. The culture solution was replaced with fresh at 2-day intervals.

The plants were grown in a greenhouse with a photoperiod of 14 hours and day/night temperatures of $24 \pm 5/17 \pm 5^\circ\text{C}$. The photosynthetic photon flux at plant height was about $1,400 \mu\text{mol m}^{-2} \text{s}^{-1}$, measured at noon with a Licor Li-1000 Data Logger.

The plants were grown for 4 weeks after starting the treatments.

Measurements

Plant parts were separated into shoots (stems and leaves) and roots. Shoots and roots were dried at 80°C , 72 hours, for dry weight (DW). The number of tiller, stolons and internode stolon lengths were determined. Average tiller angle with respect to the horizontal was measured with a protractor.

Each sample (1 g fresh weight) was ground with mortar and pestle and extracted in 5 mL of methanol-chloroform-water (MCW). Total amino acids were evaluated by the

method of Yemm & Cocking (1955). The method of Bradford (1976) was used for protein determinations using bovine serum albumin as the protein standard. Total nitrogen was measured by micro-Kjeldahl digestion and the NH_4^+ determined by the Nessler method, as described by Linder & Harley (1942). Reducing and total sugars were analyzed by the Somogy method (Cronin & Smith, 1979), in 95% (v/v) ethanol extracts. Respiration rates were measured in shoots, with a Gilson differential respirometer.

The effects of the different treatments were determined by analysis of variance (ANOVA). Differences among treatments means were analyzed by the LSD at 0.05 probability level.

RESULTS AND DISCUSSION

The aerial and root biomass showed a sharp reduction in plants treated with NH_4^+ , mostly by decreasing shoot growth compared to root growth. Plants supplied with NH_4Cl and $(\text{NH}_4)_2\text{SO}_4$ decreased the shoot growth by 65% with respect to NO_3^- , whereas, NH_4NO_3 decreased the shoot growth by 57%. Roots growth decreased by 56%, 56% and 49%, respectively (Fig. 1). In a young leaf, where

rapid photosynthesis occurs, NO_3^- reduction consumes a large quantity of reducing power. In view of the increased requirements for photochemical energy in NO_3^- reduction, one might expect NH_4^+ -N plants to grow better than NO_3^- -N plants. However, the NH_4^+ -supplied plants generally exhibit less growth than NO_3^- -N plants. Chaillou et al. (1994); Raab & Terry (1994); Rideout et al. (1994), have also observed this detrimental effect of NH_4^+ compared to NO_3^- nutrition in *Beta vulgaris* and in soybean. Other researchers have found that NH_4^+ nutrition decrease dry matter (Lewis & Chadwick, 1983; Lindt & Feller, 1987; Salsac et al., 1987; Ota et al., 1988; Lewis et al., 1989).

Fig. 2 shows that in our experiments dark respiration was 56% less in NO_3^- -N plants than it was in NH_4^+ -N ones. Elrifi & Turpin (1986) showed that NH_4^+ resulted in a large stimulation of dark respiration, so they proposed that the suppression of photosynthetic carbon fixation, in response to nitrogen supply, was the result of a competition for metabolites between the Calvin cycle and nitrogen assimilation. On the other hand, Gnanam et al (1980) and Giengenberger & Stitt (1991) conclude that an

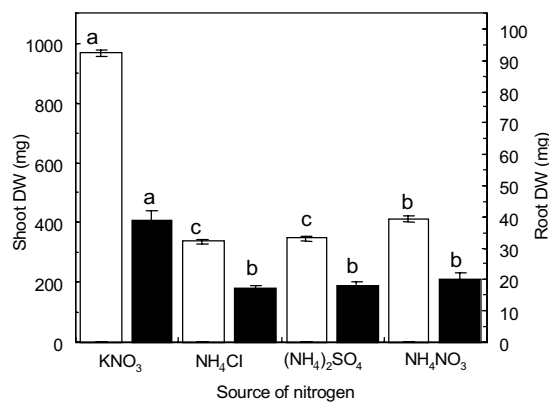


FIG. 1. Dry matter accumulation in shoot (□) and roots (■) of *P. vaginatum*, when 1.0 mM NO_3^- , 1.0 mM NH_4^+ (as NH_4Cl or $(\text{NH}_4)_2\text{SO}_4$) and 0.5 mM NH_4^+ plus 0.5 mM NO_3^- were supplied during 30 days. For each treatment values are means of 12 replicate plants. Vertical bars represent \pm SE. Bars with different letters differ significantly by LSD test, $P = 0.05$.

