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Studies on cation exchange capacity of plant roots with reference to their ecological phenomena.

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STUDIES ON CATION EXCHANGE CAPACITY OF PLANT ROOTS
WITH REFERENCE TO THEIR ECOLOGICAL PHENOMENA

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STUDIES ON CATION EXCHANGE CAPACITY OF PLANT ROOTS
WITH REFERENCE TO THEIR ECOLOGICAL PHENOMENA

by

Eliot Epstein

Thesis submitted in partial fulfillment of the
requirements for the degree of Master of Science.

University of Massachusetts
Amherst, Massachusetts

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INTRODUCTION

Plants differ greatly in their chemical composition and in their ability to take up mineral nutrients. Many investigators have commented on these differences in mineral nutrient content and on the differences in ability of plants to obtain mineral nutrients particularly on soils of low fertility. Also there seems to be some relationship between crop ecology and soil fertility.

Recent theories of cation adsorption advanced by Mattson and his students offer a new approach to the study of differences in mineral nutrient uptake and content of plants. Plant roots possess cation exchange properties as shown by De Vaux (4) and Williams and Coleman (31). Cation exchange is the process by which the plant obtains its nutrient cations. The cation exchange occurs in the greatest amount near the growing tip of the root (19,25,27). Mattson (19) found that root tips, up to 5 mm. from the end, adsorbed 125 m.mol of .001 M methylene blue solution per 100 gms. dry matter in 30 seconds; whereas, that section of root 5 to 20 mm. adsorbed only 76 m.mol of dye per 100 gms. of dry matter. Williams and Coleman (31) suggest that the root surfaces may consist of both active and inactive portions with regard to cation exchange.

The cation exchange capacity of the plant root is visualized as arising chiefly from similarly functioning cation exchange sites from carboxyl groups of pectin, pectic acid, cellulose and similar complex organic compounds.

Pectic substances have pronounced cation exchange properties (12). Large relative differences in the cation exchange capacity of the roots of different plant species appear to result from a thicker layer or denser packing of these organic compounds. At the time of formation, these compounds are probably saturated with exchangeable hydrogen ions. These complex organic compounds of the plant root are believed to be the principal source of hydrogen ions for cation exchange reactions with the soil solution, soil colloid, and primary minerals. There is a good indication of the existence of ionic swarm as shown by the suspension effect of roots (12,14,16,31).

Two theories have been advanced as to the mode of cation exchange (12). The first, the soil solution theory, assumes that cation exchange is directly related with respiratory activities of the plant. Carbon dioxide, as a result of respiration, is continuously released at the root surface where it reacts with water to form carbonic acid. It has been visualized that each root tip is also surrounded by a zone of high carbonic acid content (24). A hydrogen ion from the carbonic acid in the soil solution is exchanged for a cation (one equivalent) from the soil mineral or from the soil colloid surface (Figure I) (12). This exchanged cation is then in the soil solution. Hydrogen ions that form the root ionic swarm (Helmholtz double layer) may be exchanged for the cation which is now in soil solution (Figure I) (12).

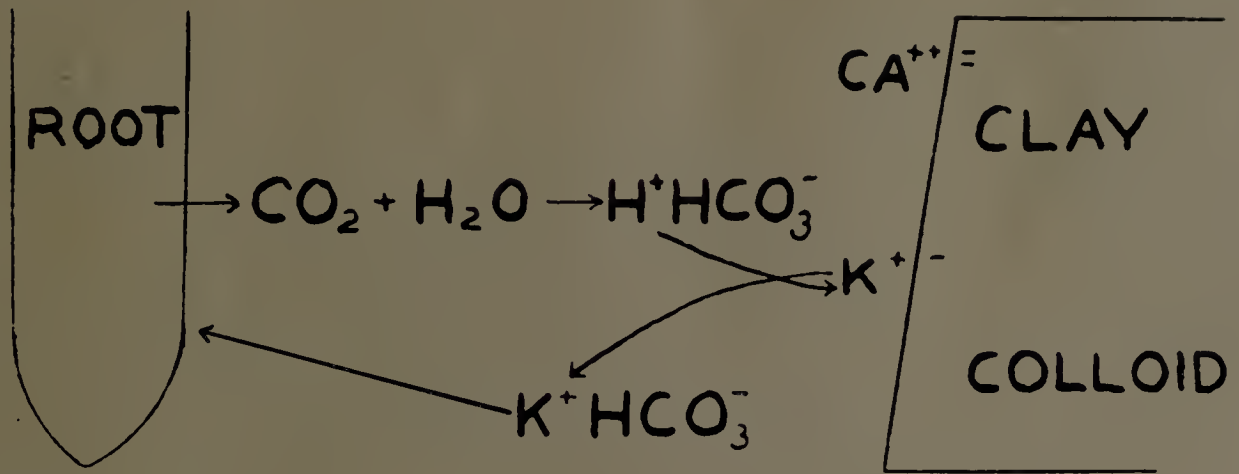


Figure I. The soil solution theory. (Jenny 12)

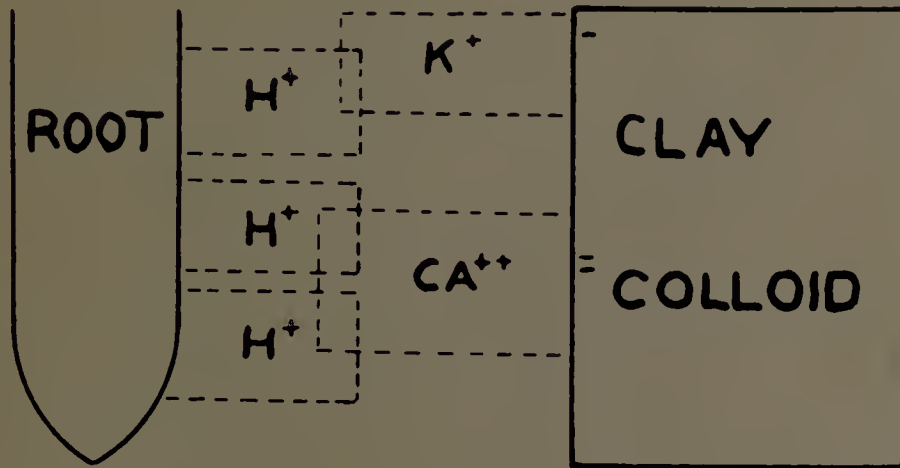


Figure II. The contact exchange theory. (Jenny 12)

Certain inadequacies of the CO_2 theory have been pointed out by Jenny (12). These inadequacies are found in the explanation of the depletion of ions from roots; the uptake of insoluble radioactive columbium which cannot be detected in the intermicellular liquid; and the difference in uptake of cations from montmorillonite and kaolinite clays.

