In the interest of public knowledge we thought it would be appropriate to post this citation.


THIS EDITION includes a discussion of general principles underlying the use of ALL methods for growing plants without soil.

> WCRICMIMPC is an all-inclusive term for the several methods of grow- ing plants in artificial media-water culture, aggregate culture, and the "adsorbed" nutrient technique.*

Most claims for the advantages of nutriculture are unfounded.
is It is not a new method for growing plants.
A Anyone who uses it must have a knowledge of plant physiology.
iz Its commercial application is justifiable under very limited conditions and only under expert supervision.

N Nutriculture is rarely superior to soil culture:
Yields are not strikingly different under comparable conditions.
Plants cannot be spaced closer than in a rich soil.
Plant growth habits are not changed by nutriculture.
Water requirement is no less in nutriculture.
Nutritional quality of the product is the same.
Nutrient deficiencies, insect attacks, and diseases present similar problems.
Climatic requirements are the same.
Favorable air temperatures are just as necessary as in soil.
is is is

## 1f, realizing these limitations, you still wish to experiment with nutriculture methods, you will find directions beginning on page 23.

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* A comprehensive treatise on methods of growing plants without soil as well as numerous references to original investigations in this field will be found in HEWITT, E. J. Sand and water culture methods used in the study of plant nutrition. Technical Communication No. 22, Commonwealth Bur. of Hort. and Plantation Crops, East Malling, Maidstone, Kent, England. Published by Commonwealth Agriculture Bur., Farnham Royal, Bucks, England. 241 pp., 1952


## Foreword

For over three decades, the California Agricultural Experiment Station has conducted investigations of problems of plant nutrition with the use of water-culture technique for growing plants, as one important method of experimentation. The objective has been to gain a better understanding of fundamental factors which govern plant growth, in order to deal more effectively with the many complex questions of soil and plant interrelations arising in the field. Many workers have participated in these investigations. One of them, Dr. W. F. Gericke, conceived the idea some time ago that the water-culture method, hitherto employed only for scientific studies, might be adapted to commercial use, and proceeded to devise special technique for this purpose.

In the nineteen thirties, this development was given widespread publicity in newspapers, Sunday supplements, and popular journals. The possibility of growing plants in a medium other than soil intrigued many persons, and soon extravagant claims were being made by many of the most ardent proponents of the commercial use of the water-culture method. Furthermore, amateur gardeners sought to make this method a new hobby. Thousands of inquiries came to the University of California for detailed information for general application of the water-culture method to commercial as well as to amateur gardening.

Because of doubts expressed concerning many claims made for the use of the water-culture method as a means of crop
production, it became evident that an independent appraisal of this method of growing crops was highly desirable. I therefore requested Professors D. R. Hoagland and D. I. Arnon to conduct certain additional investigations and to prepare a manuscript for a popular circular on the general subject of growing plants in nutrient solutions.

When this circular was first published in 1938, neither the California Agricultural Experiment Station nor the authors made any general recommendations as to the use of soilless culture methods for commercial crop production. The purpose of the publication was to make available such technical information from the researches of the Station to those who wished to experiment with the waterculture method on their own responsibility. An attitude of caution and a balanced consideration of the various factors determining success in growing crops on a large scale, whether in soil or in nutrient solutions, was commended to the attention of those contemplating commercial ventures. The purpose of this revised publication and the point of view of the Experiment Station remain the same today. The experience of the past decade, during which a number of large-scale installations for soilless crop production was established in the United States and overseas, fails to support the exaggerated claims of the early enthusiasts of the technique.

C. B. Hutchison

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Dean of the College of Agriculture

# THE WATER-CULTURE METHOD FOR GROWING PLANTS WITHOUT SOIL 

D. R. Hoagland ${ }^{1}$ and D. I. Arnon ${ }^{2}$<br>Revised by D. I. Arnon ${ }^{2}$

Nutriculture is the term applied to all methods for growing plants in a medium other than natural soil. It includes water culture, aggregate culture, and the "ad-sorbed-nutrient" technique, all of which are discussed briefly in this circular. Specific directions, however, are given for water culture only.

In the nineteen thirties, the popular press gave an immense amount of publicity to the subject of commercial or amateur growing of crops in "water culture." This is a method of growing plants with their roots in a solution containing the mineral nutrients essential for plant growth. The solution takes the place of soil in supplying water and mineral nutrients to the plant. "Tray agriculture," "tank farming," and "hydroponics," were other names given to this same process. Frequently, popular accounts left the impression that a new discovery had been made which would revolutionize present methods of crop production. Indeed, some predicted that in the future water culture would supplant the use of soils for growing many crops and would thus produce far-reaching social dislocations.

## Extravagant claims for nutriculture are unfounded

Promoters have made wholly un. founded claims that a new "profession of soilless farming" has been developed, affording extraordinary opportunities for investment of time and funds. They have attempted to convince the public that a short course of training will give preparation for entering this new "profession." The impression has also been given that the water-culture method offers an easy means of raising food for household use.

Widely circulated rumors, claims, and predictions about the water-culture production of crops often had little more to commend them than the author's unrestrained imagination. Grossly inaccurate in fact and misleading in implication, most of these claims betrayed an ignorance of even the elementary principles of plant physiology. For example, there have been statements that in the future most of the food needed by the occupants of a great apartment building may be grown on the roof, and that in large cities "skyscraper" farms may supply huge quantities of fresh fruit and vegetables. One Sunday-supplement article contained an illustration showing a housewife opening a small closet off the kitchen and picking tomatoes from vines growing in water culture with the aid of electric lights. There has even arisen a rumor that the restaurants of a large chain in New York City are growing their vegetables in basements. Stories of this kind have gained wide currency and have captured the imagination of many persons.
Many factors have doubtless contributed to arousing the surprisingly wide interest in the water-culture method of crop production. Current stress upon soil conservation, with attendant emphasis upon needless soil depletion and land erosion, has made the public especially receptive to new ideas relating to crop production. Some people have been impressed by the assumed social and economic significance of the water-culture method. Others, moved by the common

[^0]delight of mankind in growing plants, even though the garden space is reduced to a window sill, have sought directions to enable them to try a novel technique of plant culture.

The consequence of the discussion of this method has been the creation of a great public demand for more specific information. Should this newly aroused interest in plant growth lead to a greater diffusion of the knowledge of certain general principles of plant physiology, the publicity regarding the water-culture method of crop production may in the long run have a beneficial effect. Growing plants in water culture has been considered by some popular writers as a "marvel of science." The growth of plants is indeed marvelous, but not more so when plants are grown in water culture than when they are grown in soil.

The two entirely distinct lines of investigation at the California Agricultural

Experiment Station, in which the waterculture technique is used, have sometimes been confused in popular discussions. One of these concerns methods of growing plants in water culture under natural light; the other, the study of special scientific problems of plant growth in controlled chambers artificially illuminated. At the present time there is no economic possibility of growing commercial crops solely under artificial illumination, even if there were any reason for doing so.

At several other institutions, considerable attention has been devoted to a study of the effect of supplementing daylight with artificial light during some seasons of the year, to control the flowering period or to accelerate growth of certain kinds of plants (particularly floral) in greenhouses. So far, this practice has been applied mainly to plants developed in soil and has no essential relation to the waterculture method of growing plants.

## NUTRICULTURE IS NOT A NEW METHOD

Curiously enough, the earliest recorded experiment with water cultures was carried out in search of a so-called "principle of vegetation" in a day when so little was known about the principles of plant nutrition that there was small chance of profitable results from such an experiment. Woodward (1699) grew spearmint in several kinds of water: rain, river, and conduit water, to which in one case he added garden mold. He found that the greatest increase in the weight of the plant took place in the water containing the greatest admixture of soil. He concluded "That earth, and not water, is the matter that constitutes vegetables."

## Water-culture technique developed from plant nutrition studies

The real development of the technique of water culture took place over threequarters of a century ago. It came as a logical result of the modern concepts of plant nutrition. By the middle of the
nineteenth century, enough of the fundamental facts of plant physiology became known and properly evaluated to enable the botanists and chemists of that period correctly to assign to soil the part it plays in the nutrition of plants. They realized that plants are made of chemical elements obtained from three sources: air, water, and soil, and that plants grow and increase in size and weight by combining these elements into various plant substances.

Water is, of course, always the main component of growing plants. But the major portion, usually about 90 per cent, of the dry matter of most plants is made up of three chemical elements: carbon, oxygen, and hydrogen. Carbon comes from the air, oxygen from the air and water, and hydrogen from water. In addition to these three, plants contain other elements, such as nitrogen, phosphorous, potassium, and calcium, which they obtain from the soil. The soil then supplies
a large number of chemical elements, but they constitute only a very small portion of the plant. Yet the various elements that occur in plants in comparatively small amounts are just as essential to growth as those which compose the bulk of plant tissues.

The publication in 1840 of Liebig's book on the application of organic chemistry to agriculture and physiology, ${ }^{3}$ in which these facts were ably and effectively brought to the attention of plant physiologists and chemists of that period, served as a great stimulus for undertaking experimental work in plant nutrition. (Liebig, however, failed to understand the rôle of soil as a source of nitrogen for plants; and the fixation of atmospheric nitrogen by bacteria was not then known.)

Once it was recognized that the function of the soil in the economy of the plant is to furnish certain chemical elements, as well as water, it was but natural to attempt to supply these elements and water independently of soil. The credit for initiating exact experimentation in this field belongs to the French chemist, Jean Boussingault, who is regarded as the founder of modern methods of conducting experiments in vegetation.

