The Determinative Action of Environic Factors Upon Neobeckia acquatica Greene [1].

By Dr. **D. T. Mac Dougal**

(With 14 figures in text.)

The march of development of the metameres in the ontogeny of a large number of seed-plants is attended with the formation of a series of foliar organs varying progressively through a wide range of form and structure from the nepionic leaves to the floral bracts. That these leaf-characters are indicative of a complex of morphogenic and physiologic characters essentially different, in the internodes which bear them, is well evidenced by the fact that the rejuvenation phenomena and the mature individuals which may follow propagation by metameres from the earlier or later part of the series may be widely different.

One phase of this behavior is illustrated by the work of Shull with Sium in which it was shown definitely that the rejuvenescence of a bud borne on any internode was followed by the formation of foliar organs the approximation of which to the true nepionic leaves corresponded to the nearness of the internode to the senescent or floral end of the series. (Shull, G. H., Stages in the Development of Sium cicutaefolium. Publ. Carnegie Inst. of Wash. Nr. 30. 1905.)

Still another phase of this matter is exhibited by plants in which for example, propagation from juvenile individuals representing the earlier part with the ontogenetic series results only in other juvenile individuals which do not display characters included in adults in which the entire progression to senescence has been followed. There is a confluence of thought toward acceptance of the conclusion that all of these facts must rest upon a definite physical basis of formative or specialized material characteristic of the stages of development and with

1) Diverse and changing usage has made necessary the citation of this plant also under the names of Nasturtium lacustre A. Gray, Roripa Americana Britton and Radicula aquatica (Eat.) Robinson, in correspondence with American botanists during the ten years in which it has been under cultivation.

respect to the various organs. (See Goebel, Organography of Plants. Part I, pag. 45 and 145. 1900.)

The fact that the structure of the leaves of any part of the series is generally of an obvious suitability for activity under the seasonal conditions in which they usually are formed has led many writers to assign a directly determinative action to the environment. The coincidence of amplitude of range in intensity of environic conditions and of correlated diversity of structure, as exemplified by Bidens Beckii, Cabomba, Ranunculus delphinifolius, Proserpinaca palustris, Sium cicutaefolium, and of Neobeckia the subject of the study described on the following pages, might be one of simple survival by fitness, or on the other hand, fitness might in itself be induced by the agencies encountered.

Any consideration of the matter raises the question at once as to how far the various forms of a polymorphic series are morphologi-

Fig. 1. Seedlings of Sium cicutaefolium grown as terrestrials.

cally determinative, following an unmodifiable proceedure, and to what extent the morphogeny of the metameres may be modified by manipulation of the external conditions affecting their development. The results of Shull cited above seem to show that the ontogeny of Sium is independent and that external conditions may be modified to increase the range of variability or to cause rejuvenescence at any stage, yet their influence goes no farther.

This variation may be illustrated by some results which the author obtained with Sium, in the New York Botanical Garden in 1903. Two series of germinating seeds in soil were made. One was treated in the ordinary manner and the other was submerged to a depth of 10 cm in water.

The seedlings germinated as terrestrials grew more rapidly than those under water and had a main root 2 to 3 cm long with a few lateral branches, and had also some adventitions roots arising from the lower internodes of the stem, which were almost as long as the main root. The first leaf was of orbicular outline, sometimes cut nearly to the base, while in other specimens the first, second and sometimes the third leaves showed only crenation. The fourth leaf was visible on many of the seedlings on the above date (Fig. 1).

Aquatic seedlings developed an axis longer than that of the terrestrials with a slender main root of greater length and with fewer branches. The primary leaf was of a width not more than one-third of that of the terrestrial, not entire in any instance, but never divided to the base. The second and third leaves departed less from the form of the nepionic leaf than did the same organs in terrestrial plantlets (Fig. 2). Development was terminated in every case in five or six months after germination and no adult plants were secured from aquatic germinations. This result indicates that the seedling was exposed to an extreme of conditions and the divergence was probably as wide as might be produced. The death of the young plants may be ascribed to the unsuitability of the leaves for photosynthesis under submersion. Terrestrial plants a year old were of course able to endure submersion and produced finely dissected leaves comparable in spread and length with others unfolded in the air. So far as the forms of the leaves are to be taken into account the diversity noted above was well within the range of variation noted by Shull in seedlings grown as terrestrials.