In recent years, Jenny and others (12,14,15,16) have proposed a second theory, contact exchange. This is based on the assumption that there is a direct exchange between the root and the soil colloid (Figure II). It is believed that contact exchange likewise applies to cation uptake from other soil minerals.

Jenny and others (12,15) propose two phases of contact exchange, (a) contact intake and (b) contact depletion. The former deals with H^+ ions of the root exchanging for other cations (Ca^{++} Mg^{++} K^+) from the soil colloid, while the latter deals with the loss of cations from the root, in that H^+ ions from the clay exchanges for cations of the roots (Ca^{++} Mg^{++} K^+). Knowing the relative cation exchange capacity of the plant root and the clay colloid, one can predict the relative depletion of cations from the plant roots (30).

Differences in ability of plants to take up cations and phosphorous from soil colloids have been reported (6,19). This difference is expressed in the composition of the plants (2,18).

Elgabaly and Wiklander (7) stated that at given outside concentrations of ions, the relative distribution of mono and divalent ions is determined by the exchange capacity or acidoid content of the plant root; thus, the valence effect tends to be expressed in the composition of the plants. This valence effect means that at a given outside concentration of cations, high exchange colloids, roots in this case, adsorb or bind relatively more divalent than monovalent cations. In contrast, low exchange colloids adsorb relatively more monovalent and less divalent cations. By increasing the outside ionic concentration as by application of fertilizers, this valence effect as Ca/K is reduced. McLean and Baker (21) measured the energy of adsorption or mean free bonding energy of high and low cation exchange roots with the clay membrane. Roots of Kansas Common alfalfa and Ogden soybeans with high cation exchange capacity adsorbed Ca with a much higher bonding energy than the low exchange capacity roots of Reed Canary and Red Top. This relationship of bonding energy to cation exchange capacity of the root colloid is most effective at low ionic concentration. At higher concentration, the valence effect, i.e., the mono-divalent bonding energy concept, is reduced (18,30). The rate of adsorption of K has been shown by Jacobson and Overstreet (11) to increase at low K concentration. This increase might result from increased concentration overcoming the valence effect.

At high concentrations of K, there was no appreciable increase of K absorption, indicating that beyond a certain concentration the valence effect was overcome.

Drake et al (5) determined the magnitude and order of cation exchange capacities of roots of certain agricultural plants. They found considerable differences in root cation exchange values between monocotyledons and dicotyledons, and on this basis, suggested an explanation for cation compatibility of certain grass-legume associations. Gray (9) showed that potassium uptake by individual plant species at low levels of soil potassium corresponded to root-cation exchange capacities. Also relationships exist between the nature of the colloid, its exchange capacity and degree of saturation, and cation uptake by the plant (1,8,13,22,23).

The cation exchange capacity of the plant root may be an important factor in the adsorption of nutrients by plants. Hence, the relative magnitude of cation exchange capacity of plants should be useful in evaluating the ability of plants to adsorb cations. Furthermore, this information should be useful in predicting the soil fertility requirements of plants as well as the mono-divalent cation ratio in the plant material.

The objectives of this experiment were:

1. To study effects of technique on cation exchange capacity of plant roots.

2. To determine the effect of age and size of roots of a given plant on the cation exchange capacity.

3. To measure the cation exchange capacity of roots of a number of important agricultural plants.

4. To attempt to relate the cation exchange capacity of plant roots to certain ecological phenomena.

EXPERIMENTAL PROCEDURE

Plants were grown in gallon pots containing 1/4 inch granite grit. A 1/5 Hoagland solution was supplied by the constant drip method (Figure III). Growth of the plants was maintained until there was sufficient root production (30 gms. fresh roots). The plant species and the age at which roots were harvested for dialysis are shown (Table I).

TABLE I

SPECIES GROWN

ANGIOSPERMS (Angiospermeae)

Monocotyledons (Monocotyledoneae)

Grass Family (Gramineae)

<u>Common Name</u>	<u>Scientific Name</u>	<u>Age in Days</u>
Corn	Zea Mays	20
Field Brome	Bromus arvensis	20
Ryegrass	Lolium perenne	40
Reed Canarygrass	Phalaris arundinacea	50
Millet	Panicum miliaceum	60
Sudangrass	Sorghum vulgare	60
Tall Fescue	Fescuta elatior	70
Bermuda-Grass	Cynodon dactylon	100
Quackgrass	Agropyron repens	100

Dicotyledons (Dicotyledoneae)

Legume Family (Leguminosae)

Blue Lupine	Lupinus angustifolius	20
Yellow Lupine	Lupinus luteus	20
White Lupine	Lupinus albus	20
Canadian Field Peas	Pisum sativum arvense	20
Peanuts	Arachis hypogae	30
Sweet clover	Melilotus alba	30
Black Medic	Medicago lupulina	40
Bur-clover	Medicago denticulata	70
Common Crimson Clover	Trifolium incarnatum	80
Birdsfoot Trefoil	Lotus corniculatus	80
Black Locust	Robina pseudoacacia	80
Hubam Sweet Clover	Melolotus alba var annua	90
Naff's Bur-clover (Giant Improved)	Medicago arabica	95

TABLE I (Cont.)

