# POLARITY

Growth in one region or dimension is related to growth in the others and the plant thus becomes an integrated individual. A notable feature of these bodily forms of plants ( and animals ) is the presence in them of an axis which establishes a longitudinal dimension for organ or organism.

Along this axis, and symmetrically with reference to it, the lateral structures develop. The two ends or poles of the axis are usually different both as to structure and physiological activity. Thus a typical vascular plant has a major axis with the root at one end and the shoot at the other and with lateral appendages—leaves, branches, or lateral roots disposed symmetrically around it.

# This characteristic orientation of organisms, which is typically bipolar and axiate, is termed Polarity.

The structures at the two ends of an axis are unlike, as in the case of root and shoot, "stem end“ and "blossom end" of fruits, and petiole and blade of leaves. In regeneration, the organs formed at one end are usually different from those formed at the other. Cells and tissues may show polar behavior in grafting experiments. The transportation of certain substances may take place in one direction along the axis but not in the other, thus manifesting polarity in physiological activity. Both in structure and in function there are gradients of all sorts. Individual cells show polar behavior in plane of division and in the different character of their two daughter cells.

Polarity is simply the specific orientation of activity in space.

It refers to the fact that a given biological event, such as the transfer of material through an organ or the plane in which a cell divides, is not a random process but tends to be oriented in a given direction. If this were not so, an organism would grow into a spherical mass of cells, like tissue in a shaken culture. This differential directiveness is responsible for organic form. What is the cause of it?

# POLARITY AS EXPRESSED IN EXTERNAL STRUCTURE

The most conspicuous expression of polarity is in external morphology.

In higher plants the differences between root end and shoot end are determined very early, perhaps at the first division of the fertilized egg. This differentiation is not irreversible, however, for roots often appear on stems under favorable conditions and, less commonly, buds and shoots appear on roots. Polar behavior occurs in thallophytes and bryophytes, even in some very simple forms like those of many filamentous algae, though in such cases it is less sharply marked and more easily reversed than in vascular plants. Organisms without morphological polarity are rare. A few amoeboid forms have no axes in the vegetative stage but form polarized fruiting bodies. Algae like Pleurococcus are spherical and apparentlv apolar but may be induced to produce filaments, an expression of axiation. Forms like Spirogyra, desmids, and diatoms have an axis of symmetry but its two poles seem to be alike. In most filamentous types, however, a rhizoidal pole and a thallus pole can be distinguished. Experimentally, polarity can best be demonstrated through its expression

# Vochting ( 1878)

cut twigs of willow and kept them under moist conditions. Some he left in their normal, upright orientation and others were inverted. Regardless of orientation, however, roots tended to be regenerated more vigorously from the morphologically basal end and shoots from buds at the original apical end. This is the classical example of Polarity .such a shoot were cut into two or more parts transversely, each part regenerated roots and shoots in the same polar fashion. Even very short pieces of stem showed this polar character. Vochting removed a ring of bark in the middle of a shoot and confirmed earlier observations that roots were formed above the ring and shoots below, just as if the stem had been cut in two. From these and similar experiments he concluded that polarity was a fixed and irreversible characteristic of the plant axis and that probably the individual cells of which the axis was formed themselves possessed a polar character. Experiments like these have been carried out on many plants.

Klebs (1903), for example, found that roots would grow at the apical end of an inverted shoot, that water stimulated root formation at any point on the twig, and that removal of the bark could reverse polarity. He believed that environmental conditions rather than innate polarity determined the place where buds and roots develop on a stem.

Polar regeneration is also evident in the lower groups of the plant kingdom. If fern prothallia are sliced transversely, regeneration from their cut surfaces is polar (Albaum, 1938) and is related to physiological gradients, especially of osmotic concentration (Gratzy-Wardengg, 1929 ) . In isolated primary leaves of ferns, polarity is evident, but both the character and the polar distribution of regenerated structures are somewhat diverse (Beyerle, 1932).