Fig. 2. Seedlings of Sium germinated as aquatics.

Some experimental cultures were begun in 1902 which might afford further opportunity for testing the generalizations noted above and also yield some information bearing upon the transmission of environic effects to successive generations. The present contribution is concerned with the first named subject: the inheritance of environic effects, or the transmission of „acquired" characters is being treated in an extensive series of cultures at the various plantations of the Department of Botanical Research of the Carnegie institution of Washington, and it would not be profitable to discuss the fragmentary results now available.

Living plants of Neobeckia aquatica were obtained from the shores of South Bay of Lake Champlain in the autumn of 1902 and a few years later a socond supply was furnished by Prof. H. C. Cowles from pools in the vicinity of Chicago. Cultures from 1902 to 1906 were made in the soil and in water in the New York Botanical Garden. Living plants were taken to the Desert Laboratory in 1906 and grown under glass as well at the Montane plantation at 8,000 feet as terrestrials. Some of the individuals grown here were taken to the Coastal Laboratory at Carmel, California near the shore of the Pacific in 1910. Flowers were formed but once in the ten years and all reproductions were from cuttings.

Neobeckia is usually found rooted in the mud at the bottom of lakes and pools at a depth af 20 to 30 cm. Its most familiar aspect is that offered by the plant in bloom when an irregularly cylindrical stem extends above the surface of the water a few cm, the emersed part bearing a few oblong er oblong-ovate leaves or bracts subtending the terminal inflorescences. The submerged part of the stem bears finely dissected leaves and a dense cluster of these are usually found about the base of the stem. The plant is not found above the high water level. Almost any part of the shoot serves to propogate the plant and numerous individuals may be found upon the muddy strand between high and low water levels.

Nepionic leaves of seedlings have not come under observation during the course of this work. The emersion of aquatic individuals is usually followed by rejuvenescence consequent upon the changes in temperature, illumination, and moisture. The earlier leaves are entire or nearly so and successive organs show an irregularly progressive dissection of the laminae beginning at the base, which results in pinnatifid blades and finally carries the series on terrestrials into much divided organs in which the ultimate parts are narrow and strap-shaped (Fig. 3). These aerial dissected leaves have not the spread and extension of the submerged dissected leaves, and wide differences exist between the structures presented by the two types.

The senescent leaves of aquatics are formed on the terminal portions of stems above the surface of the water are in ordinary appearance quite like the senescent organs of terrestrials. No wild terrestrial plants have been found in which stems were formed, but it seems very probable that they may have been developed by many plants in a state of nature.

A number of cultures were made to ascertain the reaction of the plant under various environic conditions. Plants which had been grown as terrestrials were placed in the water. Also cuttings including several internodes were thrown into tanks in which they floated freely. The rejuvenescence of these cuttings was characterized by the development at first of two or three ovate, serrate leaves, which passed through dissected stages into the filamentous types (Fig. 5). If small cuttings were used the nepionic leaves were broadest, but were still not so broad

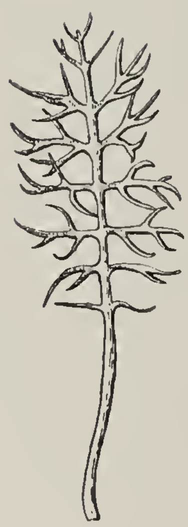

Fig. 3.