<u>Common Name</u>	<u>Scientific Name</u>	<u>Age in Days</u>
<u>Buckwheat Family (Polygonaceae)</u>		
Buckwheat	Fagopyrum esculentum	15
<u>Mustard Family (Cruciferae)</u>		
Rape	Brassica napus	60
<u>Night Shade Family (Solanaceae)</u>		
Tobacco (Havana Kl)	Nicotiana tabacum	90
<u>Beech Family (Fagaceae)</u>		
Red Oak	Quercus borealis	2 yrs.
<u>Olive Family (Oleaceae)</u>		
White Ash	Fraxinus americana	2 yrs.
<u>Mallow Family (Malvaceae)</u>		
Cotton	Gossypium hirsutum	75
<u>Compositae Family (Compositae)</u>		
Galinsoga	Galinsoga parviflora	120
<u>Pink Family (Caryophyllaceae)</u>		
Chickweed	Stellaria media	150
GYMNOSPERM (Gymnospermae)		
<u>Pine Family (Pinaceae)</u>		
White Pine	Pinus Strobus	3 yrs.

Plants were removed from the granite grit; the roots were washed to remove the grit; and the roots were cut from the tops. The roots were then placed in a Visking bag (cellulose dialyzer membrane bag) covered with distilled water. The bag was then placed in the center compartment

of a Mattson cell (Figure IV) and dialyzed at 140-150 volts at less than two amperes for a period of approximately 70 minutes or until the amperage was between 0.1 - 0.2 amperes. The center and cathode compartments were flushed at regular intervals. The temperature was kept below 50° C by flushing and with the aid of a cooling coil. Platinum and monel metal electrodes were used in the anode and cathode compartments respectively.

Roots were then removed and centrifuged at 2000 R.P.M. for five minutes in a basket-type centrifuge to remove excess moisture. Five grams of centrifuged roots were then placed in a beaker with 200 ml. of 1 N KCl. The pH of the root-KCl solution was determined to indicate the amount of base required, and the solution was titrated in five minutes with 0.02 N KOH to a pH of 7.00. The titration was completed in five minutes since the amount of the base required for longer periods of time did not increase appreciably (Figure V). The root-KCl solution was then dried on a steam bath and placed in the oven for 48 hours at 90° C. Beakers were weighed and the exchange capacity calculated and expressed as milliequivalents per 100 grams of dried roots (me/100 gms.)

Evaluation of Error:

The standard deviation was ± 1.35 for 15 samples of peas and ± 1.42 for 9 samples of ryegrass. The standard error of the mean was determined in order to evaluate the reliability of the mean for peas and for ryegrass (Appendix p.36)



Figure III. Constant drip technique used to grow plants in granite grit.

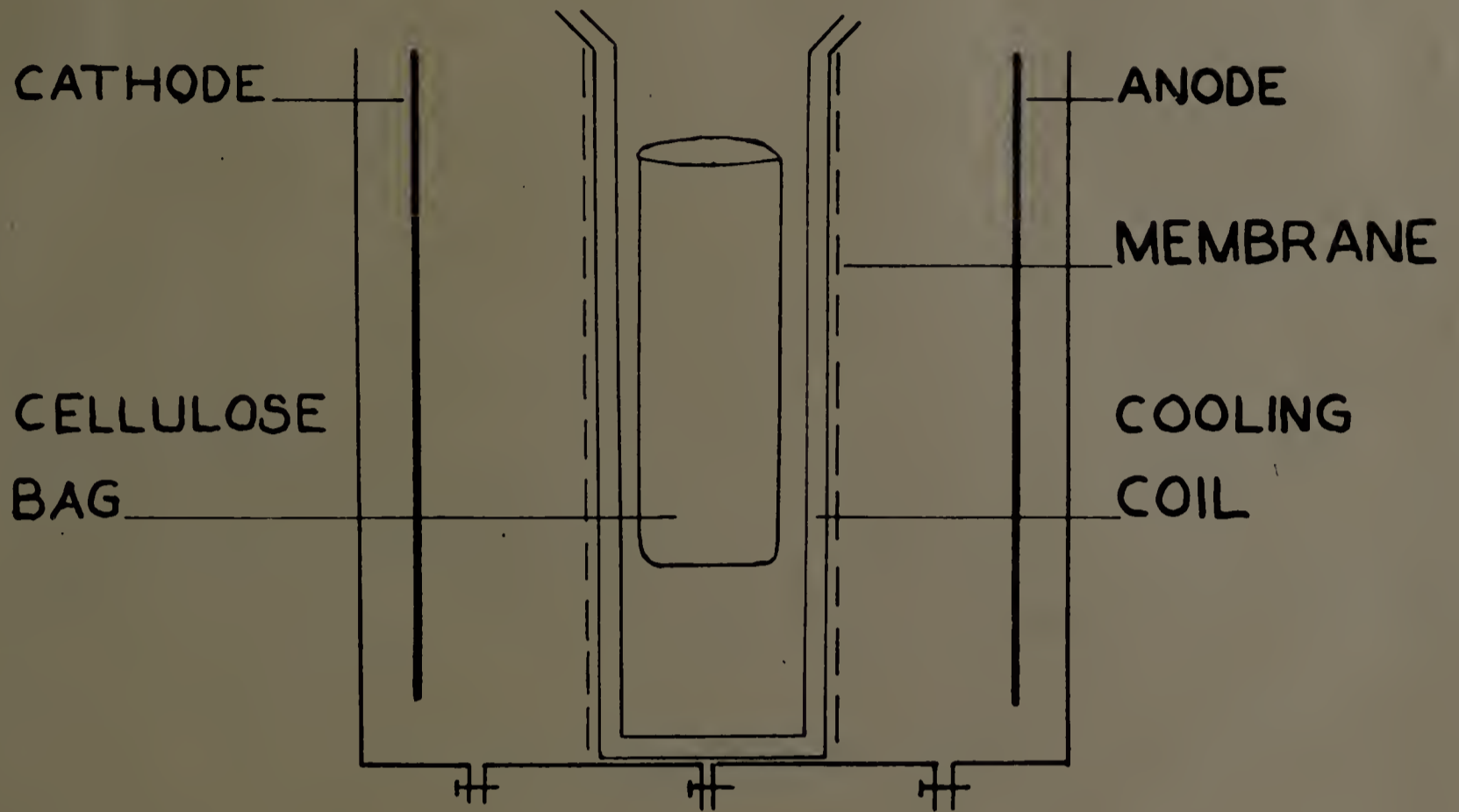


Figure IV. Mattson electro dialysis cell.

