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INTRODUCTION

Plant physiologists throughout the years have used various substrates in an attempt to secure one which would give plant responses comparable to those of soil. Plants grown in water culture method, as practiced by the physiologist of the nineteenth century, showed little correlation with those grown in solid substrates or soil. Plants grown in chemically inert sand give results closer to those in soil but serious limitations are still encountered. In recent years gravel and other coarse mineral materials have been employed and the plant growth responses obtained correlate quite closely with those found when soil is used. Certain disadvantages have been found with many mineral media which are not totally inert, physically or chemically. Often the physical phenomena of adsorption and ionic replacement have been found to seriously alter the composition of the nutrient solution when mineral substrate is used. The bringing of the mineral into soluble form by the root acid has also been a definite drawback.

At present the plant physiologists are developing the use of another type of substrate for plant nutritional studies. This new type of substrate includes a series of surface active materials which supply the nutrient elements in an adsorbed form. In experiments that have been carried out with such media, the cations were adsorbed on clay colloids (Jenny and Cowan, 1933; Albrecht and McCalla, 1938; Albrecht and Schroeder, 1939; Converse, Gammon and Sayre, 1943; Albrecht, 1946), artificial zeolites known under the trade names "Decalso" and "Zeo-Karb-H" (Jenny and Cowan, 1933; Schlenkler, 1940, 1942; Converse, Gammon and Sayre, 1943) and phenol-formaldehyde resin known as "Amberlite" (Arnon and Grossenbacher, 1947; Arnon and Meagher, 1947). Anions can be adsorbed on an aniline material named "De-Acidite" (Schlenkler, 1940, 1942; Converse, Gammon and Sayre, 1943) and on an amine-formaldehyde resin "Amberlite" (Graham and Albrecht, 1943; Jenny, 1946; Arnon and Grossenbacher, 1947; Arnon and Meagher, 1947).

Although a number of the synthetic materials have proved satisfactory for plant growth studies, the expense involved in their use is often prohibitive. A relatively abundant and cheap material thought to have the same type of adsorptive powers as these synthetic materials is pumice (Veller and Arutyunyan, 1933). A comparison of pumice with quartz gravel as a substrate for plant growth has been made by Stout (1947). Working with hemp (*Cannabis sativa* L.), he found that there was only slight differences between plants grown in gravel and those in pumice as to their metabolic efficiency although the pumice plants were more vigorous when compared on the basis of gross morphology.

The present study was carried out to determine the differences between gravel and pumice substrates as indicated by the growth and reproductive responses of prickly-seeded spinach (*Spinacia oleracea* L.) under varying conditions of temperature and photoperiod. This was done with the view to determine the suitability and limitations of pumice substrates for experiments on mineral nutrition of plants under different conditions.

METHODS

Seeds of prickly-seeded spinach (*Spinacia oleracea* L.) were germinated at ordinary greenhouse temperatures (18°-21°C.) in flats of one-half sand and one-half loam. On the 26th of February, 1947, upon the appearance of the first true leaf, the seedlings were removed from the germinating flats, the roots washed free of soil in distilled water, and transplanted into series of substrates. One series consisted of uniform weights of solute-free quartz gravel, mean size of 1.8 cubic centimeters, in three-gallon glazed jars. The second series consisted of the same type of jars filled with pieces of pumice, mean size of 345 cubic centimeters. Solute-free quartz gravel was used to fill the interstices between the pieces of pumice and to form a top layer over the pumice to enable the seedlings to become established. The pumice was not treated in any manner before it was used. This pumice was obtained from deposits near Grants, New Mexico.

