Chemical influences of other plants (allelopathy)*.

By

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With 11 figures.

I. Introduction.

The plant in innumerable chemical ways controls its own development from germination to flowering and the ripening of fruits and seeds. These chemical controls are "self" controls as certain substances, like growth hormones, germination inhibitors *etc.*, produced by the plant body itself, regulate the physiological functions of this self-same body.

Concentrating most of the research efforts on this problem the fact has often been overlooked that the plant is at the same time a chemical powerhouse, producing and secreting chemical substances with which it actively changes its abiotic and biotic environment.

Through these secretions the plant is able to influence other plants growing in its surrounding and exerts to some extent a chemical control of its environment. In some cases, as in those of many parasites, the chemical relationship between plant and plant forms a *conditio sine qua non* for the fulfillment of the normal life cycle of the plant concerned.

The detection of the antibiotics has deepened the interest of the botanist in the problem of the chemical influence of plant upon plant. But its great importance for the understanding of basic facts in plant sociology and plant ecology is still not yet fully recognized, although our knowledge about the subject is quite old.

Already KUESTER (1909) published a paper on the „Chemische Beeinflussung der Organismen durcheinander".

In 1937 MOLISCH wrote his fascinating booklet on the same subject and in accorfdance with his terminology we will define allelopathy as the *influence of one plant upon another occurring under natural conditions and exerted by chemical means other than nutritional ones.*

Lately GRÜMMER (1955) published another book on allelopathy where the main results of modern research are summed up.

In basing our discussion on this definition of allelopathy we immediately encounter some difficulties. Our definition of allelopathy excludes nutritional relations between different organisms. But in certain cases of stimulation *f.i.* it is very difficult to discern between a nutritional effect and one produced by stimulating substances.

Allelopathy exerted through secretion of hormones and enzymes should be included in our chapter. We will only touch upon this type of allelopathy as other chapters of this encyclopaedia will deal with the same question.

* B. RADEMACHER's contribution „Gegenseitige Beeinflussung höherer Pflanzen" in Vol. XI, p. 655 of this encyclopaedia deals also with allelopathy and compliments our chapter in many points. He for instance deals with the nutritional relations between different organisms which we exclude per definitionem from our own contribution.

G. Melchers (ed.), *Aussenfaktoren in Wachstum und Entwicklung*

As we decided that one of the criteria of allelopathy is its occurrence under natural conditions a laboratory experiment alone cannot prove allelopathy. Besides the difficulty to determine what are "natural conditions" we here encounter another problem. Very often potentially allelopathic substances such as antibiotics are present in a certain organism. A laboratory experiment proves their antibiotic effect on certain microorganisms. But there is no proof that under natural conditions the antibiotic is of any biological importance. But as such a proof is very difficult to give the substance in question may still have an allelopathic function. We made it a rule to exclude cases of potential allelopathy when at least no *indication* of allelopathy under natural conditions exists.

Another difficulty lies in the complexity of "natural conditions". When dealing *f.i.* with the rhizosphere effect or the mycorrhiza it is often impossible to unravel the complex conditions without the most elaborate experiments (seldom done) and to come to a clear conclusion.

We naturally included here allelopathy between host and parasite and between microorganisms. In these chapters the material is not exhaustively dealt with and mostly only examples are given as otherwise we would have transgressed to much the scope of this encyclopedia.

We dealt extensively with ethylene as an allelopathic agent because this is the only case of allelopathy which was thoroughly investigated.

The chapter by CARR on the "Chemical influence of the environment" which follows (pp. 737—794) constitutes in many ways a complement to this chapter on allelopathy.

II. Allelopathy between higher plants.

A. Volatile secretions.

a) Ethylene.

1. Occurrence and identification.

ELMER (1932) enclosed apples and potato tubers in the same container and found that under the influence of the apples the sprouting of the tubers was delayed and the sprouts formed were abnormal.

HUELIN, (1933) SMITH and GANE (1933) and KIDD and WEST (1934) obtained the same effect in using ethylene and suggested that the gas emanating from the apples in ELMER's experiment was ethylene. GANE (1934) isolated ethylene from apples and was the first to prove by chemical identification that plants secrete ethylene and that it is physiologically active when it comes in contact with other plants. Later ethylene was isolated from ripening bananas by NIEDERL, BRENNER and KELLEY (1938), from avocados by PRATT, YOUNG and BIALE (1948), from ripening tomato fruits by SPENCER (1956, 1958) and from leaves of *Silybum marianum* by PRATT (1954). Table 1 gives the amounts of ethylene liberated by different plants and plant organs.

GANE (1934) estimates that one apple during its whole life-time produces about 1 ml of ethylene.

In addition to the fruits mentioned BIALE, YOUNG and OLMSTEAD (1954) have proved by chemical identification the emanation of ethylene by the following fruits: *Annona cherimola, Feijoa sellowiana,* and *Casimiroa edulis* (Sapote). Mango, Lemon and Oranges do not produce ethylene.

The production of ethylene by citrus fruits reported by other authors (see *f.i.* MILLER 1946) was apparently based on the fact that the fungus *Penicillium digitatum,* which infects citrus fruits, produces ethylene (BIALE 1940, MILLER, WINSTON and FISHER 1940, BIALE and SHEPHERD 1941, YOUNG, PRATT and

Table 1. *Comparative ethylene production by several plant organs.* (After BIALE 1950 and others.)

Plants	Ethylene produced ml/kg/24 hrs.	Author
Apple var. Worcester / Apple var. Pearmain	0.12	GANE (1934)
Apple var. Gravenstein	0.10—0.28	HANSEN and CHRISTIANSEN (1939)
Apple var. Canada gris	2	PHAN-CHON-TON (1956)
Apple var. Reine des Reinettes	11	PHAN-CHON-TON (1956)
Avocado var. Fuerte	0.23	PRATT, YOUNG and BIALE (1948)
Banana	0.0005	NIEDERL, BRENNER and KELLEY (1938)
Pear var. Anjou	0.072—0.72	HANSEN and CHRISTENSEN (1939)
Pear var. Bartlett	1.32 —5.33	HANSEN and CHRISTENSEN (1939)
Pear var. Williams	0.7—1.8	PHAN-CHON-TON (1956)
Silybum leaves	0.46—0.8	PRATT (1954)
Cotton plants	1.96	HALL *et al.* (1957)
Cotton leaves	0.13	HALL *et al.* (1957)
Flowers (Iris, Dahlia)	1—4	PHAN-CHON-TON (1956)
Tomato	0.01—0.19	SPENCER (1956)

BIALE 1951, PHAN-CHON-TON 1957a). Some other fungi, pathogenic to humans like *Blastomyces dermatitidis* also produce ethylene (NICKERSON 1948). The pathogen *Fusarium* the cause of fusarium wilt in tomatoes produces ethylene in culture and in the diseased host (DIMOND and WAGGONER 1953a). HALL'S (1952a) report that oranges produce ethylene is apparently based on a faulty method. HALL *et al.* (1957) have shown with an improved method that cotton plants and cotton leaves produce ethylene in considerable quantities. Flowers also emanate ethylene (PHAN-CHON-TON 1956).

These are all the cases in which the production of ethylene by plant organs was proven chemically. In many other cases the emanation of volatile substances, identical with near certainty with ethylene, was tested by various biological tests, like leaf epinasty and the triple response of etiolated pea seedlings *etc.*

Leaves, petals, anthers, pistils, mature and immature fruits, tubers, twigs, roots *etc.* were shown to produce ethylene. (For details see DENNY 1935, DENNY and MILLER 1935, MOLISCH 1937 and GRÜMMER 1955.) It is even possible that soil microorganisms produce ethylene which has an allelopathic influence on higher plants growing in that soil (HALL *et al.* 1957).

2. Physiological effects.

α) *Maturation of fruits.*

Already at the beginning of the century California Citrus growers used to "cure" the fruits forcably by placing them in a tent together with burning Kerosene stoves. This treatment stimulates the colouring of the fruit. SIEVERS and TRUE (1912) proved that not the heat but the gaseous combustion products of the Kerosene were responsible for the curing effect. CHACE and DENNY (1924) and DENNY (1924a) suggested that ethylene was the active agent.

The "United Fruit Company" in shipping bananas to the United States noticed over a period of years prior to 1917 that the ripening of the bananas occurred in "pockets" which acted as a focus of ripening for the surrounding fruit. RIDLEY (1923) found that ripe bananas produce a gas which caused the accelerating of the ripening of green bananas. This gas was ethylene which proved effective in stimulating the ripening of many plant products, as shown early by DENNY (1924a, lemons), HARVEY (1925, celery), CHACE and CHURCH (1927), REGEIMBAL and HARVEY (1927, pineapples), REGEIMBAL, VACHA and

HARVEY (1927, bananas), DUFRENOY (1929, tropical fruits), HIBBARD (1930, celery, tomatoes), RAMSAY and MUSSO (1930, oranges), KOHMANN (1931, tomatoes), WOLFE (1931, bananas), DAVIS and CHURCH (1931, persimmon), to cite only a few. The effectiveness of ethylene in fruit maturation is best illustrated by the fact that one lemon infected with the ethylene producing *Penicillium digitatum* affected the maturation of 500 non infected lemons (BIALE and SHEPHERD 1941).

β) Epinasty of leaves.

Many leafy plants when exposed to smoke (MOLISCH 1911, KNIGHT and CROCKER 1913), to "laboratory air" or air containing traces of illuminating gas react with an epinastic movement of their leaves (HARVEY 1913, DOUBT 1917, ZIMMERMAN, CROCKER and HITCHCOCK 1930). The epinasty is caused by the ethylene contained in "laboratory air", smoke and illuminating gas. BOTJES (1933) when enclosing an apple emanating ethylene with a tomato in a bell jar obtained the same effect. The same epinastic response was produced by pure ethylene and the emanation of a great variety of plant organs (DENNY and MILLER 1935, DENNY 1935, 1937/38, MOLISCH 1937). DENNY (1938/39) after a great number of tests concludes that the effective epinasty inducing volatile product from various plant organs is ethylene. The amounts of ethylene needed to produce a minimum epinastic response are very small. According to CROCKER, HITCHCOCK and ZIMMERMAN (1935) 1:10,000,000 of ethylene in air already gives epinasty in tomato plants whereas 1:40,000,000 and 1:60,000,000 are enough for producing epinasty in potato and African marigold plants. Epinasty which is one of the symptoms of Fusarium wilt in tomatoes is caused by ethylene produced by the fungus inside its host (DIMOND and WAGGONER 1953). The epinastic curvatures are caused by the renewal of growth of petioles which had ceased to grow. As the upper side grows faster than the lower one epinastic bending occurs. When removed from ethylene to air a hyponastic movement brings the leaves back to their original position. The epinastic response is affected by gravity. Ethylene is most effective on upright plants. On plants rotated on a horizontal clinostat the effect is only about half of that of upright plants. There was no effect on inverted plants (CROCKER, ZIMMERMAN and HITCHCOCK 1932).

γ) Formation of intumescences.

Ethylene produces intumescences in many different plant tissues (ELMER 1932, WALLACE 1926, 1927, 1928, MOLISCH 1937). Those induced in lenticels are especially large. In the apple twig the intumescences arise from any cells between cambium and phellogen. The secondary thickenings of the cell walls and the middle lamellae are dissolved, the cells then enlarge to many times their original size and often start dividing (WALLACE 1928). There is an interesting relation between gravity and the location of the intumescences. When standing upright the intumescences are formed at the apical end of the apple twigs, when inverted at the morphologically basal end (WALLACE 1926). The amounts of ethylene producing intumescences are again very small (1 part of ethylene in 100,000,000 parts of air (WALLACE 1927) which equals 1 g. of ethylene per 658,000,000,000 g. of apple twigs (CROCKER, HITCHCOCK and ZIMMERMAN 1935).

δ) Abscission of leaves.

WALLACE (1926) was the first to point out that ethylene induces abscission in plants almost universally. It was known for a long time that illuminating gas and tobacco smoke, which contain as active ingredient ethylene, do the

same (see literature in MOLISCH 1937; Fig. 1). HALL (1957) reports serious damage to cotton crops by ethylene produced by a nearby polyethylene factory, which polluted the air over the plantations and caused early mass-abscission of leaves, floral buds and young bolls. LIVINGSTON (1950) and BROWN and ADDICOTT (1950) working with explants of the abscission layer of orange leaves and beans could show that even in the absence of the leaf blade ethylene increases the rate of abscission.

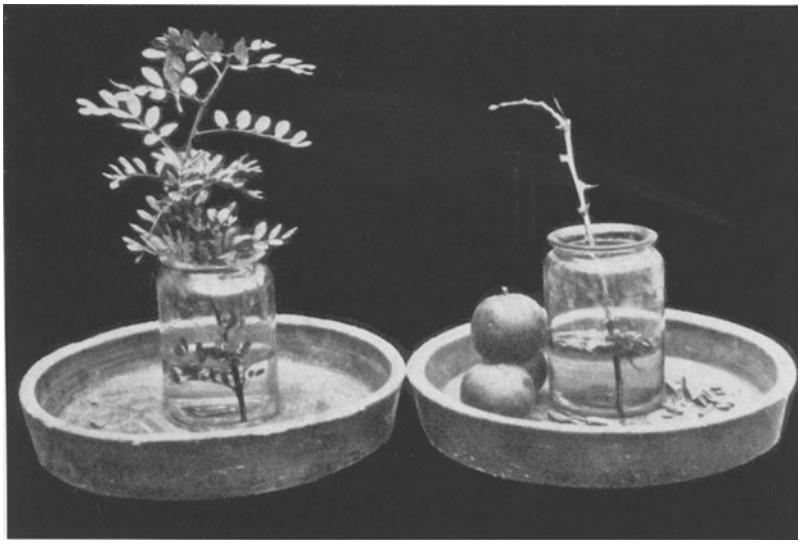

Fig. 1. Abscission of leaves on twigs of *Caragana arborescens* caused by ethylene emanation of apples. Left control. (After MOLISCH 1937.)

ε) "Triple response".

Etiolated epicotyls of the sweet pea treated with ethylene react with a "triple response" *i.e.* reduction or total inhibition of stem elongation, increasing growth in diameter brought about by the enlargement of pith and primary cortex cells (HOHENSTATTER 1942) and absence of normal geotropic response (KNIGHT, ROSE and CROCKER 1910, CROCKER, KNIGHT and ROSE 1913, KNIGHT and CROCKER 1913).

NELJUBOW (1901), SINGER (1903) and NELJUBOW (1911) had already observed that epicotyls of peas, lentils and potato sprouts when grown in laboratory air showed retarded stem elongation and enlargement of stem diameter. The tip assumed a horizontal position and continued to grow horizontally. Fig. 2 shows clearly the "triple response" caused by the emanation of apples. The same allelopathic "triple response" of the roots of *Vicia faba* and other plants was observed by MOLISCH (1937). The roots even lost their positive geotropic response. DOSTAL (1942) paid special attention to that part of the "triple response" which is characterized by the absence of the normal geotropic reaction. Pea seedlings treated with ethylene loose their negative geotropic response. The epicotyls carry out horizontal nutations which are analogous to the epinastic curvatures of the petioles treated with ethylene.

Inhibition of the elongation of shoots and roots of wheat seedlings was observed by MACK and LIVINGSTONE (1933) and by ROBERTS (1951), but the ethylene concentrations used in these experiments were unusually high (0.2—1%). A more detailed analysis of the effect of ethylene on growth was given by BORRISS (1943) who worked with etiolated hypocotyls of *Agrostemma*, the growth of which

is strongly inhibited by ethylene. This inhibition has two components, one exerts its influence directly on the elongating cells of the hypocotyl, the other brings about changes in the cotyledons which cause as a secondary result the inhibition of growth of the hypocotyl. This second component can be eliminated by cutting off the cotyledons. Root growth is also inhibited by ethylene.

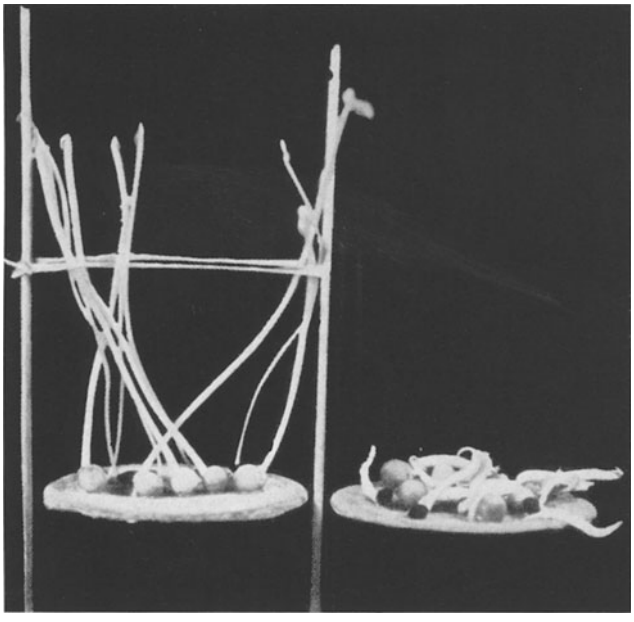

Fig. 2. "Triple response" of pea seedlings caused by ethylene. Left control. (After MOLISCH 1937.)

ζ) Breaking of dormancy.

Ethylene hastens the sprouting of potato tubers and gladiolus corms and breaks the dormancy of leaf and flower buds of many hardwood cuttings (VACHA and HARVEY 1927). It forces the development of latent rose buds (ZIMMERMAN, HITCHCOCK and CROCKER 1931), and axillary buds of the cotton plants (HALL *et al.* 1957). The forced shoots of roses grow faster and produce more dry weight than comparable shoots of the untreated controls. MOLISCH (1937) found that dormant buds of *Aesculus* and *Syringa* exposed for 24 hrs. to the emanation of apples sprout early, whereas a permanent contact with the emanation inhibits the development of the buds completely.

η) Formation of roots.

Ethylene induces the formation of adventitious roots in many plants (ZIMMERMAN and HITCHCOCK 1933, KRASSINSKY and ANDREJEWA 1935). It also stimulated the growth of preexistant root primordia in willow cuttings.

When the induced roots were in their turn treated with ethylene, they formed root hairs in abundance and produced secondary roots. In accordance with the facts reported on pp. 695 the induced roots did not possess their normal positive geotropic response (ZIMMERMAN and HITCHCOCK 1933).

ϑ) Various other responses.

Ethylene brings about germination of different dormant seeds (VACHA and HARVEY 1927). In very minute concentrations it stimulates the germination

of oat grains who had partly lost their germinability (RUGE 1947). The germination of seeds is inhibited if they are placed together with ripe apples under a bell jar (KOECKEMANN 1934, 1936). Ethylene inhibits the formation of anthocyanin. When MOLISCH (1937) put apples and roots of corn together in light the formation of anthocyanin by the roots was inhibited while under the same conditions without the apples the roots form anthocyanin abundantly. The same was observed on seedlings of *Vicia sativa*.

The extranuptial nectaries on the leaves of *Vicia faba*, which normally form anthocyanin, do not do so when treated with the ethylene-emanations of apples. They apparently produce anthoxanthins instead (KROPFITSCH 1951).

Ethylene treated epicotyls of *Pisum* show an increased phototropic reaction. As the ethylene in this case suppresses the negative geotropism (see p. 695) the epicotyls grow straight downwards if illuminated from below (DOSTAL 1942). RICHTER (1906) already reported the same for plants treated with illuminating gas.

3. Conditions influencing the production and action of ethylene.

Ethylene production in higher plants seems in certain cases to be a function of the developmental stage of the plant. Cotton seedlings and young vegetational plants show no or only a limited formation of ethylene. The production in considerable quantities starts only in the early reproductive state and reaches a maximum in the fruiting plants, indicating a connection between ethylene formation and initiation of flowering. Iris flowerbuds produce most ethylene just before the flowers open. As wilting proceeds the ethylene production decreases (PHAN-CHON-TON 1956). Senescence in cotton leaves stops the production of ethylene (HALL *et al.* 1957).

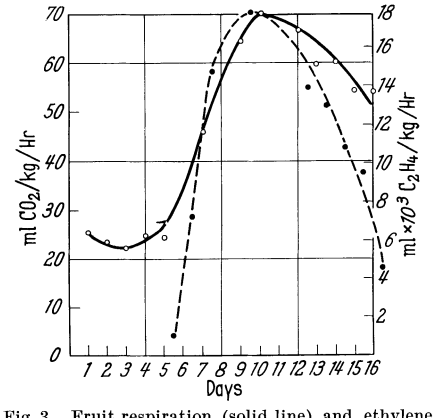

Fig. 3. Fruit respiration (solid line) and ethylene production (broken line) of avocado. (After BIALE *et al.* 1954.)

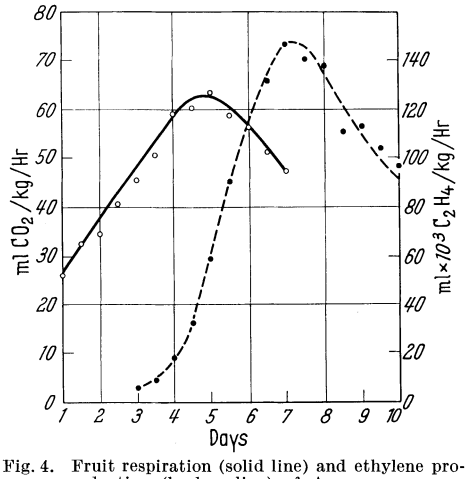

Fig. 4. Fruit respiration (solid line) and ethylene production (broken line) of Annona. (After BIALE *et al.* 1954.)

In fruits forming ethylene there is a clear cut relation between the production of ethylene and the climacteric. In the preclimacteric state the fruits do not form ethylene or do so only in minute quantities. The ethylene production increases either together with the increasing CO_2 production which characterises the climacteric (Fig. 3, Avocado) or after the climacteric peak has been reached (Fig. 4, *Annona cherimola*) (see literature in BIALE 1950 and BIALE *et al.* 1954).

In tomato fruits which show a climacteric peak of CO_2 evolution waves of CO_2 production occur during ripening and ageing accompanied by corresponding waves of ethylene production after ripening has started (SPENCER 1956).

The relation of ethylene formation and climacteric is also illustrated by the fact that fruits without climacteric (lemon, oranges) do not produce ethylene. Most of the fruits with an outspoken climacteric (avocado, banana, *etc.*) produce ethylene. However, mango which has a climacteric does not form ethylene (BIALE *et al.* 1954).

There exists a relation between ethylene evolution and longevity in storage. In apples those varieties with the longest storage capacity form least ethylene (NELSON 1939). In pears a variety with a short storage life showed a maximum of ethylene evolution, 6—7 times higher than that of a variety with a long storage life (HANSEN 1942). Pears with a short maturation period produce much more ethylene than the slowly maturing ones (HANSEN and CHRISTENSEN 1939, PHAN-CHON-TON 1956). The same is true for early and late maturing varieties of

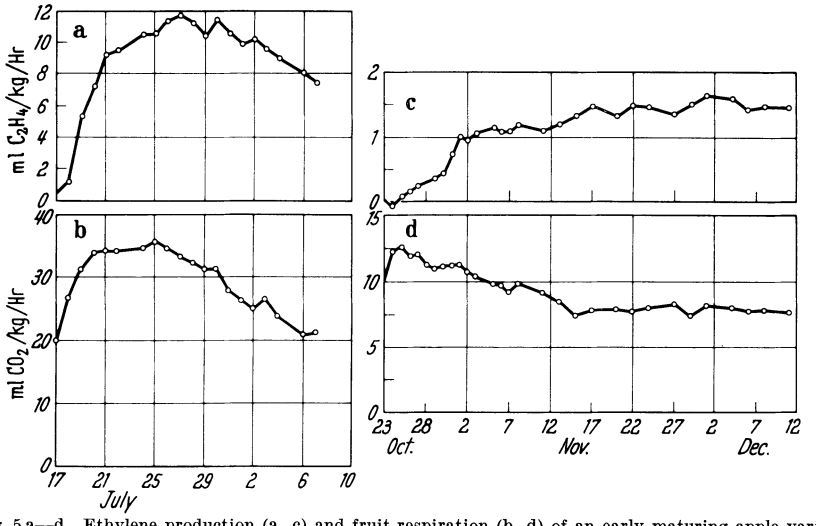

Fig. 5 a—d. Ethylene production (a, c) and fruit respiration (b, d) of an early maturing apple variety (Astrachan, a, b) and a late maturing one (Newton, c, d). (After HANSEN 1945.)

apples. Early maturing ones produce more ethylene and have a climacteric, whereas the late ones do not show a clear cut climacteric and produce less ethylene (HANSEN 1945; Fig. 5).

On the influence of temperature on ethylene production we possess only a scanty knowledge. HANSEN (1942) reports for pears that between 0—20° C CO_2 and ethylene production increases steadily. From 20—40° C CO_2 evolution increases whereas ethylene production decreases, being zero at 40° C. A severe inhibition of ethylene production by sections of apple tissue at 40° C and higher temperatures has been reported by BURG and THIMANN (1959). This inhibition is reversed by lower temperatures. According to BIALE *et al.* (1954) *Annona* fruits when kept at 5° C for 40 days had no climacteric and produced no ethylene. When transferred from 5° C to 20° C after either 20 or 45 days the CO_2 production rose climacterically. In contrast ethylene production increases only when the transfer was done after 20 days. The transfer after 45 days had no effect on the evolution of ethylene. One may conclude with BIALE *et al.* (1954) from these facts that the mechanism of ethylene production in fruits may be affected by factors which leaves the overall respiration intact. We will come back to this point later.

HANSEN (1942) reports on the influence of different gases on the evolution of ethylene in pears. Nitrogen and hydrogen leave the CO_2 production unchanged

whereas they decrease the formation of ethylene. But working with a much more sensitive method (gas chromatography) BURG and THIMANN (1959) found that ethylene production and O_2 consumption in apples show the same dependance upon oxygen tension. Although ethylene production is immediately stopped under anaerobic conditions, a precursor accumulates giving rise to rapid production of ethylene when the tissues are transferred to air. Increased oxygen pressure given at 40° C, when no ethylene is produced, does not bring about the evolution of ethylene (HANSEN 1942).

Exactly as the production of ethylene is restricted to certain phases of fruit maturation the influence of external ethylene on maturation seems to be limited to certain stages in the life of fruits (BIALE 1950). HANSEN and HARTMAN (1937) reported that the greatest repsonse of pears to ethylene is obtained with fruit picked early in the season and the least effect with fruit harvested at post mature stages. In all cases the effect of ethylene was confined to the preclimacteric period. Fruits stored for longer periods react to ethylene when treated at the beginning of the climacteric. Pear varieties with a long storage life respond for a long time towards ethylene (12 weeks) whereas short lived varieties react only for 2 weeks.

The temperature prior to and at the time of the ethylene treatment change the ethylene effect. Treatment of pears with ethylene at high temperature has no effect on the ripening (HANSEN 1942). Pears kept at low temperatures before being treated with ethylene do not show any increase in respiration or ripening (HANSEN and HARTMAN 1937).

It is important to note that ethylene also hastens maturation in fruits like mango, lemons and oranges which do not produce ethylene themselves. "The ability of the fruit to respond to external ethylene is not correlated with its capacity for reproducing ethylene" (BIALE *et al.* 1954).

The production of ethylene by *Penicillium digitatum*, which evolves this gas whether in culture or on its host (BIALE and SHEPHERD 1941), does not depend on the major nutrient components of its culture solution (PRATT 1944). The evolution of ethylene in this case seems to be a function only of active growth and respiration.

