Nitrogen Level and Form Affect Taro Growth and Nutrition

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Abstract. Nitrogen (N) is often the most limiting mineral nutrient for taro growth. Two experiments were carried out under hydroponics conditions to determine the effects of varying solution N levels and N form on taro (*Colocasia esculenta* L. Schott cv. Bun Long) growth and foliar nutrient concentrations for 42 days. In the first experiment, taro plants were grown at six NH_4NO_3 levels (0, 0.25, 0.5, 1.0, 2.0, and 4.0 mM N). In the second experiment, taro plants were grown at a total N level of 3 mM with five nitrate (NO_3^-) : ammonium (NH_4^+) percent molar ratios (100:0, 75:25, 50:50, 25:75, and 0:100). In the N level experiment, dry matter and leaf area increased up to 2 mM N and then decreased at the highest N level. The reduced growth of taro at the highest N level was attributed in part to a high NH_4^+ level that reduced uptake or translocation of cations, such as Ca^{2+} , Mg^{2+} , and Mn^{2+} . Nitrogen concentration in leaf blades increased with increasing N levels. The critical foliar N concentration that coincided with 95% of maximum growth based on a quadratic model was $40.4 \text{ g} \cdot \text{kg}^{-1}$ (dry weight basis). In the N form experiment, NO_3^- : NH_4^+ ratios of 75:25 or 100:0 favored greater plant growth compared to other treatments. Taro plants grown in NH_4^+ -rich solutions drastically acidified the solution pH, and had retarded growth and smaller leaf area compared to those grown in NO_3^- -rich solutions.

Taro is a crop commonly cultivated in the tropics, especially in the Pacific basin, where the leaves are consumed as vegetable and corms as staple (De la Pena and Plucknett, 1972). In highly weathered soils, one of the most important constraining production factors is nitrogen (N) deficiency (Sanchez and Logan, 1992). Dryland and wetland taro positively responded to N fertilization (De La Pena and Plucknett, 1972; Manrique, 1994; Silva et al., 1990). Plant growth, foliar N concentration, and yield increased as a result of N application with a maximum yield at N rates of 560 and $1120 \text{ kg} \cdot \text{ha}^{-1}$ for upland and lowland conditions, respectively.

In well-aerated, warm, nonacidic soils, NO_3^- is the predominant N form present in the soil solution due to the activity of nitrifying bacteria (Layzell, 1990). Nitrate levels in soil solution typically range from 0.8 to 2.4 mM (Barber, 1995), while NH_4^+ is usually below 1.0 mM (Marschner, 1995). In acidic or

flooded soils, in which the activity of nitrifying bacteria is reduced, NH_4^+ is the predominant N form present (Layzell, 1990). Due to the requirement for charge balance when N is absorbed as NO_3^- , the rhizosphere is alkalized, but when plants absorb NH_4^+ , the rhizosphere is acidified (Marschner and Romheld, 1983). Such soil pH changes could affect microbiological activity and pathogenic relationships with soil microorganisms (Osuna et al., 1991). The form of N supply plays a key role in the cation-anion relationships in plants, since both NH_4^+ and NO_3^- represent $\approx 70\%$ to 80% of the cations and anions absorbed by plants. At low N concentrations in nutrient solution the growth differences between plants supplied with NH_4^+ or NO_3^- are small, however, with increasing external N concentrations, the advantage of NO_3^- as sole source of N increases for most plants (Gerendas and Sattelmacher, 1990).

The response to N form varies with plant species. For example, Scoggins and Mills (1998) recently found that the growth and nutritional status of poinsettia (*Euphorbia pulcherrima* Willd. ex Klotzsch) grown in nutrient solution was favored by high NO_3^- concentrations, whereas NH_4^+ had deleterious effects. Similar results were obtained in *Vinca* sp. (Thomas and Latimer, 1995), wheat (*Triticum aestivum*) (Xu et al., 1992), cucumber (*Cucumis sativus*) (Heuer, 1991), and bell pepper (*Capsicum annuum*) (Marti and Mills, 1991) grown in nutrient solution. However, some plants prefer NH_4^+ as the major source of N. For example, rice (*Oryza sativa* L.) (Magalhaes and Huber, 1991) and maize (*Zea mays* L.) (Anderson et al., 1991). In general, the best results are obtained when there is a mix of both N forms in solution (Errebhi and Wilcox, 1990).