In the regeneration of hepatics and mosses, polar behavior varies. The gemmae of Marchantia and Lunularia form rhizoids from either surface while they are young but only from one when they grow older ( Haberlandt, 1914), indicating that embryonic tissue, as it proves to be in many other cases, is relatively unpolarized. Polarity here can be reversed by gravity, light, and other environmental factors ( Fitting, 1938 ) . Vochting found relatively little polarity in the regeneration of the thallus of Marchantia. In the mosses, cuttings formed rhizoids at the lower end and protonemata at the upper one. This behavior could be reversed by inversion of the cuttings ( Westerdijk, 1907), but regenerating structures were always more vigorous at the morphologically basal pole.

Polarity is evident in the sporophores of the higher fungi but here, also, it is not firmly fixed, for a segment of the pileus may be successfully grafted back to the same pileus in an inverted position ( Lohwag, 1939 ).

In most algae there is a sharp distinction between the rhizoidal, or hold-fast, pole and the thallus, or shoot, pole. Especially in the simple forms and in early stages of the more complex ones, this polarity may be reversed by changed relations to gravity, light, or other factors (Wulff, 1910; Zimmermann, 1923).

Manifestations of polar behavior in higher plants are much more uniform and fixed, presumably because of the higher level of organization and differentiation among them. It must have its origin verv early in embryonic development. Vochting's conclusion, however, that every cell is polarized has been challenged by those who point out that many cells theoretically may become completely embryonic again and ultimately produce an entire plant and thus can have no fixed polar character.

Pfeffer and Klebs have emphasized the probability that the cells of the terminal growing points have no original polarity of their own, any more than does an egg cell. In older parts a more stable polarization results from the influence of conditions in the environment

Polarity may be manifest in the transverse axis as well as in the longitudinal one. This is evident structurally in the transversely polar gradient often associated with regeneration. Thus Goebel (1908) found that in half slices of the root of Dioscorea sinuata shoots grew out from the central part of the axis and roots from the margin directly opposite to this. Transverse polarity is also manifest in the flow of auxin in various tropisms .The subject has been discussed in detail by Borgstrom

( 1939 )

# Polarity in stem cuttings

In stem cuttings, polar regeneration of shoots and roots is clearly obvious in most higher plants, but there are considerable differences between species. Polar behavior may be obscured in variousways, as by the tendency of monocotyledons to form roots at nodes and by the influence in many cases of the age of the cutting upon the formation of root primordia. The specific polar reactivity of tissues from which buds and roots originate must be taken into account, as well as the factthat a different complex of conditions may control each of the successive processes in the development of these structures, such as the formation of primordia, their growth, their final differentiation into roots and shoots, or the formation of callus which may give rise to either roots or shoots.

Various modifications of polar behavior in regeneration from stem cuttings have been reported. Roots, for example, tend more characteristically

to be limited to one pole in their growth than do shoots.Doposcheg-Uhlar (1911) observed this in Begonia, and Massart (1917)studied 30 species of plants, some of which showed strongly polar regeneration of both roots and shoots, some weakly polar regeneration, some only root polarity, and some only shoot polarity. Root polarity was related to the growth habit of the plant, for species with pendant branches

rooted readily at their apical ends.

# ROOT CUTTINGS

Cuttings of roots behave in polar fashion. Dandelion,chicory, and sea kale have been studied most frequently in this regard.Shoots are commonly regenerated at the basal or proximal pole (the endnext the shoot) and roots from the apical (distal) pole. This polarity is maintained even when the root cutting is grown in an inverted position. Wiesner (1892) made the observation, often confirmed since, that, in relatively short pieces of root, shoots regenerate at bothends. This was also seen by Neilson-Jones (1925) and, in stem cuttings,by Fischnich (1939). If the growing roots were continually trimmed off from the apical end, shoots finally appeared there. Czaja ( 1935) producedroots at both ends by trimming off tissue from the basal end. Centrifugationtoward the shoot pole results in bud formation at the root pole, asdoes enclosing the base in sealing wax (Goebel, 1908). These resultsare now interpreted as due to the effect of auxin , which tends to move toward the root apex. A high concentration of it tends to produceroots and a low one, shoots. This has been shown clearly by Warmkeand Warmke (1950). Callus develops more vigorously at the proximalpole. As early as 1847 Trecul reported that, in root cuttings of Maclura,buds and roots showed polar distribution and were formed endogenously but that in Ailanthus, where the buds arose in the cortex, polarity wasmuch less evident. This agrees with Plett's findings in stem cuttings and emphasizes the more intense polar behavior of the inner tissues.