There seems to be a most interesting connection between infection of leaves and their treatment with defoliants on the one hand and their production of ethylene on the other. Rose leaves infected by *Diplocarpon rosae* produce more ethylene than non-infected leaves (WILLIAMSON 1950), although the same fungus in culture does not evolve ethylene. Leaves of several plants (potato, tobacco, *Datura*) inoculated with certain viruses produce much more ethylene than uninfected controls (ROSS and WILLIAMSON 1951). Leaves treated with phytotoxic chemicals or synthetic defoliants show increased ethylene production (JACKSON 1952, HALL *et al.* 1957). It must be mentioned here that already ZIMMERMAN and WILCOXON (1935) indicated that plants treated with growth substances increased their ethylene production.

ROSS and WILLIAMSON (1951) suggest that in all these cases the ethylene is the product of dying and necrotic cells and not a direct outcome of the virus and fungus infection and the defoliants. Certain symptoms, such as abscission common to some virus diseases may therefore be due only indirectly to the virus. Virus infection causes necrosis and the necrotic cells produce ethylene which causes abscission.

4. Mechanism of action.

The difficulties in understanding the action mechanism of ethylene are due to the lack of basic information and the great variety of plant responses induced

by it. As there is no proof that all the responses are based on the same physiological action of ethylene each response must be considered separately.

α) Maturation of fruits.

In most fruits the maturation of which is hastened by ethylene the rates of starch hydrolysis and sugar formation are increased (WOLFE 1931, REGEIMBAL, VACHA and HARVEY 1927, HANSEN 1939 *etc.*). Protopectin is transformed to pectin and the amount of soluble pectin increases (HANSEN 1939, HALL 1952a) resulting in the softening of the fruit. The content in organic acids decreases, changing the taste of the fruit. The chlorophyll is decomposed bringing about the colouring of the fruit. The blanching of celery and the colouring of leaves is based on the same ethylene action (HIBBARD 1930, NELSON and HARVEY 1935).

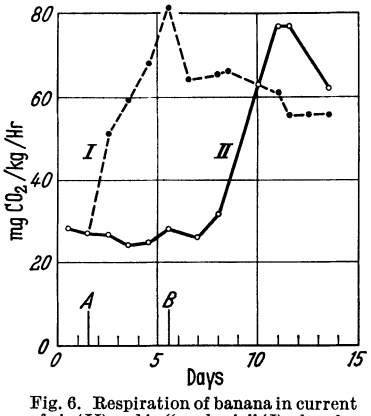

Fig. 6. Respiration of banana in current of air (*II*) and in "apple air" (*I*) whereby air was passed over an apple at *A* and the apple removed from air stream at *B*. (After GANE 1937.)

Many authors believe that these effects are brought about by the direct action of ethylene on the enzymes involved. There is no irrefutable proof for this supposition.

The most pronounced effect of ethylene is the immediate increase in the rate of respiration (Fig. 6). This increase occurs only when ethylene hastens maturation. When it does not (treatment during postclimacteric or after prolonged cold storage, *f.i.*) there is no change in respiration. This effect of ethylene on respiration is also observed with potato tubers, twigs and leaves (HERKLOTS 1928, HUELIN and BARKER 1939). The question arises if the respirational change brought about by ethylene is a side effect or the central link between ethylene and its physiological action.

The most convincing argument concerning this question is given by HUELIN and BARKER (1939). They believe that the effect of ethylene is concerned with the supply of substrate to the respiratory centres. In fruits ethylene is only effective when respiration is low and sugars are not yet formed from starch, during the preclimacteric. In potato tubers with high sugar content ethylene does not affect respiration. Therefore, where the rate of supply is already high ethylene is ineffective. The causal chain would thus be: Ethylene → mobilisation of respiratory substrate → increased flow of substrate to respiratory centres → processes leading to maturation. There may be a link between this proposed chain of events and the production of ethylene by ripening fruits. HALL (1952b) found that apple juice and extracts from *Penicillium digitatum* as enzyme sources liberated ethylene best under aerobic conditions from different sugars, alcohols and pectin. One of the steps leading from increased respiration to maturation are apparently the pectic changes. As pectin and its hydrolytic products arabinose and methyl alcohol are good substrates for ethylene formation, ethylene by increasing respiration increases its own production. "In ripening fruits apparently ethylene may paradoxically function as an autocatalyst accelerating its own production" (HALL 1952a). Though based on certain facts these speculations on the mechanism of action of ethylene have to be taken with some reservation as our information is too scanty.

Another question too remains open. Though it is certain that the allelopathic ethylene causes maturation BIALE *et al.* (1954) doubt that during normal ripening the self produced ethylene is the cause of maturation. They consider it as a *product* of ripening and not its cause.

β) *Abscission.*

Without discussing the question whether ethylene is an *endogenous* regulator of abscission (see ADDICOTT and LYNCH 1955) we can state that the abscission promoting effect of ethylene seems to be connected with the role of auxin. Before abscission occurs there is an auxin gradient across the zone of abscission. In bean leaves *f.i.* the leaflet contains about three times as much auxin as the stalk. As natural abscission approaches with the beginning of senescence the auxin content of the leaflet decreases to that of the stalk. With this loss of the auxin gradient abscission sets in (SHOJI *et al.* 1951).

Ethylene probably accelerates abscission by inactivating auxin or lowering its level (HALL 1952b, LIVINGSTON 1950). In fact there exists an ethylene-auxin antagonism as external auxin prevents ethylene induced abscission and inhibits the formation of ethylene in vitro (HALL 1952b). The suggested inactivation of auxin could be brought about through the liberation of auxin inhibitors by ethylene.

The ethylene effect on maturation and abscission has one point in common: As maturation and abscission are the result of progressive senescence ethylene accelerates in both cases the ageing of the cells and leads to cellular disintegration and breakdown (GAWADI and AVERY 1950, BROWN and ADDICOTT 1950) which in both cases are perhaps mediated through increased respiration. It is of interest in this connection that the course of respiration in ageing leaves before abscission resembles very much the climacteric rise in maturating fruits (EBERHARDT 1955a). EBERHARDT suggests that in both cases ethylene either affects the ATP/ADP ratio (PEARSON and ROBERTSON 1954) or uncouples phosphorylation and oxidation (MILLERD *et al.* 1953).

γ) *Inhibition of growth.*

With the exception of MICHENER (1938) most authors agree that ethylene in inhibiting elongation acts in some way on auxin. VAN DER LAAN (1934) found that ethylene treated coleoptiles of *Avena* and epicotyls of *Vicia faba* contained less extractable auxin than the controls and v. GUTTENBERG and STEINMETZ (1947) report similar results. As the investigations cited here did not use the chromatographic method the reliability of the results may be doubted.

BORRIS (1943) proved that one component of the ethylene induced inhibition acts directly on the elongation zone and can be eliminated by external auxin (see p. 696). The other component, which quantitatively is much more important than the first and which works through the cotyledons cannot be counteracted by auxin. The best explanation put forward so far (GRÜMMER 1955) would be that at least the second component of BORRIS consists in the liberation of a growth inhibitor by ethylene which inhibits cell elongation. This inhibition then could interfere with cell elongation only at a point other than that where auxin acts as it is not counteracted by auxin. The first component of the ethylene effect could consist in either destruction of auxin, a change of sensitivity of the cells towards auxin or a change of the permeability of the tissues towards auxin as reported by v. GUTTENBERG and STEINMETZ (1947). The destruction of auxin by ethylene could not be a direct one as there was no influence of ethylene on auxin in vitro (VAN DER LAAN 1934, v. GUTTENBERG and STEINMETZ 1947). But ethylene could increase the activity of IAA oxidase. All these are mere speculation as not enough reliable data are available. The influence of ethylene on growth does not seem to be mediated through increased respiration. For instance in wheat seedlings, the growth of which was inhibited by ethylene,

the rate of respiration was the same as in the controls (ROBERTS 1951). The respiration of a number of other plants was even inhibited by ethylene (HOHENSTATTER 1942).

δ) Various.

No explanation can be offered for the epinastic effect or for the change in geotropic behaviour of roots caused by ethylene. Both effects are so interesting as to warrant additional research.

RUGE (1947) suggests that ethylene as an intermediate respiratory product changes respiration in such a way that the energy needed for germination is produced even in seeds with lowered vitality. Germination stimulation results from this.

It may be important for the understanding of the mechanism of action to mention that the unsaturated bond in ethylene is significant as only ethylene, propylene and butylene are effective in causing *f.i.* epinasty whereas the corresponding saturated gases (ethane, propane, butane) are not (CROCKER, ZIMMERMAN and HITCHCOCK 1932, ZIMMERMAN and HITCHCOCK 1933).

5. Biogenesis of ethylene.

The exact biogenesis of ethylene in the plant body is unknown. Relevant facts may be those reported by HALL (1952a) (see p. 700). In his experiments, ethylene is best produced enzymatically (in vitro) from sugars, organic acids and alcohols (methanol, ethanol) and pectin. He suggests that perhaps all ethylene yielding substrates are reduced to alcohol which then would be the terminal substrate from which ethylene is liberated. BURG and THIMANN (1959) have proposed the following scheme for ethylene production:

$$\longrightarrow A \xrightarrow[-2H]{} B \underset{+H_2O}{\overset{-H_2O}{\rightleftharpoons}} C \longrightarrow C_2H_4$$

$$\searrow \text{Terminal Oxidase}$$

A, B and C are nonvolatile precursors. Substance A accumulates under anaerobic conditions (see p. 699). A is dehydrogenated to B and a cyanide insensitive oxidase acts as electron acceptor. This may be the same oxidase which accepts electrons from respiration. B → C is a reversible dehydration. Experiments with tritiated water and glycerol made this step probable.

b) Hydrogen cyanide and ammonia.

There is ample evidence that hydrogen cyanide, set free enzymatically from cyanophoric glucosides contained in many seeds, is a strong inhibitor of germination and growth (see literature in EVENARI 1949a, b and NIEMANN 1952). This inhibition can be allelo- or autopathic. Leaving aside the autopathical influence of hydrogen cyanide, we do not know yet if all the experiments carried out under laboratory conditions are pertinent to what happens under natural conditions. There is only one proof for the existence of allelopathy caused by hydrogen cyanide in nature. A basidiomycete causes winter crown rot of alfalfa by producing hydrogen cyanide which kills under natural conditions specific tissues or the entire crown of the host plant (LEBEAU and DICKSON 1953). It may be mentioned that another fungus *(Pholiota aurea)* also produces hydrogen cyanide.

BORSOWA (1944) and TOKIN (1956) report that buds and bark of *Prunus* and *Laurocerasus officinalis* contain volatile "phytoncides", *i.e.* substances which emanate from mashed tissues of these organs and kill bacteria, zoospores and

Phytophtora etc. Most probably the substance concerned here is hydrogen cyanide. TOKIN (1956) suggests that the biological allelopathic function of hydrogen cyanide is to kill parasites attacking these plants.

Ammonia, which strongly inhibits germination and growth is released enzymatically from nitrogenous substances contained in the pericarp of different dry fruits especially sugar beet seed balls (see literature in EVENARI 1949a, b). But whereas FROESCHEL and FUNKE (1939) report that sugar beet seeds prevent the germination of other seeds also in soil, GRÜMMER (1955) found that soil or charcoal abolish the inhibition.

c) Essential oils.

DE CANDOLLE (1832) already knew that the essential oils have a detrimental effect on plants. Most of them inhibit germination and growth and on longer contact may even kill a plant exposed to their vapours (literature in EVENARI 1949a, b; GRÜMMER 1955). Plants producing the oil are much more resistant to their own oils than other species (HELLER 1904).

Recently HAFEZ (1958a, b) has shown that the vapours of essential oils bring about a considerable closing of the stomata of different plants. It is therefore not astonishing that lately a number of authors have reconfirmed the results of earlier investigators that essential oils influence transpiration though this was denied by others as *f.i.* AUDUS and CHEATHAM (1940). HAFEZ (1939, 1957) found that the vapours of essential oils cause a decrease of transpiration. HEILBRONN (1950) reported that electrical resistance of the cuticle of *Peperomia sandersii*, a plant not containing essential oils, increased under the influence of air containing essential oils because, the oils form thin films on the cuticle, thus decreasing the water permeability. HÖHN and ELFERT (1951) working with oat plants in an atmosphere of peppermint and lemon oil report an increase in transpiration with small amounts of essential oils (5 mm^3/27 l air) whereas greater amounts cause a decrease of transpiration. The cuticular transpiration seems to be especially affected. The higher concentrations bring about guttation under conditions where it naturally would not occur. Parallel to the decreased transpiration growth is inhibited.

It would be most interesting to know if this allelopathic influence of essential oils exists under natural conditions. There are only *indications* that such an influence exists. KNAPP and THYSSEN (1952) grew medicinal plants rich in essential oils in mixed culture and found that their competition value is higher than that of plants devoid of essential oils. This question should be studied in mediterranean countries where associations of plants rich in essential oils are common.

The essential oils have been used as antiseptica for a long time (literature in HELLER 1904, EVENARI 1949a, b). Lately the strong bactericidal and protistocidal effect of essential oils has been stressed by Russian authors working with pure oils and plant organs rich in essential oils (SCHISCHKINA 1944, SWET-MOLDAWSKI 1947, PLOCHOWA in TOKIN 1956 and TOKIN 1956). It is therefore possible that essential oils protect the plants containing them against infections, an opinion already voiced by FOCKE (1881/82). But a clear cut proof is still missing.

As essential oils are chemically a very heterogeneous group the question has been asked what their active constituents are (SIGMUND 1924, ULLMANN 1940, KLOSA 1948/49, EVENARI 1949a and GRÜMMER 1955). Our incomplete chemical knowledge of them does not permit a clear answer. But apparently the aldehydes (benzol-, citrol-, cinnamal-aldehyde), and the phenols (thymol, carvacol, apiol, safrol) are the most active compounds.

d) Mustard oils and related compounds.

Mustard oils (probably especially allyl-isothiocyanate and β-phenethyl isothiocyanate though this should be reinvestigated) contained in seeds and other organs of many members of the cruciferae family, are strong germination inhibitors (literature in EVENARI 1949a, b, GRÜMMER 1955), and are very toxic to certain fungi (WALKER *et al.* 1937, PRYOR *et al.* 1940). Seedlings of *Raphanus sativus*, *Brassica alba* and *B. oleracea* form mustard oil vapors killing potato test plants (DENNY 1937/38). TOKIN (1956) and many coworkers report that onion and garlic contain volatile "phytoncides". Other authors like OSBORN (1943), LUCAS *et al.* (1946), MADSEN and PATES (1952) found the same. TOKIN claims that not one single substance but a complex of organic compounds is responsible for this antibiotic effect. Probably the most important one is Allicin isolated by CAVALLITO *et al.* (1944/45) as the antibacterial principle of *Allium sativum* and a number of closely related compounds (see Russian literature in TOKIN 1956). Allicin is apparently the substance giving garlic its typical odour.

Diallyl disulfide and diallyl polysulfides present in considerable amounts in onion and garlic, have, according to CAVALLITO *et al.*, no antibiotic activity. Though the allelopathic influence of mustard oils under natural conditions is not yet proved as far as higher plants are concerned, we may mention here and confirm an observation already made by GRÜMMER (1955): In fields planted with onions the characteristic odour of mustard oils is often very strong.

e) Unspecified volatile substances.

WINTER and WILLEKE (1951, 1952c) found volatile antibacterial substances in the macerates of leaves *(Hemerocallis species, Lepidium sativum, Tropaeolum majus, Anemone pulsatilla, Clematis vitalba)* and of roots *(Clematis)*. The one from *Tropaeolum* has some practical importance in medicine (see HALBEISEN 1954). A number of Russian authors report that certain plants *(Pelargonium roseum, Chrysanthemum indicum, Lolium perenne etc.)* give off volatile "phytoncides" which under a bell jar bring about a decrease of 50% of the bacteria contained in air (DUMOWA in TOKIN 1956). The air over forests is supposed to be practically sterile through the influence of the volatile phytoncides formed by the leaves (JANOWITCH and BRYNZEW in TOKIN 1956).

B. Non volatile excretions.

a) Leaves and shoots.

It is known for a long time (see ARENS 1934, GRÜMMER 1955) that a great number of water soluble substances are leached out from leaves by rain and washed into the ground or unto other plants. ARENS (1934), LAUSBERG (1935) and ENGEL (1939) have measured the amounts of these substances. The values given by ARENS and LAUSBERG are much higher than those of ENGEL, but the fact remains that leaves can loose about 0.5—6% of their ash content when put with their blades into water for 24 hours. DALBRO (1955) reports that 800 kg per hectar of organic material are leached out from apple leaves during one season. Lately TUKEY and coworkers (1958, 1959) have shown by using the isotope technique that the foliage of various plants looses considerable amounts of carbohydrates, carboxylic acids, amino acids and inorganic nutrients by leaching. For alkaloids, MOTHES (1950) reported that they are excreted by leaves (see also RADEMACHER'S contribution in this encyclopaedia, Vol. XI, p. 668). Regarding the allelopathic importance of these excretions it makes no difference if the leaves secrete the substances actively through their cuticle (ARENS 1934) or if they are washed out

passively (ENGEL 1939). Disregarding the older and "not too convincing" (BONNER 1950) investigations reported in EVENARI (1949a) and BONNER (1950) there are a number of cases where the allelopathic influence of leave excretions is well proven. BODE (1940) has shown that *Artemisia absinthium* inhibits, under field conditions,

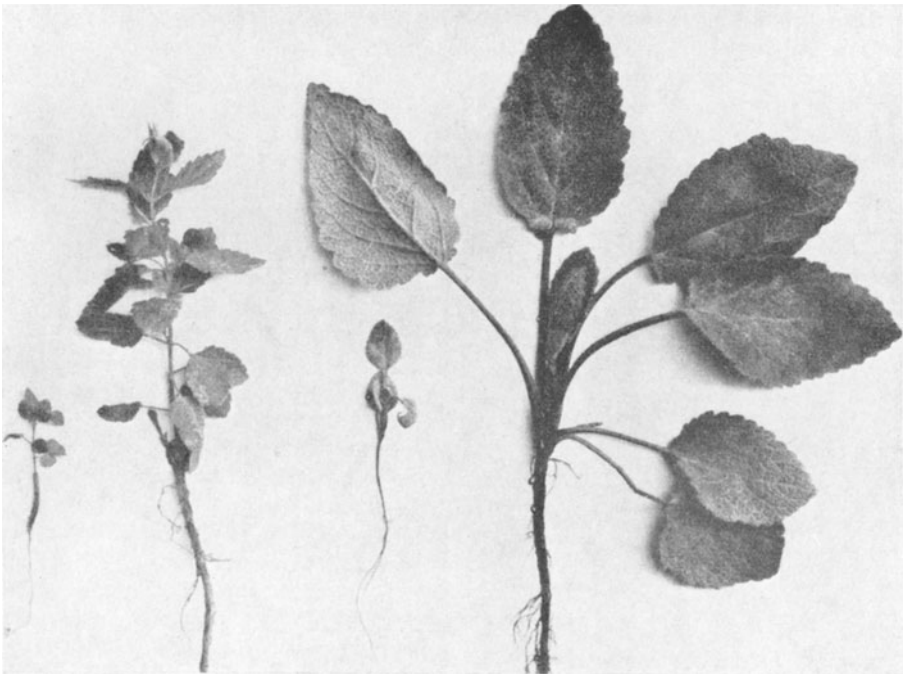

Fig. 7. *Nepeta nuda* (left) and *Salvia sclarea* (right) grown at distance of 40 cm (small plants) and 120 cm (big plants) from *Artemisia Absinthium*. (After FUNKE 1943.)

growth and development of a number of other plants in its surrounding, even at a distance of 1 m. This effect is due to leaf excretions which are washed into the ground and unto surrounding plants. The effective substance is possibly the glucoside absinthin though the excretions of the glandular hairs contain, in addition to absinthin, a number of other organic compounds. FUNKE (1943), GOLOMJODOWA (1952), SCHENDERETZKIJ (1952) and GRÜMMER (1955) have confirmed BODE's observations (see Fig. 7).

Table 2. *The germination percentage of Phaseolus multiflorus sown in open soil mixed with cut fresh absinth leaves.* (After FUNKE 1943.)

Days from sowing	Control	With leaves
8	32	0
10	93	14
11	100	36
12	100	46
17	100	61
83	100	75

Table 2 shows the inhibition and retardation of germination of *Phaseolus multiflorus* caused by the addition of foliage of *Artemisia absinthium* to the soil.

Not only the percentage of germination was affected but growth was inhibited and abnormal (rolled and undulated leaf blades).

WENT (1942) observed that the desert shrub *Encelia farinosa* does not harbour annuals as do other shrubs growing in the same locality. GRAY and BONNER (1948a) investigated this further and found that dried *Encelia* leaves applied to the surface of sand in pots containing tomato plants inhibit the growth of tomato plants (Fig. 8). The growth of *Encelia* itself was little affected. The

germination of seeds of species normally growing under desert shrubs was inhibited by placing a mulch of *Encelia* leaves over the substratum (BONNER 1950). The active compound was 3-acetyl-6-methoxy-benzaldehyde (GRAY and BONNER 1948b). Thus BONNER (1950) concluded that under natural conditions *Encelia* inhibits allelopathically the growth of certain susceptible species. MULLER (1953) disagrees, pointing out that *Franseria*, another desert shrub, the leaves of which contain an even more potent toxin, harbours many desert annuals, because debris rich in organic material accumulates under the individual plants. In his opinion the reason for the lack of shrub dependent herbs under the *Encelia* bushes is to be found only in the lack of accumulation of organic debris and not in the presence of the toxin. The toxin is not effective in the natural habitat, possibly because it is destroyed by micro-organisms of the soil.

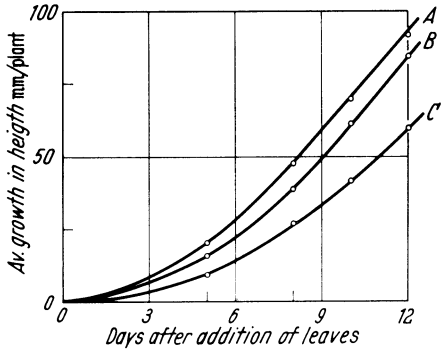

Fig. 8. Effect of tomato or Encelia leaves on the growth of tomato plants in sand cultures. *A* Control plants no leaves added; *B* 3 g tomato leaves per pot; *C* 3 g Encelia leaves per pot. (After GRAY and BONNER 1948a.)

Doubtlessly, the microbial destruction of plant produced toxic substances in the soil and/or their inactivation through absorption by the colloidal fraction of the soil are important factors which have to be taken into consideration when trying to explain certain ecological facts through allelopathy. In this respect the quality of the soil seems to be of great importance. GRAY and BONNER (1948a) for the toxin of *Encelia* and GRÜMMER (1955) for that of *Artemisia absinthium* have shown that the effect in sand is much stronger than in good soil apparently, because in sand the inactivation and destruction of the toxins is much less pronounced. This would mean that one should expect allelopathical influences to be much stronger in sandy soils than in other types of soil rich in micro-organisms and colloidal fractions.

BENNETT and BONNER (1953) isolated three toxic fourocoumarins from another desert shrub *(Thamnosma montana)* but no test under field conditions was conducted.

WENT *et al.* (1952) observed that in a Californian burn seeded artificially with *Brassica nigra*, germination and establishment of certain native species were strongly inhibited though at some distance from the mustard plants they thrived well. Laboratory experiments showed that in flats covered with a mulch of leaves and seeds of mustard germination and development of *Salvia mellifera* and *Robinia pseudacacia* was much affected. The *Salvia* seedlings which managed to germinate died back in the presence of mustard. This is due to a water soluble substance contained in leaves and seeds of *Brassica nigra* which is leached out by rain or irrigation. The substance is soluble in carbontetrachloride and ether, is heat stable and is not an ethereal oil (unpublished original).

When tomatoes are grown in rich garden soil and leaves of *Myrtus communis* or *Eucalyptus rostrata* put on the soil surface, the growth of the tomato plants was inhibited, the leaves became yellow and dropped from the stem (YARDENI and EVENARI 1952). The same happened when the containers were watered with aqueous leaf extracts (Table 3).

These experiments may explain why the soil of an *Eucalyptus* grove is almost bare of vegetation. Leaves of *Ailanthus* contain a principle toxic to tree seedlings. When pine and birch seedlings were watered with aqueous extracts of

Ailanthus, the seedlings died after some time. "The toxic substance may be one of the important factors that limits succession in *Ailanthus* stands" (MERGEN 1959).

It is known since a long time that the presence of the weed *Camelina alyssum* in a flax field considerably reduces the flax yield (see Russian authors cited in GRÜMMER 1955). GRÜMMER (1956/57, 1958) could show that this reduction of the yield is not due to toxic root excretions of the weed but to two other factors: competition between the weed and flax and inhibitors present in the *Camelina* leaves which are leached out by rain, come in contact with the flax plants and inhibit their development.

It is possible that there is an allelopathic influence of leaf and stem litter which either covers the soil in forests after the annual leaf fall or remains on the fields and is ploughed under after the harvest.

WINTER and SIEVERS (1952), WINTER (1953), WINTER and SCHÖNBECK (1953 a) and SCHÖNBECK (1956) found that acqueous extracts of the litter of different gramineae influence the germination of seeds in petri-dishes and inhibit the growth of seedlings. The inhibiting substances brought into the soil from wheat litter could be leached out even 9 months after the harvest (WINTER 1957).

Table 3. *Effect of leaf extract on stem elongation of tomato seedlings grown in garden soil. Stem elongation as % of elongation of controls after 8—10 weeks of growth. In 1 and 2 the tins watered with an aqueous extract 1:5 of first extraction, in 3 with extract 1:5 of residue of first extraction.* (After YARDENI and EVENARI 1952.)

	Myrtus extr.	*Eucalyptus* extr.
1	1.5	7
2	7.6	11
3	23	47

BÖRNER (1957) isolated 4 phenolic growth inhibitors from straw and litter of wheat, barley and rye, two of which could be identified as p-hydroxycinnamic acid and p-hydroxybenzoic acid. MASSART (1957) found the same two acids and in addition vanillic and ferulic acid, both of which are germination and growth inhibitors. KÖVES and VARGA (1958) report the presence of the following growth inhibitors in rice straw: p-oxybenzoic, p-coumaric, ferulic, caffeic, protocatechuic and salicylic acid. The most active compound was salicylic acid. But it remains doubtful whether these toxic substances derived from litter have any direct allelopathic influence under field conditions. On the one hand WINTER (1957) and coworkers have shown that they remain for quite some time in the soil and are inactivated more slowly in the soil than they accumulate. PATRICK and KOCH (1958) isolated "phytotoxic" substances from soils in which residues of different plants had been allowed to decompose. These substances inhibited respiration, germination and growth of tobacco seedlings. When no decomposition of plant residues took place in the soils, the soil extracts did not contain toxins (see also PATRICK 1955). We may mention that the authors together with COCHRANE (1948), GARRETT (1956) and others believe that these toxins arising from plant residues may predispose plants to the invasion of root rot producing microorganisms. On the other hand GRÜMMER (1955) reports that the roots of *Lepidium* were inhibited by litter extract only when growing on filter paper. When he put soil under the filter paper the inhibition disappeared. A further doubt is provoked by our lack of knowledge of the quantities of these substances present in the soil. BÖRNER (1957) maintains that the quantities of straw left on fields is not enough to bring about such concentrations of his 4 phenolic inhibitors as could inhibit growth. But he leaves open the possibility of accumulation of these substances especially under arid conditions. As pointed out by GRÜMMER (1956/57) one should also expect an allelopathic influence of the litter whenever germination takes place inside or on the litter without

the seeds being in direct contact with the soil (see also DINOOR 1959). It should also not be forgotten that there exists the possibility that these toxins even when not influencing higher plants directly may affect the microflora of the soil (see p. 721) and through this the life of higher plants.