Given the adaptation of taro to flooded conditions (De la Pena and Plucknett, 1972) we predicted that taro would prefer NH_4^+ as N-source. To our knowledge, there were no previous studies conducted on N form effects on taro. The objectives of these experiments were to determine the effects of different N levels and NO_3^- : NH_4^+ ratios on growth and foliar nutrient concentration of taro seedlings grown in nutrient solution.

Materials and Methods

Two experiments were conducted in greenhouses in the Univ. of Hawaii at Manoa ($21^\circ 19' \text{N}$, $157^\circ 58' \text{W}$). In both experiments, propagating materials (0.5 cm of upper corm plus 30 cm of lower petiole) of taro cv. Bun long were grown for a week in a 1 perlite : 1 vermiculite medium (v/v). Rooted taro propagating materials were washed to remove adhered substrate from roots and then selected for uniform size within replicates. One seedling was placed per pot on a plastic rack located directly above 10 L of an aerated nutrient solution in polyethylene buckets following the procedure of Miyasaka et al. (1993). During the first week after transplanting, some plants that exhibited poor growth were replaced.

N level experiment. This experiment was carried out from 28 Jan. to 11 Mar. 1997 with six N levels (0, 0.25, 0.5, 1.0, 2.0, and 4.0 mM) as NH_4NO_3 in the nutrient solution. The basal nutrient solution was a modified Steinberg solution (Miyasaka et al., 1993) that had the following composition (mM): 0.2 P, 1.2 K, 1 Ca, 0.4 Mg, and 0.8 S. Micronutrients were supplied in the following concentrations (μM): 2 Mn, 6 B, 1 Zn, 0.5 Cu, 0.1 Mo, and 10 Fe. The nutrient sources used were analytical grade chemicals: $\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$, NH_4Cl , $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$, K_2SO_4 , K_2HPO_4 , CaCl_2 , $\text{MnSO}_4 \cdot \text{H}_2\text{O}$, $\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$, $\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$, H_3BO_3 , $\text{H}_2\text{MoO}_4 \cdot \text{H}_2\text{O}$, KCl, and Fe-ethylene diamine Di-o-hydroxyphenyl acetic acid. The pH of the solution was adjusted to 6.0 using 0.25 mM of a buffer solution MES (2-[N-morpholino]ethanesulfonic acid) (Miyasaka et al., 1988) and NaOH.

N form experiment. This experiment was carried out from 28 Jan. to 11 Mar. 1999, and the treatments consisted of five NO_3^- : NH_4^+ ratios (100:0, 75:25, 50:50, 25:75, and 0:100) at a total N concentration of 3 mM. The basal nutrient solution had a pH of 6.4 with the following macronutrient composition (mM): 0.13 P, 0.43 K, 0.35 Ca, 0.29 Mg, 0.14 S, and 0.04 Na. Macronutrient levels were reduced from the first trial to provide adequate cation levels but to minimize Cl concentrations to below the 4.9 mM level that causes salinity stress in taro (Hill et al., 1998). Micronutrients were supplied in concentrations similar to those used in the first experiment. Solution pH was buffered with 0.25 mM MES as described for the first experiment.

Sampling and analysis. Solution pH was measured weekly throughout the course of both experiments. Nondestructive measurements of chlorophyll were taken using a chlorophyll-

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meter (SPAD-502; Minolta, Tokyo) (MacKown and Sutton, 1998) at 28 and 42 d after transplanting. Plants were removed from the nutrient solution 42 d after transplanting, washed in deionized water, and divided into roots, corms, petioles, and leaf blades. Leaf lamina area was determined with a leaf area meter (LI-3100; LI-COR, Lincoln, Nebr.). All plant parts were subsequently dried in a forced air oven at 60 °C to constant weight, and then weighed. Leaves were passed through a 1-mm mesh and then ashed in a muffle furnace and analyzed for Ca, Mg, K, P, Mn, Zn, Cu, Fe, and B using an inductively coupled plasma spectrometer (model 6500; Perkin-Elmer, Norwalk, Conn.) (Isaac and Johnson, 1998). Total N was determined by a micro-Kjeldahl method (Nelson and Sommers, 1972).