Boussingault, who had begun his experiments on plants even before 1840, used insoluble artificial soils: sand, quartz, and sugar charcoal, which he watered with solutions of known composition. His results provided experimental verification for the mineral theory of plant nutrition as put forward by Liebig, and were at once a demonstration of the feasibility of growing plants in a medium other than a "natural soil."

This method of growing plants in artificial insoluble soils was later improved by Salm-Horstmar (1856-1860) and has been used since, with technical improvements, by many investigators. In recent years, large-scale techniques have been devised for growing plants for experimental or commercial purposes in beds of sand or other inert solid material.

## Modern technique in water culture originated about 1860

After they were successfully grown in artificial culture media, it was but one more step to dispense with any solid medium and attempt to grow plants in water to which were added the chemical elements they were known to require. This was successfully accomplished in 1860 by Sachs and about the same time by Knop. To quote Sachs directly:

In the year 1860, I published the results of experiments which demonstrated that land plants are capable of absorbing their nutritive matters out of watery solutions, without the aid of soil, and that it is possible in this way not only to maintain plants alive and growing for a long time, as had long been known, but also to bring about a vigorous increase of their organic substance, and even the production of seed capable of germination. ${ }^{4}$

The original technique developed by Sachs for growing plants in nutrient solutions is still widely used, essentially unaltered. He germinated the seed in well-washed sawdust, until the plants reached a size convenient for transplanting. After carefully removing and washing the seedling, he fastened it into a perforated cork, with the roots dipping into the solution. The complete assembly is shown in figure 1 , which is a reproduction of Sachs' illustration.

Since the publication of Sachs' standard solution formula (table l) for growing plants in water culture, many other formulas have been used with success by investigators in different countries. Knop, who undertook water-culture experiments at the same time as Sachs, proposed in 1865 a nutrient solution, which became one of the most widely employed in studies of plant nutrition. Other formulas for nutrient solutions have been proposed by Tollens in 1882, by Schimper in 1890, by Pfeffer in 1900, by Crone in 1902, by

[^1]Tottingham in 1914, by Shive in 1915, by Hoagland in 1920, and by many others.

At the very beginning of the waterculture work, investigators clearly recognized that no one composition of a nutrient solution is always superior to


Fig. 1. Water-culture installation employed by the plant physiologist Sachs in the middle of the last century. (Reproduced from Sachs, Lectures on the Physiology of Plants, Clarendon Press. 1887.)
every other composition, but that within certain ranges of composition and total concentration, there could be fairly wide latitude in the nutrient solutions suitable for plant growth. Thus Sachs wrote:
I mention the quantities (of chemicals) I am accustomed to use generally in water cultures, with the remark, however, that a somewhat wide margin may be permitted with respect to the quantities of the individual salts and the concentration of the whole solution-it does not matter if a little more or less of the one or the other salt is taken-if only the nutritive mixture is kept within certain limits as to quality and quantity, which are established by experience.

## Water culfure was long used only as research technique

Until recently, the water-culture technique was employed exclusively in smallscale, controlled laboratory experiments intended to solve fundamental problems of plant nutrition and physiology. These experiments have led to the determination of the list of chemical elements essential for plant life. They have thus profoundly influenced the practice of soil management and fertilization for purposes of crop production. ${ }^{5}$ In recent years, great refinements in water-culture technique have made possible the discovery of several new essential elements. These, although required by plants in exceedingly small amounts, often are of definite practical importance in agricultural practice. The elements derived from the nutrient medium now considered to be indispensable for the growth of higher green plants are nitrogen, phosphorus, potassium, sulfur, calcium, magnesium, iron, boron, manganese, copper, and zinc. New evidence suggests that molybdenum has to be added to the list. ${ }^{8}$ Present indications are that further refinements of technique may lead to the discovery of still other elements essential in minute quantity for growth.

In addition to the list of essential ele-ments-obviously of first importance in making artificial culture media for growing plants-a large amount of information has been amassed on the desirable proportions and concentrations of the essential elements, and on such physical -and chemical properties of various culture solutions as acidity, alkalinity, and osmotic characteristics. A most important

[^2]recent development in the technique has been the recognition of the importance, for many plants, of special aeration of the nutrient solution to supplement the oxygen supply normally entering it when in free contact with the surrounding atmosphere.

## Present-day commercial water culture involves no new principles

The recently publicized use of the water-culture technique for commercial crop production rests on the same principles of plant nutrition as were discussed above. It involves the application of a large-scale technique, developed on the basis of an understanding of plant nutrition gained in previous investigations conducted on a laboratory scale. The latter have provided knowledge of the composition of suitable culture solutions. Furthermore, methods of controlling the concentration of nutrients and the degree of acidity are, except for modifications imposed by the large scale of operations, similar to those employed in small-scale laboratory experiments.

The selection of a particular type of covering for the tanks adapted to largescale water-culture operations and of methods for supporting the plants de-
pends on the kind of plant. Potatoes, for example, require a suitable bed in which tubers can develop. This is usually a porous one placed just above the level of the solution. Tomatoes need adequate support only for the aerial portion of the stem, assuming that the roots are in a favorable culture-solution medium, adequately aerated, and with light excluded. A porous bed may be convenient as a means of facilitating aeration of the solution, as a heat insulator, or as a support for the plant, but plays no indispensable rôle. Aside from such considerations, the choice of a covering is determined largely by expense and convenience, provided the materials used are not toxic to plants.

With any kind of covering for the tanks, an adequate supply of air to the roots must be provided. While the use of a porous bed instead of a perforated cover facilitates aeration of roots, the bed can be dispensed with if provision is made to bubble air through the nutrient solutions (fig. 2). Recent experiments have shown that even with the use of a porous bed, bubbling air through the solution may be advantageous or, under some conditions, indispensable.

As illustrations of some scientific problems of plant nutrition which have been

TABLE 1.-Composition of Nutrient Solutions Used by Early Investigators* $\dagger$

| Sachs' solution (1860) |  | Knop's solution (1865) |  | Pfeffer's solution (1900) |  | Crone's solution (1902) |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Ingredient | $\begin{gathered} \text { Grams } \\ \text { per } 1,0,00 \mathrm{cc} \\ \mathrm{H}_{2} \mathrm{O} \end{gathered}$ | Ingredient | $\begin{gathered} \text { Grams } \\ \text { per } 1,0,00 \mathrm{cc} \\ \mathrm{H}_{2} \mathrm{O} \end{gathered}$ | Ingredient | $\begin{gathered} \text { Grams } \\ \text { per } \hat{1}_{1,000} \mathrm{H}_{2} \mathrm{O} \end{gathered}$ | Ingredient | $\underset{\substack{\text { Grams } \\ \text { per } \\ \mathrm{H}_{2}, 000 \mathrm{Oc}}}{ }$ |
| $\mathrm{KNO}_{3}$ | 1.00 | $\mathrm{Ca}\left(\mathrm{NO}_{3}\right)_{2}$ | 0.8 | $\mathrm{Ca}\left(\mathrm{NO}_{3}\right)_{2}$ | 0.8 | $\mathrm{KNO}_{3}$ | 1.00 |
| $\mathrm{Ca}_{3}\left(\mathrm{PO}_{4}\right)_{2}$ | 0.50 | $\mathrm{KNO}_{3}$ | 0.2 | KNO ${ }_{3}$ | 0.2 | $\mathrm{Ca}_{3}\left(\mathrm{PO}_{4}\right)_{2}$ | 0.25 |
| $\mathrm{MgSO}_{4}$ | 0.50 | $\mathrm{KH}_{2} \mathrm{PO}_{4}$ | 0.2 | $\mathrm{MgSO}_{4}$ | 0.2 | $\mathrm{MgSO}_{4}$ | 0.25 |
| $\mathrm{CaSO}_{4}$ | 0.50 | $\mathrm{MgSO}_{4}$ | 0.2 | $\mathrm{KH}_{2} \mathrm{PO}_{4}$ | 0.2 | $\mathrm{CaSO}_{4}$ | 0.25 |
| NaCl | 0.25 | $\mathrm{FePO}_{4}$ | Trace | KCl | 0.2 | $\mathrm{FePO}_{4}$ | 0.25 |
| $\mathrm{FeSO}_{4}$ | Trace |  |  | $\mathrm{FeCl}_{3}$ | Small amount |  |  |

[^3]

Fig. 2. The use of the water-culture technique for studying the nutritional responses of lettuce plants under controlled conditions. The individual plants are supported in corks, which are placed in holes drilled in the metal covers. The glass and rubber tubes carry compressed air, which is bubbled through the nutrient solution.
elucidated by the aid of the water-culture method of experimentation, the effects of aeration of the roots on plant growth are shown in plate $l, A$, and the foliage symptoms of deficiencies of mineral elements required in large or minute quantity in plate $1, B$ and plates 2 to 4 .

## Solid aggregate culture provides anchorage for plant roots

In the water-culture technique the roots of plants are submerged in a liquid solution of plant nutrients. As in a soil, the roots serve as the organs of absorption for water and nutrients; unlike in soil, the roots provide no anchorage for the aerial portions of the plant. Special provisions, discussed later, are necessary for supporting plants grown in water culture.