The fact that in pure stands of *Picea excelsa* there is neither underbrush nor weeds is attributed, at least partly, to the allelopathic influence of the accumulated fallen needles. BUBLITZ (1953) found that the litter of *Picea* contains a water soluble substance which inhibits germination and development of *Picea* and *Pinus* seedlings and inhibits the development of the normal microflora of the soil (WINTER and BUBLITZ 1953).

BAUTZ (1953) reports similar results and opines that quinones, formed when *Picea* litter is being decomposed to humus, are responsible for the allelopathic effect of the litter. Tannins and gallic acid doubtlessly are washed into the soil from leaves of many plants *f.i.* leaves of *Acer platanoides* (BENDZ 1956) and from bark and fruits (KLOSA 1949, FÖRSTER 1957). In solution tannins strongly inhibit germination and growth of different plants. But addition of soil extracts and soil greatly reduces the inhibition caused by tannin (NIEMANN 1952). FÖRSTER (1957) also found that tannin and gallic acid inhibit germination and growth much more in solution and in sand than in soil. But her experiments in which she added plant material rich in both substances (meal of oak acorns, bark of *Picea*) to plants grown in sand and soil have proved that tannins may have an allelopathic influence under natural conditions, though soil in contrast to sand weakens their effectivity. *Digitalis* and *Sinapis* were strongly inhibited in their growth, oat and peas less, whereas spruce and pine seedlings were hardly affected. In a study undertaken to establish the reasons for the affinity or preference of certain plant species for "sheltered" conditions under trees of *Quercus ithaburensis* or for the open areas of this park forest of northern Israel, DINOOR (1960) found that there is a definite litter effect of the oak leaves. When sown under field conditions on the litter germination and establishment of *Avena sterilis* and *Trifolium purpureum*, two species typical for the open areas were inhibited. This is partly due to a mechanical effect and partly to germination and growth inhibitors present in the oak leaf litter. As the leaves decompose, they gradually loose their effect as germination inhibiting agents.

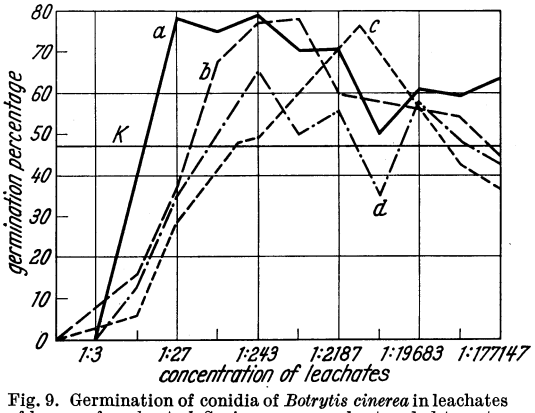

Fig. 9. Germination of conidia of *Botrytis cinerea* in leachates of leaves of *a* wheat; *b* Syringa; *c* sugar beet and *d* tomato. *K* control. (After KOVÁCS and SZEÖKE 1956.

The cuticular excretions of leaves affect not only higher plants allelopathically but micro-organisms as well. W. BROWN (1916, 1922a, b) found that the electrolytic conductivity of an infection droplet put on leaves of different plants increased and that as a function of this increase the germination of spores of *Botrytis cinerea* was stimulated. When the same was done on the leaves of *Rhoeo discolor* the germination of the spores was retarded.

The leaf excretions of different plants contain substances affecting the germination of spores and conidia of different parasitic fungi (Fig. 9) (KOVÁCS and SZEÖKE 1956). The authors state that under normal conditions the con-

centrations of these substances on the surface of the leaves leached out by dew or raindrops are sufficiently high to inhibit the germination of the conidia of *Botrytis cinerea*. The chemical nature of these substances is still unknown.

b) Roots.

We exclude from this chapter the general problem of "soil sickness" or "soil fatigue" („Bodenmüdigkeit" of the german authors), as there is still no direct irrefutable proof that toxic substances secreted by roots are one of the main causes of soil sickness. This has often been postulated and as often been refuted (see critical surveys in LOEHWING 1937, BRONSART 1949, BONNER 1950, WINTER 1952a, GRÜMMER 1955, DEMOLON 1956)[1]. The first question which concerns us here is do roots, under natural conditions, excrete substances into the soil. The older literature on this question reviewed by LOEHWING (1937) has already clearly established the fact that inorganic substances, especially phosphorus, are given off by living roots into the soil under field conditions (see ACHROMEIKO, DELEANO and others cited in LOEHWING 1937). The same is true for certain organic materials. VIRTANEN and coworkers have reported in many papers (see LOEHWING 1937), that legume nodules secrete a number of amino acids into the soil so that one pea plant furnishes enough amino nitrogen for the growth of two associated oat plants. But some authors (see *f.i.* BOND 1938, DEMOLON 1956) have doubted the correctness of VIRTANEN'S observations. VIRTANEN reported lately another 11 years experiment of growing together in one container alder and spruce without nitrogen. The spruce obtained nitrogen from the root nodules of the alder (VIRTANEN 1957).

The excretion of sugar and certain organic acids such as malic acid seems to be well established.

From the newer literature we cite ROVIRA (1956) who found that the roots of oat and pea plants grown on sand give off a number of acids and two sugars. RATNER (1954) and LINSKENS and KNAPP (1955) too report the secretion of amino acids by the roots into the soil. KATZNELSON *et al.* (1955) have shown that roots of wilting plants give off more amino acids than those of non wilted controls.

MARTIN (1957) confirms the observation of EBERHARDT (1955b) concerning the excretion of scopoletin through the roots of oat plants.

Amino acids, fructose and glucose are also given off into the medium. EBERHARDT and MARTIN (1957) state that besides scopoletin the roots of a number of plants give off fluorescent compounds. Their allelopathic importance is doubtful because the amounts are very small and scopoletin is destroyed in the soil. DEHAY and CARRÉ (1951) investigated the root secretion of many plants and found that besides amino acids nearly all secreted citric acid. A number of other organic acids were given off by some of the plants only. The different plants behaved very differently. The roots of *Sinapis alba* were the only ones to excrete $SO_4^=$, the roots of *Helianthus annuus* were the only ones not to give off any organic material. The authors point out that the amounts secreted are too small as to be the sole cause of allelopathy.

Leaving open the question whether we deal here with active secretion, passive diffusion and/or substances derived from the destruction of root cells (most possibly all three processes are involved) it is a fact that roots give off a great variety of inorganic and organic substances into the soil. A most elegant proof of this was furnished by PRESTON *et al.* (1954). They showed that the growth

[1] See also RADEMACHER'S contribution in vol. XI, p. 655 of this encyclopaedia.

regulator α-methoxy phenyl acetic acid when applied to bean hypocotyls moves into the roots, is secreted by the roots into the medium, taken up by the roots of nearby plants and transmitted to their leaves.

The active secretions of different enzymes by the roots into their substrate has been reported by KOUPREVITCH (1954), RATNER (1954) and others. Catalase, invertase, amylase, urease, phenolase, protease and glycerophosphatase are primarily involved. RATNER (1954) underlines the importance of these exo-enzymes in stating: "L'analyse ultérieure de l'activité enzymatique des racines doit ouvrir de nouveaux horizons à l'étude de l'absorption par contact comprenant l'action direct sur le sol de la plante elle même ..."

But the question remains: to what extent are the proven root secretions and exudates responsible for *direct* allelopathic action of one plant upon another.

Observing in nature that cultivated guayule plants grew much better on the edge of the plantation than in the centre and that the roots of the individual plants did not intermingle BONNER and GALSTON (1944) suspected that this was a case of allelopathy. Experiments proved that the sand in which one year old plants grew contained a leachable substance. This when suppled to the nutrient solution with which younger plants were irrigated greatly inhibited growth. Continuous recirculation of the same nutrient solution through sand cultures of young seedlings at the one hand and young seedlings and older plants on the other showed that the presence of an older plant in the recirculation system inhibited the growth of the seedlings. As in both case the nutrients removed were constantly resupplied, the effect could not have been due to lack of nutrients but only to the excretion of a toxin by the roots of the older plants.

In another experiment seedlings were planted directly in sand under an older plant and other seedlings in a glass jar inserted into the sand. In the first case the seedlings died or grew slowly, in the second growth was normal and mortality low.

The toxin isolated from root leachates was trans-cinnamic acid, a substance highly toxic to guayule seedlings. When applied to sterilized soil the cinnamic acid was stable, in normal soils it disappeared rapidly apparently due to the activity of microorganisms (BONNER 1946). Therefore we deal here with a most interesting case where the toxic root secretion and its inhibiting influence on growth in sand cultures has been proved and the toxin identified but where the toxin is rapidly destroyed in normal soil. As we possess no data about the behaviour of this toxic root excretion in the natural habitat and soil of the guayule plant it is still doubtful if it has an allelopathic influence under field conditions.

WAKS (1936) found that the roots of *Robinia pseudacacia* contain substances which inhibit strongly the growth of barley roots. The author suggests that this may explain the fact that stands of *Robinia* are almost completely without any other vegetation. But there is no proof that the inhibitors when excreted into the soil have the same effect as on barley grown in solution.

Phytosociological investigations instigated GUYOT and his coworkers to carry out a number of relevant experiments (BECKER *et al.* 1950, GUYOT 1951, BECKER and GUYOT 1951, BECKER *et al.* 1951). Different test plants (wheat, flax *etc.*) were irrigated with aqueous extracts from roots of certain plants or root leachates or extracts from the soil of the rhizosphere of the same plants. When the extracts were taken from *Brachypodium pinnatum* there was no influence whatsoever. When derived from *Hieracium pilosella, H. umbellatum, Origanum vulgare, Thymus serpyllum etc.* the test plants were inhibited in their germination and growth.

In some cases higher dilutions of the extracts stimulated growth. In other experiments seeds of different annual plants were put on sand irrigated with aqueous extracts of soil taken from the rhizosphere of *Brachypodium pinnatum* and *Hieracium pilosella*. In the first case the germination proceeded normally, in the second germination and growth were inhibited. When the seeds of *Melampyrum arvense*, a parasite growing in the *Brachypodietum pinnati* were germinated on soil taken from the rhizosphere of *Brachypodium*, germination and growth was stimulated. Whereas the same experiment on soil from *Hieracium pilosella* resulted in a more or less pronounced inhibition. Seeds of *Hieracium pilosella* when germinating in root extracts and leachates of older plants of the same species showed a much inhibited germination.

Based on these experimental facts the authors try to explain certain phytosociological observations as *f.i.* the slow disappearance of *Hieracium pilosella* in the centre of old patches of the same species or the lack of therophytes in certain plant associations whose soil contain enough viable seeds of the same annual plants (GUYOT and MASSENOT 1950). It seems to us that though some of these explanations seem quite probable, they are not proven as long as the substances involved are not isolated and tested under field conditions.

The same goes for the experiments of DELEUIL (1950, 1951 a, b, 1954), although some of them are very convincing. He wanted to find out why the *Rosmarino-Ericion* is more or less free from annual plants. This, in his opinion, is not due to lack of seeds or edaphic factors, but to the excretions of toxic substances by the roots of the perennial plants typical for this association. When seeds of therophytes growing in soil are watered with leachates of the *Rosmarino-Ericion* soil, the seedlings die. The same experiment made with seeds of perennials or biannuals results in normal plants. The same results are obtained with leachates of the roots of the perennials typical for the *Rosmarino-Ericion* like *Rosmarinus officinalis, Erica multiflora etc.* The toxicity of the soil disappears after heating and after successive leaching. Then the annuals germinate and develop normally.

The few annual plants which are found in the same association belong mostly to the leguminosae and have root nodules or are hemiparasites *(Odontites lutea)*. Seeds of therophytes were grown on soil watered with leachates of the toxic *Rosmarino-Ericion soil* or in alternation with the same leachate and water in which root nodules or roots of the hemiparasite had been macerated. Growth and germination are normal in the last case and inhibited in the first. Leachates from the aerial parts of the same plants are ineffective. DELEUIL draws the conclusion that the root nodules of the *Leguminosae* and the roots of *Odontites* produce a substance antagonistic to the toxin excreted by the roots of the perennial species characteristic for the *Rosmarino-Ericion*. A similar toxin-antitoxin mechanism has been postulated by the same author for three other species growing inside the *Brachypodietum ramosi* (DELEUIL 1954).

In addition to the papers cited here as an example there exists a very extensive literature touching upon the problem of allelopathy through root excretions. These papers deal either with the incompatibility of certain plants when growing together or with cases where certain plants grow better in the neighbourhood of others. The greater part of these investigations has been reviewed by GRÜMMER (1955). Though in many cases there are good indications for an allelopathic interaction (see *f.i.* OSVALD 1950, VARMA 1938 *etc.*) the irrefutable experimental proof is missing[1].

[1] See also RADEMACHER's contribution „Gegenseitige Beeinflussung höherer Pflanzen" in Vol. XI, p. 655 of this encyclopaedia.

III. Allelopathy between host and parasite.

A. Higher plants as host and parasite.

The germination of the seeds of some parasitic and hemiparasitic higher plants depends at least partly on the presence of certain substances contained in the tissues of their host plants (review in R. BROWN 1946), BROWN'S chapter "The germination of angiospermous parasite seeds" in this encyclopaedia, Vol. XV, part 2, and WILLIAMS 1958). The majority of the seeds of the parasitic *Striga lutea* germinate only in the proximity of a host root. SAUNDERS (1933) found that *Striga* seeds germinated when treated with water which had passed through sand in which host roots were growing. Seeds moistened with pure water did not germinate. In enlarging these experiments R. BROWN and EDWARDS (1944, 1946) proved conclusively that the majority of *Striga* seeds germinate only when exposed to a stimulating material secreted by the host root. Only a small proportion of the seeds is able to germinate without this stimulus. The concentration gradient of the stimulant is responsible for the fact that the germination percentage is a function of the proximity of the *Striga* seeds to the roots of the host (Fig. 10). The stimulating material is secreted by the root tip of the host plant. The effect of the stimulant was greatly increased when the seeds, before being treated with the stimulant, were soaked in water at 22—30° C for varying periods. The effect of the pretreatment is a function of time. At 22° C *f.i.* an optimum effect of the stimulant is reached after about 21 days. Longer treatments bring about a decrease in the efficiency of the stimulant. The same pretreatment increases the germination percentage of the seeds germinating in the absence of the stimulating substance. Other experiments determined the effect of different concentrations of the stimulant at different stages of pretreatment. It is concluded that during pretreatment the seeds themselves form a stimulant which accumulates up to the optimum period of pretreatment and then disappears gradually. In order to germinate the seeds need a critical level of the stimulant either produced by the seeds themselves or supplied from the root of the host. The chemical nature of the stimulant or stimulants is as yet unknown. They are not identical with the known vitamins and plant hormones and can partly be replaced by thiourea and allylthiourea (R. BROWN 1946).

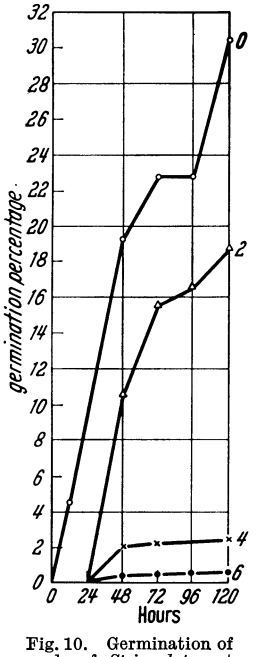

Fig. 10. Germination of seeds of *Striga lutea* at various distances (0, 2, 4, 6 cm) from roots of *Sorghum vulgare*. (After BROWN and EDWARDS 1944.)

Another case of allelopathy similar to that of *Striga lutea* was investigated in detail by VALLANCE (1950, 1951a, b). ANDREWS (1945) reported that the seeds of the hemiparasite *Striga hermonthica* germinate only in the presence of a suitable stimulator. VALLANCE (1950) found this to be present in water in which roots of *Sorghum vulgare*, one of the host plants of *Str. hermonthica*, had grown previously. In this case the germination is not exclusively dependent on the presence of a substance secreted by the host root. Pretreatment and after ripening may bring about germination of the seeds not treated with the stimulant up to 42% (Fig. 11). VALLANCE (1951a, b) succeeded in clarifying to some extent the physiological action of the stimulant, by showing that the stimulant enhances aerobic respiration and anaerobically the carbon dioxide output of the stimulant treated

seeds. But there was no correlation between the stimulation of germination brought about by the stimulant and its stimulating action on respiration. The stimulant always increased respiration even in seeds without pretreatment, whose germination was very little enhanced by the treatment with the stimulant. VALLANCE concluded from further experiments that the germination of the seeds of *Str. hermonthica* depends on the accumulation of some metabolite during pretreatment and that the stimulant can effect germination only when a sufficient amount of this metabolite is present.

The stimulation of respiration produced by the stimulant is attributed to an increase of the permeability of the seeds (their perisperm ?) to gaseous diffusion. BROWN *et al.* (1949/50) tried to isolate the stimulant ("Striga factor") from the root exudate of *Sorghum vulgare*. They found that D-xyloketose has the same effect as the stimulant and thought it probable that the activity of the natural stimulant is due to a substance very similar to or identical with D-xyloketose. But is it reported in a later paper (BROWN *et al.* 1952) that no xyloketose could be found in the solutions of the natural stimulant with paper chromatography. The authors conclude that the stimulation of germination by the "Striga factor" may be due to a complex of substances present in a resinous product obtained after chromatography on a cellulose column. The physiological effect of the stimulator was found to consist in stimulation of cell extension in the roots (BROWN, ROBINSON and JOHNSON 1949, 1949/50). BROWN and ROBINSON (1949) agree with VALLANCE that the primary effect of the stimulant may be on respiration and that as result of a stimulated respiration cell extension is promoted bringing about germination.

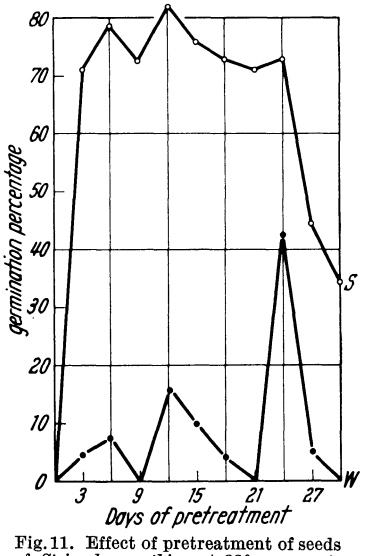

Fig. 11. Effect of pretreatment of seeds of *Striga hermonthica* at 22° on germination in the presence of *Sorghum* root-water (*S*) and in water (*W*) at 32°. (After VALLANCE 1950.)

The seeds of another angiospermous root parasite *Alectra vogelii* behave very much like those of the two *Striga* species. Their germination is dependent on the root exudate of their host plant (BOTHA 1948), pretreatment is necessary for the full effect of the stimulant but is ineffective in the absence of oxygen (BOTHA 1950). BOTHA (1950, 1951) comes to conclusions very similar to those of R. BROWN concerning *Striga i.e.* that the seed during pretreatment forms a substance necessary for germination which is the same as or similar to the stimulator secreted by the root of the host. The stimulator is an unstable substance and is not identical with heteroauxins, thiamin, riboflavin, nicotinic acid, amide, pyridoxine or ascorbic acid. Its chemical nature remains unknown. MEISSNER (1951) found that in contrast to *Striga lutea* the stimulant in the case of *Alectra* is not produced by the root tip but by the root hairs or that zone of the root which carries the root hairs.

The oldest known case of allelopathy concerning the germination of seeds of parasitic angiospermous plants is that of *Orobanche* (see older literature in BROWN, GREENWOOD, JOHNSON and LONG 1951 and GRÜMMER 1955). Here too a chemical stimulant is released from the root of the host plant bringing about the germination of the *Orobanche* seeds. The stimulant can be obtained as a dry residue from aqueous extract of host roots, is absorbed on charcoal and contains most probably an acidic or potential acidic group (BROWN, GREEN-

WOON, JOHNSON, LONG and TYLER 1951). In the case of *Orobanche crenata* KADRY and TEWFIC (1956) have shown that the host plant *(Vicia faba)* secretes the stimulant from its roots only one week before flowering.

B. Higher plants as host and microorganisms as parasites.

a) Germination of parasite.

After the classical papers of W. BROWN (1922a, b) it is well established that the germination of the spores of a considerable number of parasitic fungi depends on the presence of substances excreted by their host plants (review of older literature in W. BROWN 1936 and R. BROWN 1946). In some cases of stimulated germination reported by W. BROWN (1922a) the stimulation could have been produced by an "extraneous source of food" found in exudates of the leaves in which the spores germinated. This could not have been the case when the germination of the spores was inhibited or in those cases where a volatile substance was responsible for the allelopathic action of the host plant (W. BROWN 1922b). Water soluble phenols found in the dry outer scales of onions prevent germination of spores of *Coletotrichum circinans* (LINK *et al.* 1929, 1933, see also p. 717). Lately KOVÁCS and SZEÖKE (1956) could show that the germination of the spores of a number of fungi as *f.i. Botrytis cinerea* in an infection drop was markedly influenced (stimulated or inhibited) by the presence of substances exuded by the leaves of different plants. They conclude that under natural conditions these substances are able to inhibit the germination of the conidia of *Botrytis*. Probably the resistance of the host to certain fungal infections is a function of these chemically yet unknown substances as already stated by SUCHORUKOW (1952).

COLEY, SMITH and HICKMAN (1957) reported that the sclerotia of *Sclerotium cepivorum* (white rot disease of onions) germinated in soil or in sand only in the presence of onion roots without direct contact between root and sclerotia. Water extracts of roots of onion, shallot and leek had the same effect whereas the extracts of cabbage, brussel sprout and barley were ineffective. This shows that the roots of the host plant secrete some substances necessary for the germination of the conidia. Root excretions are apparently also involved in those cases where the conidia of certain soil fungi germinate in the soil only in the presence of seedling roots of peas, wheat and lettuce (JACKSON 1957). BARTON (1957) reported a similar case. Oospores of *Pythium mamillatum* put on glasstapes in soil germinated only when buried beneath turnip seedlings. When put into petri dishes the oospores germinated only when germinating turnip seeds were present. Exudates from turnip seedlings had the same effect. It is concluded that a stimulant is liberated from the turnip seedlings (possibly from the roots) which activates under natural conditions the germination of the oospores.

The importance of these facts for the rhizosphere phenomenon will be discussed later.

b) Secretions of parasite[1].

1. Hormones and enzymes.

As the secretion of hormones and enzymes by microorganisms like fungi *etc.* belongs to other chapters of this encyclopaedia we just want to point out that in a number of cases allelopathy in host-parasite relationship is based on the secretion of hormones and enzymes by the parasite.

[1] For this and the following chapter on "disease resistance of host" see also the contribution of KERN „Parasitismus und Symbiose. Allgemeines" to this encyclopaedia, Vol. XI, p. 429.

A classical case is the infection of rice plants by *Gibberella Fujikuroi* (Bakanae disease) where the fungus secretes gibberellins bringing about an enormous elongation of the host (see Voh. XV of this encyclopaedia).

In other cases the parasite produces indole-acetic acid and secretes it into the tissues of the host thus inducing morphological changes (GRIEVE 1939, 1941, MOULTON 1942, WOLF 1952, 1956, BERDUCON 1949, 1957). A most interesting case was lately reported by PILET (1957). The leaves of *Euphorbia cyparissias* when attacked by *Uromyces pisi* contain more auxin than the uninfected leaves. This is not caused by auxin production of the parasite. It is brought about through an "anti-enzymatic toxin" produced by the fungus which inhibits the auxin-oxidase activity of the host and so results in an abnormal accumulation of auxins. This is apparently the reason for the morphological changes in the host connected with its infection by *Uromyces*. The same was reported for *Euphorbia verrucosa* when infected by *Uromyces scutellatus*.

The secretion of pectic enzymes by certain pathogens is, in addition to wilting toxins one of the causes of the wilting diseases (review in DIMOND 1955). Replacement cultures of the incitant of the *Fusarium* wilt *(Fusarium oxysporum* f. *lycopersici)* of tomatoes and other plants contained a substance which produced some of the wilt symptoms *i.e.* browning of the vessels and wilting. The same was true for another wilt producing pathogen, *Pseudomonas solanacearum* (GOTHOSCAR *et al.* 1953, WINSTEAD and WALKER 1954). The substances responsible were pectinmethylesterase (PME) produced in great quantity by the pathogens and polygalacturonase present in much smaller amounts. Artificial enzyme preparations given to tomato cuttings produced the same wilt-symptoms. PIERSON *et al.* (1955) found histological identity between tomatoes treated with PME and wilt infected ones. WAGGONER and DIMOND (1955) reported PME in the vascular sap of wilt infected tomatoes apparently produced by the pathogen. *Fusarium vasinfectum*, the incitant of cotton wilt, also causes a marked increase in PME activity *in vivo* in the infected plants (LAKSHMINARAYAN 1957a) together with a pronounced depletion of the pectin reserves of the host (LAKSHMINARAYAN 1956). The PME formation by the fungus is of an adaptive nature (LAKSHMINARAYAN 1957b). The pectic enzymes produced by the parasite apparently hydrolyze the pectins of the host inside the infected vessels (pits?). The products of this hydrolysis form gums and gels plugging the vessels and causing wilting. KLÜPFEL (1957) suggests that one of the wilting toxins *i.e.* Vasinfuscarin belongs to this group of pectic enzymes.

We may mention here that there is good evidence that the first step of attack of certain soft-rotting bacteria on their host is the secretion of pectic enzymes (FERNANDO and STEVENSON 1952, W. BROWN 1955, LAPWOOD 1957). Possibly the same type of pectolytic enzymes is responsible for the maceration of the host cell walls and the killing of the host protoplasts produced by *Botrytis cinerea* and *Bacterium aroideae* (TRIBE 1955, FUSHTEY 1957).

2. Wilting toxins.

Already in his review on host parasite relations W. BROWN (1936) has pointed out that a number of investigators, who were concerned with wilt diseases, were inclined to accept the theory that the fungi causing the disease excreted toxins which are responsible for at least some symptoms of the disease. We will restrict ourselves here to only one of the wilt diseases, the *Fusarium* wilt of tomato caused by *Fusarium lycopersici* a fungus the mycelium of which infects

the tomato plant through the roots[1]. It penetrates to the vascular tissues. The mycelium grows inside the xylem elements through the whole plants. The main symptoms of the disease are epinasty of the leaves, vascular discoloration and wilting. As already mentioned earlier (p. 694) the epinasty is apparently caused by ethylene produced by the fungus. Are vascular discoloration and wilting brought about allelopathically through some substances produced by the fungus? Already the observation that the symptoms appear at some distance from the mycelium indicates an affirmative answer to our question. We cite DAVIS (1954) who found that after grafting eggplant, tobacco or *Physalis* which are immune to the disease on an infected tomato plant the immune scions develop the two symptoms mentioned though no fungus could be detected in the scions. KERN and SANWAL (1954) using radioactive carbon showed that *Fusarium* excretes inside the infected tomato plant toxic substances, which move upwards and cause the characteristic symptoms in parts of the host free of the fungal mycelium.