In each experiment, a completely randomized design with three replicates was used. Data were subjected to analysis of variance, trends, and regression to identify significant treatment effects ($P \leq 0.05$) (Little and Hills, 1978; Neter et al., 1996) using SAS (SAS Institute, Cary, N.C.) program. In the second experiment, the molar ratio of NH_4^+ , expressed as percentage (0–100), was used as the independent variable for the regression analysis.

Results

N level experiment. At 0, 0.25, and 0.5 mM N, leaf blades appeared chlorotic due to N deficiency. Increasing solution N levels increased and then significantly decreased total plant dry (Table 1). A quadratic model fit the data well for total dry weight (TDW) ($\text{TDW} = 7.99 + 7.29 N_s - 1.65 N_s^2$; $r^2 = 0.64$), where N_s is the concentration of N in solution. Increasing solution N levels significantly increased foliar N concentration (Table 1).

There was a significant quadratic relationship between leaf blade N concentration and total plant dry matter (Fig. 1). The critical foliar N concentration corresponding to 95% of the maximum growth determined by this quadratic model was 40.4 g·kg⁻¹ leaf tissue.

Leaf blade Ca, Mg, and Mn concentrations were negatively affected by increasing solution N levels ($P \leq 0.05$) (Table 1). Foliar P, K, Na, Fe, Cu, Zn, and B concentrations were unaffected by N treatments. Total N, P, and K contents were significantly ($P \leq 0.05$) higher when N concentration in the solution increased. Other nutrients exhibited a similar

tendency but there were no significant differences among treatments.

The initial solution pH was 6.0, but after 4 weeks of growth it dropped to ≈ 3.0 at 0.0 to 0.5 mM N, and to ≈ 2.5 at the 1.0 to 4.0 mM N levels. Solutions were changed and pH readjusted to 6.0 at 4 weeks. At harvesting, the solution pH was 3.4 in all N concentrations except in the zero-N level, which had a pH of 7.3.

Nitrogen form experiment. Plants grown in a solution rich in NO_3^- (100:0 and 75:25) had significantly greater dry weights than those grown in a solution rich in NH_4^+ (25:75 and 0:100) (Fig. 2). There were significant decreases in the dry weight of roots (DWR) ($P \leq 0.0001$), petioles (DWP) ($P \leq 0.0001$), and leaf blades (DWL) ($P \leq 0.0001$) with an increasing proportion of NH_4^+ . Quadratic regression models were significant ($P < 0.05$) and their coefficients of determination (r^2) were above 0.80 (Fig. 2). Corm dry weights were not significantly affected by treatments (data not shown), possibly due to their high coefficient of variation (32.4%) or to the short duration of growth which apparently was not sufficient for the formation of new corm material.

Increasing the proportion of NH_4^+ significantly decreased leaf area ($P \leq 0.001$, Fig. 3). A quadratic model fitted the data well ($P \leq 0.0001$; $r^2 = 0.84$). The highest leaf area was obtained at NO_3^- : NH_4^+ ratios of 75:25 or 100:0, with no significant differences between these two treatments. The treatment with 100% NH_4^+ had the lowest leaf area.

At 28 d after transplanting, significant differences ($P \leq 0.05$) in chlorophyll content were detected among treatments, with the lowest value found at the 75:25 treatment and the highest value at the 0:100 treatment (NH_4^+ -rich solution) (Table 2). Since these results were opposite to those obtained for DWL, they suggest that the inhibition of leaf expansion was greater than the reduction in the content of chlorophyll; similar to the dilution effect reported for P deficiency in some crops (Rao and Terry, 1989). At harvest, there were no significant differences among treatments with respect to chlorophyll content (Table 2).