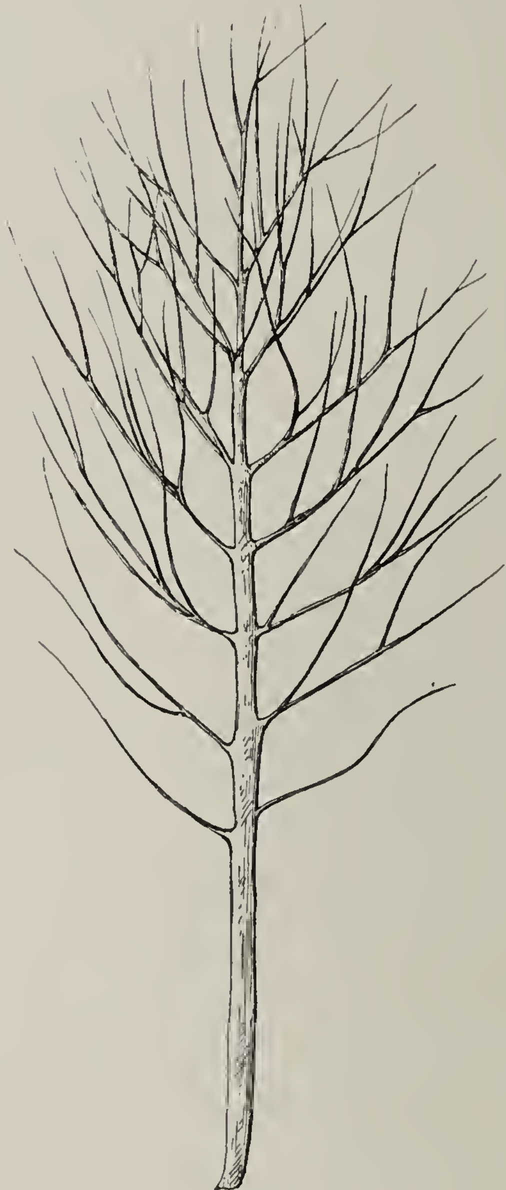

Fig. 4.

Fig. 5.

Fig. 6.

Fig. 3. Mature leaf of Neobeckia of the terrestrial type.
Fig. 4. Mature leaf of Neobeckia of the aquatic type.
Fig. 5. Plantlet of Neobeckia from cutting floating freely in water.
Fig. 6. Rejuvenation of small cutting of Neobeckia.

as those of terrestrials in rejuvenescence (Fig. 6). The rejuvenescence of lateral buds attached to stems of some length was characterized by nepionic leaves which were still narrower, being oblong-linear, more or less remotely serrate, and passed quickly into the finely dissected type (Fig. 9).

In June 1912, a number of cuttings were made from the radish-like underground members, which are probably a combination of roots and stem, which are formed in terrestrial cultures. These fusiform structures were cut into two parts by a single transverse section. The uppermost part bearing the active crown and other buds produced leaves of the broader type, but the smaller lower part, which was not so heavily stored with surplus food material and which had only axillary buds, in every case displayed nepionic leaves of the extremely narrow type.

The growth of cuttings consisting of a portion of stem in water, from plants cultivated in the soil was marked by curvatures probably

Fig. 7.

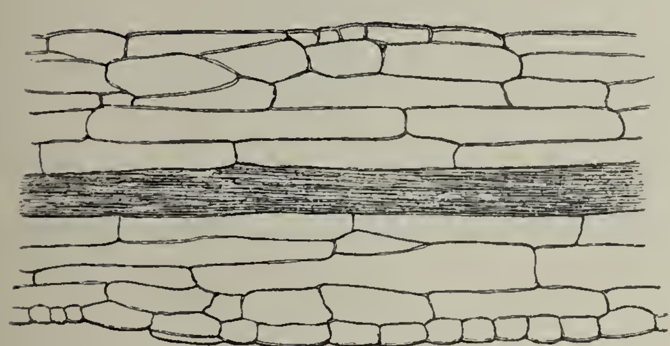

Fig. 9.

Fig. 8.

Fig. 7. Rejuvenating lateral bud of Neobeckia attached to stem with narrow nepionic leaves.
Fig. 8. Cutting from a stem of Neobeckia grown in water.
Fig. 9. Longitudinal section of segment of aquatic leaf of Neobeckia.

induced by illumination, and the terminal part formed a number of short internodes homologous with those of a submerged rosette, during the winter season in New York when the total illumination was low. With the advent of spring the formation of finely divided leaves began (Fig. 8), which might be considered as corresponding to those of the free stem of a plant rooted in the mud. The examination of these leaves showed the familiar structure of hydrophytes. The smaller subdivisions were irregularly oval in cross section, and had an epidermis of flattened elements against which the underlying parenchymatous tissue three or four layers in thickness was crowded. These thin-walled cells were irregularly cylindrical and arranged without intercellular spacing, with their longest axes parallel to that of the filament of which they formed a part (Fig. 9). Whatever the relation may be it was noted that whenever regenerating cuttings floating in the water were anchored, the influence of the anchorage was to cause the next leaves formed to take on some of the characters of terrestrials although these organs were some distance below the surface. Thus in 1913 cuttings which had progressed so far as to be forming aquatic leaves with thread-like segments, began to make strap-shaped divisions when the plantlets were fastened in the soil at the bottom of the dish.