Another indication lies in the fact that from the filtrates of pure cultures of *Fusarium lycopersici* 5 toxins could be isolated, which, when applied to cut tomato plants, produced some of the symptoms of the wilting disease. They are: Lycomarasmin (CLAUSON-KAAS *et al.* 1944, PLATTNER and CLAUSON-KAAS 1945, GÄUMANN, NAEF-ROTH and MIESCHER 1950), Fusaric acid (GÄUMANN, NAEF-ROTH and KOBEL 1952a, b), Vasinfuscarin (GÄUMANN, STOLL and KERN 1953), Dehydrofusaric acid (STOLL, RENZ and GÄUMANN 1957) and lycomarasmic acid (GÄUMANN and NAEF-ROTH 1959). But the occurrence of these toxins in the culture filtrates does not yet prove their role in the syndrome of the infected plant as has been pointed out by DIMOND and WAGGONER (1953b) and by DIMOND (1955). For this one needs at least one more additional proof, *i.e.* the production of the toxins inside the infected plant. This proof has been brought by LAKSHMINARAYAN and SUBRAMANIAN (1955) and KERN and KLÜPFEL (1956) for fusaric acid. They have shown that this toxin is a vivotoxin *i.e.* is produced inside the infected host (definition of term vivotoxin according to DIMOND and WAGGONER 1953a: Substance produced in infected host by pathogen and/or host and functional in disease production). The same vivotoxin has been found in cotton plants infected with *Fusarium vasinfectum* (KALYANASUNDARAM and RAM 1956).

There still remain many questions regarding the allelopathic action of the wilting toxins. We will mention only the following:

1. Some of the toxins are also produced by other fungi which do not cause wilting phenomena. This is true *f.i.* for fusaric acid first isolated from *Fusarium heterosporum* an unspecific parasitic fungus (see GÄUMANN 1957a).

2. Apparently fusaric acid is not formed inside the thallus of the fungus as it could not be found in the mycelium (KLÜPFEL 1957). It is possible that it is produced extracellularly by enzymatic action of the fungus on the substrate present in the host.

3. SANVAL (1955/56) using radioactive carbon has shown that fusaric acid is changed chemically inside the tomato plant. It is possible that not the acid itself but one or more of its conversion products causes the disease symptoms. GÄUMANN (1958) reported that about 10% of the fusaric acid given to the host plant was decarboxylated after 48 hrs. The new compound is apparently more toxic than fusaric acid. About 8—24% underwent methylation thereby becoming non-toxic.

[1] There are other wilting toxins produced by various fungi as for instance baccatin (from *Gibberella baccata*), culmomarasmin (from *Fusarium culmorum*) and skyrin (from *Endothia parasitica*) (GÄUMANN, KERN and OBRIST 1959).

4. The physiological action of the wilting toxins is not clear. TAMARI and KAJI (1952, 1953) assume that fusaric acid acts in forming water insoluble chelates with metals without which the host cannot carry out its normal metabolic actions as has been postulated for lycomarasmin. Another theory assumes that the toxins change the permeability of the cells (SCHEFFER and WALKER 1953, BACHMANN 1956, GÄUMANN and LOEFFLER 1956/57). Possibly both effects are inter-related (NAEF-ROTH and REUSSER 1954, BACHMANN 1956, GÄUMANN 1958).

5. It is not yet clear how far the syndrome of the wilting disease is not produced by a single toxin but by the combined action of the different toxins including ethylene (see GÄUMANN 1957b).

3. Other vivotoxins.

There are some other cases where vivotoxins cause diseases. We mention only the following: BRAUN (1950) found that *Pseudomonas tabacci* the pathogen of the wildfire disease of tobacco produces a toxin in culture and host which brings about the symptoms of the disease. As l-methionine overcomes the toxic effect, it is thought that the toxin prevents the normal utilisation of methionine.

In the *Helminthosporium* blight of oats the pathogen forms an extra-cellular toxin diffusing through the host and producing the symptoms of the disease. This vivotoxin belongs to the most potent known (0.01 μg/ml inhibits growth of oat roots) and is perhaps a polypeptide (PRINGLE and BROWN 1957). *Helminthosporium sativum* attacking barley produces a phytotoxin capable of killing the cells of its host (LUDWIG 1951). *Alternaria solani* the organism causing tomato early blight produces in culture and in the host the antibiotic alternaric acid (BRIAN *et al.* 1949, BRIAN and WRIGHT 1950). As the filtrate of the pathogen and the cristalline substance isolated from it produce the symptoms of early blight, it is highly probable that alternaric acid is the vivotoxin responsible for the syndrome of early blight (POUND and STAHMANN 1951).

SAUTHOFF (1955) and GENTILE (1951) found in culture filtrates of *Botrytis cinerea* a phytotoxic agent. RIBEREAU-GAYON *et al.* (1952) report that the same fungus forms an antibiotic active against *Saccharomyces*. We do not yet know if the two agents are identical and whether they are vivotoxins.

c) Disease resistance of host.

1. Herbaceous plants[1].

The best investigated case, where disease resistance is based on the presence of an antibiotic substance, is that of the onion smudge caused by *Colletotrichum circinans* (see WALKER and STAHMANN 1955). Onion varieties with pigmented bulb scales are resistant to this disease only as long as the *dry* outer scales are present. These contain water soluble phenols such as protocatechuic acid and catechol (LINK *et al.* 1929, 1933) which diffuse into the surface and as potent antibiotics prevent germination of the pathogen's spores and infection. The living fleshy scales apparently contain these phenols in a bound non-diffusable form and can therefore not prevent the infection. WALKER (1926) reports that the same phenolic compounds are one of the causes of the resistance of coloured onion bulbs against neck rot (*Botrytis* spp.). In the case of the common scab disease of the potato tuber, caused by *Streptomyces scabies*, polyphenolic compounds present in the periderm of the tuber seem to be the reason for the disease resistance of certain varieties. The periderm of the scab resistant varieties was

[1] See older literature in BALDACCI (1942) and GÄUMANN (1951).

consistently found to contain much higher concentrations of chlorogenic acid and of total o-dihydrophenols than the periderm of the scab susceptible ones (SCHAAL and JOHNSON 1955, JOHNSON and SCHAAL 1957).

BURROWS (1958) reported a most interesting case. The guttation fluid of a wheat variety ("Lee") resistant to certain races of *Puccinia graminis* inhibited germination and growth of uredospores of the same races of the rust to which the wheat variety was resistant. With the less resistant variety "Marquis" there was good correlation between the inhibition caused by the guttation fluid and the resistance of this wheat variety towards the rust races tested.

The strongly antibiotic volatile sulfides contained in onion juice also contribute to the resistance of onions against certain diseases as *f.i.* neck rot (HATFIELD *et al.* 1948, WALKER and STAHMANN 1955). WHITNEY and MORTIMORE (1959) found an antifungal substance in young corn stalks the presence of which is apparently the reason for the fact that stalks of young corn of certain varieties are not attacked by *Fusarium moniliforme* or *Gibberella zeae*. This substance is 6-methoxybenzoxazolinone (LUDWIG *et al.* 1960). Barley also contains an antifungal factor which "appears to be of significance in relation to *Helminthosporium* resistance" (LUDWIG *et al.* 1960).

Another interesting case is the relation between the known disease resistance of black mustard against the clubroot fungus *(Plasmodiophora brassicae)* and the presence of mustard oils. ROCHLIN (1933) suggested that the black mustard is resistant because it contains mustard oils in much higher concentration than other cruciferous species susceptible to the disease. According to evidence discussed by WALKER and STAHMANN (1955) this is not true for the following reasons: 1) From populations of the black mustard a resistant and a susceptible variety were isolated. Both contained the same amount of mustard oil. 2) By growing the resistant variety without sulphur the formation of mustard oils was prevented without affecting the resistance against *Plasmodiophora*. 3) Resistant varieties of *Brassica oleracea* were developed which are more or less free of mustard oils. We bring this case here because it is a classical example that the presence of a very potent antibiotic in a plant cannot be taken as a proof of the biological function of the same antibiotic under natural conditions.

In some cases the presence of different alkaloids is claimed to be responsible for disease resistance of certain plants. GREATHOUSE (1938) drew attention to the fact that alkaloids are to be found especially in the roots of plants resistant to *Phymatotrichum* root rot. In the case of *Mahonia trifoliata* and *M. swaseyi* which grow undamaged in regions infected with the cotton root rot *(Phymatotrichum omnivorum)* 1.33—2.25% resp. 2.15—2.48% of the dry weight of the roots is the alkaloid berberine. This is about sixty five times the concentration which in cultures completely prevented the growth of *Phymatotrichum*. The cells containing berberine form a continuous layer surrounding the root beneath the periderm constituing an anti-infection ring protecting the root against *Phymatotrichum* (GREATHOUSE and WATKINS 1938).

In the case of the *Amaryllidaceae*, which are also immune against *Phymatotrichum*, another alkaloid (Lycorine) is thought to contribute to their immunity (GREATHOUSE and RIGLER 1941). The same is reported for *Sanguinaria canadensis* where other alkaloids are thought to make the plant immune against *Phymatotrichum* (GREATHOUSE 1939). The alkaloid tomatin which is produced by the tomato plant (SANDER 1956) was suggested by different authors (see KERN 1952) to make the tomato resistant against *Fusarium lycopersici*. KERN (1952) proved that this is not true.

Special mention should be made here of the "phytoalexins" of MÜLLER (1956, 1958). He found that the cells of bean pods infected with *Sclerotinia fruticula* or *Phytophtora infestans* form an antibiotic factor ("phytoalexin") as a result of the interaction between host and pathogen. These phytoalexins are supposed to be responsible for the formation of necrotic tissue by the host which form a protective wall against the further penetration of the pathogen and for the killing of the infecting pathogen. This interesting theory needs further clarification.

2. Wood.

Special mention has to be made of the fungicidal substances contained in the heartwood of different trees as in this case the biological function of these substances under natural conditions has been established.

The heartwood of different species of trees has been known for quite some time to be resistant to certain wood decaying fungi and harmful insects (see literature in ERDTMAN 1952, ANDERSON and ZAVARIN 1958). This resistance is attributed to a number of antibiotic compounds which have been isolated.

Thuja plicata contains α-, β- and γ-thujaplicin three highly toxic topolones (ERDTMAN and GRIPENBERG 1948, GRIPENBERG 1948, GRIPENBERG and ANDERSON 1948, RENNERFELT and NACHT 1955). *Chamaecyparis nootkatensis* contains the highly fungistatic nootkatin and chamic acid (RENNERFELT and NACHT 1955), different species of *Pinus* pinosylvin and pinosylvinmonomethylester *etc.* (RENNERFELT and NACHT 1955). As *f.i.* γ-thujaplicin and nootkatin inhibit fungus growth at a concentration of 0.001—0.002% and constitute 0.05 resp. 0.03% of the heartwood it can reasonably be assumed that these substances play an important role in the natural decay resistance of the heartwood in which they are contained. Lately ANDERSON and ZAVARIN (1958) reported the isolation of a number of compounds from the wood of *Librocedrus decurrens* which had a decay inhibiting action against four wood destroying fungi. The most potent ones were λ-thujaplicin, p-methoxythymol and hydrothymoquinone. The fact that with ageing of the wood in the tree the decay resistance generally decreases is attributed to chemical changes of the antibiotic substances. One of these changes could be the dimerisation of the highly active p-methoxythymol to the ineffective librocedrol.

IV. Allelopathy in mycorrhiza and rhizosphere.

A. Mycorrhiza[1].

Though the physiological relations between mycorrhizal fungi and mycorrhizal host are not yet very clear (see review in MELIN 1953 and LEVISOHN 1958) there seem to be a few cases of allelopathy between fungus and host.

Already BERNARD (1911) and NOBÉCOURT (1923) have observed that with different *Ophrydeae* the mycorrhizal fungus *Rhizoctonia repens* regularly penetrates into the roots of the orchid but almost never enters into the tuber. When parts of the tuber were put in agar cultures at some distance in front of the growing mycelium of the fungus the hyphae were arrested in their growth at some distance from the tuber pieces. The authors ascribed this to the diffusion of a fungistatic substance contained in the tuber into the agar. GÄUMANN and JAAG (1945) confirmed this and showed that the tubers of *Orchis militaris* behaved in the same way. Additional experiments (GÄUMANN, BRAUN and BAZZIGHER 1950) proved that the amount of the fungistatic substance increased four-fold when

[1] See also MELIN's contribution "Mycorrhiza" to this encyclopaedia, Vol. XI, p. 605.

the tubers were exposed to the influence of the fungus. They conclude from this that the fungistatic substance is produced by the tuber as the result of an anti-infection defense reaction („Abwehrreaktion") of the tuber tissue against the fungus and that this is the reason for the localisation of the mycorrhizal fungus in the roots and for its non-penetration into the tuber. The substance is not specific as it is effective not only against *Rhizoctonia* but against *Fusarium solani* as well. Lately GÄUMANN and KERN (1959a, b, c) have isolated this "antibody". It is orchinol (a cryptophenol?) with the brutto formula $C_{16}H_{16}O_3$. Something similar is reported by MACDOUGAL and DUFRENOY (1946) for tree mycorrhizas where gummy tannin masses especially in cells of the pericycle and endodermis of the mycorrhizal roots form a barrier to the further penetration of the mycorrhizal hyphae.

Another case of possible allelopathy concerns the mycorrhiza of trees. It is a fact well proven by observation and experiment that the growth of trees having mycorrhiza, is stimulated in the presence of mycorrhizal fungi even when the fungi do not come in contact with the roots and do not form mycorrhizas (LEVISOHN 1953). RAYNER and NEILSON-JONES (1944) had already observed that the stimulation to tree growth by the mycelia antecedes the formation of the mycorrhiza. The same results were obtained by LEVISOHN (1956) when she tested the influence of the free living mycorrhizal mycelia of four different fungi on the development of tree seedlings. Two of them *(Rhizopogon luteolus, Boletus scaber)* brought about growth stimulation of the seedlings before infection took place. This stimulation may be due to a direct allelopathic influence or it may be caused indirectly by the fungus which decomposes organic matter in the soil, making nutrients available to the roots. There is one fact which speaks for the first alternative, without giving definite proof. SLANKIS (1948) when cultivating isolated pine roots together with mycelia of different mycorrhizal fungi found that the fungi, before contacting the roots, caused the dichotomous branching so typical for mycorrhizal roots. As the exudates of one of the fungi had the same effect it may be concluded that the fungi excrete a substance which causes the roots to change their normal growth habit.

There are some indications that not only the fungi affect the mycorrhizal host but that the host also influences the fungus allelopathically. MELIN (1954) cultivated aseptically isolated pine roots to which mycelia of different mycorrhizal fungi were added. In the culture solution whih contained in addition to the normal nutrients needed for fungus culture the known B-vitamins, purine and pyrimidine and the amino acids in caseine hydrolysates the mycelia were very much stimulated by the roots. Apparently they produce and excrete a substance not identical with the above mentioned ones which stimulates the growth of the fungi ("Factor M", MELIN and DAS 1954). As different fungi were affected and as not only pine roots but roots of tomato, *Lepidium*, *Triticum etc.* (MELIN and DAS 1954) also stimulated this substance cannot be specific. Pea roots differed from other roots, as they inhibited growth of the fungi after initial stimulation (MELIN and DAS 1954). Naturally these experiments with excised roots are no proof that under natural conditions roots will exert the same influence.

Another instance of a higher plant influencing mycorrhizal fungi has to be mentioned here. HANDLEY (unpublished data, cited in LEVISOHN 1956) reported that extracts of *Calluna* raw-humus cause total growth inhibition of a number of mycorrhizal fungi, a fact which could explain why in certain plant associations mycorrhizas are not easily formed. The question how far antifungal substances present in certain soils may effect mycorrhizae and mycorrhizal fungi is not discussed here (see MELIN 1953).

A problem of allelopathy worthy of further investigation concerns the germination of orchid seeds, as the results obtained so far are not very clear. BERNARD (1904), BURGEFF (1936), RAMSBOTTOM (1927) and others (see CURTIS 1939) have maintained that the seeds of green autotrophic Orchids can germinate and produce normal seedlings only in the presence of their mycorrhizal fungi. BURGEFF (1934) and CAPPELLETI (1935) have shown that the dead mycelium stimulates as well as the living one. They concluded therefore that an unknown compound is produced by the fungi which is necessary for the germination of the Orchid seeds. As the same stimulation is produced by extracts of different organs of higher plants the stimulant is unspecific (a vitamin or growth hormone ?) (SCHAFFSTEIN 1938). On the other hand we know since KNUDSON (1922) that Orchid seeds can be germinated in the absence of any fungus if provided with soluble sugars. CURTIS (1939) states "that Orchid seeds will germinate without the aid of any fungus or other microorganism provided they are supplied with an adequate mineral nutrient solution and a suitable sugar at the proper hydrogen-ion concentration". This is certainly true but the question remains if in nature, when no proper soluble carbohydrate is available, the germination of the Orchid seeds is not more or less completely dependent on the presence of fungi. These fungi do not have to be the same fungi which form mycorrhizae with the Orchids (CURTIS 1939). The action of the fungi may either be a direct allelopathic one as suggested by BURGEFF (1936) and others or it may be that they affect germination in decomposing insoluble carbohydrates and making them soluble and therefore available to the seeds. That soluble sugars are enzymatically formed from insoluble carbohydrates by soil fungi has been proved by a number of investigators (see *f.i.* NORKRANS 1950).

Saprophytic orchids devoids of chlorophyll seem to be more dependent on mycorrhizal fungi as far as their germination is concerned. Thus DOWNIE (1940, 1943) has found that the addition of soluble sugars to the germination medium does not bring about germination and does not substitute for the fungi.

The probable allelopathic hormone (auxin) — vitamin relationship between both partners of mycorrhizae (see MACDOUGAL and DUFRENOY 1944 and MELIN 1953) is not treated here as this will be done in other chapters of this encyclopaedia.

B. Rhizosphere.

In their review on soil microorganisms and the rhizosphere KATZNELSON *et al.* (1948) state: "That bacteria, actinomycetes and fungi of the soil find the root zone a more congenial environment for development than soil apart from the root is now generally accepted." This statement is born out by a great number of investigations (review in KATZNELSON *et al.* 1948 and STARKEY 1929). The extreme rhizosphere effect is apparently observed in desert conditions where the soil at a short distance from the roots is almost sterile and only the rhizosphere contains a microflora (SABININ and MININA 1932 and others).

The question is how far is the rhizosphere effect based on an allelopathic interplay between the roots and the microorganisms.

As pointed out already on p. 709 there is good proof that the roots of many higher plants give off amino acids into the soil. A great number of authors of which we only cite WEST and LOCHHEAD (1940), LOCHHEAD and THEXTON (1947, 1952) and GYLLENBERG 1956) have found that the development of bacteria requiring and stimulated by amino acids is greatly favoured in the rhizosphere. It can therefore be assumed that the amino acids excreted by plant roots are

one of the reasons for the greatly enhanced growth of these bacteria in the rhizosphere in comparison with the "non-rhizosphere" soil. The same is apparently true for the amino acids formed when plant litter is decomposed (KNAPP and LINSKENS 1954).

It has been shown in a number of cases that the roots exert an inhibiting influence on the rhizosphere microorganisms. CLARK (1940) and LOCHHEAD (1940) report that some plants inhibit the growth of certain bacteria in their rhizosphere. METZ (1955) found that the roots of several gramineae inhibit the development of rhizosphere bacteria of other plants as well as that of non-rhizosphere bacteria. The woody parts of some roots of trees and shrubs have an inhibiting effect on soil bacteria dependant in their growth on amino acids (GYLLENBERG and HANIOJA 1956). Only in one case is the chemical agent responsible for the inhibition of a rhizosphere organism known. A wilt resistant variety of flax excretes hydrocyanic acid into the soil and this excretion inhibits certain fungi as *f.i. Fusarium* (TIMONIN 1941).

The litter of dead plants and parts of plants can also in some cases be the cause of inhibition of soil microorganisms. MELIN and WIKEN (1946) reported the antibacterial activity of cold water extracts from litter of leaves of *Acer platanoides*. BENDZ (1956) identified gallic acid as the active agent. BÖRNER (1957) suggests that the four phenolic inhibitors found in the left-over roots and straw of rye, barley and wheat (see p. 707) inhibit the growth of soil microorganisms. Though there is no experimental proof it is probable that litter in general has a profound allelopathic influence on the microbiological equilibrium of the soil flora and on the rhizosphere and this in turn influences the growth of higher plants growing in that soil (KRASSILNIKOV 1949). But this is a speculation as we do not possess experimental proof obtained under natural conditions.

Another case of possible allelopathy in the rhizosphere concerns the claim made by a number of Russian authors (ZUKOVSKAYA 1941, KRASSILNIKOV 1944, 1949, ISAKOVA 1936, 1937, BEREZOVA 1950) that different plant species have a specific rhizosphere flora typical for each species (see also KATZNELSON *et al.* 1948). MENON and WILLIAMS (1957) also report that the microflora associated with different crops appears to be specific. If this is true we must conclude with KATZNELSON *et al.* (1949): "Sloughed of root fragments ... and excretion of specific and perhaps characteristic substances may favour the development of a rhizosphere microflora typical of a particular plant." Unfortunately here again experimental proof of such a far reaching allelopathy is lacking. We may mention here that some Russian authors (CHOLODNY 1934, 1944, TOKIN 1956) believe that volatile organic compounds given off by higher plants like *f.i.* ethylene and "phytoncides" influence soil microorganisms in their growth.

V. Allelopathy between microorganisms.

When antibiotics were first discovered many biologists thought that their biological function was an allelopathic one *i.e.* that they were produced in order either to protect the organisms against infection or to suppress other competing organisms living in the surrounding of the producer.

WAKSMAN (1950), THIMANN (1955) and others have pointed out that under natural conditions this is not the case. Their main arguments are: (1) Under natural conditions *f.i.* in the soil most antibiotics are easily destroyed or inactivated by decomposition through microorganisms, adsorption on soil particles,

oxidation, *etc.*[1] (2) The production of antibiotics depends much on special nutritional conditions rarely realised under natural conditions. (3) The antibiotic forming organisms often fail in competition with organisms not producing antibiotics. Though this is certainly true for many antibiotics we are not sure if this completely negative attitude is really justified. Without going to the other extreme represented by most Russian authors (see *f.i.* TOKIN 1956) who look at most antibiotics as a weapon of the producer in the struggle for existence we would like to cite a few cases chosen from among antagonistic organisms (reviewed in WOOD and TVEIT 1955) where the antagonism under natural conditions seems to be based on the production of antibiotics. With WOOD and TVEIT (1955) we define antagonism as "any activity of one organism which in some way adversely affects another growing in association with it".

In pure culture the fungus *Trichoderma viride* is a strong antagonist of *Rhizoctonia solani* and a number of other fungi due to the secretion of a strong toxin (WEINDLING 1932, 1934). The toxin was shown to consist of two antibiotics, gliotoxin and viridin (WEINDLING and EMERSON 1936, WEINDLING 1941, BRIAN and HEMMING 1945, BRIAN 1951).

The damping-off disease of citrus seedlings is caused by *Rhizoctonia. Citrus* seedlings grown in peat at p_H 4.5 which was put on soil inoculated with *Rhizoctonia* were infected. When a suspension of spores of *Trichoderma* was added to the peat the disease did not develop. *Trichoderma* in alkaline peat was ineffective in preventing the disease. Addition of sand or soil to the peat reduced the effectivity of *Trichoderma*. When normal soil was used at different p_H a strongly acidic soil always decreased the incidence of the disease (WEINDLING and FAWCETT 1936). As gliotoxin is stable only at an acid p_H and as the soils used contain *Trichoderma* the results can be explained by the excretion of gliotoxin by *Trichoderma*. On the other hand gliotoxin was found only in sterile soils infected with *Trichoderma*, but not in non-sterile soils (EVANS and GOTTLIEB 1952).

In the experiments of ALLEN and HAENSELER (1935) and HAENSELER and ALLEN (1934) *Trichoderma viride* grown on sterile soils was added to sterile or unsterile soil infested with *Rhizoctonia*. It decreased the disease incidence of pea and cucumber seedlings.

WOOD (1951) grew lettuce seedlings on sterilized sand or soil infected with *Rhizoctonia*. When *Trichoderma* was added the damping-off disease caused by *Rhizoctonia* did not occur. The same experiment carried out with unsterilized soil did not result in permanent control of the disease.

The damping-off disease of alfalfa caused by *Pythium* could be controlled when *Trichoderma* was added to sterile soil infected with *Pythium*. In unsterilized soil no results were obtained. But addition of *Trichoderma* and oat straw to unsterile soil again gave positive results (GREGORY *et al.* 1952). When white mustard seedlings were grown in soil infected with *Pythium* and were dusted with spores of *Trichoderma* the disease caused by *Phytium* could be controlled. Of the three strains of *Trichoderma* the gliotoxin producing one was most effective, the viridin producing one less and an antibiotically inactive one least (WRIGHT 1956a). Gliotoxin could be chromatographically identified on the coats of the seeds dusted with *Trichoderma* spores (WRIGHT 1956b).

[1] This is true for many antibiotics but not for all. WINTER (1957) added streptomycin to soil and could recover it unchanged 16 days later. WINTER and coworkers claim (see WINTER 1957) that soil contains always antibiotics of microbial or other origin in such amounts as to be together with nutrients the most important limiting factor for the development of soil microorganisms. WRIGHT (1956b) detected gliotoxin chromatographically in the seed coats of pea seeds sown in soil containing a gliotoxin producing strain of *Trichoderma viride*.

A very interesting contribution was made by BLISS (1941, 1951) showing how complex our problem is. *Armillaria mellea* causes root rot of *citrus* in California. Fumigation of the soil with carbon disulphide eliminates the disease. But fumigation of sterilized soil containing the pathogen was ineffective as *Armillaria* was not killed. Addition of *Trichoderma* without fumigation killed the pathogen. Fumigation of soil containing the pathogen and *Trichoderma* killed the pathogen. As in cultures *Trichoderma* is a most potent antagonist of *Armillaria* it was concluded that the effect of carbon disulphide on normal soils is not directly on *Armillaria*. It only disturbs the normal equilibrium of the soil microflora by partial destruction and/or inactivation of different microorganisms and permits *Trichoderma* to get the upper hand and then by its antibiotic action to destroy *Armillaria*.

When sterile soil in which sterilised wheat was grown was infected with *Ophiobolus graminis* (the incitant of the take-all disease of wheat) and with *Trichoderma*, the presence of the latter completely prevented the infection of the wheat roots by *Ophiobolus*. The infection of *citrus* seedlings by *Corticium vagum* can be prevented in the same way when the soil is infected with conidia of *Trichoderma* (GÄUMANN 1951).

Trichoderma viride is also an antagonist of fungi parasitic on trees as *f.i. Fomes annosus* (AYTOUNS 1953, RISHBETH 1950, 1951). The disease was severe on alkaline soils. On acid humus *Fomes* did not grow if the humus was not sterilized. When after sterilisation *Trichoderma* was added the growth of *Fomes* was again inhibited.