Each jar was fitted with a vertical ⅝ inch pyrex feeding tube to

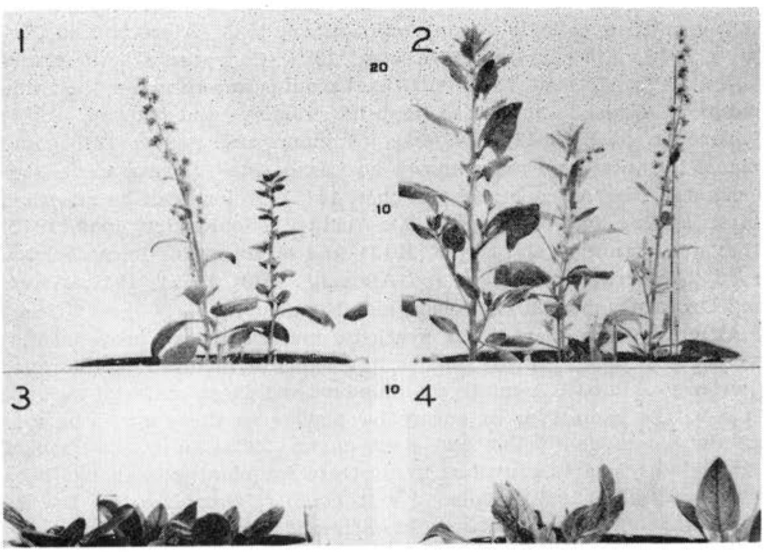

Figure 1. (1) LHP—left to right, extreme male and female; (2) LHG—female, vegetative male and extreme male; (3) SHP; (4) SHG. (Scale in centimeters).

facilitate filling the jars with nutrient solution without wetting the exposed top surface of the gravel. Two small side arms were placed on each jar through the hole in the bottom, one to serve as a level gauge and for draining, and the other for aeration. Aeration was accomplished through the use of compressed air.

Four plants were placed in each pot, but at the time the plants were subjected to the experimental environments this number was thinned to three. To facilitate establishment of the transplanted seedlings, the plants were maintained at 21°C. for a period of five days. After this period one-half of each series was subjected to a temperature of 13°C. and the remaining half maintained at 21°C. Within a given temperature one set of plants, consisting of six jars, was placed under a long photoperiod of fifteen hours and another under a short photoperiod of nine hours. The long-day group received the full length of normal daylight plus additional electric illumination in the evenings to lengthen the light period to fifteen hours. This additional illumination was provided with a series of 100-watt Mazda bulbs which gave light intensity of approximately 200 foot-candles to those plants immediately below the lights, and approximately 80 foot-candles to the peripheral plants. The jars were consistently rotated to compensate for this light intensity variation as well as for that present during the natural daylight hours. The short-day group of plants received the normal daylight of the period of the year and were segregated from the long-day plants during the latter's supplemental illumination by a light-proof, black sateen

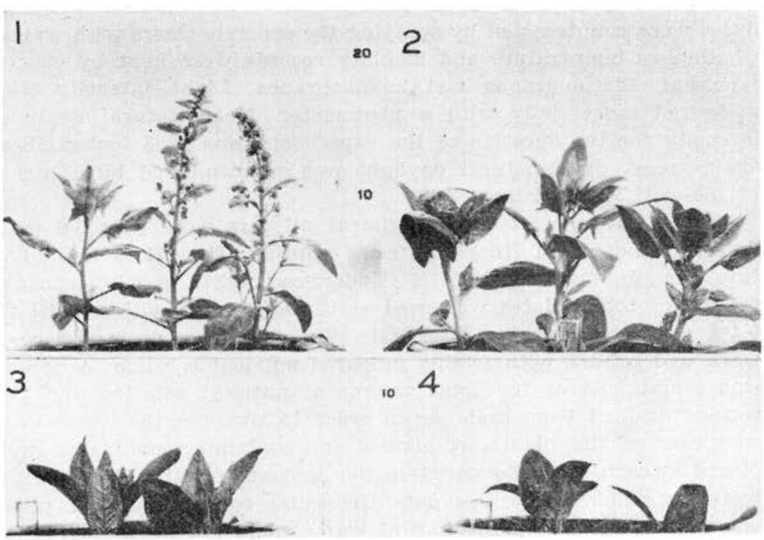

Figure 2. (1) LLP—left to right, female, vegetative male and extreme male; (2) LLG—females; (3) SLP; (4) SLG. (Scale in centimeters).

curtain. The short-day plants were also rotated to insure uniform light intensity.