Some of the experiences with this plant in various climates show the manner in which developmental proceedure might take place in dissimilar complexes of external conditions.

Six clumps of plants grown as terrestrials at the New York Botanical Garden since 1902 were received at the Desert Laboratory March 17, 1906, and were kept in pots until they were taken to the Montane plantation just being established in the Santa Catalina mountains at 8,000 ft. in May. The history of these plants shows that they underwent changes by which broadly laminar nepionic leaves would be produced from the buds to be followed by others of the finely dissected types. These alternations were not seasonally regular however. In some instances nepionic leaves were formed in midsummer with the advent of the rainy season to be followed by a series running to aerial dissected types.

Some material was taken to the Cinchona station of the New York Botanical Garden in the Blue mountains of Jamaica (7,345 ft.) by Dr. Forrest Shreve and the notes communicated by him read as follows:

„The four plants of Roripa americana taken to Cinchona were set out in the pots about October 23rd 1905 at different points in the beds or borders such as gave them different amounts of light or shade. The pots were merely sunk in the ground until the tops were flush with the level of the beds and the water received by them was only the natural precipitation. During November a number of leaves appeared which were entire and bluntly dentate, being rather spatulate in outline. These were quickly followed by leaves which were similar in the upper part to those just described but were lyrate at the basal portion. These were in turn followed by leaves which were rather finely cut, being irregularly bi-pinnate with ultimate segments more than 1 mm wide. About the end of December grubs attacked two of the plants and they lost all of their foliage. The roots were saved and a new crop of leaves soon appeared which were very finely dissected with segments less than 1 mm wide. Within a month after the appearance of the fine leaves on these plants the same sort of leaves were appearing on the plants which were not attacked. The average length of the leaves was 6 to 7 cm. From February until May the plants did well but underwent no further changes of leaf form.“

Still another series of cultures in the soil were carried out in the glass house attached to the Desert Laboratory at Tucson, Arizona. Three introductions have been made, and material has been drawn from them to various other places. Some individuals brought to Tucson in 1908 are still alive despite the extreme summer temperatures to which they are exposed (100° F to 120° F). Establishment in the soil at this place was invariably followed by the appearance of nepionic leaves merging gradually into aerial dissected forms. It was notable also that very slight disturbances would cause rejuvenescence and a return to the broadly laminar leaves, and those which were formed in the period immediately following the cooler weather of January and February were characterized by a spread and area of surface far surpassing anything seen in the natural habitat of the plant, and also all other experimental conditions.

A final introduction in September 1912 consisted of a number of stems of aquatics which had been packed in wet moss and shipped from the New York Botanical Garden by Dr. E. M. Kupfer. Those placed in small aquaria containing spring or well water showed a development of finely divided leaves from the terminal buds, while awakening lateral buds unfolded the usual series beginning with broadly laminar nepionic leaves. Other plants set in the soil formed nepionic leaves while plants already in position coincidently formed similar organs, which might be attributed to the falling temperatures of the autumnal season. It was notable that terrestrials at this place were extremely sensitive to any disturbance. Stirring the soil around the thickened roots would cause the crown buds to unfold nepionic leaves. These plants remained in the rosette stage and the apex of the stem did not rise above the level of the ground at Tucson.

About the 1st of December 1912 it was noted that the divisions of the leaves on terrestrials and aquatics were very similar both in pattern and in the fact that the ultimate divisions were flattened and strap-shaped.

The growth of the species as a terrestrial entailed among other departures from the experience of the plant the endurance of a great range of temperature during the year and also daily. It was notable that full maturity of the plant was not reached under such circumstances until conditions were provided in which this feature was of a character approximating that of the habitat of the plant. Individuals grown as terrestrials in the glass house of the Desert Laboratory were taken to the Coastal laboratory in October 1910. The climate was oceanic, the temperature falling below the freezing point but a few hours in each year, and the total exposure above 70° F is comparatively small. Under such conditions elongated aerial stems with narrow senescent leaves were formed in 1911 and in 1912, while in 1913 one plant proceeded to the development of full inflorescence.