An increasing proportion of NH_4^+ significantly increased leaf concentrations of N ($P \leq 0.05$) and B ($P \leq 0.01$) (Table 2). Other nutrient concentrations in leaf blades were not significantly affected. The treatment with 100% NH_4^+ (0:100) had a significantly greater foliar N concentration compared to other treatments.

The lowest N concentrations in leaf blades were obtained with NO_3^- -rich treatments (75:25 and 100:0); however, the total amount of N accumulated in leaf blades was significantly greater in plants fertilized with NO_3^- (data not shown). A similar situation was observed with B (Table 2), which indicated that growth was stunted to a greater degree relative to the uptake and translocation of N and B (reverse growth dilution effect, see Jarrell and Beverly, 1986). The NO_3^- -rich treatments (75:25 and 100:0) also resulted in higher total contents of all other nutrients in leaf blades compared to the NH_4^+ -rich treatments (data not shown).

In this experiment, there was also a strong decline of the solution pH in the NH_4^+ -rich treatments despite buffering and changes of nutrient solution. Solution pH values decreased to as low as 3.1 in the 100% NH_4^+ solutions.

Discussion

Total plant dry matter and leaf area increased and then decreased with increasing NH_4NO_3 levels in the first experiment (Table 1). The highest solution N level of 4 mM N had a negative effect on plant growth. Similar results were found by Miyasaka (1979) in which higher levels of NH_4NO_3 depressed yield and biomass of taro cv. Lehua Maoli grown for 6 months in solution culture.

Such an inhibitory effect of increased NH_4NO_3 levels seems to be associated with a reduction in the foliar concentration of certain cations, particularly Ca, Mg, and Mn (Table 1). Possibly, uptake of NH_4^+ interfered with the absorption and translocation of cations (Bernardo et al., 1984; Hamlin et al., 1999; Traore and Maranville, 1999). The critical foliar concentration of Ca in 49 day-old taro cv. Lehua Maoli was 4.0 g·kg⁻¹ (Miyasaka, 1979). The critical concentration of Mg in 33 day-old taro cv. Bun Long was 1.4 g·kg⁻¹ (Austin et al., 1994). The critical foliar concentration of Mn in taro cultivars Niue and Alafua Sunrise was 21 mg·kg⁻¹ (O'Sullivan et al., 1995). Based on these critical foliar concentrations, the tissue levels of Ca, Mg, and Mn were adequate but they had a tendency to decrease with the increases in solution NH_4^+ concentration. The foliar concentrations of other cations also appear to be above the critical concentrations (Ares et al., 1996; O'Sullivan et al., 1995).

Based on a quadratic model, the critical foliar N concentration that corresponded to

Table 1. Effects of the solution N concentration on the mean total dry weight (TDW), leaf area (LA), and nutrient concentration of the leaf blades of taro 'Bun Long' plants.

N solution (mM)	TDW (g/plant)	LA (cm ² /leaf)	N	P	K	Ca	Mg	Na	Mn	Fe	Cu	Zn	B
			-(g·kg ⁻¹)										
0.0	8.0	129	29	4.0	36	24	7.5	2.7	564	317	19	56	117
0.25	8.1	393	35	5.2	37	19	4.5	0.7	459	129	11	35	58
0.5	12.5	487	35	5.1	42	19	4.1	0.9	477	215	11	33	58
1.0	14.9	739	39	5.3	44	16	3.7	0.7	200	119	10	33	57
2.0	14.3	636	47	5.2	46	11	3.1	0.6	117	79	15	39	40
4.0	10.9	648	55	6.1	46	13	3.5	0.7	125	133	22	48	57
Trend analysis ^a	Q	NS	Q	NS	NS	L	Q	NS	Q	NS	NS	NS	NS
(P-value)	<0.01		<0.01			<0.01	<0.05		<0.01				

^aL = linear; Q = quadratic; $\text{TDW} = 7.99 + 7.29 N_s - 1.65 N_s^2$ ($r^2 = 0.64$), $N = 30.9 + 10.91 N_s - 1.05 N_s^2$ ($r^2 = 0.93$), $\text{Ca} = 20.39 - 2.46 N_s$ ($r^2 = 0.41$), $\text{Mg} = 6.22 - 3.09 N_s + 0.61 N_s^2$ ($r^2 = 0.47$), and $\text{Mn} = 571 - 373 N_s + 65.5 N_s^2$ ($r^2 = 0.77$), where, N_s = concentration of N in the solution.