There is a 95% probability that the true mean of these populations (peas and ryegrass) is within the limits of 43.3 - 44.7 me/100 gas for peas and 21.8 - 24.0 me/100 gas for ryegrass. This should not be interpreted as meaning that the means of future pea and ryegrass samples have a 95% probability of falling within these limits. These ranges due to analytical procedure do not apply to the variation for roots of other plants, however it does serve as a guide as to the amount of variation to be expected.

The coefficient of variability was 3.63% and 6.20% for peas and ryegrass respectively. A variation of 5-10% in the coefficient of variability in agronomic researches is considered good. The low coefficient of variation for the pea and ryegrass root samples indicate good control of variables and precision in the technique used for growing and measuring cation exchange capacity of plant roots.

Chauvenet's criterion (3) for discarding of unfit data was used on peas and ryegrass (See p.35 Appendix). Samples deviating by 2.8 me/100 gas. from the mean should be discarded for both peas and ryegrass. Since the error was evaluated for a high and a low exchange root, replicate sample values were screened on this basis.

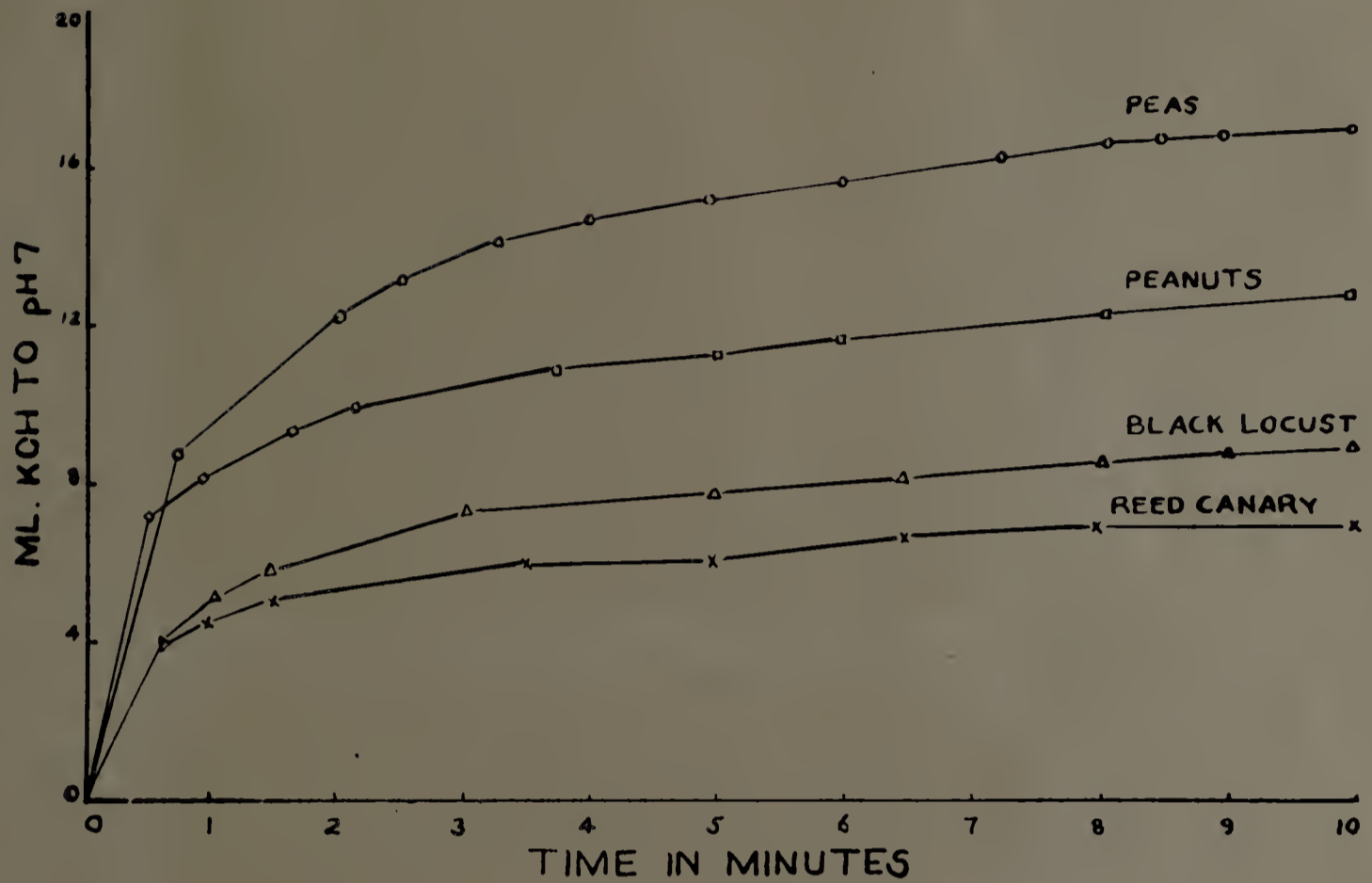


Figure V. Effect of time on titration of electro-dialyzed peas, peanuts, black locust, and reed canarygrass roots in N KCl.