## LEAF CUTTINGS

There has been much discussion as to whether, in the higher plants, polarity once established can be reversed. Reversal seems to be easier to accomplish in seedlings than in older plants. Reversal of polarity is much easier to accomplish in the lower plants

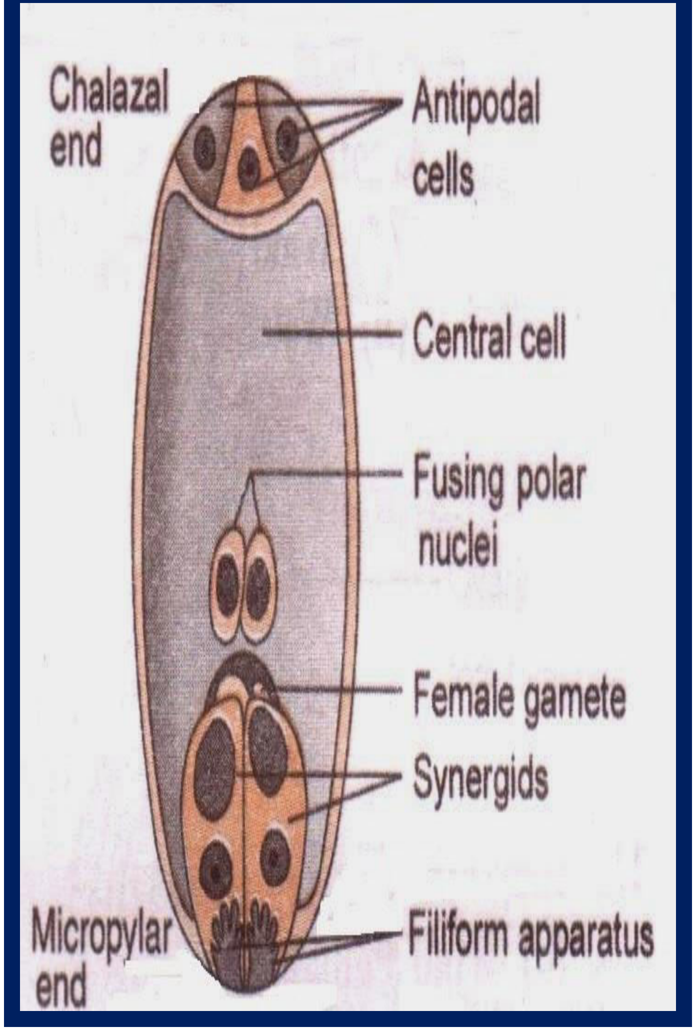
Leaves when treated as cuttings behave quite differently from stems and roots and show a somewhat different type of polar behavior, evidently related to the fact that they are organs of determinate growth. In most cases, regeneration of both roots and shoots occurs at the leaf base near the cut end of the petiole. Hagemann ( 1931 ) performed inversion experiments on various species. In certain cases he found that wound stimulus or water affects regeneration. In Achimenes, shoots were thus obtained from the apical cut surface and roots from the base under certain conditions, but Hagemann concluded that, in general, polarity as expressed in the location of regenerating structures in leaves is determined by anatomical structure. Behre (1929) reports that regeneration in the leaves of Drosera is apolar.

# INTERNAL STRUCTURES

## Embryonic Development In vascular plants

The first manifestation of polar behavior is in the division of the fertilized egg. This in most cases seems to be related to the polar character of the gametophyte.