^{NS}Nonsignificant.

Fig. 1. Quadratic relationship between 'Bun Long' taro plant dry weight and N concentration in leaf blades. The arrow indicates leaf blade N concentration at 100% of maximum plant dry weight.

Fig. 2. Effects of the N form ratio on the dry weight (DW) of 'Bun Long' taro plant parts (P = petioles; R = roots; L = leaf blades) (pNH_4 = molar ratio of NH_4^+ expressed as percentage, 0–100).

95% of maximum growth was 40.4 g.kg^{-1} (dry weight basis). Our results are consistent with the leaf N critical level of 37 g.kg^{-1} proposed by O'Sullivan et al. (1995) for the second youngest fully matured leaf of cultivars Niue and Alafua Sunrise. Also, Silva et al. (1990) proposed an adequate range of $42\text{--}46 \text{ g.kg}^{-1}$.

In the N form experiment, the best growth and leaf nutrient accumulation was observed when taro plants were grown in a solution with NO_3^- as the predominant N form. The best treatments were solutions containing either a proportion of 75% NO_3^- and 25% NH_4^+ or 100% NO_3^- . Plants are able to store NO_3^- in root cell vacuoles without detrimental effects and without the immediate necessity of metabolism in the roots (Layzell, 1990). In contrast, NH_4^+ is quite toxic even at low concentrations and must be incorporated into organic compounds in roots, requiring an abundance of carbon skeletons (Layzell, 1990; Marschner, 1995). In our experiment, root growth was inhibited when taro plants were supplied with the NH_4^+ -rich solutions (Fig. 2).

In NH_4^+ -fertilized plants, the pH in the cytoplasm decreases during NH_4^+ assimilation and must be stabilized by enhanced proton excretion or decarboxylation of organic acids for charge balance (Davies, 1986). In our experiments, high levels of NH_4^+ supply (as in the 25:75 and 0:100 treatments) resulted in drastic decline of pH even in a buffered solution. This decrease in solution pH could have a deleterious effect on root membranes and nutrient uptake (Logan et al., 1999). At low external pH, net excretion of protons is impaired and cytosolic pH may also fall (Gerendas et al., 1990). Gerendas et al. (1997) suggest that NH_4^+ toxicity may disappear if low pH is prevented. The pH changes observed in the solution culture may not happen in clay soils used for flooded crops because the pH buffer capacity that exhibit these soils (Brady and Weil, 2002).

In contrast, NO_3^- assimilation has been correlated with an about equimolar production of OH^- or consumption of H^+ (Raven, 1986), and as a consequence, the pH in the external solution was less affected. When both NH_4^+ and NO_3^- are supplied, the regulation of the pH may be achieved by similar rates of H^+ production (NH_4^+ assimilation) and H^+ consumption (NO_3^- assimilation), again resulting in little change in external solution pH (Findenegg et al., 1982; Gerendas et al., 1990). This assimilatory process may explain, at least in part, the

Table 2. Effects of N form ratio on the nutrient concentration and chlorophyll-meter readings in the leaf blades of 'Bun Long' taro plants.

NO ₃ : NH ₄ ratio	N	P	K	Ca	Mg	Na	Mn	Fe	Cu	Zn	B	Chlorophyll reading	
												28 d	42 d
												----- (g·kg ⁻¹) ----- (mg·kg ⁻¹) -----	
100:0	37	3.4	31	20	3.6	1.7	224	165	47	43	20	42	42
75:25	38	3.3	32	17	3.6	1.2	215	223	43	44	18	41	44
50:50	39	3.8	37	14	3.0	1.2	183	192	21	37	17	43	45
25:75	44	3.9	35	11	3.3	0.9	153	508	14	38	18	47	47
0:100	63	6.2	34	11	3.3	1.3	200	380	39	42	43	55	51
Trend analysis ^z	Q	NS	NS	NS	NS	NS	NS	NS	NS	NS	Q	L	NS
(P value)	<0.05										<0.01	<0.05	