RESULTS AND DISCUSSION

Modification of Technique:

A. Use of Carbon Electrodes

An attempt was made to use thin carbon electrodes for both anode and cathode compartments in place of the platinum and monel electrodes. The carbon electrodes were not satisfactory. Root exchange values for pea roots using carbon electrodes were 35.7 me/100 gms. as compared to 44.3 me/100 gms. when the metallic electrodes were used. This is believed to be due to the incomplete dialysis of the roots when the carbon electrodes were used. The amperage during dialysis with carbon electrodes, which is in general indicative of the amount of ions removed, was considerably lower during a same period of time than the amperage obtained by use of the metallic electrodes. Thus, the rate of removal was slower with carbon electrodes and incomplete dialysis resulted.

B. Removal of KCl

The relatively large weight of KCl is a source of error in determining dry weight of roots. Pea roots were removed from the KCl, placed in a Buchner funnel, and washed to remove the KCl. This method produced higher results, 50.7 me/100 gms. than by the standard procedure, 44.3 me/100 gms. During the process of decantation and washing, there was a loss of colloidal matter. Calculated cation exchange values per 100 gms. of dry roots were thereby increased.

C. Titration of Dried Roots

In another attempt to avoid the error in weighing due to KCl, electrodialed pea roots were dried, weighed, and rewet prior to titration. The value obtained by titrating the rewetted roots was 31.3 me/100 gms.; but when the rewet roots were placed in a Waring blender for five minutes and then titrated, the value was 36.4 me/100 gms. Standard N KCl procedure gave peas a value of 44.3 me/100 gms. When thoroughly dried, organic colloids do not regain their original properties. In addition it is believed that by drying, some pectin and similar compounds were partially changed or inactivated.

D. Effect of Time of Dialysis and Flushing of Compartments

The effect of length of dialysis on the cation exchange capacity of pea roots was measured. The dialysis procedures were as follows:

1. Cathode and center compartments were flushed during the first 20 minutes. After 20 minutes the anode compartment was flushed and dialysis continued for 10 minutes.

Total time - 30 minutes.

2. Cathode and center compartments were flushed during the first 40 minutes. After 40 minutes the anode compartment was flushed and dialysis continued for 10 minutes.

Total time - 50 minutes.

3. Sixty-minute lapse before anode was flushed and dialysis continued for 10 minutes.

Total time - 70 minutes.

4. Eighty-minute lapse before anode was flushed and dialysis continued for 10 minutes.

Total time - 90 minutes.

The effect of duration of electro dialysis on cation exchange is presented in Table II.

TABLE II
EFFECT OF DURATION OF ELECTRODIALYSIS ON
CATION EXCHANGE CAPACITY OF PEA ROOTS

<u>Dialysis Procedure</u>	<u>Time Lapse Prior to Anode Flushing</u>	<u>Total Time</u>	<u>Cation Exchange Capacity</u>
1.	20	30	36.9
2.	40	50	42.5
3.	60	70	46.0
4.	80	90	46.4

From the data in Table II, it can be seen that dialysis must be continued for 60-80 minutes before flushing the anode compartment. Earlier flushing of the anode compartment will result in incomplete dialysis. This probably is due to the change in concentration of the anode compartment. It is believed that the concentration of the exchangeable cations is much greater than the concentration of the exchangeable anions of the plant root. By early flushing of the anode compartment, the anions are removed, and since there are relatively few exchangeable anions on the plant root, accumulation of anions in the anode compartment is low after the first flushing. Thus, the amperage drops. Since one criterion for complete dialysis was based on a low amperage

of 0.1 - 0.2 amperes, flushing the anode gave an erroneous indication of complete dialysis.

2. Use of H⁺ from Dilute Acid to Displace Cations

Thirty grams of fresh pea roots were dipped for five minutes in each of a series of six beakers containing 200 ml. of 0.1 N H₂SO₄ instead of electro-dialysis. In a similar experiment, thirty grams of fresh pea roots were dipped for five minutes in a series of 10 beakers containing 200 ml. of 0.05 N H₂SO₄. After repeated washings in distilled H₂O, the roots were immersed in KCl and titrated as mentioned previously and the cation exchange capacity was determined.

Dipping pea roots in 0.1 and 0.05 N sulfuric acid gave cation exchange values similar to those obtained by electro-dialysis. The exchange capacity was 42.9 me/100 gms. for 0.05 N H₂SO₄ dippings, and 43.3 me/100 gms. for 0.1 N H₂SO₄ as compared to 44.3 me/100 gms. for electro-dialysis (See p.33 Appendix). There are several advantages to the dipping procedure such as (a) more uniform control of conditions (b) less expensive equipment required (c) less time required (d) allows more precise study of rate and ratio of displacement of mono-divalent cations.

During electro-dialysis both the current and the hydrogen ions, as a result of electrolysis of water, displaced the cations from the root surface; whereas, in dipping roots in H₂SO₄, the H⁺ of the sulfuric acid displaced the cations. Also, there is very little heat evolved in the dipping technique as compared with electro-dialysis. Hence, dipping roots in H₂SO₄ simulates more nearly the conditions existing in the soil. (H-clay vs. H₂SO₄).

Effect of Age and Size of Roots on Cation Exchange Capacity

A. Effect of Age

Differences due to age were found only as the plant approached maturity as expressed by the flowering of the plants (Table III). This is believed to be due to a larger amount of inactive fibrous material which decreases the exchange capacity when expressed on a weight basis. According to Williams and Coleman (31), there are exchange spots on the root surface. Steward (27), Mattson, et al (19) and others (25,31) showed that adsorption of ions was primarily in the apical region (1-20 m.m.). Based upon these conclusions, it is believed that in older, mature roots the area of adsorbing surface with respect to the entire root is considerably less than the same ratio in young, active roots. Thus, if only the lower or active portions of the older root were removed and cation exchange capacity determined, the values obtained would be expected to be more nearly the same as in the young plant. Obtaining new active roots was a serious problem encountered in determining cation exchange values for roots of trees.

B. Effect of Size of Root

Fine and coarse roots of peanuts, Berauda-Grass and quackgrass were separated. There was a difference between fine and coarse roots within a given plant (Table IV). This can be explained on the basis that the fine roots are growing portions of the plant, and thus there are more active adsorbing areas per weight of roots than in the case of coarse roots.