Plants may be grown without soil, however, by other techniques, in which the roots serve as organs of both absorption and anchorage. Instead of in a liquid
medium, the plants are placed in some solid inert aggregate, periodically irrigated by a synthetic nutrient solution. Sand culture is the earliest example of this technique. Its development paralleled that of water culture, and it was used by many investigators to study the same types of scientific problems of plant nutrition as were discussed under water culture above.
Several experiment stations in recent years have developed techniques of ag. gregate culture adapted to growing plants on a large scale. Instead of sand, many of these techniques make use of such coarser aggregates as gravel, cinders, burned shale (haydite), crushed granite, and vermiculite. These aggregates are placed in especially constructed beds to which the nutrient solutions are supplied at regular intervals.

## Subirrigation is often used in aggregate culture

With the coarser aggregates, the nutrient solution is generally supplied by a subirrigation method rather than by surface applications. Labor-saving, automatic devices for supplying nutrient solutions to the culture beds are usually a feature of the subirrigation methods. A detailed discussion of these procedures, which is beyond the scope of this circular, will be found in other publications. ${ }^{7}$
(The California Agricultural Experiment Station cannot provide copies of these publications. Inquiries should be made at the source.)

[^4]
## No new principles are used in commercial "aggregate" culture

As with large-scale water culture, the techniques for aggregates do not rest on any newly discovered principles of plant nutrition. They represent an application of engineering and technical principles to the construction of beds and the circulation of the nutrient solution, with economy and ease in construction and operation as objectives. Ingenious as these technical devices are, they cannot assure success in growing plants to any operator who does not have a sound knowledge of the physiological and horticultural principles involved in crop production. These principles, which are the same for water and aggregate culture, will be referred to in subsequent sections of this circular.

## Adsorbed-nutrient technique does use a different principle

With either aggregate or water culture, the plant nutrients are supplied in a chemical solution. The management of this solution involves the technical problems of preparing, testing, and adjusting the concentrations of the individual nutrients.

Under the sponsorship of the Army Air Forces during World War II, the possibility of using a large-scale nutrientculture technique which would have some of the "fool-proof" aspects of growing plants in a fertile soil was explored. Instead of supplying the plant nutrients in repeated applications of nutrient solutions, as is the practice in aggregate culture, a different principle was used. The plant nutrients were not furnished as chemical salts but rather as "adsorbed ions" on synthetic ion-exchange materials, in a manner similar to that in which some plant nutrients are bound to colloids in natural soils. The "charged" ionexchange materials were then mixed with sand prior to planting the crop. After the plants were in, only applications of water would be necessary to make growth possible.

These wartime experiments were promising but were discontinued as the war ended, before the "adsorbed-nutrient" technique had passed the experimental stage. The information derived from these experiments has been published, ${ }^{8}$ but no recommendations for commercial application can be made by the Experiment Station at this time.

## PRIMCIPLES AND APPLICATION OF NUTRICULTURE

## A knowledge of plant physiology is necessary

It should be stated at the outset that there is no magic in nutriculture methods. They provide only another means of supplying mineral nutrients and water to plants. The absorption of nutrients and water accounts for only two of the physiological processes of the plant. In order to evaluate the possibilities and limitations of any special technique for growing plants, one has to understand the significance of other interrelated processes, especially photosynthesis, respiration, transpiration, and reproduction. The currently prominent interest in the appli-
cation of nutriculture techniques to crop production makes it desirable to discuss briefly the various factors which need to be considered by those contemplating an investment of time and funds in this field.

## What is the justification for nutriculture in crop production?

1. The answer to this question is that the method has certain possibilities in

[^5]the growing of special high-priced crops, particularly out of season in greenhouses, in localities where good soil is not available, or when maintenance of highly favorable soil conditions is found too expensive.

Soil beds in greenhouses often become infected with disease-producing organisms, or toxic substances may accumulate. Installation of adequate equipment for sterilizing soils and operation of the equipment may require considerable expense. Also, maintenance of fertility in the soil beds is often laborious and expensive. On the other hand, a synthetic nutrient medium, expertly supervised, can serve as a continuously favorable source of nutrients and water and, especially if combined with automatic devices, can bring about economies in labor.
2. Very favorable climates in some regions may justify growing certain crops out of doors in nutriculture. The possibilities of nutriculture are not confined to greenhouses. In regions highly favored climatically and with a good water supply available, but where soil conditions are adverse, there may be reasons for growing crops outdoors by nutriculture techniques.
A case in point was the gravel-culture installation of the Army Air Forces on Ascension Island in the South Atlantic, toward the end of World War II. ${ }^{.}$This tiny volcanic island located near the equator has a climate characterized by mild temperatures and low rainfall. Over most of its area there is no agricultural soil. Because of the extreme geographic isolation and difficulties of supply, the large military garrison placed there during the war could be adequately provided only with the essential dietary staples, such as grains and meat and milk products. The supply of fruits and vegetables was limited to canned, dried, or dehydrated items. The psychological satisfactions from a supply of fresh salad vegetables and the attendant benefits to the morale and, in some cases, even to the
health of troops, were deemed important enough to justify a determined effort to provide such items as fresh tomatoes, lettuce, peppers, radishes, and cucumbers. To supply these from outside sources was not practical. To grow them on the island by conventional methods in soil was not feasible. An aggregate culture installation, using a local gravel, was therefore authorized for the soilless production of fresh salad crops.

A remarkable feature of the Ascension Island installation was the use of distilled sea water in making the nutrient solutions. Without this engineering feat of providing by distillation the large water requirements of the growing crops, the project could not have been undertaken. The nutriculture installation on Ascension Island accomplished its mission. It stands out as an example of the successful application of the principles of plant physiology and engineering techniques to the growing of crops in locations devoid of natural soils.

## What are the drawbacks of commercial nułriculture?

In the United States, nutriculture techniques have found application in greenhouses in the production of floral and vegetable crops, and outdoors, in such climatically favorable areas as in Florida. Of the various techniques, the aggregate or gravel culture is the one most commonly used in commercial installations. The commercial application of the nutriculture techniques has not been as widespread as its most ardent followers expected. As foreseen over a decade ago in the first edition of this circular, two factors have limited the displacement of soil by nutriculture and will continue to do so: first, economic considerations and second, familiarity of commercial growers with the management of soils rather than with nutriculture methods.

[^6]1. Nutriculture is costly and needs expert supervision. The initial financial investment in nutriculture facilities is high. The automatic adjustment of many of the factors determining the nutrition of the plant is found in a soil naturally fertile or in one capable of being made so by a simple treatment but is lacking in nutriculture methods.

Expert supervision is generally necessary to cope with technical difficulties which may be met. Some of these are the character of the water, adjustment of the acidity of the nutrient solution, toxic substances from tanks or beds, uncertainty as to time for replenishing salts in the nutrient solution or for changing it.

To the average grower, crop production in nutriculture is an unfamiliar undertaking, involving problems not encountered in soil culture. On the other hand, growing plants in soil is one of the oldest occupations of mankind, with a rich fund of accumulated experience to draw upon for guidance.

In the absence of such special considerations which, for example, justified the operation of the Ascension Island installation by the Army Air Forces during the war, commercial success is unlikely, unless the most careful consideration is given to economic factors. What crops, if any, could be profitably grown by nutriculture methods would depend on (1) the value of the crop in THE MARKET SERVED, in relation to cost of production,-this would include a large outlay for beds, materials, and other equipment-and (2) special costs of expert supervision and operation.
2. Nutriculture demands knowledge of all factors of plant growth. Amateurs have sometimes mistakenly assumed that nutriculture techniques can substitute for lack of horticultural skill in growing crops on a commercial scale. Indispensable to profitable crop production by nutriculture methods is a general knowledge of plant varieties, habits of growth, climatic adaptations, and pollination, and of the
control of disease and insects-in other words, the same knowledge now needed for successful crop production in soils.

## Nutriculture does not solve problems of sanitation

In certain parts of the world, agricultural soils are fertilized by human excreta. Fresh vegetables from such areas, if consumed raw, are sometimes carriers of pathogenic organisms. It has been suggested that such a hazard can be eliminated by the use of outdoor nutriculture techniques. This suggestion does not seem to be supported by enough scientific evidence. It is not clear, for example, that outdoor installations will be protected from contamination by particles of soil, carried from adjoining infected areas by wind or other agencies. Rigorous cleansing of all vegetables to be consumed raw is a safety measure in any case. It is also possible that some suitable cleansing agent can be devised for the disinfection of soil-grown vegetables. Moreover, it has not been demonstrated that the disinfection of selected local soil areas and the subsequent careful management of them are impractical or offer less health security than artificial culture techniques.

Wherever pathogenic organisms from the soil are a problem, standards of sanitation are notoriously low. Handling vegetables to be eaten raw, therefore, always constitutes a health hazard. Rigid sanitation measures are necessary against this source of infection, regardless of the method by which the crop was grown.

## Nutriculture is rarely superior to soil culture

Yields are not strikingly different under comparable conditions. The impression conveyed by many of the popular discussions of nutriculture methods is that much more can be produced on a given surface of nutrient solution than on an equivalent surface soil, even under the best soil conditions feasible to maintain. Often quoted is the yield of tomato plants grown for a


Fig. 3. Growth of tomato plants in fertile soil, in nutrient solution, and in pure silica sand irrigated each day with nutrient solution. Fruit had been harvested for 7 weeks prior to taking the photograph. All plants have made excellent growth and set large amounts of fruit in all three media. The general cultural conditions-spacing, staking, etc.-were the same.
twelve months' period in a greenhouse water-culture experiment in Berkeley. ${ }^{10}$ It is compared with average yields of tomatoes under ordinary field conditions; the yield from the water-culture plants is computed to be many times greater. But closer analysis shows that mistaken inferences may be drawn from this com-
parison. Predictions concerning yields in large-scale production are of doubtful validity when based on those obtained in small-scale experiments under laboratory control. In any event, there is little profit

[^7]in comparing an average yield from unstaked tomato plants, grown during a limited season under all types of soil and climatic conditions in the field, with that from staked plants grown in the protection of a greenhouse for a full year.
Evidence has long been available that yields of tomatoes grown in a greenhouse, in soil, can far exceed those obtained in the field. It is true that in one series of outdoor experiments, the yields of tomatoes under water-culture conditions were reported to be much higher than under ordinary field conditions; but again, the general cultural treatment of the plantsespecially with regard to spacing and staking-was so different that comparisons of yield do not mean very much.