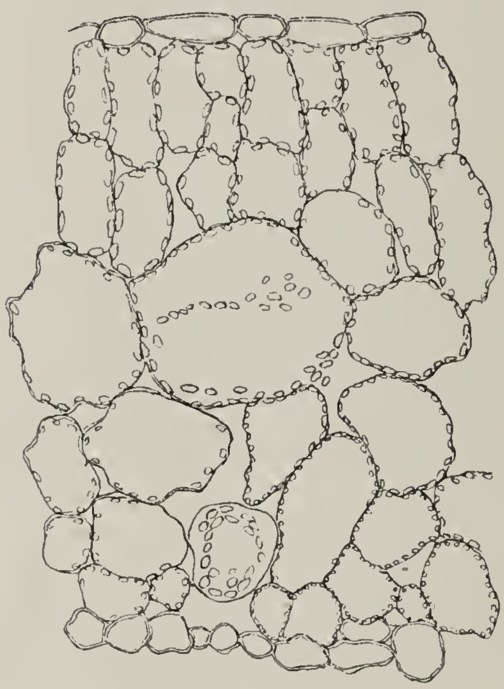

Fig. 10. Cross section through a terrestrial leaf segment of Neobeckia.

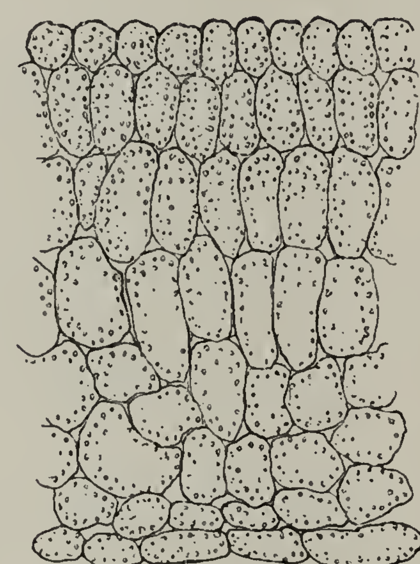

Fig. 11. Cross section through a part of a leaf from the terminal part of a stem of Neobeckia.

A comparison of the structures of aquatic and terrestrial plants was made from material grown in the New York Botanical Garden. The first lot of cuttings were placed in the soil in pots in 1902. These soon underwent rejuvenescence, sending out roots and beginning with the formation of the oblong-ovate nepionic leaves which were followed by the usual series of aerial dissected forms. The epidermal elements of such leaves were flattened but the parenchymatous elements were arranged with their greatest diameters perpendicular to the surface, and ample intercellular spaces communicated with the external air through the stomata (Fig. 10). The stomata were much more abundant per unit area on these organs than on the leaves or bracts near the inflorescence. The conducting tract was strongly developed, but the supporting tissue was weak. One or two layers of palissaded cells were found underneath the upper surfaces and the remainder of the chlorophyllose tissue was disposed in the form of spongy parenchyma with large intercellular spaces. The epidermal cells over the midribs and its branches were noticeably larger and had heavier walls than elsewhere. These aerial dissected leaves by reason of the arrangement of the dissues described are much more efficient transpiratory organs than the terminal bract-like leaves of emersed stems as was evident seen by a comparison of the structure of the two (Fig. 11).

On May 19, 1904 the cultures made from the cuttings of 1902 were turned out of the pots for examination. The large number of lateral branches previously mentioned had acted as offsets, from which new plants had arisen, but still connected with the parent in such manner that dense clumps were formed. A comparative examination of these plants and others of the same age and derivation grown in the aquarium was made in the latter part of October.

Fig. 12. Thickened roots of Neobeckia grown as a terrestrial.

The normal aquatic specimens in July showed a single main root not more than 2 mm in diameter and 10 cm in length with a very thin secondary branches. The crown consisting of the top of the root and a stem fused with it had sent off one or two branches. The terrestrially grown individuals of the same age consisted of a clump of thickened roots produced by numerous offsets and branches from the crowns. These thickened roots were in clumps and were 10 to 15 cm in length showing a diameter of as great as 1 cm at the junction with the crown. The tissues of the thickened organs were turgid and crisp resembling radishes in consistency and taste. The amount of the peculiar volatile oils present was noticeably greater than in normal plants being distinctly discernible by smell and giving a strong taste (Fig. 12).