There appears to be little relationship between the size of roots (fineness or coarseness) of different plants and the cation exchange capacity. Species with fine, medium, or coarse roots were found among high exchangers as well as low exchangers. Blue Lupine, with relatively high root exchange values, had extremely thick, coarse roots. In contrast, Bermuda-Grass, with very fine roots, had very low exchange roots.

TABLE III

EFFECT OF AGE OF PLANTS
ON CATION EXCHANGE CAPACITY

<u>Plant</u>	<u>Age from Germination in days</u>	<u>Average Cation Exchange Capacity</u>	<u>Growth Condition</u>
Peas	12	43.3	Immature
Peas	16	43.4	Immature
Peas	21	44.3	Immature
Peas	70	29.9	Flowering
Buckwheat	14	39.6	Immature
Buckwheat	30	36.1	Flowering
Naff's bur-clover	95	40.9	Immature
Naff's bur-clover	140	32.4	Flowering
Common Crimson Clover	80	41.6	Immature
Common Crimson Clover	130	37.7	Flowering

TABLE IV.

VARIATION IN ROOT SIZE WITHIN A SPECIES

<u>Plant</u>	<u>Average Cation Exchange Capacity</u>	<u>Size of Root</u>
Peanuts	38.8	Fine
Peanuts	36.5	Average
Peanuts	35.1	Coarse
Quackgrass	14.7	Fine
Quackgrass	11.8	Coarse
Bermuda-Grass	10.9	Fine-average
Bermuda-Grass	7.9	Coarse

Cation Exchange Capacity of Electrodialyzed Plants in N KCl

The value of the cation exchange capacity of electro-dialyzed plant roots titrated in N KCl is presented in Table V in milliequivalents per 100 gms. of oven-dry weight.

TABLE V

CATION EXCHANGE CAPACITY OF ELECTRODIALYZED PLANTS IN N KCl

<u>Species Common Name</u>	<u>Scientific Name</u>	<u>pH of Root-KCl Solution</u>	<u>Cation Exchange Capacity me/100 gms.</u>
Grasses			
Tall Fescue	Fescuta elatior	3.52	30.5
Ryegrass	Lolium perenne	3.53	22.5
Field Brome	Bromus arvensis	3.75	18.0
Reed Canarygrass	Phalaris arundinaceae	3.82	17.5
Sudangrass	Sorghum vulgare	4.06	13.5
Cereals			
Corn. Ind. Wf9	Zea Mays	3.89	17.0
Corn Ohio 40B	Zea Mays	3.94	13.5
Millet	Panicum miliaceum	4.28	12.2
Weeds - Monocotyledons			
Quackgrass	Agropyron repens	4.13	14.5
Bermuda-Grass	Cynodon dactylon	3.91	10.5
Forage and Cover Crop Legumes			
Blue Lupine	Lupinus angustifolius	3.23	53.3
Yellow Lupine	Lupinus luteus	3.28	47.7
Canadian Field Peas	Pisicum sativum arvense	3.38	44.3
Common Crimson Clover	Trifoleum incarnatum	3.36	41.7
White Lupine	Lupinus albus	3.31	41.3
Naff's bur-clover	Medicago arabica	3.36	40.6
Bur-clover	Medicago denticulata	3.47	39.0
Sweet clover	Melilotus alba	3.42	38.5
Hubam Sweet clover	Melilotus alba var annua	3.48	38.2
Black Medic	Medicago lupulina	3.47	34.8
Birdsfoot Trefoil	Lotus corniculatus	3.54	23.9
Manganese bur-clover	Medicago arabica (var.)	—	21.5
Crops			
Buckwheat	Fagopyron esculentum	3.39	39.0
Peanuts	Arachis hypogae	3.42	36.5
Cotton	Gossypium hirsutum	3.47	36.1
Rape	Brassica napus	3.37	33.2
Tobacco (Havana K1)	Nicotiana tabacum	3.82	24.2

TABLE V (Cont.)

<u>Species</u> <u>Common Name</u>	<u>Scientific</u> <u>Name</u>	<u>pH of</u> <u>Root-KCl</u> <u>Solution</u>	<u>Cation</u> <u>Exchange</u> <u>Capacity</u> <u>me/100 gms.</u>
Weeds-Dicotyledons			
Galinsoga	Galinsoga parviflora	3.32	55.4
Chickweed	Stellaria media	3.39	44.7
Trees			
Black Locust	Robina pseudoacacia	3.67	23.8
Red Oak	Quercus borealis	3.50	22.8
White Ash	Fraxinus americana	4.00	13.9
White Pine	Pinus Strobus	3.38	17.0

Cation Exchange Capacity as Related to Ecology

The exchange capacity of dicotyledons was in general higher than that of monocotyledons. However, the full significance of this cannot be fully evaluated since a relatively small number of plants within a few families of the two classes were tested.

High exchange roots such as legumes theoretically bind divalent cations such as calcium and magnesium with greater energy than potassium; conversely, low exchange roots should bind or adsorb monovalent cations such as potassium more readily than calcium and magnesium.

Grasses are usually much higher in potassium than in calcium and magnesium; whereas, legumes are higher in calcium and magnesium than in potassium (2, 26). The high exchange capacity obtained for roots of legumes as compared to the low exchange values for roots of grasses helps explain the differences in the cation composition of legume and grass plants.

It is possible that the cation exchange of the plant root is one important factor in the secondary succession of certain natural communities. The secondary succession of grasses followed by white pine and then by hardwoods on loamy soils in New England may be partly due to the difference in exchange capacities of the plant roots. However, the cation exchange value for roots does not account for the appearance of ragweed (high exchange roots). The cation exchange capacity of Aster, goldenrod and other annuals and perennials which appear in the early stages of succession, was not determined.