Any real test of the relative capacities of soil and nutriculture media for crop production requires that the two types of culture be carried on side by side, with similar spacing of plants and with the same cultural treatment otherwise. The soil should be of suitable depth and have its nutrient supplying power and physical condition as favorable for plant growth as possible. An experiment of this kind, with the tomato as the test plan', has been carried out in Berkeley. ${ }^{11}$ Several conclusions derived from it warrant emphasis. The yield of tomatoes grown by the usual tank-culture technique was larger than any heretofore reported for this method. That from the soil-grown plants, however, was not markedly different (fig. 3). When the greenhouse yields of tomatoes from either soil- or nutriculture-grown plants were compared on an acre basis with average yields of field-grown tomatoes, the greenhouse plants gave far greater yields. Such comparisons, however, can have no direct practical significance because of the differences in climatic factors, cultural practice, and length of season in the greenhouse and in the open field.

In one California commercial greenhouse, the yields of tomatoes grown in soil equaled those obtained in a successful commercial greenhouse using water
culture. In another greenhouse using soil, the yields were larger.

The yield of potatoes grown in a bed of peat soil in Berkeley was as large as any heretofore reported as produced by the water-culture method.

Plants cannot be spaced closer than in a rich soil. The suggestion has sometimes been advanced that plants can be grown more closely spaced in nutrient solutions than in soil, but no convincing evidence of this has been given. In our experiments, we were able to grow tomato plants as close together in the soil as in the solution (fig. 3). The density of stand giving the highest yields would be determined by the adequacy of the light received by the plants, when growth is not limited by the supply of nutrients or water derived from either soil or nutrient solution. Closeness of spacing under field conditions is, of course, limited by practical considerations involving cost of crop production. This consideration of economic factors and of the adequacy of light does not justify the view that the nutriculture medium is better adapted than soil to growing several different crops simultaneously in the same bed.

Plant gro th habits are not changed by nutriculture. Some published pictures of tomato plants grown in nutriculture show impressive height. This growth in length of vines is frequently the subject of popular comment. As a matter of fact, the ability of tomato vines to extend is characteristic of the plant and is not peculiar to the nutriculture method. Staked plants grown for a sufficiently long period in a fertile soil, under favorable light and temperature conditions, can also reach a great height and bear fruit at the upper levels (fig. 4). In commercial greenhouse practice, growers usually "top" the vines. Fruit developed at higher level is likely to be of inferior quality and is relatively

[^8]

Fig. 4. Under favorable conditions, tomato plants can grow to a great height and bear fruit over an extended period of time. This is equally possible in soil, sand, and water-culture media. The plants in the foreground were grown in a bed of fertile soil. At the time of taking this photograph, several days before the termination of the experiment, most of the fruit had already been harvested.
expensive to produce because of both the labor required to attach supports to the vines and the inconvenience of harvesting. Furthermore, it may become profitable to discontinue the tomato harvest when prices become low in the summer and to use the greenhouse space to plant another crop for the winter harvest.

Land plants have become adapted to growing in soils during their evolutionary history. It is not reasonable, therefore, to expect some extraordinary increase in their potentialities for growth when an artificial medium is substituted for soil. If no toxic conditions are present and a fully adequate supply of water, mineral salts, and oxygen is provided to the root system, either through an artificial nutrient solution or a soil, then in the absence of plant diseases and pests, the growth of a plant is limited by its inherited constitution and by climatic conditions.

Water requirement is no less in nutriculture. The view has sometimes been advanced that the water requirement is smaller in nutriculture than in soil. Utilizing climatically favored desert regions to produce crops by large-scale nutriculture is one of the recent popular misconceptions. Obviously, even if crops grown by this method in desert regions required less water, the difficulties in providing a somewhat smaller supply for nutriculture would be essentially the same as those encountered in providing a larger amount for irrigation in soil. There is no direct evidence that crops produced by nutriculture require actually less water than those grown in soil, if the climatic conditions are the same.

Tomatoes grown side by side in soil and in water culture in the same greenhouse ${ }^{12}$ afforded an opportunity to measure the relative amounts of water utilized. The numbers of gallons of water used to produce 100 pounds of fruit were as follows: soil, 222 ; water culture, 257 . These results indicate that somewhat more water was used to produce a unit weight of fruit under water culture than under soil conditions. What seems to warrant emphasis, however, is not the difference, but the essential similarity in the amount utilized by the plants grown in both media. This is in agreement with the fact that the principal use of water in producing a crop is through evaporation by the plant-a re-

[^9]quirement common to both soil and nutriculture. The physiological characteristics of each species of plant, the extent of leaf surface, and the atmospheric conditions are the determining factors in this requirement. If a large crop is produced, either in nutriculture or in soil, and if climatic conditions favor high evaporation of water from the plant, the amount of water used in either case is necessarily large.

Nutritional quality of the product is the same. Modern research on vitamins and on the role of mineral elements in animal nutrition has justly aroused great public interest. Here again much popular discussion relating to their effect in diets and on health has been without scientific basis. It is, therefore, not unexpected that claims have been advanced for the superiority of food produced by nutriculture.

As part of our investigation, careful studies of chemical composition and general quality have been made on tomatoes of several varieties grown in a fertile soil, and in sand- and water-culture media, side by side in the same greenhouse, with the same general cultural treatment. No significant difference has been discovered in the mineral content of the fruit developed on plants grown in the several media. There is no scientific basis then for referring to tomatoes grown in nutriculture as "mineralized."

Among the minerals most frequently mentioned in this connection was calcium. It may be added, as a point of general interest, that all tomatoes, regardless of the method by which they were grown, contain but small amounts of calcium and are not therefore an important source of this mineral element in the diet.

Tomatoes harvested from the soil and from water cultures could not be consistently distinguished in a test of flavor and general quality. ${ }^{13}$
No significant difference could be found in content of vitamins-carotene, or provitamin A , and vitamin C , in the fruit.

Caution: No claims of unusual nutritional value for food products should be accepted unless they are supported by results obtained in research institutes of high standing.

The similarity in composition and general quality of the tomatoes grown in soil and water culture in the present experiments, may be explained by the facts that the climate and time of harvest were comparable and that the supply of mineral nutrients was adequate in both cases. Whether plants are grown in soil or nutriculture, climate and time of harvest are, of course, the factors that most affect quality and composition of plant product.

Nutrient deficiencies, insect attacks, and diseases present similar problems.

When plants are grown in solutions deficient in any of the nutrient elements, symptoms appear, usually in the leaves. The series of photographs (plates 2 to 4 ) shows the general character of foliage symptoms developed by the tomato plant for each essential element omitted from experimental solutions.

Nutriculture does not protect plants from any diseases except those strictly soil-borne. In fact, certain other diseases peculiar to water culture may sometimes attack them.

The same insect pests attack plants grown in all media.

Climatic requirements are the same. Many inquiries have been received on the possibility of growing plants in nutriculture in dimly lighted places, or at low temperatures, under conditions which would prevent growth of plants in soil. Obviously, no nutrient solution can act as a substitute for light and suitable temperature. If there is doubt of the suitability of a particular location or season for the growth of any kind of plant, a preliminary experiment should be made

[^10]

Plate 1. A, B, Effect of forced aeration on asparagus plants grown in culture solutions: A, plants grown in solution through which air was bubbled continuously; B, plants without forced aeration, C, Asparagus plants grown in a nutrient solution in which boron, manganese, zinc, and copper were present in such small amounts as one part in several million parts of solution; D, plants grown in solutions to which these elements were not added.
by growing the plant in good garden soil. If the plant fails to make satisfactory development in the soil medium recause of unfavorable light or temperature, failure may also be expected under waterculture conditions.

Sunlight and suitable temperatures are essential for green plants, in order that they may carry on one of the fundamental processes of plant growth, known as photosynthesis. In this process, the element carbon, which forms so large a


Plate 2. Symptoms of mineral deficiencies shown by tomato plants: A, complete nutrient solution; B, solution lacking nitrogen; $C$, solution lacking phosphorus; D, solution lacking potassium.
part of all organic matter, is fixed by plants from the carbon dioxide of the atmosphere. This reaction requires a large amount of energy, which is obtained from sunlight.

Plants depend on photosynthesis for their food, that is, for organic substances, such as carbohydrates, fats, and proteins,
which provide them with energy and enter into the composition of plant substance. The mineral nutrients absorbed by roots are indispensable for plant growth but do not supply energy and, in that sense, cannot be regarded as "plant food."

Animal life is also absolutely dependent


Plate 3. Symptoms of mineral deficiencies shown by tomato plants: E, solution lacking calcium; $F$, solution lacking sulfur; $G$, solution lacking magnesium; H , solution lacking boron.
on this ability of the green plant to fix the energy of sunlight.

