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Ionic Balance and Growth of Carnations - I. Recent Literature

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Summary

The difference between the total cation and inorganic anion contents of the tissue, the (C-A) content, in most of the plant species studied was equal to the organic acid content of the plant. The relation between (C-A) content and plant yield was a positive linear relationship. Tissue analysis determining the (C-A) content was indicative of the nutrient status of the plant. For the few species studied, each specie had a characteristic (C-A) content associated with optimum yield.

The (C-A) content of the leaf tissue was affected by internal ion-uptake systems in the plant and by external environmental factors, e.g., nutrient solution composition, light, and carbon dioxide content of the plant atmosphere.

In the study to be reported in the next several issues the normal (C-A) content for the carnation plant and the qualitative and quantitative effects of external and internal factors on this (C-A) content are reported. The following literature review provides a background for planning experiments to determine the (C-A) content of additional species.

Present Status of Carnation Tissue Analysis

The chemical composition of the green leaf varies with the position of the leaf on the stock (23). Prior to conducting comparative studies on the chemical composition of tissue in a given plant species, a sampling site must be standardized. The fifth leaf pair from the base of the main shoot was determined by Nelson and Boodley (11) to be the best general area for sampling carnation tissue until primary lateral shoots developed seven pairs of leaves. Then the fifth pair of leaves from the terminal end of primary lateral shoots was sampled until flower buds became visible. At that time sampling was shifted to the same leaf pair on secondary lateral shoots. The same procedure was followed for sampling tertiary and quaternary lateral shoots. This procedure minimized physiological variation.

Seasonal variation of ion content of plant tissue in general was reported by Ulrich (22). Seasonal variation in ion content of greenhouse-grown carnations was reported by Nelson and Boodley (12). They found that the P and Mg ion concentrations in the tissue were constant throughout a two-year period. N, K, and Ca tissue concentrations were lowest during the months of June through August and increased during the winter.

Within the greenhouse environment, the main seasonal variations are probably daily total radiation and

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carbon dioxide content of the plant atmosphere, and possibly temperature. In a study on carnation nutrition, Goldsberry (4) assumed that a nutrient solution containing a higher total ion concentration was required to avoid apparent deficiency symptoms as the CO_2 level was increased. Swasey, Shank and Link (19) over a four-period found no indication of different fertilizer requirements with different CO_2 levels.

Ion Uptake and Water Loss

The literature related to the effect of light and carbon dioxide on stomatal movements and the postulated mechanisms of response % reviewed (6, 7). The effects of light and CO_2 on stomatal aperture may be related to the ion content of the plant tissue by their effect on the transpiration rate of the plant. Transpiration rate decreased with partial closure of the stomatal apertures because of increasing CO_2 content of the air (15). A level of 575 ppm compared to a level of 310 ppm CO_2 reduced the transpiration rate of corn by 23% (27). Chemical closure of the stomatal apertures also resulted in a reduction of transpiration (18, 20, 28).

The relationship between transpiration and nutrient-ion uptake has not been definitely established. Wide variations in the rate of transpiration had very little effect on the transfer of nutrients to the shoot and leaves of intact plants receiving a solution having a low nutrient-ion concentration. Under conditions of low transpiration and low water loss, the concentration of ions in the transpiration stream exceeded that in the external medium by as much as 100 fold. But the rate of transfer of ions to shoots varied closely with the rate of transpiration when the ion concentration of the external nutrient solution and the nutrient status of the plant were both high. Under these conditions the concentration in the transpiration stream was equal to or less than the concentration in the external nutrient solution (16).

A high rate of transpiration presumably would favor the establishment of a steeper gradient of mineral-ion concentration across the root. In this way transpiration rates would indirectly influence the rate of movement of salts across the root and from the xylem elements of the roots to the leaves (10). Most researchers agree that under some conditions transpiration rate can influence the rate of salt movement to leaves.

There may be a differential effect of transpiration on ion uptake with only certain ions being affected. Nitrate and potassium uptake were not influenced by the transpiration stream movement in intact and decapitated tomato plants (1).