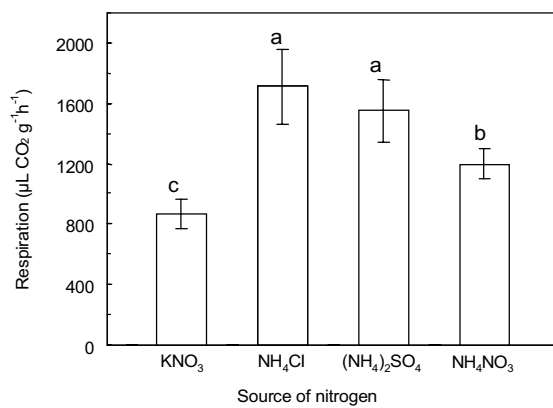


FIG. 2. Shoot respiration of *P. vaginatum*, when 1.0 mM NO_3^- , 1.0 mM NH_4^+ as $(\text{NH}_4\text{Cl}$ or $(\text{NH}_4)_2\text{SO}_4$) and 0.5 mM NH_4^+ plus 0.5 mM NO_3^- were supplied during 30 days. For each treatment values are means of 12 replicate plants. Vertical bars represent \pm SE. Bars with different letters differ significantly by LSD test, $P = 0.05$.

increase in the respiration may be due to a faster turnover of pyruvate and Krebs cycle, so speeding up carbohydrate breakdown and, as a consequence, there are more carbon chains to form amino acids.

In our experiments NH_4^+ -N caused a significant increase in amino acids content ($80.29 \mu\text{mol g}^{-1}$ DW) as compared with NO_3^- -N plants ($33.17 \mu\text{mol g}^{-1}$ DW) (Fig. 3). Similar results were encountered in other species, that is the amino acids content was higher in NH_4^+ -N plants compared to NO_3^- -N ones (Chaillou et al., 1986a, 1986b; Rideout et al., 1994; Osaki et al., 1995). Our results are also consistent with those of Mohamed & Gnanam (1977), Platt et al. (1977), Bassham et al. (1981) and Chaillou et al. (1986a) who proposed that NH_4^+ ion diverted the assimilated carbon mainly towards amino acids.

Although plants grew less under NH_4^+ than in NO_3^- solution, their leaves accumulated nitrogen at almost equal rate. Fig. 4 shows no significant differences in the total nitrogen content. On the other hand, NH_4^+ -N supply increased the synthesis of soluble protein (Fig. 3). These results agree with those of Raab & Terry (1994), who found that soluble leaf

protein increased significantly in NH_4^+ -N plants compared to NO_3^- -N.

In the experiments of this work, plants treated with NH_4^+ , as exclusive nitrogen source, showed lower level of total sugars (8.13% shoot DW) than those treated with NO_3^- (11.30% shoot DW) (Fig. 4). The rapid assimilation of NH_4^+ in glutamine led to a consumption of carbon skeletons, causing depletion of the foliar starch, sucrose and maltose (Raab & Terry, 1995), likewise Mehrer & Mohr (1989) concluded that the consumption of fixed carbon during the assimilation of NH_4^+ could appreciably reduce carbohydrates storage. Also with NH_4^+ -N supply, the endogenous content of nonreducing sugars decreased significantly, the Fig. 5 shows that the accumulation of non-reducing sugars was substantially less than in NO_3^- -fed plants (1.04% DW and 2.87% DW, respectively). Raab & Terry (1994) showed that NO_3^- -N plants had higher activities of sucrose synthase than NH_4^+ -N plants, in the latter system the activity of acid invertase doubled that of NO_3^- -N plants.

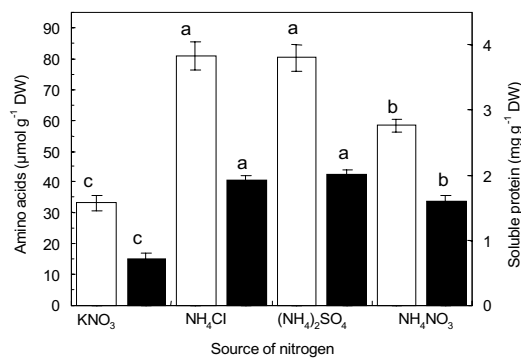


FIG. 3. Total amino acids (□) and soluble protein (■) in shoots of *P. vaginatum*, when 1.0 mM NO_3^- , 1.0 mM NH_4^+ (as NH_4Cl or $(\text{NH}_4)_2\text{SO}_4$) and 0.5 mM NH_4^+ plus 0.5 mM NO_3^- were supplied during 30 days. For each treatment values are means of 12 replicate plants. Vertical bars represent \pm SE. Bars with different letters differ significantly by LSD test, $P = 0.05$.