The lower root cation exchange value obtained for white pine as compared to red oak and black locust helps explain why white pine is found on gravelly, sandy and sandy loam soils low in available K. Potassium is more rapidly lost by leaching from sandy or gravelly soils than from sandy loam or clay loam soils. Black locust makes its best growth on moist, fertile loamy soils or soils of limestone origin usually well supplied with available K, and red oak is found on fertile loams and sandy loams; whereas, white pine makes its best development on moist, sandy soils, which are usually low in available K. Then in general, with respect to K fertility, one would expect black locust on the most fertile, red oak on intermediate, and white pine on the least K fertile soil. On light soils, white pine encounters less difficulty in maintaining itself; but on the heavier, more K fertile soils favorable for rapid growth of hardwoods, white pine has a difficult time competing with the hardwoods and maintaining itself (29). The occurrence of white pine or hardwoods can be partly explained by the differences in cation exchange capacities of their roots, for in general heavy soils are better supplied with K. Thus, on heavy soils the hardwoods can obtain the required K and compete with white pines, and eventually crowd out white pine. The low cation exchange value obtained for white ash roots is believed to be due to inactive or dead roots.

On the basis of the cation exchange theory and the low cation exchange values for grasses as compared to legumes, it would be expected that, on low levels of

fertility, grasses in association with legumes should compete better for K. Gray (9) showed this to be true. However, one must keep in mind also the fact that the growing season of the grasses in association with pasture legumes is considerably earlier. During this seasonal growth, the grasses take up large amounts of K, thereby seriously depleting the level of available soil K. Thus, when the legumes start their growth, the level of soil K and other mineral nutrients has been reduced and in addition the grasses have already made appreciable growth, thereby seriously competing with the legumes for light and moisture as well as for fertility. Important management practices based upon the results obtained can be postulated. In the selection of pasture species, the closer the cation exchange capacity of the plants to be grown in associations, the better the compatibility for K. Based on cation exchange values of plant roots, tall fescue (30.5 me/100 gas.) should be more compatible than Reed canarygrass (17.5 me/100 gas.) when grown with ladino clover, red clover, or alfalfa (relatively high exchange roots). Similarly with respect to K annual ryegrass (22.5 me/100 gas.) should be more compatible than field brome grass (18.0 me/100 gas.) when grown with crimson clover. Furthermore, frequent small K fertilizer applications will favor the legumes since the mono-divalent cation exchange theory applies primarily at low fertility levels. In the past one large K bearing fertilizer application was applied at the onset. Following the first cutting, the K fertility level dropped, thus

favoring the grasses. By small K fertilizer applications, the K fertility level can be maintained. Moreover, at high K fertility levels, the valence effect is reduced. It is appreciated that K fertility level is one factor and that other factors such as period of growth, moisture, light requirements, temperature, etc., are important in grass-legume associations. A grass which starts spring growth at about the same time as the associated legume should be more compatible with respect to K uptake, and hence highly desirable.

The unusually low cation exchange value for the roots of the legume, birdsfoot trefoil (23.9 me/100 gms.) helps to explain why this plant grows well on soils low in available K. It also helps explain the compatibility of birdsfoot trefoil with Kentucky bluegrass (21.6 me/100 gms.)¹, timothy (22.6 me/100 gms.), and even redtop (17.3 me/100 gms.) on many soils in New York, Pennsylvania, and Indiana. Similarly the unusually low cation exchange value for manganese bur-clover (21.5 me/100 gms.) helps explain the ability of this legume to persist on southern soils of very low K fertility and to grow in association with Bermuda-Grass (10.5 me/100 gms.).

The relatively low cation exchange values for the roots of sudangrass (13.5 me/100 gms.) and millet (12.2 me/100 gms.) would indicate that these plants should effectively utilize K even on soils low in available K. One must bear in mind

¹ Values determined by Drake et al (5).

that these forage crops, sudan and millet, greatly deplete the soil K. Thus, those farmers who wish to establish seedings of the superior legumes, alfalfa or ladino clover, and the superior grasses, smooth brome or orchard grass, following millet or sudangrass, must supply liberal amounts of K.

High cation exchange values obtained for roots of Galinsoga and chickweed helps explain why these plants occur chiefly on fertile soils high in available K. Galinsoga and chickweed are found on rich, moist soils high in K and they compete seriously with cultivated crops for mineral nutrients, light and water.

Roots of some other weeds such as yellow foxtail, Bermuda-Grass, and quackgrass have low cation exchange values. This helps explain their occurrence and relatively high production of dry matter on soils of low fertility as well as on moderate to highly fertile soils. The low cation exchange value for Bermuda-Grass roots helps explain its ability to grow well in the South on sandy soils, very low in available K. Most plants with low cation exchange roots thrive on soils well supplied with available K. However, on such soils the plants with low exchange roots as compared to plants with high exchange roots do not have as great an advantage in K uptake, since the differential mono-divalent cation uptake diminishes with increasing cation concentration.

Species and varietal differences were found to exist. This can be seen in the values obtained for corn and in values obtained by Drake et al (3) in other corn varieties.

Since in theory a root with low cation exchange capacity adsorbs Mg with relatively less energy than a high cation exchange root, the difference in cation exchange capacity of the two inbred lines of corn, Ind. Wf9 (17.0 me/100 gms.), and Ohio 40B (13.5 me/100 gms.), helps account for lower Mg uptake and observed Mg deficiency of inbred corn Ohio 40B, which has relatively low exchange roots. Cation exchange measurements of the roots of inbred lines or new crop varieties may prove a useful criterion in selection.

SUMMARY AND CONCLUSION

The cation exchange capacity of a large number of plants and several factors affecting the cation exchange measurements were determined.

The following conclusions were drawn:

1. Dipping pea roots in H_2SO_4 compared favorably with the electro dialysis procedure. Further investigation of this problem will be required.

2. Measureable differences in cation exchange due to age of pea roots of plants studied were found only after flowering. Values for other plants had decreased at flowering.

3. Size of root within a given plant affected the cation exchange capacity as coarse roots had lower exchange values than fine roots. However, no relationship was found between cation exchange capacity and the size of roots of different plants.