Genetic Effect on Ion Content

Leaf samples from 16 cultivars of the Sim, Littlefield, and miniature varieties were analyzed for nutrient content by Nelson and Boodley (13). They were able to group the cultivars, grown under 'similar nutrient regime', according to their nutrient content. The 16 cultivars were divided into 3 groups corresponding to the 3 main varieties, Sim, Littlefield, and miniature. They concluded that it might be necessary to establish 3 sets of tissue nutrient standards to interpret tissue analyses of these three genetically different groups. Genetic variation must be considered in interpreting tissue analysis (22, 26).

Effect of Nutrient Supply on Ion Content

Because the plant exercises certain selective properties in ion uptake, the question may be raised as to the effect of the chemical composition of the nutrient solution on growth and development of the plant. The term "chemical composition" comprises the 1) concentrations of the component ions, 2) total ionic concentration, and 3) pH. In carnation nutrition, the relative anion proportions in the nutrient solution were important only within wide limits, but the relative cation proportions were very important. The total ion concentration was important within the limits of ± 0.2 atmospheres osmotic pressure. In many cases, the pH of the nutrient solution was important within the limits ± 0.2 pH units (17).

The use of critical values to diagnose nutrient disorders was not always satisfactory because the range in plant tissue composition associated with deficient and normal plants frequently overlapped. The response of plants to a given nutrient depended upon the level of other nutrients (24).

The plant exercises ion-selectivity through the competitive ion uptake systems. Two competitive uptake systems for cations have been detected in grass (26). A four-ion system operated in the uptake of K, Na, Mg, and Ca. A monovalent ion system operated in the uptake of K and Na. The anions NO_3 and Cl competed during uptake by grasses (26).

In addition to the effect of the ion composition of the nutrient solution, the total ion concentration of the solution is important (17). In regulating plant growth, the total ion concentration was a greater factor in reducing growth than was the effect caused by specific ions (9).

But, Boyko (2) found that plants in a physiologically balanced solution could stand much higher osmotic pressures than plants in a solution of a single salt or an unbalanced solution.

Reduction of plant growth in solutions of high osmotic pressure has been reported (3, 5). Carnation yield was reduced with each addition of soluble salts (8, 25).

Effect of Ion Content of the Tissue on Plant Growth

Studies involving effects of salt solutions on the ion contents of plant tissue, competitive phenomena among ions, selective ion uptake by growing plants, regulation of the (C-A) content and yield were conducted by Wit, et al. (26) on plantain, orchard grass, and rye-grass. Acknowledgment is due Wit, et al., Tuil (21), and Noggle (14), whose publications on nutrient studies of grasses served as a background for planning and interpreting this experiment.

A given plant species has an optimum (C-A) content which is one of the requirements for optimum yield, (the (C-A) content being the difference between the total concentration in the plant tissue of the inorganic cations K, Na, Ca, Mg, and the total concentration of the inorganic anions NO_3, H_2PO_4, SO_4, Cl) (26). In most plant tissue the (C-A) is an estimate of the organic anion concentration (21).

In small grains a lower than optimum (C-A) content developed when 1) availability of cations was low, 2) uptake of inorganic anions, e.g., Cl, that stayed as such in the plant was high, and 3) reduction of nitrates in the shoot proceeded at a low rate. Reduction of the (C-A) content was accompanied by a reduction of the growth rate.

A high (C-A) content occurred in the case of K shortage in the presence of any other cation, e.g., Na, that was readily taken up. Although other cations may have functioned as a positive charge in uptake, the K ion seemed to be the only one that accompanied the excess organic anions in their downward movement.

Ammonium fertilization resulted in a reduced growth rate (26). This reduction was attributed to a stress on the (C-A) content induced by competition between NH_4^+ and other cations, e.g., K^+, and the release of H^+ ions during the transformation of NH_4^+ to organic nitrogen.

Within limits, the plants maintained the (C-A) content at a constant level. The plant responded to a stress on the (C-A) by a reduced growth rate maintaining status quo (26). Sixteen plant species, with one possible exception, had reduced growth rates with reduced organic anion concentration (14).

Evidence for the dependence of organic-salt content on the salt supply has been available since the beginning of this century (21). But its direct application to plant nutrition is comparatively recent. A review of the literature pertaining to the (C-A) content concept with special emphasis on the organic acids comprising the normal organic-salt content of perennial rye-grass, sugar beet, poplar, and birch is contained in Tuil's paper (21).