In ferns the planes of division in the young embryo are related to the axis of the prothallium and that the segment that will form the first leaf is always directed toward the growing point (notch), a fact also evident later in the orientation of the young leaf itself. This relationship persists regardless of the direction of the incident light. In Isoetes, the first division of the fertilized egg is at right angles to the axis of the archegonium, and early embryo development is not affected by external factors (La Motte, 1937;)



In seed plants the embryo has a definite orientation in the ovule, thetip of the young radicle always being directed toward the micropyle and the plumular end toward the chalaza. This has its origin in the polar relation between embryo sac and ovule, since the archegonium, or egg

apparatus, lies at the micropylar end of the sac. Even the group of four megaspores is polarized, and it is the one at the micropylar end that germinates into the female gametophyte. The planes of division of the proembryo are related to the axis of the ovule. In the young embryo as it develops at the end of the suspensors, the distinction between root and shoot begins very early, with the first transverse divisions. The direction of the polar axis is evidently impressed upon the embryo, as upon the egg, by the axial organization of the embryo sac and ovule, and once established this polar behavior persists and is apparently irreversible. The first manifestation of differentiation in any embryo,

whatever its origin, is the appearance of a polar axis.

A number of cases have been reported (Swamy, 1946) in which the polar character of the angiosperm embryo sac is reversed,

# Tissue Reorganization.

Various histological changes occur in cuttings grown in an inverted position, as described by Vochting ( 1918 ) and others. Such plants are evidently abnormal in a number of respects. There is often a tendency in them to form swellings and tumors, particularly near the insertion of branches, which now tend to grow upward. The cause of these swellings may lie in the fact that the original tissues cannot function properly under the changed orientation and that considerable cellular rearrangement must be brought about in the new tissue formed after inversion. Vochting here has described the structure of such tumors in Salix fragilis and other species and believes them to be due to the innate polar tendency of individual cells.

There has been considerable controversy as to this hypothesis. Neeff (1922) made an extensive series of studies of the changing orientation of cambial cells in decapitated stems, finding that these tend to turn until they become parallel to the newly regenerating axis instead of to the old one and he explains this in terms of the inherent polar behavior of the cells, which tends to conform to that of the functional axis. Both Jaccard (1910) and Kiister, on the other hand, disagree with Vochting's explanation and attribute the changing orientation of the cells mainly to mechanical factors. Twisting whorls may also appear in normal callus where mechanical factors can hardly be operative. More intensive studies are needed of the conditions that cause change in direction of cell growth. It is clear that in some way histological changes are related to the new conditions under which an inverted cutting has to grow.

Vochting ( 1918 ) used the swollen stem of kohlrabi for a series of such experiments. If the top of a stem is sliced off transversely and a V-shaped cut made in its upper surface and if the lower portion of another stem is sharpened to fit this cut and inserted firmly into it, the tissues of the two stems will knit together. If, however, a piece is sliced off from the lower part of a kohlrabi stem and it is then inverted, and the surface now uppermost cut as before, and if a sharpened upper piece is inserted into this cut, the tissues will not knit. Furthermore, rootlets will begin to grow out from the upper piece into the lower one, as ifgrowing in a foreign substratum. Thus a root pole will fuse with a shoot pole but two similar poles, when brought together, will not fuse. These facts can be explained by assuming that the tissues of the plant, even such relatively undifferentiated parenchymatous ones, have definitely polar behavior

Bloch (1952), however, observed that tissues of the fruits of Lagenaria do not behave in this way but that plugs, cut out and replaced, will knit in any orientation. Microscopic examination after a few days showed normal cellular fusion. In horticultural practice it has long been recognized that buds must be placed in normal orientation on the stock if they are to knit well.

Colquhoun ( 1929 ) removed buds and pieces of bark in Casuarina and reapplied them in an inverted position. Observation of the anatomical structure showed that the cells of the cambium joined freely and continued to grow regardless of orientation. Wood fibers and vessels, however, show the characteristic turns and twists reported by Vochting.

This suggests that the cambial cells are unpolarized or in a condition of unstable polarity and that, as wood elements differentiate, polarity is gradually impressed upon them.

# Cell polarity

Vochting's contention that polar behavior of a tissue is the result of the polarity of its individual cells.The fact that very small tissue pieces retain their original polarity and that inversely grafted tissues donot fuse supports Vochting.