^aL = linear; Q = quadratic, $N = 38.74 - 0.24 (pNH_4) + 0.0046 (pNH_4)^2$ ($r^2 = 0.71$), $B = 21.95 - 0.45 (pNH_4) + 0.0064 (pNH_4)^2$ ($r^2 = 0.64$), and $Chl_{28} = 39.32 + 0.13 (pNH_4)$ ($r^2 = 0.40$), where, pNH_4 = molar ratio of NH_4^+ expressed as percentage (0–100).

^{ns}Nonsignificant.

Fig. 3. Effects of N form ratio on the leaf area of 'Bun Long' taro plants (pNH_4 = molar ratio of NH_4^+ expressed as percentage, 0–100).

reason why optimal growth and high nutrient accumulation for taro was obtained either with 100% NO_3^- or with a mixed supply of both N forms (75:25 treatment).

The retarded plant growth observed at high NH_4^+ levels in solution may be due, at least in part, to the antagonism between NH_4^+ and cation absorption and translocation (Bernardo et al., 1984; Hamlin et al., 1999). Although significant decreases in foliar concentrations of cations in trial 2 were not found as the proportion of NH_4^+ increased (Table 2), significant decreases in Ca, Mg, and Mn concentrations in leaf blades were found as NH_4NO_3 levels increased in the experiment 1 (Table 1).

Taro is a plant species well adapted to flooded conditions (De la Pena and Plucknett, 1972; Miyasaka et al., 1993), in which NH_4^+ is the predominant N form (Layzell, 1990). Consequently, we expected a higher preference of taro for this N form, however, under our experimental conditions, taro preferred NO_3^- .

Ammonium concentration in soil solution rarely exceeds 1 mM (Marschner, 1995). At low total N concentrations in the external solution, the growth differences between NH_4^+ and NO_3^- are small, but with increasing external concentrations the advantage of NO_3^- as sole source of N increases (Gerendas and Sattelmacher, 1990). In the N form experiment, taro plants grown in the NH_4^+ rich solutions (50:50, 25:75, and 0:100) were exposed to very high concentrations of NH_4^+ (1.5, 2.25 and 3 mM, respectively), which appeared to be toxic to taro. Similarly, in the N level experiment, the NH_4^+ : NO_3^- ratio was 50:50, resulting in an NH_4^+ level of 2.0 mM at the highest N level. It is likely that reduced plant growth observed at the highest total N level was due to toxic NH_4^+ effect. It is necessary to examine: 1) the effects of N form on taro growth at a lower total solution N level; and 2) the interaction between solution pH and NH_4^+ toxicity effects.

Conclusions

Total plant dry weight and leaf area of 'Bun long' taro increased with increasing solution N levels up to 2 mM and then decreased at 4 mM. At a total solution N level of 3 mM, taro plants grew best when NO_3^- was the predominant N form in nutrient solution (e.g. at NO_3^- : NH_4^+ ratio of 75:25 or 100:0). The decrease in plant growth at the highest N level was attributed to a toxic level of NH_4^+ that interfered with cation absorption and translocation. In addition, the decrease in pH to 3.1 in NH_4^+ -rich solutions could be a contributing factor to NH_4^+ -toxicity.