4. Roots of dicotyledons were generally higher than monocotyledons in cation exchange capacity. Birdsfoot trefoil and manganese bur-clover had much lower cation exchange capacity roots than other dicotyledons.

5. The root exchange capacity of a plant may be one of the important factors in distribution of natural communities and in management practices in crop production.

6. Important species and varietal differences were found between the three species of lupines and the two inbred lines of corn.

APPENDIX

The following figures are the replicates obtained for the various species:

MONOCOTYLEDONS:

GRASSES

Tall Fescue

31.7
29.4
30.4

Ryegrass (annual)

21.9 22.6
23.2 23.6
22.5 22.6
23.2 25.6
 20.3

Field Brome

18.9
17.7

Reed Canarygrass

17.5
17.4
19.1

Sudangrass

14.1
12.5
13.4

CEREALS

Corn Ind. Wf9

16.7
17.1
17.2

Corn Ohio 40B

13.7
13.8
12.3
14.4

Millet

12.6
12.2
12.6
11.0

WEEDS

Quackgrass

15.3
14.2

Galinsoga

55.2
55.6

Bermuda-Grass

10.8
10.4
10.3

Chickweed

44.0
45.5

DI COTYLEDONS:

LEGUMES

Blue Lupine

53.1
53.6

Yellow Lupine

47.7
46.3

White Lupine

41.3
41.2

Canadian Field Peas 15-20 da. (electrodialyzed)

44.9	44.2	42.8	43.9	44.4
45.2	44.7	42.5	43.0	44.8
45.9	45.2	43.7	42.6	42.1

Flowering Peas
70 da.
(electrodialyzed)

29.4
30.5

Acid Dipped Peas
15-20 da.

0.05 N H ₂ SO ₄	42.85
0.1 N H ₂ SO ₄	43.25

Common Crimson Clover

41.7
41.4
42.6

Flowering Common Crimson Clover

37.1
38.2

Naff's bur-clover

40.8
42.3
40.6
40.1

Bur-clover

38.8
39.1

Flowering Naff's bur-clover

31.8
32.9
32.4

Sweet clover

38.9
37.9
38.6

Huban Sweet clover

37.4
39.0

Black Medic

35.6
34.0

Birdsfoot trefoil

23.8
24.4
23.1

Manganese bur-clover

22.3
20.6

Peanuts

36.8
36.2

CROPS

Buckwheat

41.5
38.2
39.2

Flowering Buckwheat

36.5
37.9
35.2

Cotton

35.2
35.4
37.9

Rape

33.6
33.0

Tobacco

24.3
24.2

TREES

Black Locust

24.7
23.7
23.1

Red Oak

22.9
22.7

White Ash

13.9
10.0

White Pine

17.4
17.5
16.3
16.7

COMPUTATIONS OF EVALUATION OF ERROR

Peas

<u>Sample</u>	<u>M.E.</u>	<u>d</u>	<u>d²</u>
1	45.9	+ 1.9	3.61
2	44.9	+ .9	.81
3	45.2	+ 1.2	1.44
4	44.2	+ .2	.04
5	44.7	+ .7	.49
6	45.2	+ 1.2	1.44
7	42.1	- 1.9	3.61
8	42.5	- 1.5	2.25
9	43.7	- .3	.06
10	43.9	- .1	.01
11	43.0	- 1.0	1.00
12	42.6	- 1.4	1.96
13	44.4	+ .4	.16
14	44.8	+ .8	.64
15	<u>42.8</u>	- 1.2	<u>1.44</u>
	2659.9		$\Sigma d^2 = 18.96$

Ryegrass

1	21.9	- 1.0	1.00
2	25.6	+ 2.7	7.29
3	22.5	- .4	.16
4	23.2	+ .3	.09
5	22.6	- .3	.09
6	20.3	- 2.6	6.76
7	22.6	- .3	.09
8	23.2	+ .3	.09
9	<u>23.6</u>	+ .7	<u>.49</u>
	205.9		$\Sigma d^2 = 16.16$

Calculations:

For peas:

$$\text{Mean} = \frac{659.9}{15} = 44.0$$

$$s = \sqrt{\frac{\sum d^2}{n-1}} = \sqrt{\frac{18.96}{14}} = \pm 1.35$$

$$\text{P.E.} = \pm .6745 s = \pm .6745 \times 1.35 = \pm .91$$

Chauvenet's criterion is P.E. x 3.12 for 15 samples.

$$\text{Chauvenet's criterion} = \pm 2.84$$

Any value deviating by ± 2.8 from the mean should be discarded.

For ryegrass:

$$\text{Mean} = \frac{205.9}{9} = 22.9$$

$$s = \sqrt{\frac{\sum d^2}{n-1}} = \sqrt{\frac{16.16}{8}} = \pm 1.42$$

$$\text{P.E.} = \pm .6745 s = \pm .6745 \times 1.42 = \pm .96$$

$$\text{Chauvenet's criterion} = \pm .96 \times 2.91 = \pm 2.8$$

$$\text{Standard error of the mean: } s_{\bar{x}} = \frac{s}{N}$$

$$\text{For peas: } s_{\bar{x}} = \frac{\pm 1.35}{15} = \pm 0.344; \text{ For ryegrass: } s_{\bar{x}} = \frac{\pm 1.42}{9} = \pm 0.473$$

"t" value for 14 D.F. of peas is 2.145

"t" value for 8 D.F. of ryegrass is 2.310

$$\text{For peas: } 44.0 \pm 2.145 \times 0.344 = 44.0 \pm 0.7; \text{ Range: } 43.3 - 44.7$$

$$\text{For ryegrass: } 22.9 \pm 2.310 \times 0.47 = 22.9 \pm 1.1; \text{ Range: } 21.8 - 24.0$$

$$\text{Coefficient of variation: } C = \frac{s}{\bar{x}} \times 100$$

$$\text{For peas: } C = \frac{\pm 1.35}{44.0} \times 100 = 3.63\%$$

$$\text{For ryegrass: } C = \frac{\pm 1.42}{22.9} \times 100 = 6.20\%$$

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