For the purpose of brevity, the following designations of the various series are used through this paper:

1. LHP—15 hour photoperiod, 21°C. temperature, and pumice substrate.
2. LHG—15 hour photoperiod, 21°C. temperature, and gravel substrate.
3. SHP— 9 hour photoperiod, 21°C. temperature, and pumice substrate.
4. SHG— 9 hour photoperiod, 21°C. temperature, and gravel substrate.
5. LLP—15 hour photoperiod, 13°C. temperature, and pumice substrate.
6. LLG—15 hour photoperiod, 13°C. temperature, and gravel substrate.
7. SLP— 9 hour photoperiod, 13°C. temperature, and pumice substrate.
8. SLG— 9 hour photoperiod, 13°C. temperature, and gravel substrate.

Temperatures were maintained by thermostatically controlled radiators and ventilator regulation. Due to the season during which the experiment was carried out, no difficulty was encountered in maintaining the designated temperatures. The maintenance of uniform temperatures throughout the rooms was accomplished by means of electric fans placed under the benches. A mean relative humidity of 25% was maintained over the period of the experiment. Low humidities were counteracted by spraying the concrete floors with water. Continuous temperature and humidty records were kept by use of recording thermographs and humidographs. Light intensity was measured twice daily with a photometer. Mean natural daylight intensity for the duration of the experiment was 1266 foot-candles. On overcast days, natural daylight was supplemented by a series of 100-watt Mazda lamps.

At the initiation of the experiment all jars were supplied with uniform amounts of Knop's nutrient solution. The pH of this solution was adjusted with NH_4OH (Underwood, 1934). A 0.2% concentration of total solutes was used at the beginning, with a shift to 0.4% concentration at a later date. The jars were drained once a week and refilled with freshly prepared nutrient solution. A record was maintained of the total volume of nutrient solution and the residue drained from each jar in order to compute the water consumption of the plants. A control jar containing no plants was placed in each series to ascertain the amount of water lost directly by evaporation. From this data the water consumption per plant was calculated. The absorption of water could not be computed on the basis of sex in that both males and females were present in the same jar. The pH of the original nutrient solution and that of the solution residue was measured with a Beckman pH meter. A quantitative determination of the minerals in the residual solution was made by evaporation of ten cubic centimeters of the solution to a constant weight at a temperature of 80°C. No attempt was made to make a qualitative determination of the elements present.

Bi-weekly growth records were maintained from the time the 13°C. and 21°C. temperatures were initiated until completion of the experiment.

At the termination of the experiment fresh and dry weights were determined for the various series. In the long-day plants the shoots were divided into leaves, stems, flowers and roots, while the short-day plants were segregated into shoots and roots. Before fresh weight of roots was determined, roots were washed free of gravel

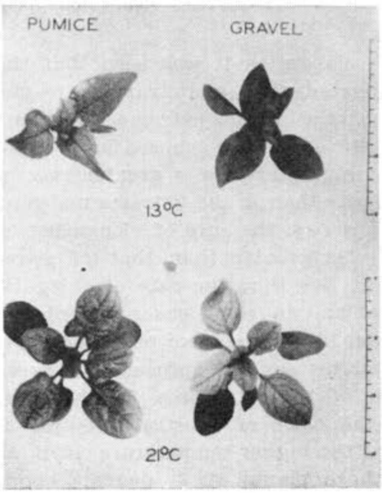

Figure 3. Rosette formation of plants in 9-hour photoperiod. (Scale in centimeters).

in tap water and quickly dried between blotting paper to remove excess moisture. Dry weights of all samples were computed from percentage of moisture content as determined with a Brabender Moisture Tester. Samples were dried at 100°C.

DATA AND DISCUSSION

With reference to the form of the mature plant, spinach is tetramorphic (Rosa, 1925). These four classes are as follows: (a) Extreme males. Only staminate flowers are produced and the leaves at the flowering apex of the central axis are completely suppressed or much reduced. (b) Vegetative males. These plants also bear only staminate flowers but differ from the extreme males in that the leaves in the flowering region are not suppressed. (c) Females. Pistillate flowers are the only type formed by these plants. As in the vegetative males, fully developed leaves extend completely to the apex of the main axis. (d) Monecious plants. This group bears varying proportions of both staminate and pistillate flowers in the same cluster. This latter group is relatively rare in occurrence in the variety of spinach used for this problem and was not encountered.