Many other facts can also be cited. The two daughter cells following a division are oftenunlike. In these cases, each of the two types is found invariably on the same side, toward or away from the tip of the axis. Thus in many young roots the last division of the surface cells is unequal, the smaller daughter cell becoming a trichoblast and producing a root hair. This cell is always on the side toward the tip of the root. In the leaf epidermis of monocotyledons some cells divide unequally, and the one toward the leaf tip becomes a stomatal mothercell. These facts suggest that the cells themselves have a polar orientation. Whether polarity is a quality of the whole developing organ or simply of its component cells is still uncertain and is a problem involving the deeper one of the relation between cell and organism.

Even when the cell does not divide,the difference between its two ends is often evident. That the cytoplasm is the seat of this polar difference is shown by the fact that, when vacuolate cells divide, the first indication of the plane of division, and thus of the polar axis, is the appearance of a cytoplasmic diaphragm in the position where the future partition wall will be formed . In such cells the direction of the axis may be related to gradients in hormone concentration, oxygen, or other factors. This polar difference may be visible in the contents of the cell, for in Enteromorpha ( Muller-Stoll, 1952), in Isoetes (Stewart, 1948), and other plants the chromatophore is almost always on the side of the cell away from the base of the thallus, or plant body.

# Cellwall polarity

The wall itself may show polar behavior, a fact which is of particular importance in producing differences in cell shape. Most cells are nearly isodiametric at the beginning, and if one at maturity is much longer than wide, this is the result of more rapid growth in length. Such differential growth, in turn, presumably comes from differences in the fine structure of the wall, which itself is ultimately dependent on factors in the cytoplasm. Wilson (1955) has shown that in the wall of the large cells of the alga Valonia there are two systems of orientation of cellulose fibrils which converge to two poles at the ends of the cell. The complex and remarkable shapes of many cells, both in simple organisms and within the tissues of larger ones, are probably due to a complex patternof wall polarities that determine growth in a number of directions.

# Miehe(1905) cell polarity

He plasmolysed the cells of Cladophora enough to pull them away from the walls and break whatever connections there may have been with other cells, but without killing them. The plant was then deplasmolyzed. Each cell, now as effectively isolated as though it had actually been removed, began to enlarge, broke out of its wall, and proceeded to regenerate a new filament. The significant fact is that from the basal end of each cell a new rhizoid was formed and from the apical end, a new thallus. The polar character of the cells, otherwise impossible to demonstrate, could thus be established. To prove the existence of polar behavior in the cells of one of the higher plants is more difficult.

# Polarity in isolated cells

The unfertilized egg is naked, and its nucleus is at the center of the cell. It shows at the beginning no polarity whatever nor is there any visible differentiation in its cytoplasm. After fertilization, the egg falls to the bottom and in about 12 to 24 hours, under normal conditions, a protuberance appears on its lower surface. This develops into a rhizoid by which the young plant becomes anchored to the bottom. Soon the egg divides in a plane at right angles to the axis of the protuberance. The two cells that result are very different in shape and in their future development. The upper, rounded cell gives rise to the main portion of the thallus. The lower one forms little besides the rhizoid. The growth of the rhizoid and the first division of the egg establish a permanent polar axis in a system which at first is quite without one. Here is evidently one of the simplest expressions of polarity among plants. Gravity seems not to be an important factor in the induction of thepolar axis for, if the eggs are kept in the dark, the rhizoid develops inany direction. Light is clearly a very importantfactor in Fucus (Hurd, 1920). In eggs lighted from one side by whitelight of a certain intensity (or light of particular wave lengths), therhizoid always forms on the side opposite the source of light, and thefirst wall is laid down at right angles to this direction

Whitaker ( 1937 ) subjected Fucus eggs to centrifugal force and showed that in such cases the rhizoid grows from the centrifugal pole. Polarity here seems to be dependent on the rearrangement of materials in the egg.

Other factors, such as pH, temperature, auxin, and even the shape

Nienburg ( 1922b) showed more specifically that it is not the direction of light but the intensity gradient that is the determining factor.Lund ( 1923 ) was able to prove that the first division wall in the Fucus egg was at right angles to the flow of an electric current and that the rhizoid grew toward the positive pole

In the germination of a moss spore, the young protonema pushes out on the side of the spore toward the light, and the rhizoid forms at the opposite end, indicating that here, as in the Fucus egg, its polarity is determined by light.