Favorable air temperatures are just as necessary as in soil. An earlier report of a preliminary experiment by other investigators suggested that under greenhouse conditions, heating the nutrient solution would produce large increases in the yield of tomatoes. ${ }^{14}$ This is not confirmed by experiments we undertook in a Berkeley greenhouse, which was un-
heated except on a few occasions to prevent temperatures from falling below $50-55^{\circ}$ Fahrenheit. Under the climatic conditions studied, the beneficial effects of heating the nutrient solution (to $70^{\circ} \mathrm{F}$ in the fall-winter and to $75^{\circ} \mathrm{F}$ in the spring-summer period) were not of significance. If favorable air temperatures

[^11]

Plate 4. Symptoms of mineral deficiencies shown by tomato plants: A, right, iron deficiency; left, complete nutrient solution; $B$, left, manganese deficiency; right, complete nutrient solution; C, left, copper deficiency; middle, complete nutrient solution; right, zinc deficiency; D, left, molybdenum deficiency; right, complete nutrient solution. (Illustration from recent unpublished results of D. I. Arnon and P. R. Stout.)
are maintained, there seems to be no need to heat the solution.

Attempts should not be made to guard against frost injury or unfavorable low air temperatures merely by heating the nutrient solution. Proper provision should be made for direct heating of the greenhouse. This may be found desirable even when danger from low temperatures is absent, in order to control humidity and certain plant diseases.

These experiments on tomatoes sug. gest that if greenhouse temperatures are properly controlled, the solution temperature will take care of itself. Certainly no expense should be incurred for equipment for heating solutions, either in a greenhouse or outdoors, until experimentation has shown such heating to be profitable.

There is no one best solution temperature. The physiological effects of the temperature of the solution are interrelated with those of air temperature and of light conditions.

Most amateurs who try the nutriculture method will grow plants in warm seasons and probably will not wish to complicate their installation by the addition of heating devices. Anyone who desires to test the influence of heating the culture solution should make comparisons of plants grown under exactly similar conditions, except for the difference of temperature in the solutions.

## Composition of nutrient solutions may vary

No one nutrient solution is superior to all other solutions. Thousands of requests have been received by the Station for formulas for nutrient salt solutions. It is often supposed that some remarkable new combination of salts has been devised and that the prime requisite for growing crops in solutions is to use this formula. The fact is, there is no one composition of a nutrient solution which is always superior to every other composition. Plants have marked powers of adap-
tation to different nutrient conditions. If this were not so, plants would not be growing in varied soils in nature. We have already emphasized that within certain ranges of composition and total concentration, fairly wide latitude exists in the preparation of nutrient solutions suitable for plant growth. Many varied solutions have been used successfully by different investigators. Even when two solutions differ significantly in their effects on the growth of a particular kind of plant under a given climatic condition, the relation between the solutions will not necessarily be the same with another kind of plant, or with the same kind of plant under another climatic condition.

Concentration of the solution changes as the plants grow. Another point concerning nutrient solutions needs to be stressed. After plants begin to grow, the composition of the nutrient solution changes because the constituents are absorbed by plant roots. How rapidly the change occurs depends on the rate of growth of the plants and the volume of solution available for each plant. Even with large volumes of solutions, some constituents may become depleted in a comparatively short time by rapidly growing plants. This absorption of nutrient salts causes not only a decrease in the total amounts of salts available, but a qualitative alteration as well, since not all the nutrient elements are absorbed at the same rates. One secondary result is that the acid-base balance $(\mathrm{pH})$ of the solution may undergo changes which in turn may lead to the precipitation of certain essential chemical elements (particularly, iron and manganese) so that they are no longer available to the plant. Also to be considered are the effects of salts added with the water (discussed later).

Constant control of the solution is necessary. For these various reasons, the maintenance of the most favorable nutrient medium throughout the life of the plant involves not merely the selection of an
appropriate solution at the time of planting but also continued control, with either the addition of chemicals when needed or the replacement of the whole solution from time to time. Proper control of culture solutions is best guided by observations of the crop and by chemical analyses of samples of the solution taken periodically.

The objective of controlling the nutrient solutions is not to maintain a fixed composition of some "ideal" nutrient solution, but rather to provide the plant at each stage of its growth with a sufficient quantity of each essential element, within suitable ranges of total concentration and fairly broad limits of ionic proportions.

Test tap water for salt content. For the purpose of exact control in his experiments, the plant physiologist prepares his solutions with distilled water. The commercial grower and the amateur are usually limited to the use of domestic or irrigation water, which contains various salts, including such sodium salts as sodium chloride, sodium sulfate, and sodium bicarbonate, as well as calcium and magnesium salts.

Most waters suitable for irrigation or for drinking can be utilized in the waterculture method, but the adjustment of the reaction $(\mathrm{pH})$ in the nutrient solution depends on the composition of the water. Some waters may be unfit for use in the solution because of high sodium salt content. Even with a water only moderately high in it, the salt may concentrate in the nutrient solution with possible unfavorable effects on the plant. This is particularly true when large amounts of water have to be added to the tanks and the solutions are not changed. In one instance, a well water was highly toxic because it contained too high a concentration of zinc, apparently derived largely from circulation through galvanized pipes. This same water, however, was not injurious to tomato plants grown in soil because of the absorbing power of the soil for zinc.

Nutrients cannot take the place of sunshine. As already indicated, the successful growth of a crop is dependent on sunlight and temperature and humidity conditions, as well as on the supply of mineral nutrients furnished by the culture medium. Complex interrelations exist between climatic conditions and the utilization of these nutrients. The relation of nitrogen, nutrition, and climatic conditions to fruitfulness has often been stressed. In some localities, deficient sunshine in winter months may limit the growth of many greenhouse crops, no matter what nutrient conditions are present in the culture solution.

The same initial composition may supply nutrient requirements of many kinds of plants. The question is frequently asked: Does each kind of plant require a different kind of nutrient solution? The answer is that if proper measures are taken to provide an adequate supply of nutrient elements, then many kinds of plants can be grown successfully in nutrient solutions of the same initial composition. (The same fertile soil can produce high yields of many kinds of plants.)

The composition of the nutrient solution should always be considered in relation to the total supply as well as to the proportions of the various nutrient elements. To give a specific illustration: assume that several investigators prepare nutrient solutions of the same formula, but one uses 1 gallon of the solution for growing a certain number of plants, another 5 gallons of solution, and still another 50 gallons. If plants were grown to large size, each investigator would reach a different conclusion as to the adequacy of the nutrient solution employed, although the initial composition was the same in all cases. The investigator using the small volume might find that his plants became starved for certain nutrients, while the one using the larger volume experienced no such difficulty. In fact, the precise initial composition of a culture solution has very little signifi-
cance, since the composition undergoes continuous change as the plant grows and absorbs nutrients.

The rate and nature of this change depends on many factors, including total supply of nutrients. An adequate supply of nutrients involves (1) volume of solution in relation to the number of plants grown, stage of growth of the plant, and rate of absorption of nutrients, and (2) frequency of changes of solution.

Apart from the question of adequate supply of nutrients, certain special responses of different species of plants have to be taken into account in the management of nutrient solutions. Plants vary in their tolerance to acidity and alkalinity. They also differ in their need for root aeration and in susceptibility to injury from excessive concentrations of elements like boron, manganese, copper,
and zinc. Some plants may be especially prone to yellowing because of difficulty in absorbing enough iron or manganese. Some may succeed best in a nutrient solution more dilute than is employed for most kinds of plants. Unfavorable responses by certain plants to high nitrogen supply in relation to fruiting, under certain climatic conditions, may require consideration.

Since the adaptation of a nutrient solution to the growth of any particular kind of plant depends on the supply of nutrients and on climatic conditions, there is no possibility of prescribing a list of nutrient solutions, each one best for a given species of plant. ${ }^{15}$ Some general type of solution, such as one of those described in this circular, should be tried first. It may be modified later by experiment if found necessary.

## DIRECTINS FOR THE WATER-CULTURE METHOD

The preceding discussion dealt with general considerations bearing on the use of any soilless method of plant growth, especially by those who contemplate commercial ventures. What follows, deals with specific directions on how to proceed. These are given in response to numerous inquiries received from amateurs, prospective growers, teachers, and many others. As stated earlier, this circular describes only one technique for growing plants without soil, namely, the waterculture method. Other publications available elsewhere (see footnote 7, page 9) give details of other techniques.

## The type of container

The selection of a container depends on the kind of plant to be grown, the length of the growing period, and the purpose for which the plants are grown.

In investigational work, 1- or 2 -quart Mason jars provided with cork stoppers often serve as culture vessels (fig. 5).

Sometimes 5- or 10-gallon earthenware jars are more suitable. Small tanks of various dimensions have been extensively used. For certain special investigations, shallow trays or vessels of Pyrex glass are required. Figure 6 shows the varied types of containers used at the Station for nutrient solutions in research problems.

For demonstrations in schools. Mason jars covered with brown paper to exclude light are excellent for demonstrations in schools (fig. 5). The jars should have cork stoppers in which one or more holes have been bored (sometimes a slit is also made in the cork; see fig. 1). Plants are fixed in the holes with cotton. Wheat or barley plants are very suitable for these

[^12]demonstrations, since they may be grown in the jars without any special arrangements for aeration.