Shoots

The plants in the 15-hour photoperiod showed immediate stem elongation and not the characteristic rosette formation frequently described in the literature. Taking into account the intensity of the light in this photoperiod, it is quite evident that this is not an etiolation response but rather the effect of the photoperiod on early plant development.

Comparing stem elongation it was seen that the LHP and LHG series usually elongated at a more rapid rate than the LLP and LLG series. In the case of the extreme males in the LLP series, the pumice substrate apparently caused an initial reduction in the effect of the low temperature for a greater rate of elongation was present in these plants than in the extreme males of the LHG series. In all the long-day series, the rate of elongation of the plants in a pumice substrate was greater than that of gravel until anthesis or near anthesis. At this time the rate of elongation in the pumice series was reduced and in some cases exceeded by the plants in the gravel substrate. In all cases except in the vegetative males, the total stem height at the time of anthesis was greater in the gravel series. Comparison of the total stem height of the 15-hour light period plants on the basis of substrate reveals that the greatest height is present at the higher temperature. If, however, substrate is disregarded and those plants at 21 degrees compared with those at 13 degrees, it is observed during early growth of the extreme males that a greater height is present in the LLP series than in the LHG series. In all other cases the plants at 21 degrees exceeded those at 13 degrees in stem height. In the 9-hour photoperiod series, the plants at a given temperature regardless of substrate seemed to elongate at about the same rate.

New nodes were initiated at a slightly greater rate in the series at the higher temperature. At a given temperature nodes were initiated more rapidly in the pumice substrate. It is of interest to note that more active node initiation is closely correlated with anthesis at an earlier date (Parker and Borthwick, 1939). A comparison of the two types of substrate shows that with the exception of the vegetative males, a greater number of nodes was initiated before anthesis in the gravel plants. Regardless of the fact that temperature caused a variance within a given substrate group as to the time of anthesis, the number of nodes of the extreme males and females at anthesis was comparable for the two temperatures.

There was no apparent correlation in the mean number of leaves or leaf area at any particular developmental phase in any of the long-day series. Usually the 21 degree temperature maintained a greater number of leaves at any given date because of accelerated ontogeny. Pumice in each temperature group sustained a slightly higher number, probably due also to earlier maturity. The leaf area as opposed to the leaf number was greatest in the 13 degree temperature. In the extreme males and females at the 21 degree temperature, the area of the third leaf at any given date was greatest in pumice substrate. At the lower temperature the area was largest in the gravel series. Measurements of the sixth leaf showed the area to be larger in the gravel series at both temperatures. In the short-day series of plants the leaf number was much the same in both substrates at both temperatures. As in the long-day series, the leaf area was greatest at the 13 degree temperature. The pumice substrate at 21 degrees had an initially larger third leaf area, but the gravel series attained equality in the 21st day and surpassed it by the 28th. The pumice plants at the lower temperature maintained a slightly larger third-leaf area throughout, but a gradual decrease in this difference was noted during the time of experimentation. The area of the sixth leaf was greater in the gravel substrate at the time of the first measurement in both temperatures and remained so throughout.

In the 9-hour photoperiod, a consistent difference was observed in the type of vegetative rosette growth in the two temperatures. In both LHP and LHG, the rosette took on a flattened appearance with the leaves in a more or less horizontal position (Fig. 1). In the LLP and the LLG series, on the other hand, the leaves of the rosette assumed a more vertical, erect position (Fig. 2). The leaf shape also varied with difference of temperature (Fig. 3). The leaf apex of the LHP and the LHG series was characteristically obtuse and that of the LLP and the LLG series more acuminate. This variance in habit of growth is suggestive of nutritional differences in the high and low temperature groups.

The total fresh weight of the leaves and stems at a given temperature in a long day was greater in those plants grown in gravel. In the short-day plants a comparison of total fresh shoot weight showed this to be true at the higher temperature but at the lower, the shoot weight of the pumice plants was almost two times that of the gravel plants. Except for the stems in 13 degree extreme males and leaves and stems in 13 degree vegetative males, the per cent dry weight at a given temperature in leaves and stems in the 15-hour photoperiod was greatest in the pumice plants. At both temperatures in the 9-hour photoperiod the shoots showed a higher per cent dry weight in the pumice plants. The top-root ratio at a given temperature was greatest for the gravel plants except in the 13-degree females. In this group a higher ratio was present for the pumice plants.