In summing up the case of *Trichoderma viride* one can neither state with certainty that the antibiotics produced by this fungus have in nature an allelopathic function nor can one draw the opposite conclusion. The fact is that *Trichoderma* in pure culture is one of the most potent and most universal antagonists and that this antagonistic action is exerted through the excretion of antibiotics. In soil the antagonistic action of *Trichoderma* also exists but only under certain conditions. Circumstantial evidence indicates that this antagonistic action is exerted via the excretions of antibiotics but a decisive proof is still lacking. The experiments with sterilized and unsterilized soil and the fumigation experiments suggest that as long as there exists an equilibrium between the different microorganisms the antagonistic action of *Trichoderma* is kept in check. When the equilibrium is disturbed *Trichoderma* acts antagonistically. All this goes to show that the question of the allelopathic function of antibiotics is far from solved and is certainly worthy of further investigation.

There are a number of other cases where it is very probable that we deal with allelopathy concerning two microorganisms though the chemical nature of the substances involved is unknown. *Helminthosporium sativum* and *Fusarium culmorum* cause the foot-rot disease of cereals. They are mutual antagonists. Though each of them separately brings about infection, infection is reduced through their antagonistic action when wheat is inoculated with both pathogens (LEDINGHAM 1942). In culture a number of fungi antagonistic to both pathogens could be found which were effective also in sterilized soil (KOMMEDAHL and BROCK 1954, GREANEY and MACHACEK 1935). *Helminthosporium* does not grow on unsterilized wheat stubble, but does grow on it after sterilization as the microflora of the unsterilized stubble was antagonistic to it. It grew on green culms but stopped doing so after the green culms were moistened and incubated (SIMMONDS 1947).

NISSEN (1956) reports that the mycelium of *Polyporus annosus* the cause of the root rot of *Picea abies* does not grow on unsterilized soil. A number of

actinomycetes isolated from these soils showed in vitro a clear antagonism towards the *Polyporus* mycelium. Sterile soils were then inoculated with the same actinomycetes. When the inoculated and the sterile control soils were infected with mycelia of *Polyporus* these spread only on the soils not containing the actinomycetes.

When tomato plants or their roots are treated with cultures of *Micromonospora* or with filtrates of it and then planted in soil infected with *Fusarium*, the symptoms of *Fusarium* wilt do not develop. As in vitro also *Fusarium* is inhibited by *Micromonospora*, it may be assumed that *Micromonospora* excretes substances inhibiting the growth of *Fusarium* (SMITH 1957).

We mention here without going into details the success claimed by Russian authors in fighting seed born fungal diseases by using antagonistic mycolytic bacteria or filtrates of their cultures (NOVOGRUDSKI 1936, KHUDYIAKOFF 1935 *etc.* cited after WOOD and TVEIT 1955).

We may be permitted to mention here the antagonism existing between different viruses and fungi though this may not belong to our chapter on allelopathy sensu stricto. BARTELS (1955/56) found that culture filtrates of *Fusarium oxysporum* and *Sclerotinia fructigena* inactivate to 90% tobacco mosaic virus. BLUMER *et al.* (1955/56) report that mildew diseased cucumber plants (infected with powdery mildew, *Erysiphe polyphaga*) show a strong resistance against infection with cucumber mosaic virus. When conidia of the mildew are suspended in juice containing the virus the infecting power of the virus decreases strongly. It is assumed that the virus is inactivated by metabolites produced by the fungus.

An interesting case of allelopathic action of fungi on ferns was reported lately. It was found that in pure cultures the germinating spores of *Pteridium aquilinum* developed only into an unicellular prothallus whereas the presence of a number of fungi and actinomycetes enabled these prothalli to grow into the normal adult form (WILKIE 1954). HUTCHINSON and FAHIM (1958) confirmed these results. They also found that the spores which lose their germinability during dormancy are stimulated when germinated in cultures containing fungi. This effect is attributed to some secretion from the living hyphae.

There also some cases of allelopathy between algae. It is known already for a long time, that some algae produce auto-inhibitors (HARDER 1917). LEFÈVRE *et al.* (1949) found that filtrates of *Scenedesmus quadricauda* inhibit the growth of other algae. In the filtrate of *Pandorina* some other algae were stimulated, some inhibited. LEFÈVRE *et al.* (1951) report that the filtrate from ponds containing the bloom of blue green algae contain a substance inhibiting the growth of other algae. JORGENSEN (1956) observed in some lakes that during the time of maximum development of planktonic diatoms only very few epiphytic diatoms are found. The maximum development of the epiphytic diatoms occurs only when the planktonic diatoms are few. The same relationship was found between the epiphytic diatoms and green phytoplankton. It was concluded that the growth of the epiphytic diatoms was inhibited by substances produced by planktonic diatoms and green algae. In experiments it was shown that *Scenedesmus quadricaudata* forms a substance inhibiting the epiphytic diatom *Nitzschia palea*. *Nitzschia* and *Asterionella* formed substances inhibiting the growth of other species, whereas the growth of *Chlorella* was stimulated by the filtrates from *Nitzschia*.

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Chemical influences of the environment.

By

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With 3 figures.

I. Introduction.

The chemicals in the environment which have effects on growth and development of plants include, of course, many inorganic and organic substances of which the purely nutrient function is dealt with elsewhere in this Encyclopaedia. No account will be given here of the mineral nutrients or of the vitamins or other organic substances which heterotrophic organisms must obtain from their environment. In the preceding chapter, EVENARI (pp. 691—736) has already dealt with the chemicals which are released by certain organisms into their surroundings and which feed, stimulate or inhibit other organisms. The role of hormones, which may be present in the environment, is already sufficiently covered by the articles in Volume XIV. The function of oxygen in aerobic respiration and the metabolic aspects of carbon assimilation or nitrogen fixation are also beyond the scope of this chapter, despite the fact that these substances, together with the essential mineral elements, supply the fuel, building materials and machinery for growth and development. We thus create an artificial distinction between metabolic physiology and the physiology of growth and development, but this distinction has some advantages in releasing us from the necessity of considering the detailed biochemistry of the processes of growth and development, and concentrating on their more morphological aspects.

It must not be forgotten that in any response, the factor in the environment is interacting with the specific constitution of the organism and that the outcome is determined by both. The potentialities inherent in the genetic constitution of the organism are realized, or prevented from being realized, by this interaction. This implies that there can be no unique way in which chemical influences affect biological processes since different kinds of organisms and different individuals differ in genetic constitution. Nevertheless, by the tenets of comparative biochemistry and physiology, which are fundamental to our concept of evolution, we recognize that certain modes of behaviour are widespread among organisms and may even be compulsory by reason of the universality of basic physical and chemical laws.

It is possible to consider the chemical effects of the environment in various ways. We may distinguish, for instance, between chemical and physicochemical effects. The latter would include such phenomena as osmotic pressure (dealt with elsewhere in this Volume), p_H, adsorption phenomena and redox potentials. Of these p_H is so universally involved in physiological experiments as to render any treatment of its effects almost superfluous. The measurement and interpretation of redox potentials is so fraught with difficulties that they are of real value only with systems which can be simplified to a few chemical components.

They are best left in the hands of those who are concerned with the energetics of metabolic reactions.

In this treatment of the effects of chemicals on plant growth and development only such chemicals as occur in "natural" environments where plants grow will be considered. The effects of synthetic hormones or of fertilizers will, therefore, be neglected, but some attention must be given to certain gases which, as pollutants, must be considered as part of the atmosphere of any industrialised country.

II. The effects of gases and vapours.

1. The constituents of the atmosphere.

The main invariant constituents of the air are nitrogen, oxygen, argon, neon, krypton and xenon. In addition, the air contains variable amounts of water vapour (see WANGERMANN, this Volume, pp. 618—633), carbon dioxide, ozone, ammonia and other nitrogenous compounds, sulphur dioxide, hydrogen sulphide, hydrogen peroxide, hydrocarbons, tar and dust particles. The oxygen/nitrogen ratio remains constant for all practical purposes (BENEDICT 1912). The content of carbon dioxide varies between 2.5 and 4.0 parts per 10,000 by volume (LUNDEGÅRDH 1924; see also HUBER 1958, CHAPMAN *et al.* 1954). The fluctuations of carbon dioxide content are small over the oceans, but considerable and important over the land, increasing at night or with proximity to large towns, or to the soil, and in the presence of fog or snow. Winds blowing over land often contain more CO_2 than onshore winds. Water dissolves appreciable amounts of carbon dioxide and a litre of rain-water contains 1.5 ccm of carbon dioxide. Despite views expressed long ago and still more recently (by the physicist TELLER, see MATTHEWS 1959), the carbon dioxide content of the atmosphere is not likely to be markedly increased by the burning of fossil fuels because the carbonate content of the sea effectively buffers the atmosphere against such changes (SCHLÖSING 1880, see LUNDEGÅRDH 1924, p. 34). The rate at which this buffer acts may be gauged by the fact that near the poles the air is poorer in carbon dioxide because of the greater solubility of the gas in water at lower temperatures.

Ozone, hydrogen peroxide and nitrous oxide are formed in relatively small quantities by electrical discharges. Ozone also arises in considerable quantities from ultra-violet irradiation in the upper atmosphere and the content of ozone increases with altitude (PRING 1914). Ozone and hydrogen peroxide oxidise organic substances in the air, particularly hydrocarbons. Nitrous oxide dissolves in water to form nitric acid and may then combine with ammonia. Ammonia is produced as an effluent of coal fires. City air is richer in ammonia than country air. Apart from carbon dioxide, sulphur dioxide is the main effluent of the burning of coals and other fuels. It has been estimated that the burning of 100 tons of coal yields about 1.5 tons of sulphur dioxide. The gas dissolves in rain-water and is thus returned to the soil as sulphuric acid or as ammonium sulphate. Chloride is present in the air mainly as sodium chloride which is caught up by the wind blowing over the sea and deposited in rain over the land near the sea. The salt content of the air is much greater near the sea than further inland. Small amounts of iodine and potassium are also carried in the air near the sea. Dust particles in the air come from many sources. Near the sea coast there may be sand and small crystals of salt; inland, particles of soil or plant remains are carried away by the wind, especially from places where the soil is bare. By their abrasive action such particles can damage plants when driven by a high wind. Appreciable amounts of dust derived from soil may be carried

down in rain, giving rise to phenomena such as the "red rains" of Australia. A litre of rain may also contain as much as 0.3 to 0.5 mg of free ammonia, 0.1 to 0.5 mg of nitrogen as nitrate or nitrite, 2 to 7 mg of chlorine (as much as 55 mg near the coast) and 2 to 3 mg sulphur dioxide (MEIGEN 1929). In towns the amounts are greater. Rain over London may contain as much as 2.8 mg of ammonia, 13 mg hydrochloric acid and 24 mg of sulphur dioxide per litre.

2. Oxygen.

a) Modes of life in relation to oxygen.

Organisms may be classified on the basis of their oxygen requirements for growth as anaerobes (either facultative or obligate) or aerobes. Most, if not all obligate anaerobes are bacteria, *e.g. Clostridium* spp., *Thiobacillus denitrificans*, *Desulphovibrio* spp. Oxygen is toxic to these organisms, which are agents of decay in habitats in which there is no gaseous oxygen or only traces of it, *e.g.* in the depths of the sea and in organic materials (*e.g.* silage) from which air is excluded. *Clostridium butyricum* will not withstand concentrations of oxygen beyond 0.003 per cent (PORODKO 1904) but various obligate anaerobic sulphur bacteria will tolerate up to 0.2 per cent oxygen. Anaerobic bacteria may be cultivated on normal media with somewhat less rigorous exclusion of oxygen by the addition of reducing agents such as cysteine, sodium thioglycollate, or on neutral media with the addition of very small amounts of sodium sulphite (STANIER *et al.* 1958; see also THIMANN 1955) or on nutrient-poor media (BEIJERINCK 1898). The addition of reducing agents decreases the redox potential of the medium but in certain cases these agents may act more directly to remove the toxic effects of hydrogen peroxide produced by the bacteria. The assimilates and respiratory substrates of organisms are reduced compounds accumulated in opposition to the general tendency in nature towards oxidation. Biological oxidation consists essentially in the uniting of hydrogen, removed from substrates, with oxygen to form water or hydrogen peroxide. It is true that certain chemolithotropic bacteria cause the reduction of strongly oxidised substances such as nitrate or sulphate but they do so only by oxidising other inorganic substances or by using inorganic substances as hydrogen acceptors instead of oxygen (see KLUYVER and VAN NIEL 1956; WOODS and LASCELLES 1954).

HEWITT (1950) has pointed out that certain sites in the cell or at the cell wall must be maintained in a reduced condition if metabolism is to continue and that hydrogen peroxide, which is formed in the presence of oxygen in many auto-oxidation reactions, is antagonistic to the maintenance of a reduced state in such sites, particularly those dependent on SH groups. Hydrogen peroxide must therefore be removed from the cell and catalase is the main enzyme responsible for this removal. However, some anaerobes do not possess catalase. HEWITT remarks: "The subdivision of bacteria into aerobic and anaerobic organisms is artificial since a constant gradation of oxygen requirements is seen. Although some bacteria will grow only when there is a plentiful oxygen supply and others only when air is totally excluded, most bacteria have requirements falling between these two limits and some are able to multiply under all conditions varying from the fully aerobic ... to completely anaerobic". MCLEOD and GORDON (1923) found that obligate anaerobes contained no catalase and suggested that their sensitivity to oxygen was in reality a sensitivity to peroxide which was formed in the presence of air and could not be destroyed by the bacteria (HEWITT 1957). HEWITT cites the case of the haemolytic streptococci which actually prefer aerobic conditions for growth but lack catalase. In a closed vessel a culture of these organisms gradually acquires a negative potential but in aerated cultures the redox potential becomes very positive and steady. This is due to the formation of hydrogen peroxide which accumulates in the medium and kills all the organisms in about 18 hours. Cultures of typical aerobes such as *Micrococcus lysodeikticus*, which possess catalase and do not permit peroxide to accumulate acquire a more negative potential when more strongly aerated because they grow more vigourosly under those conditions. These concepts have been strongly contested by STEPHENSON (1949),

who does not regard it as proven that the sensitivity of the *Clostridia* to oxygen involves the production of hydrogen peroxide. No direct evidence of the production of peroxide by these bacteria has been obtained. According to STEPHENSON the phenomenon "still-awaits satisfactory explanation".

Oxygen must therefore be considered together with the oxidising or reducing conditions of the medium in attempts to determine the tolerance of organisms to aeration. Redox potentials may be of importance in the germination of bacterial spores. Those of *Clostridium tetani* will tolerate oxygen up to about 20 mg per litre. KNIGHT and FILDES (1930) showed that at p_H 7 these spores germinate only at redox potentials below 0.01 volt. Starting with different redox potentials and using various oxygen-nitrogen mixtures they succeeded in obtaining germination at a redox potential as high as 0.12 volt. The time required for germination reflects the time required for the redox potential of the medium (a wound, for instance) to fall to 0.01 volt at p_H 7.

Many organisms, including higher plants, can exist for shorter or longer periods in the absence of oxygen but the term "facultative anaerobe" is reserved for those which can grow and develop under such conditions. Some flagellates, many bacteria, yeasts and some filamentous fungi and some algae are capable of growing and developing anaerobically. The capacity to become adapted to anaerobic conditions is found in all the main phyla of the algae (FOGG 1953). No higher plants are facultative anaerobes in the strict sense, although the spores and seeds of a few (*e.g.* rice) have been shown to be capable of germinating in the complete absence of oxygen. A supply of oxygen is essential, however, for any prolonged manifestation of growth in higher plants and even such algae and fungi as are capable of prolonged anaerobiosis usually grow more slowly and have a simpler morphology in the absence of oxygen than in its presence.

For organisms which require considerably more than trace amounts of oxygen for normal growth and function it may be advantageous to use the term "macro-aerophilic". Organisms which require a definite but small concentration of oxygen are usually termed by microbiologists "microaerophilic" and obligate anaerobes would perhaps be better termed "aerophobic" organisms. The following discussion will be concerned with the effects of oxygen concentrations higher or lower than those normally present in the atmosphere or dissolved in natural waters, and aerophobic organisms will be neglected.

b) Anabiosis.

There are certain stages in the life-cycle of an organism namely, the seed or the spore, when all activities of growth and development may be suspended and life appears to cease. It is a matter for controversy whether or not such organisms require oxygen for the retention of viability. BÜNNING (1953) takes the view that "in complete dormancy or anabiosis, respiration is more or less completely excluded so that the organism is independent of oxygen" but VAN TIEGHEM'S view was that "respiration continues during dormancy and if it cannot do so, the organism dies". However, VAN TIEGHEM'S experiments on this matter were conducted with peas, which have thin seed-coats, a small degree of dormancy, and a rather short life in storage. JAMES (1953) has pointed out that the more effectively seeds are dried out the more difficult it becomes to demonstrate the emission of carboin dioxide from them, and has cited experiments to show that, with refined techniques, such an emission may nevertheless be detected. However, OHGA (1926a, b) was unable to find even traces of carbon dioxide emitted from the dry seeds of *Nelumbo nucifera*. Moreover JAMES (1953) mentions an experiment of BECQUEREL'S (1907) "in which isolated testas, which contain only a small portion of the living tissues, gave off as much carbon dioxide as the whole seeds before stripping". But the testas of seeds often have fungal hyphae and bacteria on their outer and inner surfaces and it is therefore necessary

first to exclude the possibility that the residual respiration of dried seeds is due to these organisms (PRINGSHEIM *et al.* 1931, MILNER and GEDDES 1945) before one can conclude that the seeds, too, respire. Oxygen consumption in stored oats (BAKKE and NOECKER 1933) and carbon dioxide production in stored wheat (OXLEY and JONES 1944, LARMOUR *et al.* 1935) has been attributed to the fungi and bacteria present in the pericarp (see CROCKER and BARTON 1953).

According to BÜNNING (1953) the different degrees of respiration in dried pollen and spores are indicative of different degrees of dormancy. Some kinds of pollen are said not to respire at all when dried. However, spores of many fungi rapidly lose viability with even moderate drying (ZOBL 1943) although many can be lyophilized (frozen-dried) successfully (for references see COCHRANE 1958). Attempts to lyophilize pollen, thus removing the last traces of water, in order to prolong the storage-life have not generally been successful (PFEIFFER 1936, 1955). It is possible, therefore that in some spores and kinds of pollen the retention of a certain amount of water, which might act as the solvent for respiratory substrates, may be essential for the retention of viability in storage. Some kinds of seeds will not withstand intense drying. Maize grains, birch seeds and some pine seeds will not survive drying to less than about 5 per cent moisture content (CROCKER 1948).

On the whole, there is good circumstantial evidence that oxygen-consumption is not essential for the maintenance of viability in seeds and spores and that respiration is a function of their moisture status which with suitable techniques can be reduced to nil without affecting (or even prolonging) life in storage. JAMES says that "BLACKMAN thought that the slow gas exchanges (which go on in dried seeds) might indicate a purely photochemical oxidation of seed materials, which would in time destroy the organization necessary to maintain viability". BLACKMAN thus appears to have adopted the view that these slow gas exchanges might not be respiratory in nature but JAMES has referred to the difficulty of defining respiration. It is clear that the retention of viability in bacteria after freeze-drying, by *Marsilea* sporocarps and clover seeds stored in mercuric chloride and absolute alcohol for very many years, and by wheat and maize stored in the presence of HCN for a year (TOWNSEND 1901) is evidence contrary to the view that oxidative respiration is necessary. Indeed, it would seem that conditions of moist storage, increased partial pressure of oxygen, and elevated temperature, all of which reduce the longevity of seed in storage (CROCKER 1948) do so by encouraging respiration to take place, whereas those conditions of storage (low temperature, absence of moisture, reduced partial pressure of oxygen) which increase the longevity of seeds reduce the level of respiration. It is somewhat paradoxical to discover (OHGA 1926a, TOYODA 1958) that fruits of *Nelumbo nucifera* at least 700 years old contain more oxygen and less carbon dioxide than fresh fruits of the same species. However, this discovery also argues against the idea that dormant seeds maintain their viability by consuming oxygen, and that they simultaneously evolve carbon dioxide. Indeed the very old (1040 ± 210 years) fruits of *Nelumbo nucifera* have been shown to contain fully viable seeds (LIBBY 1951). Finally, most seeds lose their viability long before even the major respiratory substrates have been exhausted, so that it is unlikely that lack of substrate for respiration can be held responsible for loss of germinability. It is possible, however, that respiration may result in depletion of phosphate carriers so that, in poor storage conditions, protoplasmic structures (particularly membranes or nuclear structures) may break down. CROCKER (1948) favours the hypothesis that chromosomal changes (fragmentation and degeneration) are responsible for the loss of viability and draws a comparison

between the reduction of germinability brought about by irradiation and heat, and the chromosome mutations which can also be induced by these treatments. This concept is supported by evidence that aged, heated or irradiated seeds may give rise to a greater percentage of genetically abnormal seedlings than fresh or untreated seeds.

Seeds may possess morphological structures, particularly of the seed coats, which serve to prevent access of water and in some instances of gases to the embryo and by thus preventing the initiation of an active respiration, prolong the life of the seed. According to BECQUEREL, hard-coated legume seeds have 2 to 5 per cent. of water and their coats are impervious to oxygen. The water content is maintained fairly constant under varying conditions of external moisture, by means of a special mechanism in the hilum (HYDE 1954). Hard-coated seeds are frequent in species of *Papilionaceae*, *Mimosaceae*, *Cannaceae* and *Ranunculaceae* and it is these which contribute most to the lists of long-lived seeds such as those given by CROCKER (1948) and BARTON and CROCKER (1948). There are, however, many species which do not have coats impervious to water and which are yet long-lived (EWART 1908, BECQUEREL 1932). Some of these are said to have seed coats which are relatively impervious to gases, particularly oxygen. The classical instance is that of the "upper" of the two seeds in the burr of cocklebur, *Xanthium* spp. (SHULL 1911, 1914; DAVIS 1930).

c) The role of oxygen in germination.

α) Seeds.

It is common to find, in elementary or even in more advanced text-books (*e.g.* STILES 1950) the statement that "a supply of oxygen is necessary for germination", despite the fact that the seeds of a number of plants have been shown to be able to germinate in the absence of oxygen, and that many seeds are even injured by oxygen during the period when they are imbibing water prior to germination (BARTON 1950). Seeds must be wetted before they will germinate and when they germinate in water or in a very wet soil they inevitably go through a brief period of anaerobiosis. JAMES and JAMES (1940) have shown that the RQ of barley grains allowed to imbibe water from moist sand rises from a value of 0.64 (in the stored grain) to a value above 1.5 and then falls. Even higher values (above 7.0) can obtain in more liberally wetted grains due to obstruction to the entry of oxygen to the grain by the film of water. The film of moisture which forms over the grain disappears in the later phases of imbibition. During the anaerobic phase lactic acid may be formed (PHILLIPS 1947) but if the period of anaerobiosis is not longer than a few hours no injury results. Evidently a critical stage in germination is reached when, if anaerobiosis is continued for a much longer period, germination ceases and the seedling may die. Before this stage, however, carbon dioxide seems to be more favourable for germination than oxygen (BARTON and MCNAB 1956).

The requirements for oxygen in germination vary greatly from one species to another. It is evident that the seeds of water-plants must normally be able to germinate in concentrations of oxygen lower than those required by the seeds of most land-plants. Even among land-plants the requirements vary considerably. It was found by MORINAGA (1926) that 34 of 78 different species of land plants would not germinate under water, 21 species would germinate well under water, and of these all but one would germinate in water previously boiled and sealed with paraffin oil. Of these latter species, two *(Cynodon dactylon* and *Poa compressa)* actually germinated better under water than on blotters in Petri dishes. The small residual oxygen content of the water was of some importance, apparently, for there was better germination with fewer seeds per flask and no germination at all if the seeds were sown in Petri dishes in a sealed jar containing pyrogallol to absorb oxygen. Moreover, most seeds germinated better in water if it was in contact with oxygen rather than with air, and some

which would not germinate in water would do so if the air over it was displaced by oxygen. Some criticisms may be raised against this work. For instance, pyrogallol solutions freshly made-up give off carbon monoxide and need to be aged before use. There is no indication that this precaution was attended to. Also the suspicion arises that the nitrogen which in some experiments was shown to suppress germination might have been impure with carbon monoxide. Despite these objections, the main thesis, that the seeds of many land-plants will germinate in the presence of very low concentrations of oxygen is well substantiated by MORINAGA'S work. BÖHMER (1928) reports greater germination of light-sensitive seeds *(Lythrum salicaria, Epilobium hirsutum etc.)* in darkness with reduced oxygen tension than with air.

The seeds of many water-plants will germinate in the virtual or complete absence of oxygen (SCHAUMANN 1926). CROCKER and DAVIS (1914) showed that, after removal of the seed coats, which are impervious, seeds of *Alisma Plantago* would germinate in water boiled at 30° C at reduced pressure (0.1 mm Hg) and sealed at that pressure and temperature. The seedlings did not develop chlorophyll, grew less than control seedlings in water, and the leaves remained undifferentiated. About 5 mm of air pressure was required to bring about chlorophyll formation and more than 5 cm for leaf differentiation. TAKAHASHI (1905), NAGAI (1906) and AKEMINE (1914) have established that rice *(Oryza sativa)* will germinate in the absence of oxygen, and TAYLOR (1942) has attributed the capability of rice to grow in nitrogen to an unusually high rate of anaerobic respiration. The seedlings thus grown accumulate alcohol (PHILLIPS 1947). Most authors (TAKAHASHI, NAGAI, EDWARDS 1933) agree that the plumule of rice grows but that the roots do not develop in anaerobic conditions and a possible explanation of this will be mentioned later. In TAYLOR'S experiments wheat did not germinate at all in the absence of oxygen.

Anaerobic germination of *Typha latifolia* (MORINAGA 1926 b, SIFTON 1959), *Nelumbo nucifera* (OHGA 1926 a), *Trapa natans* (TERESAWA 1927), *Euryale ferox* (OKADA 1930) and *Peltandra virginica* (EDWARDS 1933) has been reported. EDWARDS remarks that "perhaps the most striking feature of these experiments is the evidence they present of the unusual tolerance these plants must possess to the products of their own anaerobic respiration". In most, if not in all cases, germination and seedling growth of these water plants is better in the presence of some oxygen (or air) than in its complete absence, and although they may be able to germinate and make some growth in the virtual absence of oxygen, they are in later stages of growth just as dependent on oxygen as are plants less well-adapted to enduring a period of anaerobiosis. Unlike those of most water plants the seeds of *Nelumbo nucifera* (OHGA 1926a) germinate just as well in air as in water. SIFTON (1959) finds that the parenchyma cells of the embryos of *Typha latifolia* seeds are rich in aleurone grains which swell during germination. Swelling and vacuolation of the aleurone grains are increased by reducing the oxygen tension (or by white light — see EVENARI, Vol. XV/2). The resultant swelling ruptures the seed coats. Vacuolation of the protoplast is increased by access to oxygen and, in some samples of seed, this compensates for the reduced swelling of the aleurone grains so that the germination of seeds of these samples is less affected by oxygen tension.

Many seeds are known to have thin seed coats, permeable to water, but relatively impermeable to gases, and the excised embryos of many of these will germinate in conditions which will not permit the germination of the whole seeds (see review by TOOLE, HENDRICKS, BORTHWICK and TOOLE 1956). Even in such seeds as germinate readily in water the oxygen tension at the embryo is much reduced by the barriers imposed by the testa, endosperm, carpel wall or enveloping glumes or bracts (see AXENTJEV 1930). This may explain why germination rates are often improved by increasing the partial pressure of oxygen in the atmosphere surrounding the fruits or seeds. The seed coats of *Cucurbita pepo* are much more permeable to oxygen than to carbon dioxide, according to BROWN (1940), the greater resistance being due to the inner coat. The rate

of uptake of oxygen by the excised embryos is much higher than that of the intact seeds (BROWN 1942) and the same holds for barley (BROWN 1943), sunflower and flax (LARMOUR *et al.* 1944).