For small-scale cultures. Two or 4gallon crocks may be serviceable for small-scale cultures. Perforated corks fitting into specially constructed covers, or a porous bed of the kind described later, support the plants. Other useful containers are sheet metal tanks, such as those shown in figure 6. The dimensions of tanks are determined by the objective. A tank of moderate size, adapted to many purposes, is 30 inches long, 30 inches wide, and 8 inches deep (fig. 2, p. 9 and fig. $6, B$ ). A smaller one, 30 inches long, 12 inches wide, and 8 inches deep, is con-- venient for use in many experiments (fig. $6, C)$. In general, the tanks should be shallow, their length and width determined by convenience and economy. They should have metal or wooden covers perforated to hold corks (fig. $6, A, C$, $D)$ which support the plants and in which the plants are fixed with cotton (fig. 2).

For commercial water culture. For largescale experimental installations or for commercial water culture, long, narrow, shallow tanks have been employed. They may be constructed of wood, cement, sheet metal, or other sufficiently cheap materials which do not give off toxic substances. Wooden tanks must be made water tight. Redwood has been reported to give off toxic substances and, therefore, may require their removal by preliminary leaching. Concrete tanks should also have thorough leaching before use.
Caution: All tanks should be painted on the inside with asphalt or some other paint harmless to plants. Most ordinary paints cannot be used because of their toxic substances. Galvanized iron, even when coated with asphalt paint, may cause trouble if any of the paint scales off. Black iron tanks, well painted with asphalt (fig. 6, A) have proved satisfactory for experimental work.

In experimental installations requiring large tanks, plants such as tomatoes were


Fig. 5. Corn and sunflower plants grown in' nutrient solution contained in 2 -quart Mason jars. Note method of placing plants in perforated corks. The jars are covered with thick paper to exclude light.
supported in perforated cork, fitted into specially constructed metal covers. In commercial culture, however, a porous bed is commonly used.

## Nature of the bed

Any good carpenter or mechanic can design and construct tanks and frames suitable for commercial nutriculture. Such installations generally consist of large tanks with porous beds for supporting the plants. (In experimental work, the perforated cork often serves this purpose.) The beds in turn are supported by heavy chicken wire netting (l-inch mesh) coated with asphalt paint and stretched tightly across a frame that fits the top of
the container. This technique was first suggested by W. F. Gericke. ${ }^{16}$

Some suggestions for building the frame.
1 . The wire-netting must be stretched tightly across the frames and must be immediately above the surface of the solution when the tank is full.
are: pine excelsior, peat moss, pine shavings or sawdust, rice hulls..Certain materials are toxic to plants. For this reason, redwood should usually be avoided. In experiments carried on in Berkeley with tomatoes, potatoes, and certain other plants, a layer of pine excelsior 2 or 3


Fig. 6. Various types of containers for carrying on water-culture experiments:
A, Large iron (not galvanized) tank painted inside with asphalt paint, outside with aluminum paint. Dimensions: $10 \mathrm{ft} . \times 21 / 2 \mathrm{ft} . \times 8 \mathrm{in}$. Shows one section of metal cover. Perforated corks for supporting plants are fixed in the holes (fig. 2). Wooden frames containing bedding material may also be set over these tanks, as shown in figure 7.
B, Iron tank of dimensions: $30 \mathrm{in} . \times 30 \mathrm{in} . \times 8 \mathrm{in}$.
C, Iron tank of dimensions: $30 \mathrm{in} . \times 12 \mathrm{in} . \times 8 \mathrm{in}$
D, Iron tank of dimensions: $151 / 2 \mathrm{in} . \times 10 \frac{1}{2} \mathrm{in} . \times 6 \mathrm{in}$.
E, Graniteware pan $16 \mathrm{in} . \times 11 \mathrm{in} . \times 2 \frac{1}{2} \mathrm{in}$. used for growing small plants. Perforated metal covers, as shown in A, C, and D, may be used on all metal tanks or trays. The number of holes in the cover can be varied according to the number and size of plants to be grown.

F and G, Pyrex dish and beaker used for special experiments designed to study the essentiality of certain chemical elements required by plants in minute quantity, such as zinc, copper, manganese, and molybdenum. The covers for these containers, shown in the illustration, are molded from plaster of Paris and then coated with paraffin.
2. Cross supports may be needed to keep the wire from sagging (fig. 7).
3. Several narrow sections of the frame may be left uncovered by wire and fitted with wooden covers instead. The latter may be removed easily for inspection of roots and for adding water or chemicals to the solution.

Some porous materials that may be used. The layer of the porous material is generally 3 or 4 inches thick-thicker when tubers or fleshy roots develop in the bed. Some inexpensive bedding materials
inches thick, with a superimposed layer of rice hulls about 1 or 2 inches thick, has produced no toxic effects. For plants that develop tubers or fleshy roots, some finer material may possibly need to be mixed with the excelsior. This is also essential when small seeds are planted in

[^13]the bed to prevent their falling into the solution and to effect good contact of the moist material with the seed. In all cases the bed must be porous and permit free access of air.

Care of the porous material. Seeds may be planted in the moist beds, or young plants from flats may be set in them with
for plants differ greatly in this requirement. In general, shallow, open tanks with porous beds facilitate aeration of the root system. It need not be assumed, however, that these beds assure the best growth for such plants as tomatoes, which have a high oxygen requirement. In one series of experiments, ${ }^{17}$ tomato plants


Fig. 7. General arrangement of tank equipment and method of planting: $A$, a frame supporting a wire screen fits over the metal tank (fig. 6, A) filled with the nutrient solution; $B$, tomato plants are placed with their roots immersed in the nutrient solution; a layer of excelsior is spread over the netting, as shown in the far end of the tank; $C$, the planting is completed by spreading a layer of rice hulls over the excelsior.
their roots in the nutrient solution. When seeds are planted in the bed, they must of course be kept moist until the roots grow into the solution below. Occasional sprinkling will provide enough moisture for the development of tubers, bulbs, and fleshy roots. Great care should be observed to prevent waterlogging of the bed. This results from immersion of the lower portion of the bed in the solution and leads to exclusion of air and to undesirable bacterial decompositions.

## Aeration of the root system

In water culture, special attention has to be given to aeration of the root system,
were grown in large shallow tanks provided with porous beds, but without any special provision for aeration. A parallel culture was aerated by bubbling air through the solution. The latter showed a significant improvement in growth and yield, although the yields from the unaerated beds were at least as large as any previously reported for this technique.

Roots may develop in beds as well as in the solution, when porous beds are used. It has been suggested that for such plants as tomatoes, the additional roots in the bed may be essential for supplying certain factors required for the growth

[^14]of stem and for the prevention of chlorosis. According to this hypothesis, even with adequate aeration, normal growth would be impossible if the roots were continuously submerged in the nutrient solution. No support for this hypothesis was found in an experiment with tomatoes in Berkeley. The plants were grown in metal tanks provided with metal covers, so constructed that the level of the nutrient solution was automatically maintained at the top of the tanks. When adequate aeration was provided, normal growth and development resulted without a porous bed and with the roots continuously submerged.

Bubbling air through the solution. It is sometimes difficult to supply adequate oxygen when plants are grown in small containers and a large root system is to be developed. Bubbling air or circulating the solution is helpful in such cases. Various devices, such as porous carbon pipes and glass tubes, can be used for this purpose. In general, too vigorous agitation of the solution should be avoided as it may harm tender roots. A continuous stream of small bubbles of air gives good results. Certain methods of circulating culture solutions not only bring about effective aeration but, in addition, equalize the supply of nutrients. Circulation of the nutrient solution from a central reservoir was used successfully in one commercial greenhouse. For small scale or experimental installations, special devices for bubbling air or circulating the nutrient solution have been described. ${ }^{18}$

## Planting jprocedures

How to plant. Seeds may be planted directly in the moist bed. In that case, the whole bed must be installed and moistened before planting is begun.

Other seeds-cereals, for examplemay be germinated between layers of moist filter paper or paper toweling. This method is recommended if plants are to be fixed in corks and grown in jars or tanks with perforated metal or wooden
covers. As soon as germination begins, the upper layer of moist paper is removed and the seedlings allowed to grow on the moist paper bed until they are large enough to be placed in corks. An excess of water is then added to the paper and the seedlings carefully removed without damage to the roots.

Sometimes it is preferable to grow seeds in flats of good loam and then choose the most vigorous seedlings for transplanting into the bed. Just before transplanting, the soil must be thoroughly soaked with water so that the plants may be removed with the least possible injury to the roots. These should be rinsed free of the soil with a light stream of water and immediately set either in corks or in beds with the roots immersed in the solution. In the latter case, the layer of excelsior is built up over the wire screen as the roots are placed in the solution, and the layer of rice hulls is added last (fig. 7).
How to space plants. No general advice can be offered as to the best spacing. This depends on the kind of plant and on light conditions. Individual experience must guide the grower. In our experiments, tomato plants were set close together, in some instances 20 plants to 25 square feet of solution surface.

## Managing the solutions

When to add water to tanks. In starting the culture, the tank is filled with solution almost to the level of the wire netting on the bottom of the bed. As they grow, the plants absorb water, or it evaporates from the surface of the solution, thus reducing its level in the tank. After the root system is sufficiently developed, this level is usually maintained from one to several inches below the lower part of the bed to facilitate aeration. Since the solution

[^15]level should not be permitted to fall very far, however, water must be added at regular intervals.
As pointed out earlier, when large amounts of water have to be added, excessive accumulations of certain salts contained in the water may occur. This is especially likely to happen if the salt content of the water is high. To avoid this difficulty, the entire solution is changed whenever the salt concentration becomes high enough to influence the plant adversely. Should plants be injured, however, by the presence in the water of high concentrations of elements like zinc, changing solutions will not prevent injury. Because of the wide variation in the composition of water from different sources, no specific directions to cover all cases can be given.
When to change the nutrient solution. As they begin to grow, the plants absorb the nutrient salts, thus causing the acidity of the solution to change. More salts and acid may be added. To know how much, requires chemical tests on the solution. When these cannot be made, an arbitrary procedure may be adopted of draining out the old solution every week or two, immediately refilling the tank with water and adding nutrients as at the beginning of the culture. The number of changes of solution required will depend on the size of plants, how fast they are growing, and on the volume of the solution.