Roots

The habit of root growth in the pumice and gravel substates was quite different. The roots grown in pumice were largely confined to the pumice surface or penetrating down into the numerous pores as though in chemotropic response. Roots were not found to any extent in the gravel between the pumice pieces. The roots in the gravel substrate were widely spread throughout the gravel. No roothairs were observed in either substrate. In all cases except the 9-hour 13-degree group, at a given temperature the plants grown in gravel had a greater fresh weight of roots. Since the amount of roots a plant produces is related to the extent and character of its foliage development, it seems logical that with a greater shoot weight being present in the pumice series of this group that the roots should also be larger. The more rapid development of the pumice-grown plants would undoubtedly account to some extent for their smaller root system in that the onset of flowering seems to reduce root formation (Roberts and Struckmeyer, 1938). At 21 degrees the highest per cent of dry weight of the roots was in the pumice-grown plants. At 13 degrees, however, with the exception of the extreme males, the greater per cent dry weight was in the gravel series.

Flowering

While the temperature of substrate did not substitute or nullify photoperiodic responses in this experiment, these factors definitely influenced the date of anthesis in a favorable photoperiod. Neither of the substrates or temperatures were effective in bringing the plants under the 9-hour photoperiod into the reproductive phase in the time allowed in this experiment.

In the 15-hour light period series, it was observed that both temperature and substrate influenced the period of time it took the plants to reach anthesis. Comparing the LHP to the LLP series and the LHG to the LLG, it was observed that the lower temperature had a definite retarding effect on seed stalk maturity (Thompson, 1934; Knott, 1939). In this long-day photoperiod and at a given temperature, the plants in a pumice substrate reached anthesis more quickly than those in gravel. The time lag of the gravel behind the pumice was approximately three days in all cases. The exact cause of the earlier maturity in pumice is unknown. Reduced nitrogen supply has frequently been cited in the literature as a cause for early flowering of spinach (Schapelle, 1936; Knott, 1940; Withrow, 1945).

pH, water and salt absorption

In the consideration of pH, water intake and salt absorption, it was impossible to take the tetramorphic forms into account separately because of the technique of the experiment. An initial reduction in pH of the nutrient solutions in all series was noted. This initial decrease was probably due primarily to preferential cation absorption along with the minor factor of acid excretion of the roots. Subsequently selective anion absorption occurred and there was a progressive pH rise. It was noted in the LHP series that the pH dropped much lower than any of the other series. This drop is probably correlated with a higher metabolic rate in this series. An additional factor which should not be overlooked is that hydrogen ions may have been released from a pumice adsorption system by the cations of the nutrient solution. This, however, does not seem to be in accord with the results of any of the other pumice series in which there was less reduction of pH than in the gravel cultures.

As the developmental stage of bud inception was attained in the long-day plants, there was a definite shift in the water uptake. It was noted that a definite decrease in the mean daily water consumption per plant took place (Fig. 4). This decline in water ab-

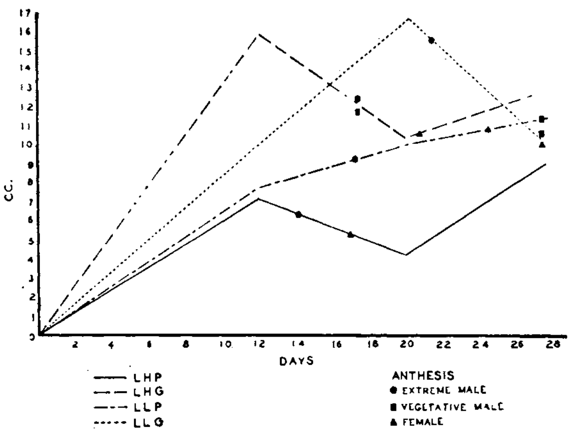

Figure 4. Mean daily water consumption per plant in cubic centimeters.

sorption at flower-bud initiation has also been noted by other workers (Loehwing 1942; Dennison, 1945). With the onset of fruiting there was again an increased rate of water absorption.