The internal structure of the roots showed correlated divergences. The central cylinder becomes greatly enlarged by secondary thickening in the terrestrial organs and a corresponding increase takes place in the cortex. In addition to the greater number and size of the various elements concerned the terrestrial organs are crammed with starch which appears to be wholly lacking from aquatic organs, thus showing that the roots have been altered from a form suitable to fixation only to a structure adapted for receiving quantities of sugars and converting this substance into starches which are stored in all of the parenchymatous elements. The embryonic tissues remain active in the periphery of the central cylinder and the phelloderm was visible in both cases although its growth did not keep pace with the enlargement of the terrestrial roots in all instances some of these organs having undergone splitting.

The terrestrial cultivation of these plants was continued. The plants of the original lot set out in 1902, produced aerial stems in 1905 which had internodes 3 to 20 mm long, by September of that year. The leaves and stems underwent an autumnal death however. Cuttings put out in 1904, showed clusters of thickened roots in 1905 which were much smaller than those set out in 1902 and material was preserved for a comparative examination, which might detect any developmental changes with continued cultivation.

It was not possible to take up this point until the summer of 1912 when the structure of the two lots of material was compared. The chief advance or change to the older condition of the thickened roots consisted in the more pronounced development of sclerenchymatous thickenings of the cortical cells. The greatest number of elements modified in this manner lie immediately internal to the phellogen, but numbers of cells with such thickened walls are scattered throughout the cortex. The central cylinders of the older roots also showed an exaggerated development.

The observations the results of which are described in the preceding pages extended over many years and included a consideration of the behavior of the plants under widely dissimilar climatic and other conditions. It is believed that very nearly the possible range of behavior has been noted. After these cultural experiments were well under way a series of special tests were made to determine under what experimental conditions rejuvenescence, as indicated by the formation of nepionic leaves might be induced. Cultures in tap water to calcium nitrate had been added in various proportions failed to show any results different from those of ordinary water. Recourse was then taken to water cultures with unusual proportions of potassium nitrate. Nany of these were made and as the results were fairly uniform the behavior of the plants may be best illustrated by citation of certain selected examples.

A glass aquarium in the greenhouse at the New York Botanical Garden was filled with 20 liters of water and to this was added 100 grams of potassium nitrate, on May 23, 1903. Small plants grown

Fig. 13. Cutting of Neobeckia which was producing finely divided aquatic leaves which after being placed in solution of potassium nitrate formed a series of leaves with broader laminae.

Fig. 14. Terrestrial stem of Neobeckia showing series of leaves in which a simplification first ensues then progression toward division of the laminae.

as aquatics but rooted in small pots of soil were set in the solution so as to be completely submerged. These plants were producing the finely divided leaves of the filamentous type at time of the change. The first leaves produced in submergence in every instance were less refined than those formed last, then others followed with coarser divisions until the ovate-serrate type recognizable as true nepionic forms were developed. These were the beginning of a series which finally returned to the finely divided filamentous type (Fig. 13; see also Fig. 14).

A more concentrated solution was next made by adding 2 kg of potassium nitrate to 20 liters of water in a glass aquarium. The osmotic pressure which would be set up by this solution would be about 35 atmospheres. A number of plants grown as aquatics withe mature form of finely divided filamentous leaves, and others which had been cultivated as terrestrials and formed the mature type of finely dissected leaves were placed in the solution in 1904. The filamentous aquatic leaves were quickly killed, and the plants bearing them were checked and showed no marked activity of any kind during the few weeks the experiment was continued. The individuals taken from terrestrial conditions showed a marked difference in reaction. The finely divided leaves were not killed, but the terminal buds which produced them became inactive. At the same time lateral or axillary buds on the terrestrially grown stems underwent rejuvenescence, beginning with the formation of broadly laminar leaves, which merged in a series in which incision and division became more marked. The preparation was taken down before filamentous threads were produced.