The nutrients should be distributed to different parts of the tank. To effect proper mixing, fill the tank at first only partly full (but keep most of the roots immersed), add the salts, and complete the filling to the proper level with a rapid stream of water, so directed as not to injure the roots.

How to test and adjust acidity of water and nutrient solution. Ordinarily some latitude is permissible in the degree of acidity $(\mathrm{pH})$ of the nutrient solution. For most plants, a moderately acid reaction (from pH 5.0 to 6.5) is suitable. If distilled water is used in the preparation of
nutrient solution, no adjustment of its reaction is necessary. If tap water is used, a preliminary test of its reaction should be made. Water found alkaline should bc acidified before adding the nutrient salts. This should be done when the solution is first made up and at each subsequent change of solution.
The chemicals required for testing acidity of water or nutrient solution are:

1. Bromthymol blue indicator. This can be obtained, with directions for use, from chemical supply houses, in the form of solutions or impregnated strips of paper.

Strips of other test papers covering a wide range of acidity are also now available on the market. The amateur who understands their use will find them convenient for adjusting the acidity of water as well as that of the nutrient solution.
2. Sulfuric acid. Purchase a supply of 3 per cent (by volume) acid of chemically pure grade. (Concentrated, chemically pure sulfuric acid may be purchased and diluted to 3 per cent strength, but the concentrated acid is dangerous if handled by inexperienced persons.) This 3 per cent acid may be further diluted with water, if a preliminary test indicates the need of only small additions of acid.
Test the degree of acidity of a measured sample of the water or nutrient solution (a quart, for example) by noting the color of the added indicator or test paper immersed in the solution. When bromthymol blue indicator is used, a yellow color indicates an acid reaction (with no further adjustment necessary) ; green, a neutral reaction; blue, an alkaline one.
If the original color is green or blue, add the dilute sulfuric acid ( 3 per cent or less in strength), slowly with stirring until the color just changes to yellow (indicating approximately pH 6 ). Do not add more beyond this point, since the yellow color will also persist when excessive amounts of acid are added. Record the amount of acid required.
Finally, add a proportionate amount of the acid to the water or nutrient solu-
tion in the culture tank or vessel, having first determined how much it holds.

Modification of the solution. Since considerable latitude is permissible in the composition of nutrient solution, analysis of tap water is not indispensable, unless the content of mineral matter is very high. Some waters may contain so much calcium, magnesium or sulfate, however, that further additions of these nutrient elements are unnecessary, or even undesirable. As the objective should be to approximate the intended composition of the nutrient solution, taking into account the salt already present in the water, analysis of it is useful.

Prepared salt mixłures not recommended. Many amateurs have become interested in the purchase of mixtures of nutrient salts ready for use. Various individuals and firms have offered such mixtures for sale in small packages. Clearly a prepared salt mixture does not obviate the difficulties which may be met in growing plants in water culture. Recently, some firms have made highly misleading claims for the salt mixtures they sell. The Station makes no recommendation with regard to any salt mixture. The fact that a mixture is registered with the California State Department of Agriculture, as required by the law governing sale of fertilizers, implies no endorsement for use of the product. The directions given later will, we hope, help the amateur to prepare his own nutrient solutions.

Chemically pure salts commonly employed in making nutrient solutions for scientific experiments would be too expensive for commercial practice. A number of ordinary fertilizer salts can serve in the production of crops by nutriculture methods. Recent developments in the fertilizer industry have made available cheap salts of considerable degree of purity. Some commercial salts, however, contain impurities (fluorine, for example, is commonly found in phosphate fertilizers) which may be toxic to plants under water-culture conditions.

## Selecting the nutrient solution

As stated before, there is no one nutrient solution which is always superior to every other solution. Many solutions may be used with good results. Those described below have been found satisfactory with various species of plants in experiments conducted in Berkeley, with a source of good water.

The composition of the solutions is given in two forms: $(A)$ by rough measurements adapted to the amateur without special weighing or measuring instruments, and ( $B$ ) in more exact terms for those with some knowledge of chemistry and the proper facilities for more accurate experimentation. These facilities would include chemical glassware, a chemical balance, and a supply of C.P. (chemically pure) chemicals.

## Preparing the nutrient solution

Directions for amateurs. Either one of the solutions given in table 2 may be tried. Solution 2 may often be preferred because the ammonium salt delays the development of undesirable alkalinity. The salts are added to the water, preferably in the order given.

To either of the solutions, add the elements iron, boron, manganese, and in some cases, zinc, and copper, which are required by plants in minute quantities. There is danger of toxic effects if much greater quantities of these elements are added than those indicated later in the text. Molybdenum and possibly other elements required by plants in minute amounts will be furnished by impurities in the nutrient salts or in the water, and need not be added deliberately.
a) Boron and Manganese Solution. Dissolve 3 teaspoons of powdered boric acid and 1 teaspoon of chemically pure manganese chloride ( $\mathrm{MnCl}_{2} \cdot 4 \mathrm{H}_{2} \mathrm{O}$ ) in a gallon of water. (Manganese sulfate could be substituted for the chloride.) Dilute 1 part of this solution with 2 parts of water, by volume. Use 1 pint of the
diluted solution for each 25 gallons of nutrient solution.

The elements in group $a$ are added when the nutrient solution is first prepared and at all subsequent changes of solution. If plants develop symptoms characteristic of lack of manganese or boron (see plate $4, B$, and plate $3, H$ ), solution $a$, in the amount indicated in the preceding paragraph, may be added between changes of the nutrient solution or between addition of salts needed in large quantities. ${ }^{10}$ But care is needed, for injury may easily be produced by adding too much of these elements.
b) Zinc and Copper Solution. Ordinarily this solution may be omitted, because these elements will almost certainly be supplied as impurities in water or chemicals, or from the containers. When needed, (plate $4, C$ ) additions are made as for solution $a$. To prepare solution $b$, dissolve 4 teaspoons of chemically pure zinc sulfate $\left(\mathrm{ZnSO}_{4} \cdot 7 \mathrm{H}_{2} \mathrm{O}\right)$ and 1 teaspoon of chemically pure copper sulfate
$\left(\mathrm{CuSO}_{4} \cdot 5 \mathrm{H}_{2} \mathrm{O}\right)$ in a gallon of water. Dilute 1 part of this solution with 4 parts of water. Use 1 teaspoon of the diluted solution for each 25 gallons of nutrient solution.
c) Additions of Iron to Nutrient Solution. Generally, iron solution will need to be added at frequent and regular intervals, perhaps as often as twice a week. If the leaves of the plant tend to become yellow (see plate $4, A$ ) even more frequent additions may be required. A yellowing or mottling of leaves, however, can also arise from many other causes.
The iron solution is prepared as follows: Dissolve 1 level teaspoon of iron tartrate (iron citrate or iron sulfate can be substituted, but the tartrate or citrate is often more effective than the sulfate) in 1 quart of water. Add $1 / 2$ cup of this solution to 25 gallons of nutrient solution each time iron is needed.

[^16]TABLE 2.-Composition of Nutrient Solutions*
(The amounts given are for $\mathbf{2 5}$ gellons of solution)

Directions for schools or technical laboratories. For experimental purposes, the use of distilled water and chemically pure salts is recommended. Molar stock solutions (except when otherwise indicated) are prepared for each salt, and the amounts indicated below are used.
Solution l ccin a liter of

$M \mathrm{KH}_{2} \mathrm{PO}_{4}$, potassium acid | $\begin{array}{c}\text { cc in a hiter of } \\ \text { nutrient solution }\end{array}$ |
| :---: |

phosphate .................. 1
$M \mathrm{KNO}_{3}$, potassium nitrate ..... 5
$M \mathrm{Ca}\left(\mathrm{NO}_{3}\right)_{2}$, calcium nitrate ... 5
$M \mathrm{MgSO}_{4}$, magnesium sulfate... 2

## Solution 2 <br> cc in a liter of nutrient solution

$M \mathrm{NH}_{4} \mathrm{H}_{2} \mathrm{PO}_{4}$, ammonium acid phosphate...................... I
$M \mathrm{KNO}_{3}$, potassium nitrate ..... 6
$M \mathrm{Ca}\left(\mathrm{NO}_{3}\right)_{2}$, calcium nitrate $\ldots 4$
$M \mathrm{MgSO}_{4}$, magnesium sulfate... 2
To either of these solutions, add solutions $a$ and $b$ below.
a) Prepare a supplementary solution which will supply boron, manganese, zinc, copper, and molybdenum, as follows:

| Compound ${ }_{\text {in }}^{\text {a }}$ | Grams dissolved in 1 liter of $\mathrm{H}_{2} \mathrm{O}$ |
| :---: | :---: |
| $\mathrm{H}_{3} \mathrm{BO}_{3}$, boric acid. . . . . . . . . | ... 2.86 |
| $\mathrm{MnCl}_{2} \cdot 4 \mathrm{H}_{2} \mathrm{O}$, manganese chloride $\qquad$ | 1.81 |
| $\mathrm{ZnSO}_{4} \cdot 7 \mathrm{H}_{2} \mathrm{O}$, zinc sulfate. | 0.22 |
| $\mathrm{CuSO}_{4} \cdot 5 \mathrm{H}_{2} \mathrm{O}$, copper sulfate | . . 0.08 |
| $\mathrm{H}_{2} \mathrm{MoO}_{4} \cdot \mathrm{H}_{2} \mathrm{O}$, molybdic acid <br> (assaying 85 per cent MoO | $\left.\mathrm{O}_{3}\right) \quad 0.02$ |

Add 1 cc of this solution for each liter of nutrient solution, when solution is first prepared or subsequently changed, or at more frequent intervals if necessary.