A decrease in the intake of mineral elements was also seemingly correlated with flowering. This conclusion is drawn from the fact that at the time of flowering the mineral matter in the nutrient solution residues was at the highest point. At no time, however, did the amount of mineral in the residues exceed the concentration at which the solutes were originally added. This would indicate that if exudation of salts by the roots took place (Loehwing, 1940, 1942) sampling was too infrequent for this fact to become apparent.

Table I. Comparison of Pumice and Gravel Substrates as to Their Influence upon Growth and Development of Spinach

FACTORS OF COMPARISON	PUMICE	GRAVEL
Faster rate of stem elongation	X	
Greater stem height at anthesis		X
Faster rate of node initiation	X	
Greater node number at anthesis		X
Greater leaf number at a given age	X	
Greater 3rd leaf area, 15-hour photoperiod, 21 degree temperature	X	
Greater 3rd leaf area, 15-hour photoperiod, 13 degree temperature		X
Greater 6th leaf area, 15-hour photoperiod, 13 and 21 degree temperature		X
Greater fresh weight of shoots and roots		X
Higher percent dry weight of shoots and roots	X	
Roots most widely spread in substrate		X
Greater top-root ratio		X
Earlier anthesis	X	
Greater mean water intake per plant		X

CONCLUSIONS

Of the environmental conditions in this experiment, photoperiod seemed to be the major factor in the determination of seed stalk initiation and flowering. A definite relationship, however, has been shown to exist between photoperiod, substrate and temperature. Although in no case was it found that substrate or temperature altered the photoperiodic requirements, these factors were found to exert a definite influence on growth and development within a given photoperiod. If a distinction between growth and development is made on the basis of size as opposed to the progression of the plant throughout its life cycle, the 13 degree temperature is most important in growth while the 21 degree temperature is more favorable for development. At a given temperature, maximum growth is obtained on the gravel substrate while pumice accelerates the development cycle. It is difficult to ascertain whether substrate or temperature is more influential in development. In the case of the extreme males, for example, the effects of lower temperature on the developmental cycle were overcome by the pumice substrate. This fact is suggestive although far from conclusive as to importance of substrate over temperature.

All of these results indicate that so far as growth and development are concerned, pumice and gravel are not comparable substrates for plant growth studies. A comparison of the growth and developmental responses of spinach on the two substrates is given in Table I. This variance may be due to an adsorption system in the pumice which is not present in the gravel.

SUMMARY

The major growth and reproductive responses observed were as follows:

1. In the 15-hour photoperiod plants, there was no characteristic rosette formation.
2. With a 15-hour photoperiod, the higher temperature caused a greater rate of stem elongation and node initiation. At a particular temperature, the pumice plants sustained a greater rate of both factors. In all cases except in the vegetative males, the total stem height at the time of anthesis for a given temperature was greater in the gravel series. This is true also for node number. The rate of elongation was independent of substrate in the 9-hour photoperiod plants at a given temperature.
3. There was no apparent correlation of the number of leaves with any developmental phase. Due to accelerated development, the larger number of leaves usually appeared in the 21-degree and pumice series. The leaf area was greatest in the 13-degree series.
4. Root development was quite different in the pumice and gravel series. The pumice series had small root systems which were largely confined to the surface or interstices of the pumice while the gravel-grown plants had extensive root systems spread throughout the gravel.
5. The gravel-grown plants showed a greater fresh weight at both temperatures and photoperiods. The per cent dry weight was, however, usually greater in the pumice plants indicating a greater degree of hydration in the gravel plants.
6. The top-root ratio at a given temperature was greatest for the gravel plants except in the case of the 13-degree temperature females.
7. In general, seed stalk formation was accelerated by a higher temperature. At a given temperature the plants grown in pumice substrate reached anthesis about three days earlier than those grown in gravel.
8. An initial reduction of the pH of the nutrient solution in all combinations of temperature and photoperiod was noted which probably can be attributed to preferential absorption of cations in early stages of the growth of spinach. The greatest reduction was observed in the 15 hour-21 degree-pumice substrate series and was undoubtedly correlated with the high metabolic activity of these plants.
9. The absorption of water declined sharply at the inception of flower buds.

10. The intake of mineral elements by the plant decreased at anthesis.

The data indicates that spinach plants grown in gravel and pumice substrates are not comparable in their growth and development.

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