Literature Cited

- Anderson, D., R.H. Teyker, and A.L. Rayburn. 1991. Nitrogen form effects on early corn root morphology and anatomical development. *J. Plant Nutr.* 14:1255–1266.
- Ares, A., S.G. Hwang, and S.C. Miyasaka. 1996. Taro response to different iron levels in hydroponic solution. *J. Plant Nutr.* 19:281–292.
- Austin, M.T., M. Constantinides, and S.C. Miyasaka. 1994. Effect of magnesium on early taro growth. *Commun. Soil Sci. Plant Anal.* 25:2159–2169.
- Barber, S.A. 1995. Soil nutrient bioavailability: A mechanistic approach. Wiley, New York.
- Bernardo, L.M., R.B. Clark, and J.W. Maranville. 1984. NO_3^- / NH_4^+ as a source of N for corn and their influence on the uptake of other ions. *Agron. J.* 82:463–467.
- Brady, N.C. and R.R. Weil. 2002. The nature and properties of soils. Prentice Hall, Upper Saddle River, N.J.
- Davies, D.D. 1986. The fine control of cytosolic pH. *Physiol. Plant* 67:702–706.
- De la Pena, R. and D. Plucknett. 1972. Effects of nitrogen fertilization on the growth, composition and yield of upland and lowland taro (*Colocasia esculenta*). *Expt. Agr.* 187–194.
- Errebhi, M. and G.E. Wilcox. 1990. Tomato growth and nutrient uptake pattern as influenced by nitrogen form ratio. *J. Plant Nutr.* 13:1031–1043.

- Findenegg, G.R., M. Salihu, and N.A. Ali. 1982. Internal self-regulation of H^+ -ion concentration in acid damaged and healthy plants of *Sorghum bicolor* (L.) Moench. *Proc. 9th Plant Nutr. Coloq. Cmwth. Agr. Bur., Bucks, U.K.*, 174–179.
- Gerendas, J. and B. Sattelmacher. 1990. Influence of nitrogen form and concentration on growth and ionic balance of tomato and potato, p. 33–37. In: M.L. Van Beusichem (ed.). *Plant nutrition-physiology and application*. Kluwer Academic Publishers, Dordrecht.
- Gerendas, J., R.G. Ratcliffe, and B. Sattelmacher. 1990. ^{31}P nuclear magnetic resonance evidence for differences in intracellular pH in the roots of maize seedlings grown with nitrate or ammonium. *J. Plant Physiol.* 137:125–128.
- Gerendas, J., Z. Zhu, R. Bendixen, R. G. Ratcliffe, and B. Sattelmacher. 1997. Physiological and biochemical processes related to ammonium toxicity in higher plants. *Z. Pflanzenernahr. Bodenk.* 160:239–251.
- Hamlin, R.L., H.A. Mills, and W.N. Randle. 1999. Growth and nutrition of pansy as influenced by N-form ratio and temperature. *J. Plant Nutr.* 22: 1637–1650.
- Heuer, B. 1991. Growth, photosynthesis and protein content in cucumber plants as affected by supplied nitrogen form. *J. Plant Nutr.* 14: 363–373.
- Hill, S., R. Abaidoo, and S. Miyasaka. 1998. Sodium chloride concentration affects early growth and nutrient accumulation in taro. *HortScience* 33: 1153–1156.
- Isaac, R.A. and W.C. Johnson. 1998. Elemental determination by inductively coupled plasma-atomic emission spectroscopy, p. 165–170. In: Y.P. Kalra (ed.). *Handbook of reference methods for plant analysis*. CRC Press, Boca Raton.
- Jarrell, W.M. and R.B. Beverley. 1986. The dilution effect in plant nutrition studies. *Adv. Agron.* 34: 197–224.
- Layzell, D.B. 1990. N_2 fixation, NO_3^- reduction, and NH_4^+ assimilation, p. 389–406. In: Dennis, D.T., and D.H. Turpin (eds.). *Plant physiology, biochemistry, and molecular biology*. Wiley, New York.
- Little, T.M. and F.J. Hills. 1978. *Agriculture experimentation. Design and analysis*. Wiley, New York.
- Logan, K., R. Thomas, and J. Raven. 1999. Hydrogen ion production and ammonium uptake by two tropical forage grasses. *J. Plant Nutr.* 22:53–66.
- MacKown, C.T. and T.G. Sutton. 1998. Using early-season leaf traits to predict nitrogen sufficiency of Burley tobacco. *Agron. J.* 90:21–27.
- Magalhaes, J.R. and D.M. Huber. 1991. Response of ammonium assimilation enzymes to nitrogen form treatments in different plant species. *J. Plant Nutr.* 14:175–185.
- Manrique, L. A. 1994. Nitrogen requirements of taro. *J. Plant Nutr.* 17:1429–1441.
- Marschner, H. 1995. *Mineral nutrition of higher plants*. Academic, London.
- Marschner, H. and V. Romheld. 1983. In-vivo measurement of root-induced pH changes at the soil-root interface: Effect of plant species and nitrogen source. *Z. Pflanzenphysiol.* 111: 241–251.
- Marti, H.R. and H.A. Mills. 1991. Calcium uptake and concentration in bell pepper plants as influenced by nitrogen form and stages of development. *J. Plant Nutr.* 14:1177–1185.
- Miyasaka, S.C. 1979. Calcium nutrition of taro [*Colocasia esculenta* (L.) Schott] and its possible relationship to guava seed disease. MS Thesis, Dept. Agron. Soil Sci., Univ. of Hawaii, Honolulu.