In general, the analysis of the organic anions showed that the anions of the water-soluble, nonvolatile organic acids represented about 90% of the total organic anions in rye-grass. Other fractions were: succinate, malonate, glycerate, shikimate, quinate, and oxylate. Malate contributed mainly to the change in the organic-salt content. Chloride accumulated instead of organic acids, and mainly at the expense of malate. When ammonium was supplied in place of nitrate, the (C-A) content of the foliage was lower than normal and chromatographic analysis showed that this was due to a fall in the oxalate content.

General Theory of Plant Nutrition

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The uptake of salt cations (C) may occur in amounts which, depending on the salt cations available, differ from the number of equivalents of the salt anion absorbed (A). In the ionic balance a positive difference (C-A) represents an excess uptake of cations compared to inorganic anion uptake. This excess uptake of cations is balanced by organic anions formed by metabolic processes within the plant. The ions in the plant tissue are present as the inorganic salts (A) and organic salts (C-A) of the salt cations (C).

As a result of the uptake of the inorganic ions of the nutrient solution, there results an accumulation in the plant tissue of the inorganic cations: K^+, Na^+, Mg^{++}, and Ca^{++}; and the inorganic anions: NO_3^-, Cl^-, $H_2PO_4^-$, and SO_4^{--}. (It is not necessary to account for the very low quantities of other inorganic ions such as Fe, Mn, Zn, and Cu.) The sum of these cations and anions in milligram equivalents per killogram dry plant material is given by C (cations) and A (anions), respectively. C equals the total salt content of the plant material. The organic anions (salts of the organic acids) which combine with the excess cations are formed by metabolic processes, specifically by the processes of photosynthesis and respiration. These organic acids are: succinic, malonic, malic, citric, glyceric, shikimic, quinic, and oxalic. Malic, which forms malate organic salts, is the main constituent of the total organic acids and varies to a much greater extent with (C-A) than the other organic salts.

Cations function to allow the plant to accumulate organic salts to be used in protein synthesis, respiration, etc., instead of losing them to the medium surrounding the roots as bicarbonate formed by decarboxylation of the organic salt.

The normal organic-salt content is the value obtained at optimum growth. Suboptimal growth can also occur at the normal organic-salt content if some factor such as the nitrate supply is limiting.

Definitions:

Ion= An electrically charged atom; there are two kinds of ions:
  Cations =positively charged ions, e.g., Ca^{++}, Mg^{++}, K^+, and Na^+;
  Anions =negatively charged ions, e.g., NO_3^-, SO_4^{--}, and $H_2PO_4^-$.

Inorganic ions =Do not contain carbon; are derived from mineral sources, e.g., Ca, Mg, K, Na, NO_3, SO_4, H_2PO_4, and Cl.

Organic ions= Carbon containing compounds, e.g., Malate, oxalate, and other salts of carboxylic acids.

Chemical Equivalent = $\frac{\text{Atomic or formula weight}}{\text{valence}}$

Miligram equivalent (me) =1/1000 of an equivalent

ABBREVIATIONS:

C = Cations:	A = Anions:
Ca^{++} = calcium	Cl^- = chloride
Mg^{++} = magnesium	NO_3^- = nitrate
K^+ = potassium	SO_4^{2-} = sulfate
Na^+ = sodium	$H_2PO_4^-$ = phosphate