How the polar axis is determined in the spores of vascular plants has been demonstrated in a few cases. In Equisetunm the spore of which

shows no external or internal polarity, germination is followed by division

into two cells. The division wall, as in Fucus, is laid down at right angles to the gradient of light absorption (Stahl, 1885). The more strongly

illuminated daughter cell becomes the primary prothallial cell and the one on the darker side, the rhizoidal cell. Polarity is also to be found in the microspores and pollen grains of

higher plants, though here it is not easily open to experimental analysis.

# POLARITY IN PLASMODIA AND COENOCYTES

In larger and multinucleate protoplasmic units, notably coenocytic forms, polarity finds a somewhat different expression than in uninucleate protoplasts. Thus in the plasmodium of Plasmodiophora brassicae, as reported by Terby (1933), the axes of the many nuclear division figures lie parallel to one another, indicating that the whole mass of protoplasm has a uniform anisotropic orientation, though here without a polar axis.

True coenocytes show some remarkable examples of organized systems where there is pronounced differentiation of parts but no cellular partitions in the cytoplasmic body. Conspicuous among these are the algae Bryopsis and Caulerpa.

# PHYSIOLOGICAL MANIFESTATIONS OF POLARITY

Differences in the external or internal structure of the plant body are almost invariably accompanied by physiological differences, though the latter are usually more difficult to demonstrate. Among these are the unidirectional flow commonly shown by auxin and often by other substances; the differences in bioelectric potential which can be demonstrated between different parts of the plant; and the many examples of physiological gradients in the plant body—in pH, rate of respiration, osmotic concentration, auxin concentration, and others. These are doubtless related to visible morphological polarities but the character of the relationship is obscure. Whether such physiological polarities control the morphological ones or whether both are determined by more deeply seated morphogenetic factors in the living material, which are physiological only in the broadest sense, is not known. Physiological gradients of various kinds, particularly metabolic ones, and their significance have been extensively discussed by Child ( 1941 ). Such gradients are along the major axes of the organism, and indeed their existence is thought by some to establish these axes and to be a major factor in the origin of polarity. Child believed that they arise early in development as the result of some unilateral difference in the environment and that, once established, they persist. He points out that they often can be obliterated or redirected by external differentials and infers that they are of great importance in determining patterns of development.

Gradients in respiratory activity such as have so often been described in animal axes are found in plants ( Wanner, 1944 ) . Ball and Boell ( 1944 ) , however, have shown that in some plants the rate of respiration at the meristematic tip is less rapid than in the zone immediatelv behind this.Hurd-Karrer (1926) found that in corn stalks the minimal concentration of solutes is in the basal internodes and increases upward, a

gradient reported by others for leaves at different levels in a tree. In plant exudates there is a concentration gradient with the highest values near the apex (Tingley, 1944). The proportion of ash to dry weight in herbaceous plants was shown by Edgecombe ( 1939 ) to increase toward the tip of the plant. Many other examples might be cited