The continuation of the observations upon material from the original introduction resulted in a long vegetative series. Some of this material had been carried to the Coastal Laboratory at Carmel, and was being cultivated as aquatics with the mature filamentous type of leaf-divisions in 1912. Three of the plants were placed in a glass dish containing 1000 ccm of water and 5 gram potassium nitrate on August 2. The following entries are taken directly from my notebock:

"Early in September it was seen that the series of leaves included forms which passed by gradual stages into organs with divided laminar segments with fewer incisions until finally organs were produced in which the indentations were entirely marginal and the small but relatively broad laminae were those of the nepionic type, which thus had come about by gradual stages rather than as an abrupt reaction."

It was thus demonstrated again that in Neobeckia as in Sium and Proserpinaca the addition of such compounds as potassium nitrate to a water culture in which aquatic individuals were growing "resulted in the production of primitive leaf-forms in a simplifying series rather than as abrupt appearange following rejuvenescence."

The interpretation of these reactions involves the whole question as to the nature of the physical changes underlying rejuvenation, and no pretence is made that the facts cited above solve the main problem. The general trend of the evidence afforded by the behavior of Neobeckia for ten years however may be best apprehended when the facts in question are considered in totality.

The full series of foliar organs of Neobeckia ranges from broadly oblong lanceolate or ovate leaves in the nepionic stages to narrowly ovate or lanceolate floral bracts in the senescent stage. The mature or adult leaf of the highest type in aquatics is cut into fine thread-like divisions, and the mature leaf of terrestrially grown plants is much divided with narrow strap-shaped segments (Fig. 4 and 5). The spread and size of the nepionic leaves varies with the conditions under which they are formed. The structure of the mature leaves varies between the limits of the two types indicated according to the environment.

Nepionic leaves show a more pronounced development of the lamina on free cuttings than on awakened lateral buds on entire stems, on the upper parts of thickened root-stocks rather than on the lower. Cuttings placed in water invariably produce nepionic forms immediately, but when the water is allowed to evaporate leaving the plantlets growing as terrestrials the type of leaf changes gradually from the aquatic to the terrestrial type without the intervention of nepionic forms. Abrupt change from aquatic to terrestrial conditions however is followed by the interposition of nepionic types indicative of rejuvenescence. Anchorage of floating aquatic plantlets while submerged was followed by modification of the aquatic leaves toward the terrestrial types without the interposition of nepionic forms. Anchorage and exposure of the stems to the air would occur together under natural conditions, but either may bring about the modifications ensuing when the two act together.

The development of nepionic leaves indicative of rejuvenation occurred in terrestrial cultures with the change from cool to warm seasons from warm to cool conditions, with rapid changes in the supply of moisture either way, and might also be induced simply by the increased aeration following stirring of the soil about the roots.

Aquatically grown plants remained alive when placed in strong (10 $^0/_0$) solutions of potassium nitrate, but the aquatic leaves were killed. Terrestrially grown plants retained the strap-like divisions of the leaves unharmed under the same conditions: the terminal buds remained inactive but the lateral buds were awakened unfolding the broadly laminar nepionic leaves of the customary type. In this connection it is pertinent to call attention to the fact that the aquatic leaves, and the main actively growing points would be most easily dehydrated and to an injurious extent by the solution. The terrestrial leaves and the lateral buds would endure the concentration and in case of the latter undergo the changes which constitute the basis of rejuvenation.

Aquatically grown plants with the characteristic thread-like segments continue to be active when placed in a solution one part in two hundred to one part in two thousand of potassium nitrate, with a range of osmotic pressure from two to about seventeen atmospheres. and form a series of leaves passing gradually toward and into the broadly laminar leaves of the nepionic type. Continuance in the solution was followed by a gradual return in the series to the finely segmented aquatic type. The reaction was as if the immersion in the solution produced a brief and temporary effect only. Leaves already partly formed in the bud were affected but little, others less developed might be altered to a greater extent. Later the unknown accommodations of the plant having taken place, the return or progression from the nepionic to the aquatic or mature type occurred in the usual manner.