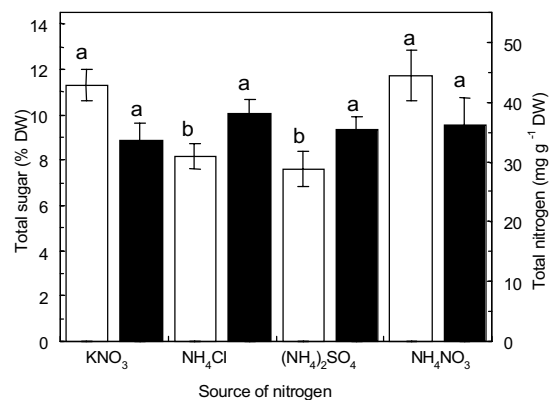


FIG. 4. Total sugar (□) and total nitrogen (■) in shoots of *P. vaginatum*, when 1.0 mM NO_3^- , 1.0 mM NH_4^+ (as NH_4Cl or $(\text{NH}_4)_2\text{SO}_4$) and 0.5 mM NH_4^+ plus 0.5 mM NO_3^- were supplied during 30 days. For each treatment values are means of 12 replicate plants. Vertical bars represent \pm SE. Bars with different letters differ significantly by LSD test, $P = 0.05$.

The decrease in non-reducing sugars content with NH_4^+ -N treatment caused the tillers to grow tending toward an orthogravitropic position ($\text{NH}_4\text{Cl} = 68^\circ$; $(\text{NH}_4)_2\text{SO}_4 = 45^\circ$) with longer internodes (18.9 and 19.5 mm, respectively) and less stolons. On the other hand, plants treated with NO_3^- -N that reached a higher content of endogenous non-reducing sugar, their tillers tended to become diagravitropic (23°), with shorter internodes (11.3 mm), and a significant increase in the stolon number per plant (2.91, NO_3^- -N versus 0.45, NH_4^+ -N) (Figs. 6 and 7).

The lower sucrose content of erect shoots of NH_4^+ -N plants, as compared with prostrate stolon of NO_3^- -N plants, is consistent with the hypothesis that the nitrogen nutrition and endogenous levels of reducing-non-reducing sugar determine the growth habit of tiller in *P. vaginatum*. Therefore, the canopy architecture of plants supplied with NO_3^- was strikingly different from that of plants treated with NH_4^+ (Fig. 8). Morphogenic differences among plants as a consequence of different nitrogen sources, result from a variation in the orthogravitropic/diagravitropic ratio of the tiller growth, the length of internodes and the growth angles of shoots and stolons with respect to the horizontal. Those characteristics were found also in *C. dactylon* by Montaldi (1970, 1974)

and in *P. vaginatum* by Willemoës et al. (1988). Moreover, in agreement with Kojima & Sonoike (1985) and Osaki et al. (1995), it was found that the nitrogen form affects the development and growth pattern of the plant.

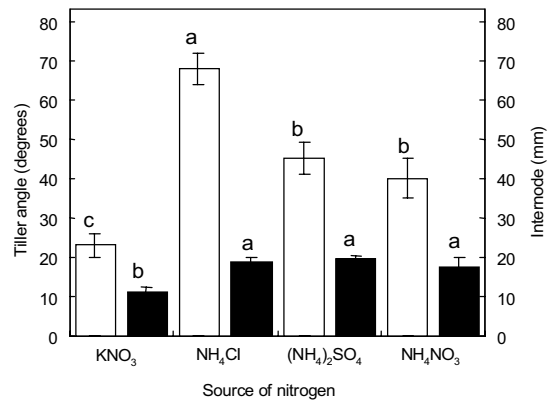


FIG. 6. Average tiller angle the horizontal \square and internodes length \blacksquare of *P. vaginatum*, when 1.0 mM NO_3^- , 1.0 mM NH_4^+ (as NH_4Cl or $(\text{NH}_4)_2\text{SO}_4$) and 0.5 mM NH_4^+ plus 0.5 mM NO_3^- were supplied during 30 days. For each treatment values are means of 12 replicate plants. Vertical bars represent \pm SE. Bars with different letters differ significantly by LSD test, $P = 0.05$.