In the *Gramineae*, many instances have been reported in which removal of the glumes facilitates germination, although some authors have attributed the effectiveness of this treatment, not to removal of structures constituting a barrier to oxygen diffusion, but to the removal of specific inhibitors in the glumes themselves. GASSNER (1915) found that the glumes of *Chloris ciliata* hinder access of oxygen to the grain, and the pericarp of *Tetrarrhena juncea* has also been found to restrict the entry of oxygen to the seed and thus apparently to inhibit germination (CARR and CARR 1957). LEHMANN and AICHELE (1931), AKAMINE (1944), JOHNSON (1935), TOOLE (1939, 1940, 1941) and ELLIOTT and LEOPOLD (1953) have all shown that seeds of various grasses germinate better when the glumes are removed or the pericarp pierced, and the simplest, although not necessarily always the correct, explanation for this, namely that it improves the gaseous exchange of the seed, has been adopted by most authors, but not by ELLIOTT and LEOPOLD, who prefer to attribute the inhibition by the glumes of *Avena sativa* to an amylase inhibitor (said to be a polypeptide of high molecular weight but nevertheless quite soluble in ether!). Evidence that access to oxygen and not removal of inhibitors is required to bring about germination is seen in the fact that the apparent dormancy of *Avena fatua*, and various cereals including wheat (ATWOOD 1914, HARRINGTON 1923, JOHNSON 1935) can be relieved by increasing the partial pressure of oxygen (see also SIFTON 1959). There are, of course, well-authenticated cases in which apparent dormancy is not attributable solely to the imperviousness to gases of seed coats or other structures surrounding the embryo, and CROCKER and BARTON (1953) even go so far as to say that "it is doubtful that a limited oxygen supply plays a considerable part in dormancy of seeds". In view of the cases cited above and of many others (*e.g.* SCHAIBLE 1900, SPAETH 1932) this conclusion seems unwarranted. Indeed, the classical case of germination limited by gaseous exchange is that of the dimorphic fruits of *Xanthium* spp., the elucidation of which is due largely to CROCKER (1906) and his co-workers.

It is well-known that many plants produce fruits or seeds differing in morphology and possibly in physiology (heterocarpy) (PAVOLINI 1910, ZOHARY 1937). Dimorphic and trimorphic fruits are especially common in the *Compositae*, particularly the *Calendulae* and *Cichorieae* and the physiology of the dimorphic fruits of *Dimorphotheca pluvialis* was investigated by CORRENS (1906) at the same time as ERNST (1906) was studying those of *Synedrella nodiflora* and CROCKER those of *Xanthium*. While the fruits of the disc florets (or of the "lower" floret in *Xanthium*) germinate very much more rapidly and to a higher percentage than the fruits of the ray florets (or that of the "upper" floret in *Xanthium*) these differences were found by CORRENS and CROCKER and by BECKER (1912) to disappear when the testas were removed. Intact seeds from the "upper" florets of *Xanthium* germinated 100 per cent in pure oxygen and not at all in air (CROCKER 1906). CORRENS and CROCKER found that the seed coat of ray seeds (or of the "upper" seeds in *Xanthium*) was somewhat thicker than that of the disc seeds ("lower" seeds in *Xanthium*) and CROCKER was able to show that the increase in oxygen uptake of the embryo of the "upper" seed of *Xanthium* upon excision was twice as great as that of the embryo of the lower seed. The oxygen uptake of both kinds of seeds at 33° C was more than twice that at 19° C. The "upper" seeds, which scarcely germinate at all at 23° C, germinate very readily at 33° C, even in air. At 31° C the excised embryo of the upper seed will germinate with

a minimum pO_2 of 7 mm but at 21° it requires 12 mm (SHULL 1911, 1914) whereas the embryo of the lower seed will germinate at 21° C with only 3 mm of oxygen. SHULL's data were confirmed and extended by THORNTON (1935) who showed that the intact coat of the upper seed increases the oxygen requirement for germination more than 60-fold.

In many cases in the *Compositae* (BECKER 1912) the disc fruits germinate more quickly and to a higher percentage than the ray fruits (for example, in *Heterotheca Lamarckii, Achyrachaena mollis, Ximenesia encelioides,* most *Layia* and *Chrysanthemum* species, *Geropogon* and certain *Zinnia* species) but in others (for example, *Galinsoga parviflora, Hypochaeris glabra*) the relationship is reversed. There is no regularity in the difference in physiology of the dimorphic fruits even within a single genus *(e.g. Layia).* In *Zinnia elegans,* the disc fruits germinate better, in *Zinnia pauciflora* worse, than the ray fruits. BECKER showed that in all these cases the germination of both ray and disc fruits was promoted by increasing the partial pressure of oxygen. The excised embryos all germinated readily in air. Taken together, these two facts could mean that the relative impermeability of the testa and pericarp to gases plays an important role in the dormancy of these fruits.

The relationship of oxygen to dormancy may be complicated by other factors which may be of more general importance than we realise. *Kochia indica* seeds germinate better when submerged than on moist filter paper. This is attributed by EL-SHISHINY and THODAY (1952) to the leaching-away of a saponin-like substance which, when the seeds are in contact with air, forms a film, impervious to oxygen, over them. This hypothesis is questionable. Seeds of *Atriplex,* on the other hand will not germinate when they are submerged or even when surrounded by a film of water (BEADLE 1952).

β) Secondary dormancy in seeds.

If insufficient oxygen is supplied to imbibed *Xanthium* or *Ambrosia* seeds, kept about 28° or above, the embryos may not only not germinate, but they may become secondarily dormant in about two months or more (DAVIS 1930a, b; THORNTON 1934, 1935). The induction of dormancy requires the presence of some, but little oxygen (DAVIS 1930b). The dormant embryos will germinate if excised from the seeds, but they give rise to dwarf plants, the radicles of which grow slowly although the cotyledons expand normally and become green. After growing for about 40 days such dwarf *Xanthium* plants begin to grow normally. The imbibed seeds of *Sorghum halepense* (HARRINGTON 1917), *Taraxacum megalorhizon* (POPSTOV 1935), lettuce (THORNTON 1936) and *Eucalyptus regnans* (CUNNINGHAM 1958) become secondarily dormant when exposed to air and moisture at temperatures above those which permit germination. Similar effects are obtained by storing lily bulbs in the absence of oxygen (THORNTON 1939). Secondary dormancy is induced in seeds of *Brassica alba* and other weed seeds (BARTON 1945) by excess carbon dioxide (KIDD 1914a). It is relieved by removing the seed coats *(Brassica,* lettuce, *Xanthium),* by allowing the seed to dry and then re-wetting it *(Brassica)* or by prolonged moist storage at 5° C *(Xanthium).* It appears to be a condition of the embryo rather than of the seed coat and as it is likely to be more common among seeds than these few examples disclose, it may be of considerable ecological and economic importance (KIDD 1914a).

γ) Spores.

The fungi. GOTTLIEB (1950) has reviewed the recent literature on the role of oxygen in the germination of the spores of fungi and has pointed out that lack of germination following submergence, enclosure in sealed capillary tubes or displacement of air with carbon dioxide does not alone constitute proof that oxygen is required for germination, because these treatments involve other and possibly inhibitory factors. Nevertheless, there is good evidence that the spores of at least some fungi can germinate in the absence of oxygen. The most interesting cases are those of species in the *Peronosporales,* studied by UPPAL (1924,

1926). The conidia of many of these parasitic fungi may germinate in two different ways, either "indirectly" to give rise to a zoosporangium which releases zoospores, or "directly" to give rise to a germ-tube and a mycelium. *Phytophthora* species *(e.g. P. infestans, P. palmivora)* will germinate indirectly at 12° even in the absence of oxygen. At higher temperatures, in air, the conidia of these fungi usually germinate directly, but they will germinate only in the presence of oxygen. Other species of the *Peronosporales*, which are able to germinate indirectly at lower temperatures, will not do so in the absence of oxygen *(e.g. Albugo candida, Plasmopara parasitica, P. trifoliorum)*. The anaerobic germination of the *Phytophthoras* may have biological significance since anaerobiosis is most likely to occur in water, the medium of life for the zoospores, and evaporation is less rapid at lower temperatures. But the physiology of the processes which select between direct and indirect germination still remains to be investigated. Spores of *Sclerotinia fructicola* (LIN 1940) and conidia of *Erysiphe graminis* (DOMSCH 1954) are also said to be able to germinate anaerobically.

In contrast to the rarity of authentic cases of anaerobic germination of fungal spores, there are many well-substantiated instances of failure to germinate in the absence of oxygen. DE BARY observed that fungal spores germinate better near the edge of a drop of water covered by a cover-slip than near the centre, and held this to indicate a requirement for oxygen in germination. DUGGAR (1901) also considered that oxygen tension governs germination. Species, the spores of which have been shown unequivocally *not* to germinate in the absence of oxygen, include *Neurospora tetrasperma* (GODDARD 1939), *Ustilago avenae* (PLATZ *et al.* 1927), *Coccomyces hiemalis* (MAGIE 1935), *Puccinia graminis tritici* (ALLEN 1955) and *Melampsora lini* (HART 1926). The amounts of oxygen required for full germination are comparatively small, in most cases of the order of 4 to 5 per cent (BROWN 1923). The spores of *Synchytrium endobioticum* however are said to be "severely inhibited" with 23 mm of oxygen (VLADIMIRSKAYA 1954, cited by COCHRANE 1958) and germinate fully only in a well-aerated environment.

Immediately after, or even during germination the oxygen requirement of the germling suddenly increases (FRAMPTON and MARSH 1941, GODDARD 1939) and if germination has occurred under somewhat anaerobic conditions the morphology of the germ-tube may be affected by a continuance of these conditions. In water the teleutospores of the *Uredinales* produce much longer germ-tubes (which may even fragment into chlamydospore-like cells) than in air (BLACKMAN 1903).

The algae. Prior to the work of CROCKER (1906) and SHULL (1911) on the oxygen requirement of *Xanthium* seeds it was often supposed (for instance by CORRENS and ERNST) that germination was "triggered" by some chemical stimulus emanating from the environment, and that a brief exposure to this chemical (*e.g.* oxygen) could act as such a stimulus. The observation by FISHER (1907) that seeds of many water-plants *(Alisma, Sagittaria, Potamogeton, Hippuris etc.)* germinate better in polluted water, containing large numbers of bacteria, than in "pure" water was interpreted, for instance, as meaning that their germination is induced by substances produced by the bacteria. Following FISHER'S work, ERNST (1918) suggested that *Chara* oospores might be caused to germinate by applying organic acids or alkalis to them, but there is no evidence that he succeeded in obtaining their germination by this means. Those of *Chara gymnopitys* can be caused to germinate aseptically in anaerobic conditions in water (CARR and ROSS, unpublished; ROSS 1959). Germination will also take place in water under nitrogen but not under air, so that it appears that the

"stimulus" provided by the bacteria consists essentially in an increase in the biological oxygen demand of the putrescent mud, which ERNST found to give good germination. Germination is facilitated to some extent by the inevitable etching of the oospore wall by the sterilising agent. Since the oospores become fully turgid in water, impermeability to water can be ruled out as a cause of failure to germinate. As with the fungi, morphological abnormalities occur if, after germination, some air is not admitted to the sporelings.

δ) The mode of action of oxygen in germination.

Since some seeds and spores are capable of germinating (at least facultatively) in the absence of oxygen the requirement for oxygen cannot always be due solely to the necessity for energy derived from aerobic respiration for the initiation of cell expansion and cell-wall growth, or of cell division. Suggestions have recently been made that oxygen may be involved in the elimination of germination inhibitors produced by or present in the seeds or spores themselves or that it may be involved in the elaboration of hormone-like substances which promote germination.

FORSYTH (1955) and ALLEN (1955) have shown that uredospores of *Puccinia graminis tritici* contain a substance (or substances) which inhibits their own germination. The inhibitor is somewhat volatile, is readily adsorbed on to glass surfaces and accumulates in the water on which the spores are floated, but much more so in aerobic than in anaerobic conditions. On the other hand, the spores will not germinate anaerobically, but the presence of oxygen reduces the effectiveness of the inhibitor in germination. Finally, the inhibitor is converted into two stimulatory substances (one of which is pelargonaldehyde; FRENCH and WEINTRAUB 1957) on distillation (FRENCH *et al.* 1957). The inhibitor is not trimethylene, as suggested by FORSYTH (ALLEN 1957). It seems probable in view of this work that oxygen plays an important part in the germination of the uredospores (and possibly of the spores of other fungi) firstly, by promoting the formation of the inhibitor (which prevents germination when the ratio of inoculum to water is of the order of 300,000 spores to 1.5 ml); secondly, as an oxidant in normal metabolism; and thirdly, by reason of the conversion of the inhibitor to a stimulator of germination. The inhibitor may be of biological importance, possibly in preventing germination of too many spores on insufficient leaf area, but more probably in acting, when converted, to promote the formation of appressoria, infection pegs and structures resembling sub-stomatal vesicles (ALLEN 1957). Inhibition appears to involve the Krebs' cycle oxidation of fatty acids, which is inactivated. Oxygen consumption is reduced by inhibition, but both it and fatty acid oxidation are restored by pelargonaldehyde or other stimulants (FARKAS and LEDINGHAM 1959).

It has long been a paradox that many different kinds of seeds behave as though they contained germination inhibitors which could be leached out of them, but that these same seeds may be caused to germinate, without leaching, merely by removing the seed coats. As has already been stated, these "seed coat effects" have usually been attributed to the imperviousness of the seed coats to oxygen. WAREING and FODA (1957) have re-investigated the situation in *Xanthium* and have found that (1) the embryos contain two fluorescent germination inhibitors which can be leached from the excised embryos but not from the intact seeds (2) the apparent dormancy of "upper" seeds cannot be explained solely in terms of interference with gaseous exchange by the testa since, if precautions are taken to prevent leaching after sowing, excised embryos

require increased oxygen tensions for germination. The authors present evidence (WAREING and FODA 1956) that the fluorescent substances, which will inhibit the growth of cress and *Xanthium* radicles and lettuce seeds) are capable of being broken down, in the presence of oxygen, by an oxidase system in the *Xanthium* radicles. They conclude that "stimulation of germination by increased oxygen tensions is due to a specific effect upon the breakdown of the inhibitors rather than to an increase in the rate of respiration and general metabolism". This conclusion is applied also to the results of work on birch *(Betula pubescens* and *B. verrucosa)* (BLACK 1956, BLACK and WAREING 1956), the single inhibitor of which appears to be present only in the pericarp. There are some difficulties in the hypothesis. For instance, no differences in inhibitor content could be demonstrated between dormant (freshly-harvested) and non-dormant (after-ripened) "lower" seeds, and between "upper" (dormant) und "lower" (non-dormant) after-ripened *Xanthium* seeds. This is explained (WAREING and FODA 1956) by assuming that it is the degree of activation of the oxidase enzyme which changes with the change from dormancy to non-dormancy.

No recognition is made of the stimulation of germination which can be achieved by increased pCO_2. With a mixture of 20 per cent oxygen and 40 per cent each of nitrogen and carbon dioxide, THORNTON (1935) doubled the rate of germination of intact "lower" seeds. Intact "upper" seeds require 80 to 100 per cent oxygen at 25° C but THORNTON found that they germinate just as well with 80 per cent carbon dioxide and 20 per oxygen. Moreover, the germination of intact "upper" seeds forced with high pCO_2 proceeds in a normal manner, that is the radicle emerges before the cotyledons enlarge, but forcing with high pO_2 always results in abnormal germination, the cotyledons enlarging two or three times before the radicle commences to grow. Stimulation by carbon dioxide cannot be ascribed to a general increase in the permeability of the seed coat to oxygen because the seed coat is thinner over the cotyledons than over the radicle and it is for this reason that, according to THORNTON, the cotyledons enlarge first after stimulation by high pO_2.

Similar dormancy-breaking effects of carbon dioxide are described by THORNTON (1936) for lettuce seeds which ,when dormant, appear to be relatively insensitive to oxygen but germinate in increased pCO_2. Secondarily-dormant embryos of *Brassica alba* (KIDD and WEST 1917) germinate abnormally on removal or breaking of the seed coats. KUGLER (1955) has recently demonstrated the existence of germination-inhibiting substances in embryos and seed coats of *Brassica alba*. These comparisons suggest that the unresponsiveness of "upper" *Xanthium* seeds is due to an embryo dormancy, smaller in degree but of the same kind as that present in freshly-harvested seeds and seeds made secondarily dormant.

In BLACK and WAREING's work with birch the embryo is said to have a very low oxygen requirement, so that to explain the lack of germination of intact seeds the pericarp would have to be very much more impermeable to oxygen than the seed coat of *Xanthium*. Unlike *Xanthium*, it is impossible to cause germination of intact birch seeds by high pO_2. This was provisionally attributed to the "extremely low permeability of the seed coat to oxygen". Yet if the pericarp, testa and endosperm are slit, only 20 per cent of the seeds germinate in air and only in 50 per cent oxygen does the percentage rise to 100. The inhibitor is said to be in the seed coat in birch, so that it can be leached out. There is no evidence that it is broken down enzymatically.

In a rather similar fashion, the dormancy of freshly-harvested potatoes has been attributed to inhibitors in the periderm (HEMBERG 1946, 1949) and is relieved by removing it. But the effects of oxygen on the potato (THORNTON 1939, 1944b) are just the reverse of those on *Xanthium* — reducing the pO_2 to between 15 and 75 mm causes sprouting. Thus WAREING's ingenious hypothesis cannot be applied without modification to the potato. Despite these difficulties, the general hypothesis is of considerable importance, for it resolves the paradox mentioned earlier by postulating that the seed coat may play a dual role (1) to keep inhibitors from getting out and (2) to prevent oxygen, which might be used to break down the inhibitors, from getting in. In recent work the emphasis has shifted towards the formation of substances stimulating germination, rather than the breakdown of inhibitors (VILLIERS and WAREING 1960).

d) The effects of oxygen on growth.

α) The general effects of oxygen.

Work on this topic up to 1900 is summarised in PFEFFER (1903, Vol. 2) and CLEMENTS (1921). In much of the pre-1900 work the effects of reduced or increased pO_2 were compounded with effects due to reduced or increased total pressure, which are dealt with elsewhere in this Volume. The main effects of oxygen on the growth of higher plants were already known to DE SAUSSURE (1804). Non-photosynthetic organs, especially those having a high rate of respiration, such as flower-buds, leaf-buds and young seedlings, are unable to grow without oxygen and rapidly succumb to anoxia. Green plants, particularly water-plants, grow in weak light as well in nitrogen as in air, presumably because they are able to produce oxygen in photosynthesis. In the absence of oxygen, however, growth is very slow and with increasing pO_2 up to some level usually below that of the ordinary air the growth-rate of the higher plant increases. According to WIELER (1883) *Helianthus annuus* requires 23 mm, *Vicia Faba* 40 to 45 mm oxygen for optimal growth and *Cucurbita pepo* is still oxygen-limited at 40 to 45 mm. NABOKICH (1903, 1909) claimed that many plants such as *Helianthus* are capable of growing (although abnormally) in the absence of oxygen, but most of his plants did not survive more than three days, although many recovered after a somewhat shorter period of anaerobiosis. It is possible that the initial growth was made at the expense of oxygen in the intercellular spaces. NABOKICH believed that eventual cessation of growth in nitrogen (in the dark) was due to lack of sugar, but LEHMANN (1911) was unable to make plants such as *Helianthus annuus* and *Vicia Faba* grow, even by supplying them with sugar, in the complete absence of oxygen. Thus although some land plants can germinate in the absence of oxygen they are unable, at a later stage in development, to grow when the air around them contains less than from 3 to 0.1 per cent (23 to 0.8 mm) of oxygen. Consequently the pO_2 in the normal atmosphere is always in excess of the minimal requirements of these plants, although if the concept is correct that the oxygen content of the atmosphere is attributable to photosynthesis, it may well have been of a very low order in the remote past.

There is even some suggestion that the oxygen content of the normal air may be supra-optimal for growth of shoots. Using a modified Königsberger auxanometer (RANSON and HARRISON 1955), RANSON and PARIJA (1955) found that the growth, in length or fresh weight, of coleoptiles of wheat, rice and barley, and the hypocotyls and epicotyls of *Vicia Faba*, marrow and buckwheat was greater at pO_2 less than that in ordinary air, although reduced at 37 mm or less. The stimulatory effect of reduced oxygen supply was shown even within 15 minutes of transfer from air, but continued in most cases during at least the first seven days from germination. The minimum oxygen requirements of water plants are in general much less than those of land plants (BERGMANN 1920) and according to LAING (1941) the optimal range of oxygen concentration for the growth of the rhizomes of water plants range from 0 to 1 *(Nuphar advenum)*, 0 to 10 *(Pontederia cordata)*, 4.6 *(Typha latifolia)* and 10 per cent oxygen *(Acorus calamus, Scirpus validus)*. Since some of these plants *(e.g. Nuphar advenum)* are actually inhibited by concentrations of oxygen of the order of 3 to 4 per cent, they may be described as "microaerophilic".

The minimum requirements for fungi are in some cases extremely low (references in COCHRANE 1958). *Blastocladia pringsheimii* is microaerophilic, having a definite but extremely low requirement for oxygen which can be satisfied by the traces present in commercial nitrogen or carbon dioxide (EMERSON and CANTINO 1948). *Fusarium oxysporum* will survive and grow for at least 13 weeks in completely waterlogged soils (HOLLIS 1948). The minimum requirements for sporulation are usually higher than those for growth. Aquatic *Phycomycetes* produce spores under water, but most other fungi will not do so. *Neurospora sitophila* requires at least 0.5 per cent oxygen for the formation of perithecia but grows quite well with 0.3 per cent oxygen (DENNY 1933), but not at all in the complete absence of oxygen.

There are some instances in which growth is restricted by the oxygen tension of the normal environment. The inner tissues of the more massive organs of

the higher plants and *Basidiomycetes* may often be near or below the minimum oxygen concentration (see GODDARD 1945) and an increase in the external pO_2 may overcome the internal deficiency. Resistance to inward penetration of oxygen may be due to the lack of (or waterlogging of) intercellular spaces (*e.g.* in germinating seeds), to epidermal structures (*e.g.* the waxy cuticle of the apple) to the presence of an endodermis (in thick roots) or to sheer distance from the surface of the organ to the inner tissues. JAMES (1953) has calculated, however, that it is likely that the oxygen concentration of the inner tissues of even the most bulky plant organs rarely sinks below the critical minimum for the avoidance of toxic anaerobiosis under normal circumstances. At temperatures above 25° C, however, there exists a danger that such anaerobiosis might occur and indeed it is responsible for the rapid internal blackening of potatoes kept at 37° C. Limitations to oxygen diffusion may also be of greater importance in rapidly-growing organs, which are also rapidly respiring (such as primary roots) than in less active organs.

In the wood-destroying fungi such as *Polystictus versicolor* (SCHEFFER and LIVINGSTON 1937) growth may be oxygen-limited because of the relative imperviousness of the wet medium in which they grow. Increase of the oxygen tension may then increase the growth rate and the rate of utilisation of the substrate. RHOADS (1917) suggested that the zone of black hyphae formed by some wood-rotting fungi in tree-trunks is an indication of oxygen-limited growth, but this is denied by the work of THACKER and GOOD (1952) on the fungi causing decay in sugar maple (see also GOODWIN and GODDARD 1940). In the sound wood of the maple tree oxygen concentrations below 2.9 per cent were never found and even in rotted and soft heartwood, the lowest recorded concentration was 0.8 per cent. All the fungi grew well at oxygen concentrations between 0.8 and 35 per cent, but their growth was decreased by a change in oxygen concentration from 10 to 0.8 per cent. Mushrooms *(Agaricus bisporus)* grown in unusually high pO_2 are heavier and more compact than those grown in air (LAMBERT 1933). Reducing the content of oxygen in the air to one-tenth normal, has slight inhibitory effects on growth of *Penicillium roquefortii* at 30°, but no effect at 21°, and it is actually stimulatory at 9° C (GOLDING 1937, 1940a, b).

It is partly the lack of oxygen but more probably the acidity and low mineral status which delays decay in deep high-moor peats. HESSELMAN (1910), quoted by LUNDEGÅRDH (1924), could detect no oxygen in peat 20 cm below standing water, or in the interior of *Sphagnum* hummocks. Low-moor peat is also anaerobic but it is well supplied with minerals by drainage from higher ground. It has a rich flora of cellulose-decomposing and nitrifying bacteria (WAKSMAN 1938).

β) Inhibition of growth by high pO_2.

An increase in the oxygen concentration may have favourable effects on the growth of some plants or plant organs, but adverse effects are generally found with high concentrations . Concentrations of oxygen of the order of 95 to 100 per cent are usually toxic (BOEHM 1873). The toxicity may be due in part to the absence of carbon dioxide, which appears, in small amounts, to have tonic effects on cells, for instance, of roots. ELIASSON (1958) finds that pure oxygen inhibits the growth of wheat roots completely after two or three days, partly as a result of cessation of cell division, partly through cessation of cell elongation (see also BAILEY 1958, STEINITZ 1943). Neither the roots of *Pinus lambertiana* (LEYTON and ROUSSEAU 1958) nor those of cotton (LEONARD and PINCKARD 1946) grow well in nutrient solutions aerated with 95 per cent or 100 per cent oxygen. Cotton roots thus grown are more susceptible to attack by chytrids and *Fusaria* than roots aerated with ordinary air. Excessive aeration

of nutrient solutions is inimical to the growth of roots of beans and sunflowers (LOEHWING 1934), tomatoes (ERICKSON 1946), avocados (CURTIS 1949), barley (HOAGLAND and BROYER 1936), and soybeans SHIVE 1941). The toxic effects of excess oxygen are accentuated by supplying nitrogen as ammonium salts (GILBERT and SHIVE 1942).

The fact that, in LEONARD and PINCKARD'S (1946) experiments certain fungi grew well in the presence of cotton roots aerated with pure oxygen may be attributed to the loss of solutes from these roots. There is no evidence that in the absence of such indirect effects these fungi would grow better in pure oxygen than in solutions aerated with ordinary air. On the other hand, WHITE and MUNNS (1951) have presented data which seem to show that the growth of yeast in synthetic media increases with increased rates of aeration up to 0.75 gm of oxygen per litre per hour, but that further increases lead to a decrease in growth, as measured in gm/litre of yeast cells. The apparent inhibition might, as THIMANN (1955) suggests, be due to the cooling effect of the air at very high rates of aeration.

BRITTAIN (1957) see also PANNIER (cited in GESSNER 1959) found that the growth of *Chlorella* in the light and in the presence of CO_2 was decreased when the O_2 concentration was raised from 21 to 95 per cent. The individual cells grown in high pO_2 were larger than those grown in low pO_2. Dry weight and "packed cell volume" were unaffected by concentrations between 0.5 and 20 per cent oxygen but considerably so between 20 and 95 per cent oxygen. The relative growth rate decreased linearly with increasing oxygen concentration from 0.5 per cent upwards. These depressant effects of oxygen on growth rate resemble those on photosynthesis (see TURNER *et al.* 1956, TAMIYA and HUZISIGE 1949, MIYACHI, IZAWA and TAMIYA 1955). To explain them it is suggested that if glyceraldehyde phosphate dehydrogenase (GPD) acts (at high light intensities and high CO_2 concentration) as a pacemaker in photosynthesis then "inhibition of the enzyme by oxygen could inhibit photosynthesis (1) by depressing the rate of re-oxidation of reduced pyridine nucleotides derived from the photolysis of water, so that this process, and oxygen evolution would slow down; (2) by causing a block at the 3-phosphoglyceric acid level which could interfere with the operation of the carbon cycle". It is shown that GPD from leaves, for which both TPN and DPN act as co-factors, is inhibited by pure oxygen but not by nitrogen or air (TURNER *et al.* 1958). Other explanations have also been put forward, for instance that oxygen acts as an oxidant in the Hill reaction, and competes with the normal hydrogen acceptors (MEHLER 1951).