It seems impossible to ascribe rejuvenation of buds and the formation of leaves to any hydration effect, or to any other simple change in colloidal condition which might be described as liquidity or lability. The disturbance resulting in rejuvenescence, like many other striking phases of reaction in plants may be initiated by a wide range of agencies, changes in temperature, changes in moisture, alterations in concentration of the medium, separation of a segment of the vegetation body, injury to neighboring buds, etc. The direct effect of all of these so-called stimuli would embrace far too wide results to be included in any distinctive colloidal or osmotic reaction. The only allowable supposition is that which refers the entire matter back to modifications of the supply of formative nutritive material. Rejuvenescence in nearly all of the cases described above was connected with an increased supply of nutritive material available for the awakening buds. In some instances the increase resulted from the removal of competition. In other cases as in plantlets arising from leaves used as cuttings the material accumulated instead of being translocated. Cuttings in solutions containing much potassium nitrate showed awakening of the lateral buds and death of the terminal buds, the osmotic pressure being injurious to the tender tissues of a bud accommodated to a medium of much lower concentration, while the densely granular cells of the latent buds were in a condition to absorb the solution, and make use of it.

Neobeckia is thus seen to exhibit a wide range of diversity in its ontogeny, as indicated by the form and structure of its mature leaves which may be either of the terrestrial or aquatic type or of an intergraded structure. Any of these stages may be induced by seasonal changes or by variations in components of the environic complex as well as by a number of agencies to the action of which the plant is not ordinarily subject. Development may be induced in which the series of leaves formed on successive internodes will retrogress from the mature terrestrial or aquatic form to the nepionic or juvenile type.

Nearly all of the alterations noted in the series of foliar organs were of a kind which yielded structures suitable for functionation and existence under the conditions which induced their formation. To this there is the exception of flattened leaf-divisions which are sometimes formed on aquatic leaves. The retrogressive series in which successive leaves were caused to vary from a mature aquatic or terrestrial type toward the juvenile or nepionic form is an example of an entirely different reaction. Here the influence of the transplantation or some external agency induces rejuvenation or the condition of the plasma characteristic of the earlier stages of ontogeny. One may imagine a bud with leaf-primordia in all stages of development toward the mature divided type either of the aquatic or terrestrial form. The rejuvenated protoplasm now may be taken to be in a condition in which the differentiation necessary to the development of the adult form is made impossible and consequently simple growth without such further differentiation ensues with the result that each leaf comes to its full size with an arrested development the youngest of the series having all of the characters of the nepionic type. A fair parallel is offered by the behavior of etiolated organs in which growth without differentiation is very marked.

Summary.

The experiments through wich this plant have been carried include cultures as terrestrials and aquatics in a temperate house of the New York Botanical Garden, cultures in the soil in the open in the same place, cultures in a tropical climate at Cinchona in Jamaica (7,345 ft.) in the soil in the open, in the montane plantation of the Desert Laboratory in the Santa Catalina mountains in Arizona at 8,000 ft., in the glass house of the Desert Laboratory 2,700 ft. in a sub-tropical climate with extreme temperatures, and in the garden of the Coastal Laboratory at Carmel, California, in a foggy cool, equable oceanic climate. Full development with the formation of flowers of this aquatic was secured at the last named place only. The plant however is seen to endure an extremely wide range of conditions, in which the diversity of its leaf structure may be a factor of importance.

The cultivation of Neobeckia as a terrestrial was accompanied by the development of thickened roots, in which an exaggerated formation of cortical and fibrovascular tissues ensued. Large amounts of starch accumulated in these members, the entire reaction being one which probably does not occur in nature.

Variations in the form of nepionic leaves have been seen to be coupled with the composition of the medium or substratum, the availability of a supply of food to buds and with competitions. No connection was established between the form of such organs and the stage of the material taken for rejuvenescence, although it is to be said that in most of the experiences such effects would have been masked by other effects. While it is true that most of the diverse structures exhibited by the leaves of Neobeckia show some degree of suitability to the conditions under which they are formed, yet this is by no means always the case as instanced by the occurrence of terrestrial types in submerged plants. This of course is still more noticeable in the various regenerative proceedings in which the form and structure of the leaves are determined by the presence or abundance of certain formative materials. The form and structure of roots, and foliar organs of Neobeckia are seen to be determined by environic conditions to a much greater extent than in Proserpinaca, Sium, or probably any other so-called "polymorphic" species, yet the reaction to such external agencies is not a direct or physical adjustment.