- Miyasaka, S., R.T. Checkai, D.L. Grunes, and W.A. Norvell. 1988. Methods for controlling pH in hydroponic culture of winter wheat forage. *Agron. J.* 80:213–220.
- Miyasaka, S.C., C.M. Webster, and N.V. Hue. 1993. Differential response of two taro cultivars to aluminum. I. *Plant Growth. Commun. Soil Sci. Plant Anal.* 24:1197–1211.
- Nelson, D.W. and L.E. Sommers. 1972. Determination of total nitrogen in plant material. *Agron. J.* 65:109–112.
- Neter, J., M. Kutner, C. Nachtsheim, and W. Wasserman. 1996. *Applied linear statistical models.* McGraw-Hill, Boston.
- O'Sullivan, J.N., C.J. Asher, and F.P.C. Blamey. 1995. Diagnostic criteria for nutrition disorders of taro, p. 83–90. In: E.T. Craswell, C.J. Asher, and J.N. O'Sullivan (eds.). *Mineral nutrient disorder of root crops in the South Pacific.* Watson Ferfugon, Brisbane.
- Osuna, F.J., S.K. De Datta, and J.M. Bonman. 1991. Nitrogen form and silicon nutrition effects on resistance to blast disease of rice. *Plant Soil* 135:223–231.
- Rao, I.M. and N. Terry. 1989. Leaf phosphate status, photosynthesis, and carbon partitioning in sugar beet. I. Changes in growth, gas exchange, and Calvin cycle enzymes. *Plant Physiol.* 90: 814–819.
- Raven, J.A. 1986. Biochemical disposal of excess H^+ in growing plants. *New Phytol.* 104:175–206.
- Sanchez, P. and T. Logan. 1992. Myths and science about the chemistry and fertility of soils in the tropics, p. 35–46. In: R. Lal and P. Sanchez (eds.). *Myths and science of soils of the tropics.* Soil Sci. Soc. Amer., Madison, Wis.
- Scoggins, H. and H. Mills. 1998. Poinsettia growth, tissue nutrient concentration, and nutrient uptake as influenced by nitrogen form and stage of growth. *J. Plant Nutr.* 21:191–198.
- Silva, J. A., D.M. Sato, P.S. Leung, G. Dantos, and J. Kuniyoshi. 1990. Response of Chinese taro to nitrogen and potassium fertilization, p. 60–70. In: *Proc. Wkshp. on Taro and Plant Population*, Univ. Hawaii, Honolulu.
- Thomas, P.A. and J.G. Latimer. 1995. Nutrient charge, composition of media, and nitrogen form affect growth of vinca. *J. Plant Nutr.* 18: 2127–2134.
- Traore, A. and J. Maranville. 1999. Effect of nitrate/ammonium ratio biomass production, nitrogen accumulation, and use efficiency in sorghum of different origin. *J. Plant Nutr.* 22:813–825.
- Wolf, B. 1974. Improvements in the azomethine-H-method for the determination of boron. *Commun. Soil Sci. Plant Anal.* 5:39–44.
- Xu, Q.F., C.L. Tsai, and C.Y. Tsai. 1992. Interaction of potassium with the form and amount of nitrogen nutrition on growth and nitrogen uptake of maize. *J. Plant Nutr.* 15:23–33.