Injury caused by pure oxygen has been observed by ALBAUM *et al.* (1942) in oat coleoptiles, and by GALSTON and SIEGEL (1954) in pea roots. TURNER and QUARTLEY (1956) and QUARTLEY and TURNER (1957) working with pea seeds attribute the injurious effect of high pO_2 to interference with the metabolism of citric acid thus blocking the citric acid-cycle which they believe to be a major respiratory pathway in peas. The content of oxaloacetic acid fell during treatment with oxygen. The inhibition is apparently reversible on transfer to air.

When fungi are grown on agar most of them grow as well at an oxygen tension of 20 to 40 mm as in air (DENNY 1933, THACKER and GOOD 1952) but the dry weight is usually depressed with further increase in oxygen tension. *Ophiobolus graminis* grows less with pO_2 105 mm than with lower oxygen tensions (FELLOWS 1928, GARRETT 1937). Very high oxygen tensions may have effects on morphology as well as on growth rates, but they are not usually lethal (WEBLEY 1954, KLAUS 1941).

γ) Redox potentials in soils and natural waters.

PEARSALL (1938, 1950) and others have proposed that the redox potentials of soils and natural waters are of considerable importance in determining the suitability of the habitat for the growth of higher plants. Apart from the difficulties in making measurements of these potentials in soils and natural waters, and in interpreting the measurements in terms of reversible oxidation-reduction systems, as far as higher plants are concerned the main effects appear to be on

the availability of minerals such as iron and manganese rather than on oxygen status, since most of the plants which normally grow in the more "difficult" reducing conditions have special aerating systems (see below, pp. 751—759). In a critical review mainly devoted to a discussion of the value of redox potentials as ecological indices, CONWAY (1940) points out that many of the conclusions drawn by PEARSALL and his colleagues (*e.g.* PEARSALL and MORTIMER 1939) are not in accord with their own observations. Certain peat soils considered on ecological grounds not oxygen deficient may have a potential at p_H 5 of +400, although there are data of PEARSALL and MORTIMER which show that such a potential may be associated with very low oxygen concentrations. The data of PEARSALL and MORTIMER for lake water samples show that the oxidation-reduction potential in them remains poised in the E_5 +400 region until the oxygen concentration is reduced to 1 mg/litre. This may well be due, as PEARSALL suggests, to the platinum electrode acting as an oxygen electrode in the presence of some oxygen and in the absence of other powerful oxidation-reduction systems, but it casts doubt on the validity of the measurements as indicators of the oxidising or reducing status of the environment, since it does not reveal the capacity but only the intensity of this. RUSSELL (1952) points out that the capacity for oxidation and reduction might be determined from potentiometric titrations with an oxidising agent such as potassium permanganate, and cites references to American work on the redox potentials of soils.

In experiments of SCOTT and EVANS (1955) the oxygen in soils (containing about 8 ppm) disappeared completely about 6 to 10 hours after flooding, apparently as a result of microbial activity, although the redox potential remained poised, apparently by solution of oxidation-reduction systems from the soil. There was initially no apparent effect of the concentration of dissolved oxygen on these systems but after the oxygen had completely disappeared the oxidation-reduction potential eventually decreased. PEARSALL (1950) claims that measurements show that the potential of +350 at p_H 5 is a critical one, because below this value iron is always found in a reduced state in soils, and above it, the relatively insoluble ferric state predominates. For further references see the article by WIKLANDER, Vol. IV, p. 140.

δ) Soil aeration and plant growth.

Although the oxygen content of the air around the shoot of the higher plant in its normal habitat rarely if ever sinks low enough to limit its growth, the oxygen content of the soil atmosphere is often near the critical minimum concentration and may sink below it. The aeration of the soil thus plays a very important role in the physiology of growth, not only of the roots, but through them of the whole plant. The composition of the soil air resembles that of the atmosphere, but the oxygen content of the soil air is usually lower, the water vapour content much higher, and the carbon dioxide content very much (often 100 times and sometimes 1000 times) higher than that of the atmosphere (RUSSELL and APPLEYARD 1915, Fig. 1).

The oxygen content of heavy subsoils is usually near to zero in winter and early spring and increases from then onwards (BOYNTON and REUTNER 1939), whereas the oxygen content of a light sandy loam at 2 metres depth may fall only transiently below 16 per cent. The oxygen content of grassland soils is lower than that of arable land. It is reduced following heavy rain or irrigation (ALBERT and ARMSTRONG 1931) although rain water may bring dissolved oxygen (of the order of 10 ppm) into the upper parts of the soil profile (RICHARDS 1917). As with other porous media, diffusion of gases is relatively slow in the soil and this limits the exchange of soil air with atmospheric air. Mass flow, due to changes in air temperature or pressure, is of comparatively little importance in this exchange. Winds blowing

over the surface may exert some slight accelerating effect, but the main factor in exchange of air between soil and atmosphere is gaseous diffusion of each constituent gas under its own partial pressure gradient from soil to air. The rate of diffusion is a linear function of the air-space volume of the soil and is governed largely by the capillary air-spaces, since it is they, and not the larger non-capillary spaces, which lengthen the diffusion path. The rate of diffusion is strongly affected by the degree of compaction and the moisture content of the soil, which in turn affect the air-space volume (TAYLOR 1949, ROMELL 1935).

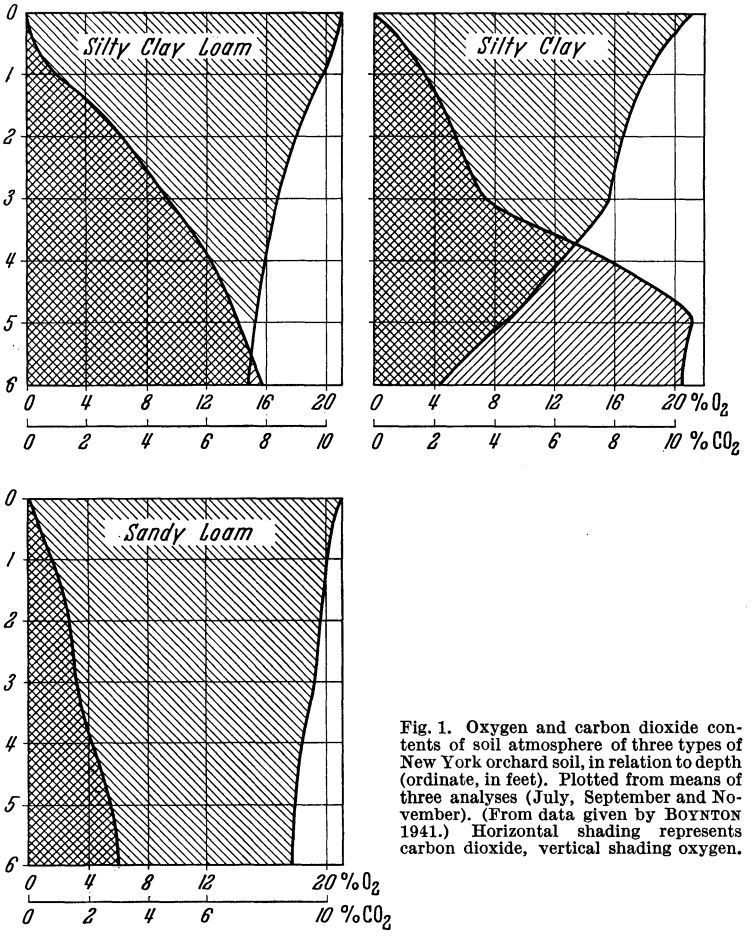


Fig. 1. Oxygen and carbon dioxide contents of soil atmosphere of three types of New York orchard soil, in relation to depth (ordinate, in feet). Plotted from means of three analyses (July, September and November). (From data given by BOYNTON 1941.) Horizontal shading represents carbon dioxide, vertical shading oxygen.

Radical changes in the composition of the soil air affect the valency-states and therefore availability of a number of important minerals and organic compounds. In anaerobic or reducing conditions iron and manganese are converted to the ferrous and manganous states and sulphates are liable to be converted to hydrogen sulphide. Carbon dioxide and organic acids, produced by soil organisms, are important in the weathering of soil minerals, particularly those containing phosphorus and calcium. The availability of these and other minerals is therefore regulated (to some extent) by the activities of micro-organisms which in turn reflect the aeration and redox potential of the soil. The changes brought about by aeration on soil-forming processes affect plant growth through their effects on the availability of minerals and in the formation of toxic substances in the soil. They have been well reviewed by LYON, BUCKMAN and BRADY (1952) and by RUSSELL (1952).

The direct effects of aeration on root growth have been reviewed by CLEMENTS (1921), RUSSELL (1952) and BERGMAN (1959). Owing to technical difficulties with soils, most of the work has been done with water cultures and the results must be applied with caution to roots growing in soil because of

the secondary effects of aeration on soil micro-organisms and soil-forming processes. In unaerated water cultures the roots deplete the oxygen content of the solution almost completely (ALLISON and SHIVE 1923a) and because of the relatively low solubility of oxygen in water the gas must be brought continuously and intimately into contact with the solution to secure adequate aeration (ALLISON and SHIVE 1923b) (see HEWITT 1952 for techniques). There are many important sources of error in extrapolating from the results of aerated water cultures to the effects of aeration in soil. (1) Forced aeration drives out carbon dioxide which might otherwise accumulate in the solution (100 cc of water will dissolve 75 cc of carbon dioxide at room temperature and normal barometric pressure). The results are therefore open to objection, on the grounds that they might be due to reduction in carbon dioxide concentration rather than to increase in aeration. On the other hand, with intermittent aeration, the oxygen tension will fall rapidly and carbon dioxide will accumulate fairly rapidly from the respiration of roots and micro-organisms. (2) In the soil the oxygen and carbon dioxide concentration show some reciprocity; as oxygen decreases, carbon dioxide increases, and *vice versa*. Moreover, root growth is not strongly affected by the complete removal of carbon dioxide from the nutrient solutions, but LEONARD and PINCKARD'S (1946) work with cotton shows that small amounts of carbon dioxide may have a slight stimulating effect on root growth. (3) Another source of error is the cooling effect which may occur if large volumes of air are swept through the solutions.

With soils the difficulties are even greater. Even an intermittent and slow aeration would, by its stirring action, greatly accelerate the attainment of equilibrium between the free and solution phases of the soil gases, which must be of considerable importance in the films of water around the roots. Forced aeration would also remove from the soil atmosphere volatile materials and gases (such as ammonia) as well as carbon dioxide. Temperature is an important factor in the effects of aeration on root growth (CANNON and FREE 1925). At high temperatures, more oxygen is required to produce a given growth response than at lower temperatures. This is due partly to the effect of temperature on the solubility of oxygen in water, partly to the increased rate of oxygen consumption by roots and soil micro-organisms at the higher temperatures. For instance, cotton roots will grow with slightly more than 1 per cent oxygen at 17° C but not at 30° C (CANNON and FREE 1925).

Many attempts have been made to investigate more directly the effect of aeration on root growth in soils. MELSTED, KURTZ and BRAY (1949) used large lysimeters filled with a soil of good structure and planted with corn or soybeans. Increased yields were obtained by forced aeration of the soil in the lysimeters. BOICOURT and ALLEN (1941) forced air for an hour a day through drainage tiles placed beneath the soil of rose beds. The oxygen content of the soil was thus increased and the carbon dioxide content reduced to about that of the free atmosphere with a concomitant increase in growth (about twice the linear growth of non-aerated controls). However, the control soil is said to have had an oxygen content of 19 per cent and since SEELEY (1948) found no improvement in the growth of roses with oxygen concentrations above 10 per cent in culture solutions, RUSSELL (1952) suggests that the technique for sampling the soil air gave "probably a poor estimate of the aeration conditions at the root-soil interface". It seems dangerous to argue from the results of the water culture experiments to explain those of the soil experiments. In a less direct approach, BAVER and FARNSWORTH 1940) have plotted the non-capillary pore space of fine-textured, but poorly drained, soils of Ohio, against the yield of sugar-beet in different

years. The yield was found to be very positively correlated with the pore space, and hence by inference with aeration.

One of the most important features of the relationship between oxygen and root growth is the large difference between species. Even where special morphological features (such as special aerating tissues or organs) are absent, there are differences in the physiological adaptation of different species to aeration. This was clearly shown by CANNON'S work on aerated sand cultures (1925). *Fagopyrum esculentum* (FREE 1917, STILES and JORGENSON 1917) and some species of *Salix* (LEYTON and ROUSSEAU 1958) grow quite well with very little access of oxygen to the roots. The roots of many conifers grow tolerably well with 10 per cent oxygen but very poorly with less than 5 per cent (Fig. 2).

The fresh weight of Biloxi soybean and Maryland Mammoth tobacco roots and shoots was not increased by an increase of oxygen concentration from 3.2 per cent to 21 per cent (HOPKINS *et al.* 1950). The growth responses of Marglobe tomato plants were proportional to the logarithm of the oxygen concentration from 0.5 per cent to 21 per cent. Root growth of soybean, tobacco and tomato plants ceased at a concentration of 0.5 per cent oxygen, although the shoots continued to grow for a time. The high sensitivity of tomato roots to oxygen tension was also found by DURELL (1941) and by ERICKSON (1946). According to GILBERT and SHIVE (1942) the growth of tomatoes and oats is increased progressively with aeration (of nutrient solutions) even up to concentrations of oxygen twice that in atmospheric air. The roots of a number of conifers also grow much better, at least for a few days, in nutrient solutions aerated with a gas mixture containing 50 per cent oxygen than with ordinary air (LEYTON and ROUSSEAU 1958). The roots of these conifers are very sensitive to any reduction of oxygen content to less than that of ordinary air. Cotton roots are also sensitive to oxygen tension. With 10 per cent carbon dioxide in the gas mixture, the growth of the tap root of cotton is strongly dependent on oxygen content (LEONARD and PINCKARD 1946). Maximum growth occurs with concentrations in the region of 10 to 25 per cent. With 21 per cent oxygen, carbon dioxide concentrations above 30 per cent are very inhibitory to root growth (Fig. 2) and shoot growth is also much affected. REED (1946) asserts that maize is not particularly sensitive to aeration. When soil was aerated at the rate of onethird of the pore-space volume per day, the growth was almost as good as with aeration at two-hundred times this rate. However, the oxygen content of the soil of even non-aerated controls ranged between 12 per cent and zero, so that even the slow rate of aeration was probably sufficient to establish the 10 per cent of oxygen which CANNON (1925) claims gives "normal growth". The growth of both root and shoot of barley is reduced by any reduction of pO_2 below 50 mm, but is not increased by increase in pO_2 above this level, according to VLAMIS and DAVIS (1943). It is therefore surprising to find that, according to RANSON and PARIJA (1955), even rice roots grow better with 21 per cent oxygen than with any lower concentration. In MACK'S (1930) experiments on wheat the growth measurements were too crude and the sampling too inadequate to warrant the conclusion that there exists a "double optimum of oxygen pressure for each temperature as in the case of CO_2-production". The fall in CO_2-output between zero oxygen and 10 per cent oxygen in his experiments was presumably consequent on the extinction of anaerobic respiration, but the actual output of carbon dioxide at pO_2 below 16 to 23 mm was very small because the processes of germination did not then commence. TANG'S (1931) evidence for a "double aeration optimum" at 24° C in the germination of wheat is even more slender and less probable than that of MACK.

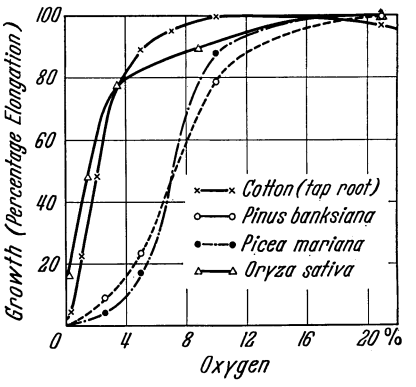


Fig. 2. Growth of roots (elongation as a percentage of the maximum) in aerated nutrient solutions, in relation to the content of oxygen in the aerating gas mixtures. Data for cotton tap roots from LEONARD and PINCKARD (1946), and for *Oryza sativa* from RANSON and PARIJA (1955). Graphs for *Pinus banksiana* and *Picea mariana* redrawn from LEYTON and ROUSSEAU 1958.

A great deal of work has been done on the root growth of fruit trees. GIRTON (1927) found that roots of orange trees stopped growing with 1.2 to 1.5 per cent oxygen and at 28° C much more than 8 per cent was required for good growth. BOYNTON *et al.* (1938) assert that apple tree roots larger than 1 mm in diameter lose weight with 1 per cent and require

at least 3 per cent oxygen for even slow growth. Unless they receive more than 10 per cent, the root and shoot growth are less than optimal. According to DE VILLIERS (1938) growth of the seedling apple root with 5 per cent oxygen is about half that with air. In orchard soils aeration conditions suitable for root growth may be available during a relatively brief season of the year (COLLISON 1935). BOYNTON and COMPTON (1943) state that apple, peach and prune trees grown in nutrient solutions grow maximally with 20 per cent or more oxygen in the gas around the roots.

One may conclude that, while roots of many species grow well with 8 to 10 per cent oxygen, they grow much better with an increased oxygen concentration, and only at low temperatures will they grow at all in soil with oxygen concentrations of the order of 0.5 to 2 per cent. It seems probable that the internal atmosphere of the root is somewhat deficient in oxygen under normal conditions in the soil. According to BETZ (1957) the zone of elongation of *Pisum sativum* roots does not show a Pasteur effect and ferments even at fairly high concentrations of oxygen. KANDLER (1950) attributes the high RQ of roots to difficulties of gaseous diffusion in the intercellular spaces. In pure oxygen, or in the absence of exogenous substrate, excised, sterile maize roots were found to have an RQ less than 1.

There is evidence that the pericycle of roots, of which the apical meristems have ceased to grow (or to be able to resume growth) due to a period of anaerobiosis, may remain capable of giving rise to new lateral roots when aerobic conditions are restored (LEONARD and PINCKARD 1946). This is of considerable importance to species which must withstand periodic waterlogging of the soil.

ε) Effects of oxygen on the development and functioning of mycorrhiza and root nodules.

According to HARLEY (1959) mycorrhizal roots of higher plants are very sensitive to oxygen and need to be adequately supplied with it for their full development and functioning. The mycorrhizal roots of beech *(Fagus sylvatica)* attain their maximum growth rates when supplied with oxygen at concentrations near that of atmospheric air and they will not function with less than 3 per cent oxygen. PENNINGSFIELD (1950) and BRIERLEY (1955) have measured the concentrations of oxygen in the air-spaces of forest soils. In the humus near mycorrhizal roots the oxygen concentration fluctuated between 20.6 and 19.5 per cent during the year, according to BRIERLEY. Orchid mycorrhiza are also sensitive to oxygen and are readily damaged by anaerobic conditions.

Root nodules of leguminous and other plants are also sensitive to reduction of the external oxygen supply (BOND 1951; ALLISON, LUDWIG, MINOR and HOOVER 1940). VIRTANEN and V. HAUSEN (1936), BOND (1951) and FERGUSON and BOND (1954) have found that the yield of nodulated legumes is reduced by any reduction in the oxygen tension around the roots. MACCONNELL (1959) has found that the initiation and subsequent development of nodules on the roots of *Alnus* is also very sensitive to oxygen supply, and that the growth of nodulated plants is much more sensitive to aeration of the roots than is that of non-nodulated plants. BOND and MACCONNELL (1955) had already shown that the fixation of nitrogen by detached *Alnus* root nodules is markedly sensitive to the oxygen supply.

Carbon monoxide inhibits nitrogen fixation, presumably through the formation of carboxyhaemoglobin, but when all the haemoglobin of the nodule is thus combined with carbon monoxide the oxygen uptake is not affected (SMITH 1949). According to EBERTOVA (1959) the oxidation-reduction potential of soybean nodules falls to a low level (—200 mV at p_H 7.2—8.7) at a time coincident with the beginning of nitrogen fixation. The nodules are then pink, indicating ferrous iron. She cites references (particularly HAMILTON, SHUG and WILSON 1957, FEDOROV 1952) to show that the maintenance of a very reduced condition is essential to the efficient functioning of nodules in nitrogen fixation.

ζ) Internal aeration of roots.

There is good evidence (see the article by STREET and SHEAT, Vol. VIII, p. 156) that more oxygen is required for assimilation of ammonium nitrogen than for the assimilation of nitrate nitrogen, whether by roots or by bacteria. If manganese is available to barley roots, they will continue to grow and will assimilate nitrate even in the absence of any supply of oxygen to the nutrient medium, but they will not do so if nitrogen is supplied in the form of ammonium (ARNON 1937). VLAMIS and DAVIS (1944) have confirmed this for rice and barley. The explanation may lie in the fact that so long as the shoots of the plants are in the air, the roots can obtain enough oxygen by downward diffusion through the intercellular spaces to support their growth (CANNON 1932, CERIGHELLI 1920, VAN RAALTE 1940, GLASSTONE 1942, BROWN 1947). Whether or not the roots obtain some oxygen from the nitrate as suggested by SHIVE (1941), GILBERT and SHIVE (1942) and JONES *et al.* (1949) (see the article by SPENCER in Vol. VIII, p. 205) is a matter of controversy. In any case, WOODFORD and GREGORY (1948) working with barley and JONES *et. al.* (1949) working with soybeans have shown that in the presence of nitrate in the culture medium, these plants can grow at least for a week or two, with no external oxygen supply to their roots. By increasing the nutrient concentration WOODFORD and GREGORY were able to obtain almost as good growth with the roots under anaerobic conditions as with them fully aerated. On the other hand, LEONARD and PINCKARD (1946) could not obtain anaerobic growth of cotton seedling tap-roots with either nitrate or ammonium nitrogen. Perhaps too little nitrate was supplied, or the culture media were too contaminated by micro-organisms.

KRAMER (1949) makes the point that, if plants with roots developed in soil are transferred to nutrient solutions the roots produced in the soil die off and are replaced by new ones. He draws attention to the fact that most crop plants can be grown in nutrient solutions without special aeration (about 1.5 to 2 per cent oxygen) but that these same plants are severely injured in water-logged soil. Apart from the effect of water-logging on the microbial population, and the possibility of the release of toxic substances into the soil, there is some evidence that roots become adapted to the conditions of aeration under which they were produced. Barley roots grown in nutrient solutions, not specially aerated are thicker and have larger cortical air-spaces than roots grown in aerated solutions (BRYANT 1934). Wheat behaves like barley (BEAL 1918, ANDREWS and BEAL 1919). HUNTER (1915) found a similar development in *Vicia Faba*. SETHI (1930) describes two kinds of roots in rice grown in pot and field trials, one like normal wheat roots and the other with large air-spaces like those of the roots of submerged rice plants. It would appear that all these are cases of biologically advantageous *morphological* responses to poor aeration. There may also be *physiological* responses which although more subtle are just as adaptive. *Pinus rigida* roots, which do not have extensive air spaces, will grow into waterlogged sandy soils and even form mycorrhiza (MCQUILKIN 1935). Some shrubs which grow on peat hummocks are said to be sensitive to aeration (CAUGHEY 1945). Since it is established that the activity of nitrifying bacteria is high in low-moor peat well-supplied with minerals, particularly calcium (HESSELMAN 1917), if free nitrate is present in these waterlogged soils the oxygen requirement of the roots may be reduced accordingly. Most moor plants are shallow-rooted and have poorly-developed aerenchyma. Those which are deep-rooted have well-developed lacunae and air ducts (METSÄVAINIO 1931).

Water-plants usually have special morphological structures which enable their submerged parts to be independent of the oxygen supply in the surrounding

water or mud, and they may even grow better when submerged than on periodically drained soil (BERGMAN 1920). The roots of aquatic plants such as *Typha* and *Sagittaria* are more numerous and more profusely branched in unaerated soils submerged in water, but the root systems are larger when the plants are grown in aerated sand or mud (DEAN 1933). On the other hand, WEAVER and HIMMEL (1930) claim that the marsh plants *Phragmites* and *Spartina michauxiana* grow just as well in waterlogged soil as in alternately drained and saturated soil, and that *Typha* grows better in waterlogged soil or submerged than on well-drained soil. In waterlogged soils all these species produce a relatively shallow root-system of fine, much-branched roots with few root-hairs (WEAVER and HIMMEL 1930).

Because certain floating aquatics, such as *Pistia stratiotes* (and *Salvinia* and *Azolla*) have large amounts of aerenchyma, CONWAY (1940) does not regard this feature as necessarily adaptive, but as a "tendency in the development of normal parenchyma when it differentiates in a plant organ surrounded by water". Actually the aerenchyma in these plants enables them to float, and in any case the water around the roots of such plants may not be well-aerated when there is a complete cover of plants and the temperature is high. With a less dense cover of vegetation and in the light, the water near the surface will have a relatively high oxygen content due to the photosynthesis of the plants, but if the plant cover is dense and the temperature high the lower parts of the plants and the roots may be oxygen deficient. BUSCEMI (1958) found that the water at a depth of 2 feet in a lake in Minnesota had an oxygen content of 6 to 7 cc per litre, but the water near the mud in which tall plants of *Elodea* were rooted was very deficient in oxygen, due apparently to the respiratory demands of the lower, internally shaded parts of the plants. *Elodea* grows only along the shallow margins of deep lakes and in summer the surface mud at three metres depth (that is, beyond the littoral zone of *Elodea*) actually has more oxygen (4.6 ppm) than the mud under the dense canopy of *Elodea*, which may reduce the oxygen content to zero.

CONWAY finds that the gas in the air-spaces of roots of water-plants such as *Phragmites communis* and *Cladium Mariscus* contains about 17 per cent oxygen, but if the tops are removed the oxygen falls to a very low level. This has been confirmed by VAN RAALTE for rice (1940). LAING (1940) found that the oxygen content in the gas in the air-spaces decreased from the leaves towards the roots in several aquatic plants *(Nuphar, Peltandra, Pontederia, Typha, Sparganium* and *Scirpus)* and the oxygen concentration suffered diurnal changes in relation to light and darkness, It is assumed therefore that oxygen produced in photosynthesis diffuses from the leaves through the internal spaces towards the roots. VALLANCE and COULT (1951) do not believe that simple diffusion can account for the 13 to 18 per cent of oxygen in the roots of *Menyanthes trifoliata*. The large lacunae of the roots and rhizome are connected by very small pores rarely more than 2—3 μ in diameter, and these constitute a barrier to mass movement of gases in these organs. COULT and VALLANCE (1958) find that with increasing levels of CO_2 in the rhizome and roots, the consumption of oxygen falls off, and this enables more oxygen to diffuse down from the shoot to the more distal parts of the plant. Air passes in through the surface of the leaf and down the air ducts of the petiole by reason of the excess pressure due to evaporation into the lacunae of the leaf (with absorption of heat energy) (URSPRUNG 1912). GESSNER (1959) suggests that the excess pressure is relieved by mass flow (rate proportional to the 4th power of capillary diameter) along the internal air ducts, whereas inflow of air from outside the leaf is by diffusion (rate proportional to square of capillary diameter) through the stomata. He describes a model consisting of a funnel fitted with a sintered glass filter and packed below with wet cotton wool. When the funnel is placed in warm water air bubbles are generated continuously from the submerged end of the funnel, as long as water is being vapourized from the cotton wool. According to SCHOLANDER, VAN DAM and SCHOLANDER (1955) the pneumatophores of *Avicennia nitida* and *Rhizophora mangle*,

two species of mangrove growing on the coast of Florida, have lenticels which permit entry of air at low tide but do not allow access to sea-water at high tide. If these lenticels are plugged with grease, the oxygen tension in the roots falls in two days to 2 per cent or less. When the roots are covered at high tide the stored oxygen becomes considerably depleted, without a corresponding increase in the carbon dioxide content. Negative pressures are therefore built up in the pneumatophores and when the lenticels become uncovered again they suck in air. Similar but less conclusive work has been carried out by KRAMER, RILEY and BANNISTER (1952) on *Taxodium* and by TROLL and DRAGENDORFF (1931) on *Sonneratia*. Morphological investigations on air-space tissue in plants are summarised by SIFTON (1945, 1957) and aerenchyma in water plants is dealt with by GESSNER (1959).