**Hicks (1928) found that nitrogen tends to move toward the morphological tip of a stem and**

**carbohydrates toward the base, even in inverted shoots, so that a gradient**

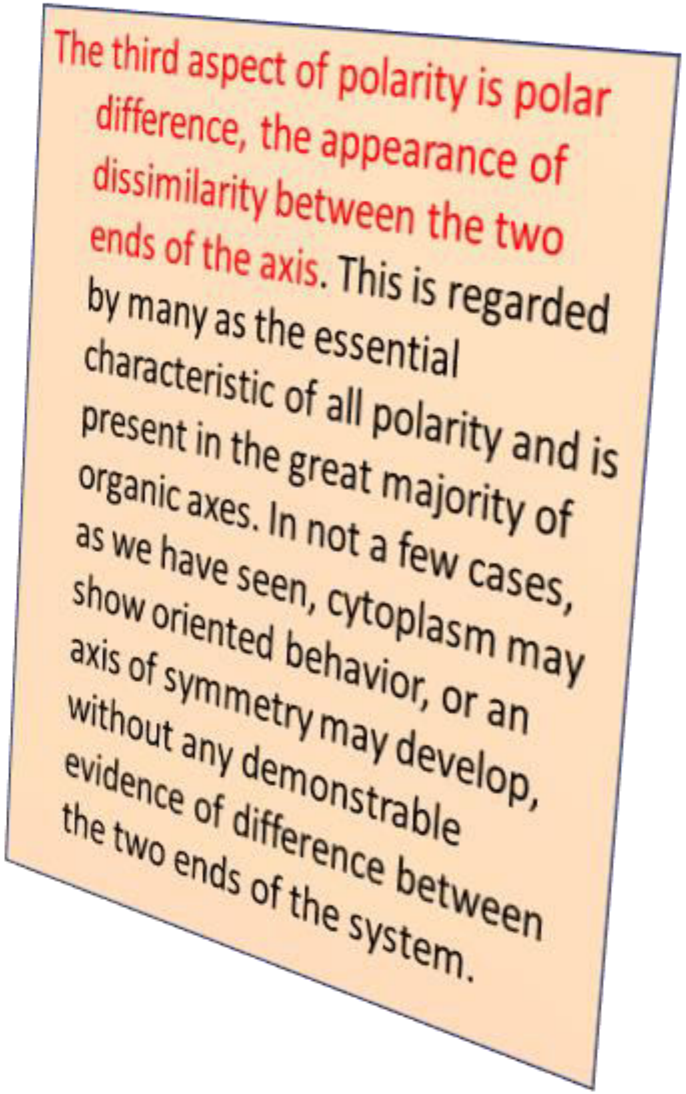
**in C/N ratio results in the stem. She believes that this may be responsible for the phenomena of polarity, but this may be a parallelism rather than a causal relation.**

# Three Aspects of Polarity.

1.the **oriented behavior** of living substance, as distinct from axiation or bipolarity. This is evident in the differential growth of cells and tissues, where one dimension increases more rapidly than the others; in the controlled plane of cell division, in which the cytoplasm, as evident especially in vacuolate cells, sets up a pattern oriented in a definite direction; and in coenocytes and plasmodia where growth, movement, or direction of nuclear spindles is similarly oriented. It is reasonable to suggest that some sort of cytoplasmic anisotropy is concerned in this oriented behavior.

# Three Aspects of Polarity.

A second aspect or element of polarity is axiation. The oriented behavior of living material most commonly, though not invariably, is expressed in cellular systems which develop symmetrically in relation to an axis or plane of symmetry parallel to the direction of orientation. Most cells and most multicellular structures possess an axis. Such structures as the cells and filaments of unattached filamentous algae may show no evident difference between the two ends of the axis, either in cell or filament, but they are clearly axiate. The problem of the symmetrical growth of a living system about this axis, so characteristic of almost all organic development, is an essential part of the general problem of pattern. Experimental attack upon this phenomenon of symmetry is promising, for its character can often be changed by modifying the environment.



The third aspect of polarity is polar difference, the appearance of dissimilarity between the two ends of the axis. This is regarded by many as the essential characteristic of all polarity and is present in the great majority of organic axes. In not a few cases, as we have seen, cytoplasm may show oriented behavior, or an axis of symmetry may develop, without any demonstrable evidence of difference between the two ends of the system.

The relation between these three aspects of polarity involves the problem of the origin of polarity itself. If they can be shown to form a progressive series, in phylogeny or ontogeny, this would indicate that polarity may increase in complexity. Whatever its origin, the direction of this bipolar axis is often continually changing but under definite control, and upon this fact depends the orderly development of organic patterns. How such a system of changing polarities is controlled so that growth in one direction is precisely related to that in another is a part of the same problem of orderly development. The ease with which polarity may be reversed in the simplest plants suggests that even in more complex ones it is not irrevocably fixed by genetic factors. Like any trait with a genetic basis, polarity is not a specific characteristic but a specific reaction to a specific environment. The environmental factor may be external, such as the direction of light, orinternal, like the correlation between the axis of the young embryo and that of the archegonium, but unless there is an environment to which the organism can orient itself, the phenomena of polarity will rarely appear. Sometimes this environmental reaction is determined early and is later irreversible, as in cases where polarity becomes firmly fixed in the fertilized egg. In other instances polar behavior is subject to induction through environmental factors at all stages.