This will give the following concentrations:

| Element | Parts per million of nutrient solution |
| :---: | :---: |
| Boron | 0.5 |
| Manganese | 0.5 |
| Zinc | 0.05 |
| Copper | . 0.02 |
| Molybdenum | . . . 0.01 |

b) Add iron in the form of 0.5 per cent iron tartrate solution or other suitable iron salt, at the rate of 1 cc for each liter, about twice a week, or as indicated by appearance of plants.

The reaction of the solution is adjusted to approximately pH 6 by adding 0.1 N $\mathrm{H}_{2} \mathrm{SO}_{4}$ (or some other suitable dilution).

Molar Solutions. The concentrations of stock solutions of nutrient salts used in preparation of nutrient solutions are conveniently expressed in terms of molarity. A molar solution is one containing 1 gram-molecule ( mol ) of dissolved substance in 1 liter of solution. (In all nutrient-solution work, the solvent is water.) A gram-molecule or mol of a compound is the number of grams corresponding to the molecular weight.

Example 1, how to make a molar solution of magnesium sulfate: The molecular weight of magnesium sulfate, $\mathrm{MgSO}_{4} \cdot 7 \mathrm{H}_{2} \mathrm{O}$ is 246.50 . One mol of magnesium sulfate consists of 246.50 grams. Hence, to make a molar solution of magnesium sulfate, dissolve 246.50 grams of $\mathrm{MgSO}_{4} \cdot 7 \mathrm{H}_{2} \mathrm{O}$ in water and make to 1 liter volume.

Example 2, how to make a one-twentieth molar $(0.05 \mathrm{M})$ solution of monocalcium phosphate, $\mathrm{Ca}\left(\mathrm{H}_{2} \mathrm{PO}_{4}\right)_{2} \cdot \mathrm{H}_{2} \mathrm{O}$ (used in deficiency studies, below): The molecular weight of monocalcium phosphate, $\mathrm{Ca}\left(\mathrm{H}_{2} \mathrm{PO}_{4}\right)_{2} \cdot \mathrm{H}_{2} \mathrm{O}$ is 252.17 . Hence 0.05 mol of $\mathrm{Ca}\left(\mathrm{H}_{2} \mathrm{PO}_{4}\right)_{2} \cdot \mathrm{H}_{2} \mathrm{O}$ is $\frac{252.17 \text { grams }}{20}$ $=12.61$ grams. Therefore, to make a 0.05 $M$ solution of monocalcium phosphate, dissolve 12.61 grams of $\mathrm{Ca}\left(\mathrm{H}_{2} \mathrm{PO}_{4}\right)_{2}$. $\mathrm{H}_{2} \mathrm{O}$ in water and make to 1 liter volume.

## Nutrient solutions for use in demonstrating mineral deficiencies in plants

In any experiment to demonstrate mineral deficiencies in plants, solution 1 or solution 2 should be used as a control to show normal growth in a complete solution. Below are given six solutions, each lacking in one of the essential elements. Similar solutions were used in producing the deficiency symptoms shown in plates 2 and 3 , with plants which had previously been grown for several weeks in complete nutrient solutions.

Distilled water should be used in making these solutions.


To any of these solutions, add iron and the supplementary solution supplying boron, manganese, zinc, copper, and molybdenum as previously described (p. $29-31$ ). For use with solution $f$, lacking sulfur, a special supplementary solution should be-prepared in which chlorides replace the sulfates. Also, sulfuric acid should not be used in adjusting the reaction of the nutrient solution.

In order to produce iron-deficiency symptoms, plants should be grown in glass containers; no iron should be added to the otherwise complete nutrient solution. Similarly, it may be possible to produce boron- or manganese-deficiency symptoms with certain plants (tomatoes, for example) by omitting either one of these elements from the supplementary solution. Zinc-, copper-, and molybdenumdeficiency symptoms can usually be produced only by the use of a special technique, the description of which was published in a technical paper. ${ }^{20}$

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[^0]:    ${ }^{1}$ Professor of Plant Nutrition and Plant Physiologist in the Experiment Station, deceased.
    ${ }^{2}$ Professor of Plant Physiology and Bio|chemist in the Experiment Station, Berkeley!

[^1]:    ${ }^{3}$ Liebig, Justus von. Chemistry in its applications to agriculture and physiology. [English translation.] 401 pp . John Wiley, New York, N.Y. 1861.
    ${ }^{4}$ Sachs, Julius von. Lectures on the physiology of plants. 836 pp . Clarendon Press, Oxford. 1887.

[^2]:    ${ }^{5}$ However, nutrient solutions such as are employed in water-culture experiments are not applied directly to soils. For discussion of fertilizer problems consult: Hoagland, D. R., Fertilizers, soil analysis, and plant nutrition. California Agr. Exp. Sta. Cir. 367: 1-24. Revised, 1949.
    ${ }^{6}$ Arnon, D. I., and P. R. Stout. Molybdenum as an essential element for higher plants. Plant Physiology 14: 599-602. 1939 .

[^3]:    * These and other formulas are given in: Miller, E. C., Plant physiology, p. 195-97. McGraw-Hill Book Co. New York, N. Y. 1931.
    $\dagger$ For best results, these solutions should be supplemented with boron, manganese, zinc, copper, and molybdenum; see discussion in the text, pp. 29-31.

[^4]:    ${ }^{\tau}$ Withrow, R. B., and Alice P. Withrow. Nutriculture. Indiana (Purdue Univ.) Agric- Exp. Sta. S. C. 328: 1-60. 1948.

    Kiplinger, D. C., and Alex Laurie. Growing ornamental greenhouse crops in gravel culture. Ohio Agric. Exp. Sta. Research Bull. 679: 1-59. 1948.

    Davidson, O. W. Large-scale soilless culture for plant research. Soil Science 62: 71-86. 1946.
    Robbins, W. R. Growing plants in sand cultures for experimental work. Soil Science 62: 3-22. 1946.

    Shive, J. W., and W. R. Robbins. Methods of growing plants in solution and sand cultures. New Jersey Agric. Exp. Sta. Bull. 636.

[^5]:    ${ }^{8}$ Arnon, Daniel I., and Karl A. Grossenbacher. Nutrient culture of crops with the use of synthetic ion-exchange materials. Soil Science 63: 159-180. 1947.

    Arnon, Daniel I., and William R. Meagher. Factors influencing availability of plant nutrients from synthetic ion-exchange materials. Soil Science 64: 213-221. 1947.

[^6]:    ${ }^{0}$ Nutriculture. War Department Technical Manual TM 20-500.

[^7]:    ${ }^{10}$ Gericke, W. F. Crop Production without soil. Nature 141: 536-40. 1938. See also the article cited in footnote 14, on page 19.

[^8]:    ${ }^{11}$ Arnon, D. I., and D. R. Hoagland. Crop production in artificial culture solutions and in soils with special reference to factors influencing yields and absorption of inorganic nutrients. Soil Science 50: 463-485. 1940.

[^9]:    ${ }^{12}$ See footnote 11 on page 14.

[^10]:    ${ }^{13}$ The quality tests were conducted by Dr. Margaret Lee Maxwell Kleiber of the Division of Home Economics, and the carotene determinations were made by Dr. Gordon Mackinney of the Division of Food Technology, College of Agriculture.

[^11]:    ${ }^{14}$ Gericke, W. F., and J. R. Tavernetti. Heating of liquid culture media for tomato production. Agricultural Engineering 17: 141-42, p. 184. 1936.

[^12]:    ${ }^{15} \mathrm{~A}$ number of inquiries have been received regarding the culture of mushrooms. The waterculture method under discussion is unsuited to the culture of mushrooms. These plants require organic matter for their nutrition and differ in this way from green plants, which can grow in purely mineral nutrient solutions like those described in this circular.

[^13]:    ${ }^{10}$ Gericke, W. F. Aquaculture: a means of crop production. American Journal of Botany $16: .862$. 1929. The general arrangement of this type of bed was described by: Gericke, W. F., and J. R. Tavernetti. Heating of liquid culture media for tomato production. Agricultural Engineering 17: 141-42, p. 184. 1936.

[^14]:    ${ }^{17}$ See footnote 11 on page 14 .

[^15]:    ${ }^{18}$ Furnstal, A. F., and S. B. Johnson. Preparation of sintered Pyrex glass aerators for use in water-culture experiments with plants. Plant Physiology 11: 189-94. 1936. Compare also J. W. Shive and W. R. Robbins in the citation given in footnote 7, page 9 .

[^16]:    ${ }^{19}$ The University is not prepared to diagnose symptoms on samples of plant tissues sent in for examination.

[^17]:    ${ }^{20}$ Stout, P. R., and D. I. Arnon. Experimental methods for the study of the rôle of copper, manganese, and zinc in the nutrition of higher plants. American Journal of Botany 26: 144-49.