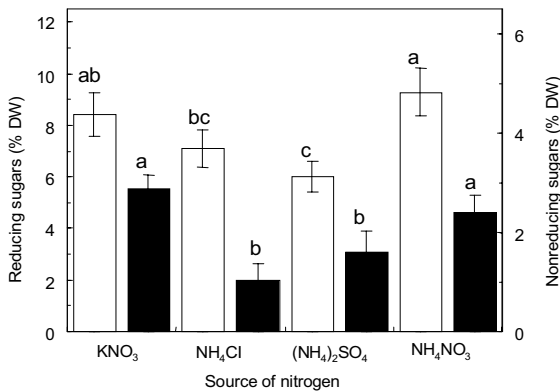


FIG. 5. Reducing sugars \square and nonreducing sugars \blacksquare in shoots of *P. vaginatum*, when 1.0 mM NO_3^- , 1.0 mM NH_4^+ (as NH_4Cl or $(\text{NH}_4)_2\text{SO}_4$) and 0.5 mM NH_4^+ plus 0.5 mM NO_3^- were supplied during 30 days. For each treatment values are means of 12 replicate plants. Vertical bars represent \pm SE. Bars with different letters differ significantly by LSD test, $P = 0.05$.

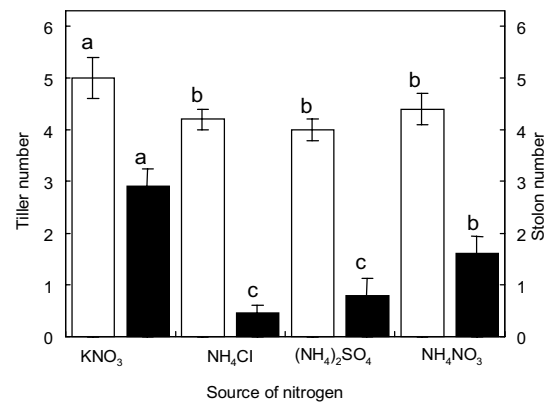


FIG. 7. Tiller number \square and stolon number \blacksquare of *P. vaginatum*, when 1.0 mM NO_3^- , 1.0 mM NH_4^+ (as NH_4Cl or $(\text{NH}_4)_2\text{SO}_4$) and 0.5 mM NH_4^+ plus 0.5 mM NO_3^- were supplied during 30 days. For each treatment values are means of 12 replicate plants. Vertical bars represent \pm SE. Bars with different letters differ significantly by LSD test, $P = 0.05$.

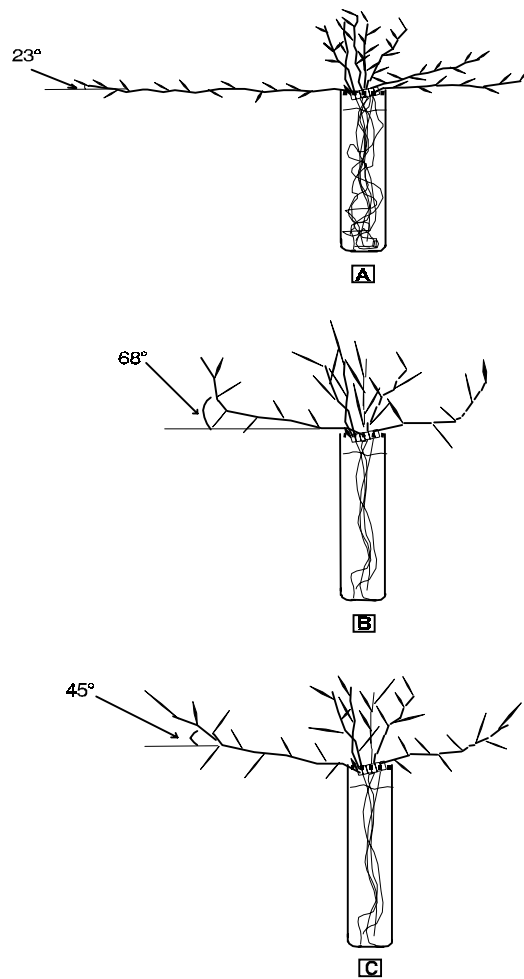


FIG. 8. Seedling scheme of *P. vaginatum*, 30 days old, illustrating the effects of the nitrogen supply on plant architecture (i.e. tiller angle, internode length and stolon number).
 [A] 1.0 mM NO_3^- ; [B] 1.0 mM NH_4^+ ;
 [C] 0.5 mM NO_3^- plus 0.5 mM NH_4^+ .

CONCLUSIONS

1. The morphogenic impact of different nitrogen sources absorbed by *P. vaginatum* results from changes in the endogenous sucrose content.

2. Such changes determine the plant architecture, modifying the orthogravitropic/diagravitropic ratio of tiller growth.

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