(C-A) = organic anions

Literature Cited

1. Alberda, T. H. 1964. Uptake of nitrate, potassium, and water in intact and decapitated tomato plants. Biol. Abstr. 100257, 1965.
2. Boyko, Hugo. 1967. Salt-Water agriculture. Sci. Amer. 216 (March): 89-96.
3. Browver, R. 1963. The influence of the suction tension of the nutrient solutions on growth, transpiration, and diffusion pressure deficit of bean leaves. Acta Bot. Neerland 12:248-260.
4. Goldsberry, K. L. 1963. Effects of carbon dioxide on carnation. Proc. Amer. Soc. Hort. Sci. 83: 753-760.
5. Hagan, R. M., Y. Vaadia, and M. B. Russel. 1959. Interpretation of plant responses to soil moisture regimes. Advances in Agron. 11:77-98.
6. Heath, O.V.S. 1959. Light and carbon dioxide in stomatal movements, p. 415 to 464. In W. Ruhland (ed.) Encycl. of plant physiol. V. 17. Springer-Verlag, Berlin.
7. Ketellapper, H. J. 1963. Stomatal physiology. Annu. Rev. Plant Physiol. 14:249-270.
8. Lunt, O. R., H. C. Kohl, Jr., and A. M. Kofranek. 1956. Tolerance of carnations to saline conditions and boron. Carnation Craft 36:5-6.
9. Magistad, O. C., Alvin D. Ayres, C. H. Wadleigh, and H. G. Gauch. 1943. Effect of salt concentration, kind of salt, and climate on plant growth in sand cultures. Plant Physiol. 18:151-166.
10. Meyer, Bernard S., Donald B. Anderson, and Richard H. Bohning. 1960. Introduction to plant physiology, D. Van Nostrand Company, Inc., New York. 541 p.
11. Nelson, P. Victor and James W. Boodley, 1963. Selection of a sampling area for tissue analysis of carnation. Proc. Amer. Soc. Hort. Sci. 83: 745-752.
12. Nelson, P. Victor and James W. Boodley, 1965. Development of a set of standard leaf composition values for carnation. Proc. Amer. Soc. Hort. Sci. 86: 641-649.
13. Nelson, P. Victor and James W. Boodley. 1966. Classification of carnation cultivars according to foliar nutrient content. Proc. Amer. Soc. Hort. Sci. 89:620-625.
14. Noggle, J. C. 1966. Ionic balance and growth of sixteen plant species. Soil Sci. Soc. Amer. Proc. 30:763-766.
15. Pallas, J. E., Jr. 1963. Transpiration and stomatal opening with changes in carbon dioxide content of the air. Science 147:171-173.
16. Russell, R. Scott and V. M. Shorrocks. 1959. The relationship between transpiration and the absorption of inorganic ions by intact plants. J. Exp. Bot. 10:301-316.
17. Steiner, Abram A. 1961. A universal method for preparing nutrient solutions of a certain desired composition. Plant and Soil Sci. 15:134-154.
18. Stoddard, E. M. and P. M. Miller. 1962. Chemical control of water loss in growing plants. Science 137:224-225.

19. Swasey, James E., James B. Shank, and Conrad B. Link. 1966. The effect of maintaining winter carbon dioxide levels in the greenhouse for roses, chrysanthemums, carnations, and snapdragons under different fertility levels or in several soil mixtures. Maryland Florist. 130:1-9.
20. Thorn, G. D. and W. H. Minshall. 1964. The effect of sodium dimethyldithiocarbamate on water uptake, transpiration, and stomatal opening. Canadian J. Bot. 42:1405-1410.
21. Tuil, H. D. W. van. 1965. Organic salts in plants in relation to nutrition and growth. Versl. Landbouwk. Onderz 657, Wageningen, 83 p.
22. Ulrich, Albert. 1952. Physiological bases for assessing the nutritional requirements of plants. Annu. Rev. Plant Physiol. 3:207-228.
23. Vickery, H. F. 1961. Chemical investigations on the tobacco plant XI. Composition of the green leaf in relation to position on the stalk. Conn. Agri. Exp. Sta. Bull. 42 p.
24. Watanabe, F. S., W. L. Lindsay, and S. R. Olsen. 1965. Nutrient balance involving phosphorus, iron, and zinc. Soil Sci. Soc. Amer. Proc. 29: 562-565.
25. White, John W. and W. D. Holley. 1957. Some effects of soluble salts and soil moisture on carnation growth and quality. Colorado Flower Growers Association Bull. 95.
26. Wit, C. T. de., W. Dijkshoorn, and J. C. Noggle. 1963. Ionic balance and growth of plants. Versl. Landbouwk. Onderz. Nr.69.15, 68 p., Wageningen.
27. Zelitch, I. 1961. Biochemical control of stomatal opening of leaves. Proc. Nat. Acad. Sci. 47: 1423-1433.
28. Zelitch, Israel and Paul Waggoner. 1962. Effect of chemical control of stomata on transpiration of intact plants. Proc. Nat. Acad. Sci. 48:1101-1108, 1297-1299.