η) Morphogenetic effects of different oxygen tensions.

Some of the morphogenetic effects brought about by manipulation of the oxygen tension have already been mentioned above. Fungi grown in aerated culture (for references see COCHRANE 1958) may grow at double the rate in unaerated culture (CRASEMANN 1954) or may be unaffected by aeration (BECKMAN, KUNTZ and RIKER 1953, WHITE 1955). In aerated cultures the mycelia are often globular, owing to the equilateral supply of all growth factors, but the form of the colonies depends also on the medium (BURKHOLDER and SINNOTT 1945, MCLEOD 1959). According to HOFSTEIN and HOFSTEIN (1958) low oxygen tension causes *Ophiostoma multiannulatum* to produce unbranched non-septate filaments in nitrogen-deficient media. They suggest that this is due to "uncoupling of cell division from cell growth". PANNIER (cited by GESSNER 1959) finds the cell size of algae to be reduced by lack or by excess of oxygen. With normal oxygen concentrations *Hydrodictyon reticulatum* cells were (on average) 1280 μ long and 480 μ wide. With three times normal oxygen concentration they were $350 \times 40\,\mu$ and with one-fifth normal, $194 \times 40\,\mu$. From similar data on *Ulva lactuca* GESSNER concludes tentatively that excess oxygen stimulates, deficiency inhibits, cell division in plant cells, a conclusion which is in direct contrast to that of WAGNER (1957) for animal cells.

Root-hair formation is generally supressed by low oxygen tensions in solution cultures or soils (DEAN 1933, SNOW 1905, WEAVER and HIMMEL 1930, ELLIOTT 1935). The root system may become less branched and the roots thicker by the development of cortical air-spaces. If water-uptake and nutrient accumulation by the roots is impaired, shoot growth will be affected, various forms of chlorosis will ensue and flowers or fruits may be shed.

Although oxygen is essential for respiration and therefore for shoot growth, there seem to be few specific ways in which oxygen affects morphogenesis of the shoot. Oxygen is necessary for regeneration, whether of organs such as shoot-buds on roots (WILLIAMS, DORE and PATTERSON 1957) (see also PREVOT 1939) or of wounded tissues such as those which form protective layers of cork (see references in KÜSTER 1925). The formation of callus tissues on cut surfaces of shoots and grafts requires the presence of oxygen (SHIPPEY 1930), but is not particularly affected by reducing the oxygen concentration down to 10 per cent, or raising it to 70 per cent. Pure oxygen is inhibitory. According to SCOTT (1950) and SCOTT and LEWIS (1953) wherever surfaces of cells come into contact with air (as in intercellular spaces) they form a thin pellicle of "suberin". Although it is well-recognized that oxygen is necessary for the growth of tissues in sterile culture the view put forward by WHITE (1939) that a diminished or limited supply of oxygen is required to initiate differentiation of organs on such tissues is not in

agreement with the results of LEVINE (1947) or of WARDLAW and ALLSOPP (1948). WHITE found that callus tissue of *Nicotiana* grown on semi-solid media produced leafy branches (but no roots) when submerged under 8 mm of a liquid culture medium. LEVINE (1947) (see also REINERT 1958) obtained similar organ formation on carrot tissue without submergence. WARDLAW and ALLSOPP found oxygen necessary for the growth of apical meristems of ferns. The rate of development of plantlings from detached meristems increased with oxygen concentration up to 45 per cent, but there were no differential effects of oxygen on morphogenesis, except for some abnormalities in 100 per cent oxygen. Tissue cultures also grow better with better aeration, as MELCHERS and ENGELMANN (1955), MELCHERS and BERGMANN (1959) and STEWARD and SHANTZ (1955) have shown.

There is little work on the effects of oxygen tension on leaf growth and development. LAING (1941) has found that although the rhizomes of certain water-plants can endure anaerobic conditions in the dormant state they require appreciable amounts of oxygen to sustain growth and respiration when they become active. This partly accounts for the fact that these plants *(Typha, Sparganium, Scirpus validus,* and *Acorus calamus)* grow only in shallow waters and "the manner of growth is such that usually some of the shoots are in contact with air all the year round".

The leaf growth of plants which inhabit deeper waters *(Nuphar, Peltandra, Pontederia)* is adversely affected by atmospheric air, and the young leaves of *Nuphar advenum* will grow as rapidly in nitrogen as in 1 per cent oxygen. With higher concentrations growth is much less rapid . On the other hand, the mature leaves, after they have reached the surface of the water, rapidly succumb to anaerobic conditions, like the leaves of many land plants (see article by TURNER, Vol. XII). Although anaerobic conditions are necessary for the rapid growth of the young leaves of *Nuphar,* the gas in the intercellular spaces of the rhizome contains as much as 10 per cent of oxygen in the daytime. Little if any of this can enter the young leaf, because of the absence of air-spaces in the mass of undifferentiated tissue at the base of the young petiole. As the petiole grows, the intercellular spaces of the lamina become contiguous with those of the rhizome across the abscission zone.

It would be interesting to know what are the physiological mechanisms which govern the growth of the leaves and petioles of these water-plants, and in particular, why they cease to grow when the lamina reaches the surface of the water. CARR and MCCOMB (unpublished) have found that small amounts of gibberellic acid will cause elongation of the internodes of the surface rosettes of *Callitriche verna,* but a similar elongation can only be induced by submergence, not by anaerobic conditions, as suggested by KARSTEN (1888) (see PFEFFER 1903). According to GESSNER (1959) the "depth compensation" growth of petioles of water plants such as *Nymphaea* species is regulated, not by change in oxygen tension, but by access to free carbon dioxide and the commencement of assimilation when the lamina arrives at the water surface. If the CO_2 is removed from the air over the water surface such petioles continue to elongate when control petioles have stopped. Restoration of the CO_2 to the air around the lamina causes growth of the petiole to stop. Growth inhibition by atmospheric CO_2 is said to be peculiar to water plants, land plants being affected only by much higher concentrations. The hypothesis cannot explain the case of *Callitriche,* the leaves of which are produced above the water surface and eventually, by elongation of the subtended internode are moved down into the water. GESSNER cites the phenomenon mentioned by SEIDEL (1955) in *Scirpus lacustris,* in which a fairly constant proportion of the haulm is produced above the water

surface, so that there is a direct proportionality between depth and total length of haulm. GESSNER believes the action of CO_2 on depth compensation growth to be indirect and makes the onset of photosynthesis in the lamina responsible. This does not accord with the fact that petiole elongation also ceases in the dark, when the lamina reaches the surface.

Coleoptiles and other organs used in auxin assays are notoriously sensitive to oxygen and grow best when not submerged, but the coleoptiles of rice grow much better submerged than emersed. YAMADA (1954) has investigated this phenomenon in relation to auxin destruction. Coleoptiles of rice in air require 20 to 30 times as much auxin to bring about maximal growth, as compared with submerged coleoptiles. YAMADA suggests that the respiration of the coleoptiles is aerobic (it is affected by KCN as well as by dinitrophenol) and that the favourable effects of submergence respresent a compromise between the decreased aerobic respiration and the decreased auxin destruction at lower oxygen tensions.

3. Carbon dioxide.

a) Solubility and acidity, in relation to plants.

Carbon dioxide affects growth and development in several ways:

(1) It is assimilated by photosynthetic organisms in the light.

(2) It is assimilated by many if not all organisms in the dark.

(3) Dissolved in water it forms carbonic acid and affects the p_H of the environment and may affect that of the organisms themselves.

(4) It has apparently narcotic effects on cells, that is, in low concentrations it may stimulate, in high concentrations inhibit activity of one kind or another.

It is not intended here to say much about modes of action (1) and (2) nor can the mechanisms of action of carbon dioxide in activities such as germination and growth be discussed at any length. Indeed, these mechanisms may be exceedingly complex and we can do little more than speculate on their possible nature.

Carbon dioxide is taken up by plants either as a gas, dissolved in water or as the hydrated forms of this gas, carbonic or bicarbonic acid. The factors affecting the solubility of carbon dioxide in water and other solvents have been discussed at length by RABINOWITCH (1945) from which the data in Table 1 are taken.

Table 1. *The solubility of carbon dioxide in water.*

pCO_2 (atm)	CO_2 mol/litre		
	solution	HCO_3^-	p_H
10^{-4}	3.37×10^{-6}	1.24×10^{-6}	5.91
3.1×10^{-4}*	0.94×10^{-5}	2.07×10^{-6}	5.68
10^{-3}	3.37×10^{-5}	3.92×10^{-6}	5.41
10^{-2}	3.37×10^{-4}	1.24×10^{-5}	4.91
10^{-1}	3.37×10^{-3}	3.92×10^{-3}	4.41
1	3.37×10^{-2}	1.24×10^{-3}	3.91

* Normal carbon dioxide content of free atmosphere.

From this table it can be seen that in very dilute solutions an appreciable number of the dissolved carbon dioxide molecules are present as HCO_3^- ions. In distilled water which has been allowed to come into equilibrium with the atmosphere and has attained a p_H of 5.7 the ratio CO_2:HCO_3^- is as 5:1. Hydration of the carbon dioxide molecules to bicarbonate ions, and more particularly to carbonate ions, is relatively slow and is accelerated by many weak acids such as phosphoric and acetic acids, and in blood cells by the enzyme, carbonic anhydrase. The evidence, such as it is, for the presence of this enzyme in plant cells is surveyed by BROWN and FRENKEL (1953). Electrolytes dissolved in water reduce the solubility of carbon dioxide in it (see EDSALL and WYMAN 1958). For electrolyte solutions of the order of 10^{-1} mole/litre (such as those typical of plant saps) the solubility is reduced about 5 to 10 per cent.

All plants can absorb amounts of carbon dioxide many times greater than those which can be accounted for by solution in the water of the plant (SPOEHR and MCGEE 1924). According to SMITH (1940) the main systems responsible for carbon dioxide absorption in plants are:

(1) the water of the plant;

(2) solid carbonates, principally of the alkaline earths (Mg, Ca) which form soluble bicarbonates.

(3) soluble phosphates. These absorb carbon dioxide according to the equation:

$$CO_2 + H_2O + HPO_4^{--} \rightleftharpoons HCO_3^- + H_2PO_4^-$$

RABINOWITCH (1945) mentions other systems which have not yet been investigated, but which might be involved in carbon dioxide absorption in plants. These are as follows:

(1) Solution in lipoids. CO_2 is many times more soluble in lipids than in water.

(2) Carboxylation of polyphenols, such as tannins and quercetin (RUBEN and KAMEN 1940).

(3) Carbamination, a process which is important in the transport of carbon dioxide in blood. In alkaline solution, amines combine with carbon dioxide to form carbamic acids and carbamates.

There seems little possibility that carbamination can take place under the acid conditions of plant cells but carbon dioxide might form dissociable compounds with the amino groups of proteins (SIEGFRIED 1905). The recent literature on this topic has been reviewed by WYMAN (1948) and by EDSALL and WYMAN (1958) who write: "since virtually all proteins contain some free amino groups ... it may be expected that all proteins should form carbamino derivatives, at least in moderately alkaline solution."

The internal atmosphere of bulky plant parts may contain considerable quantities of carbon dioxide (up to 35 per cent in potatoes, according to MAGNESS 1920) and as this must be in equilibrium with the protoplast, it is certain that the latter is usually very well buffered against changes in pCO_2 and p_H. Taken in conjunction with the ability of plants to absorb considerable quantities of carbon dioxide this means that one must expect that many of the more slowly-developed responses of higher plants, such as those of germination and cell elongation, would be relatively insensitive to carbon dioxide over a fairly wide range of partial pressures. THORNTON (1933, 1934) has drawn attention to the fact that many physiologists expect on theoretical grounds, or claim to have found by experiment (see SMALL 1954), that increasing the pCO_2 in the environment should increase the acidity of plant tissue. In fact, THORNTON (1933) finds that the p_H of flowers and vegetables, stored in atmospheres containing as much as 50 per cent carbon dioxide, increases. In asparagus there is a significant change in 15 minutes of treatment with 50 per cent carbon dioxide, but in potatoes there is no change within 12 hours, but a change does take place in two or three days. The p_H change is of the order of 0.5 to 0.75 unit and it is less with lower temperatures. The development of an increase in p_H is dependent on the presence of oxygen as well as of carbon dioxide. It is reversible on transfer to air. THORNTON (1934) finds a similar but even larger change in the fungus *Sclerotinia fructicola*, the p_H of which increases from 5.6 to 7.2 with 15 per cent carbon dioxide in 24 hours. On the other hand, the external medium showed, in the experiments, the expected change towards acidity, falling from p_H 6 to p_H 4.3. The increase in p_H of the fungus is lethal to it and THORNTON attributes the inhibitory effects of carbon dioxide on many fungi to such an enforced increase in alkalinity. In succulent plants the rate of deacidification is *reduced* (*i.e.* the plants remain acid) by increase of the pCO_2 (see THOMAS, RANSON, and RICHARDSON 1956).

b) Carbon dioxide essential for growth.

Carbon dioxide is essential for the growth of all photolithotropic organisms, that is those which obtain most of their energy from photochemical reactions and depend on exogenous inorganic hydrogen donors. Not all photosynthetic organisms are autotrophic and even some higher plants, such as some orchids, may be saprophytic in early stages of development and become autotrophic only when they have unfolded their first green leaves. Indeed, to the extent that all seedlings must live on the reserves of the seed until their leaves have developed the ability to carry out photosynthesis, all higher plants are, at an early stage in their development, independent of an external supply of carbon dioxide and those with endosperm might be classed as saprophytic. Many bacteria are capable of living as autotrophic organisms, obtaining energy for the reduction of carbon dioxide from light or from the oxidation of inorganic substances (see WOODS and LASCELLES 1954), and some of them are capable also of living heterotrophically, utilising organic compounds.

HEATH (see article in Vol. XVII, Part 1) has provided evidence that there is a limiting minimum carbon dioxide concentration which is in equilibrium with the cells of leaves. If carbon dioxide-free air is drawn through a leaf, the air-stream emerges with a content of about 0.01 per cent carbon dioxide. When illuminated leaves are enclosed in an atmosphere containing carbon dioxide they reduce its concentration down to about 0.01 per cent but no further (MILLER and BURR 1935). The limiting concentration varies with temperature, increasing steadily (in coffee and onion leaves) up to 30° C and then sharply to a value of 0.025 per cent at 35° C. If this phenomenon is true also of organs other than leaves, then it is virtually impossible to observe the responses of higher plants to atmospheres devoid of carbon dioxide, and the situation is worse the higher the temperature. It also means that quite small concentrations of carbon dioxide are likely to have tonic effects on cells with the internal carbon dioxide concentration of which they will be in equilibrium.

Carbon dioxide is an essential metabolite for the growth of species of *Mucor* (KREBS 1943) and *Aspergillus* (RIPPELS and BORTELS 1927). *Penicillium chrysogenum* also requires CO_2 for growth. The gas may be supplied directly or indirectly in the form of oxaloacetate, which can be decarboxylated to yield CO_2 (GITTERMAN and KNIGHT 1952). According to GLADSTONE, FILDES and RICHARDSON (1935) carbon dioxide is an essential factor for the growth of certain bacteria. If carbon dioxide-free air is passed through the culture medium these bacteria stop growing. A similar effect has been observed by JAHN (1936) with the *Cryptomonad* flagellate, *Chilomonas*. The growth of this organism is reduced to less than one-fifth when the culture medium is swept with carbon dioxide-free air, as compared with ordinary air. The obligate CO_2 requirement for the growth of a certain strain of the bacterium *Neisseria meningitidis* (TUTTLE and SCHERP 1952) can be replaced by some substance present in yeast extract.

It is possible, therefore that the existence of a critical minimum carbon dioxide concentration at the cell surface is widespread among many kinds of organisms.

c) Effects of carbon dioxide on dormancy and germination.

α) Buds and seeds.

Increasing the concentration of carbon dioxide in the atmosphere around seeds or buds has in many cases proved to be very effective in breaking dormancy. JESENKO (1912) showed that immersion for 12 hours in water saturated with carbon dioxide was a very good means of breaking the dormancy of buds of *Larix decidua* and *Sambucus nigra*, although it had no effect on *Salix aurita*. WEBER (1916) also found that carbon dioxide will break bud dormancy in *Syringa vulgaris*. He used pure carbon dioxide with no oxygen and considered the effect to be indirect. BORESCH (1928) also believed that the forcing of tree buds by a warm bath or low pO_2 was due to an increased rate of anaerobic respiration, but it could also be an effect of increased internal pCO_2. (Other work on the forcing of tree buds is reported in the articles by VEGIS, this volume, pp. 65—67, and BÜNNING, Vol. XI, p. 873). A considerable amount of work has been done on the effects of carbon dioxide on bud dormancy of the potato (see HEMBERG'S article in Vol. XV). BRAUN (1931) states that concentrations up to 12 per cent hastened sprouting, but larger percentages were somewhat inhibitory in his experiments, in which the tubers were kept in closed containers in which the carbon dioxide of respiration was allowed to accumulate. KIDD (1919) had found that when potatoes were stored in this way their growth was retarded by about 10 per cent, and 20 per cent carbon dioxide was quite inhibitory. THORNTON (1933) treated

freshly-harvested whole or quartered tubers with various mixtures of carbon dioxide and oxygen, made up to 1 atmosphere with nitrogen, for only three or six days, after which he planted them out in sand. Concentrations of carbon dioxide between 13 and 58 per cent caused buds to sprout. In later work (1939 and 1945) THORNTON showed that freshly-harvested tubers remain dormant in air because the tissues are readily permeable to oxygen and the oxygen content of the air is too high to permit sprouting. If the oxygen content of the air is reduced to between 2 and 10 per cent the buds sprout. In relatively dry conditions sprouting can be induced by 2 per cent oxygen in nitrogen or even by pure nitrogen. In moister conditions 5 to 10 per cent oxygen permits sprouting. As the tuber ages its permeability to oxygen decreases due to the thickening of the periderm and eventually reaches a point where the internal pO_2 is sufficiently low to allow bud growth to commerce. THORNTON'S results agree with those of KIDD (1919) in that forcing was better with 10 per cent oxygen than with 20 per cent and that 50 per cent and 80 per cent oxygen were toxic. THORNTON'S (1935) work on the effects of carbon dioxide in stimulating germination of *Xanthium* seeds has already been reviewed. There is no stimulating effect in the absence of oxygen, even 10 per cent oxygen being insufficient. In 100 per cent carbon dioxide no germination of either "lower" or "upper" seeds of *Xanthium* takes place. If, after germination has been forced by carbon dioxide, the seedlings are kept in the presence of 60 or 40 per cent carbon dioxide, the radicles become damaged after emergence, but if, on germination, the seeds are promptly transferred to air no subsequent damage is incurred.

BALLARD (1958) has found that the "hard" (dormant) seeds of *Trifolium subterraneum*, the dormancy of which can be removed by storage of the imbibed seeds at 5° C or by removal of the testa, can be caused to germinate by very low concentrations of carbon dioxide, in the region of 0.5 to 5 per cent. The dormancy of such seeds can be removed merely by sealing them in a tube, in which the carbon dioxide of respiration accumulates. In Petri dishes the respiratory carbon dioxide from a seed already germinated may also accumulate to a level sufficient to stimulate "hard" seeds to germinate. GRANT-LIPP and BALLARD (1958) have shown that the dormant seeds of many species of *Medicago*, *Trifolium* and *Trigonella* are stimulated to germinate by atmospheres containing 2.5 per cent carbon dioxide.

The very low pCO_2 which is effective in these experiments is remarkable. There are other reports of stimulation of germination by carbon dioxide, but always at much higher percentages than those used by BALLARD. Perhaps the difference lies in the amounts of carbon dioxide with which the embryo is already in equilibrium in the seed. It may be connected with the valve-like action of the fissure in the hilum in the seeds of the *Trifolieae*, described by CORNER (1951) and studied by HYDE (1954). This fissure opens in dry air and closes in moist air. The suggestion lies to hand that it may remain open under the influence of relatively low concentrations of carbon dioxide, in a manner not unlike that of stomata which also respond to small changes in the carbon dioxide content of the air, but at a much lower level than those which are effective in the germination experiments of BALLARD (see article by HEATH, Vol. XVII, Part 1). According to KIDD (1914b) mature dried peas and beans contain about 45 cc of carbon dioxide per 100 mg of seed and this content increases on soaking. There seem to be no comparable figures for *Trifolium* seeds. In a very brief report, ANDERSON (1933) says that 100 per cent carbon dioxide will force germination of *Poa compressa* fruits. THORNTON (1936) found that lettuce seeds whether freshly-harvested or secondarily dormant may be caused to germinate even at temperatures above the normal maximum by four days of treatment with air containing 20 per cent or more of carbon dioxide and

20 per cent of oxygen. Even 5 per cent of carbon dioxide will replace the need of freshly-harvested seed for light at 26° C. As might be expected from the effect of temperature on the solubility of gases, the carbon dioxide tensions required to bring about germination increased with temperature. Increasing the pO_2 did not increase the percentage of germination at the higher temperatures, nor would oxygen cause the breaking of secondary dormancy. HARRINGTON (1917) has shown that 60 to 80 per cent carbon dioxide is an effective forcing agent for *Sorghum halepense* grains.

In contrast to these reports of germination stimulated by carbon dioxide, there are many references (CLEMENTS 1921) to the inhibitory effects of carbon dioxide on germination. LEHMANN and AICHELE (1931) cite work which showed that barley will germinate with not more than 20 per cent carbon dioxide. KIDD (1914a) found the upper limit for barley, peas and onion seeds to be of the order of 30 per cent but THORNTON (1944) points out that these upper limits are modified by temperature, and that KIDD's data apply only for temperatures of 20° or less. At 35° C many seeds, including those of wheat, will germinate with only a slight delay in concentrations as high as 40 per cent, although delphinium seeds are particularly sensitive to concentrations above 20 per cent of carbon dioxide.

Most of these seeds germinate readily on transfer from the inhibitory atmospheres to normal air. KIDD and WEST (1917) found that *Brassica alba* seeds were made secondarily dormant, however, and would not germinate until either (1) they were subsequently dried and then re-wetted or (2) the seed coats were pricked or removed. About 24 per cent of carbon dioxide was necessary to make these seeds dormant. The excised embryos can be made dormant (KIDD 1914a) so that the onset of dormancy cannot be more than accentuated by the presence of the seed coat, nor is the permeability of the seed coat to gases affected by the carbon dioxide treatment (KIDD and WEST 1917). Not less than 15 per cent oxygen must also be present in the atmosphere around the seeds to induce secondary dormancy (*c.f. Ambrosia;* DAVIS 1930a). With reduction of the oxygen content of the atmosphere around the seeds to 4 per cent or by lowering the temperature to 3° C, between 4 and 6 per cent carbon dioxide was sufficient to induce secondary dormancy.

This phenomenon is of considerable importance in connection with the dormancy of seeds in the soil (BARTON and CROCKER 1948), since high percentages of carbon dioxide and correspondingly low percentages of oxygen are characteristic of the soil atmosphere and many weed seeds must therefore be kept dormant thereby for long periods. BARTON (1945) has found that the respiration of such dormant seeds in an imbibed condition is very much less than of non-dormant seeds, and this fact probably helps to prolong the life of dormant seeds. From these early investigations of KIDD and KIDD and WEST has been developed the method of carbon dioxide storage of seeds and other plant organs ("gas storage"), and this is now widely used in the storage of fruit. LEHMANN and AICHELE (1931) cite many references which show that many kinds of seeds rapidly lose viability when stored in atmospheres enriched in carbon dioxide, so that the method is not universally applicable. On the other hand in the literature on seed storage reviewed by PORTER (1949) there is abundance evidence that gas storage prolongs the life of certain kinds of seeds.

β) Spores.

Spore germination of the fungi (GOTTLIEB 1950) may be stimulated by low concentrations of carbon dioxide, inhibited by high concentrations. High concentrations decrease the p_H of the medium, an effect which must be taken into

consideration in assessing the direct action of carbon dioxide. Platz, Durrell and Howe (1927) found *Ustilago zeae* spores to germinate best with a carbon dioxide concentration of 15 per cent. They suggest that the "emanations" from plants which stimulate the spores to germinate may be carbon dioxide and not ethylene or ethyl acetate, as suggested by Brown (1922b). Carbon dioxide is said to have greater effects than oxygen on the spore germination and growth of fungi.

Conidia of *Aspergillus niger* require carbon dioxide for germination (Rippels and Bortels 1927). Increased carbon dioxide concentrations up to 2.5 per cent stimulated germination of *Puccinia graminis tritici* uredospores (Allen 1955) (see 2 c δ). Since it has no effect on spores from which the self-inhibitor has previously been removed the carbon dioxide seems to act by reducing the effectiveness of this inhibitor. Inhibition of spore germination by relatively low concentrations of carbon dioxide is comparatively rare (Magie 1935, Stock 1931). The germination of spores of *Mucor mucedo* is somewhat inhibited by 10 per cent carbon dioxide (Lopriore 1895), as is that of several mould fungi (Brown 1922b). Concentrations in the region of 20 to 30 per cent inhibit the germination of a large number of fungi, but not *Penicillium glaucum* (Brown 1922a). *Ustilago zeae* and *Basisporium gallarum* are preventing from germinating only by 50 per cent carbon dioxide (Durrell 1925). The relatively high carbon dioxide content of certain soils may be sufficient to keep fungal spores or sclerotia dormant for several years (Hawker 1950).

Clostridium botulinum spores require carbon dioxide for germination, but since organic acids can replace this requirement it is suggested that organic acid metabolism (possibly fixation of carbon dioxide into organic acids) is the operative factor (see Williams 1952).

No general hypothesis has been put forward which would account for the effects of carbon dioxide on germination. Stimulation by low concentrations and inhibition by high concentrations is usually attributed vaguely to the "narcotic" action of carbon dioxide, but exactly what this means in terms of chemical or physical mechanisms is quite unknown. A similar criticism may be levelled at the use of terms such as "the auxin-like action" of carbon dioxide to explain its effects on growth (Wood 1953). It would seem more profitable to seek an explanation along the lines of that offered by Cantino to explain the effects of carbon dioxide on morphogenesis in the *Blastocladiales* (see below, and Vol. XV).

d) Injury to seeds caused by soaking them in water.

It has been found by many observers (*e.g.* Kidd and West 1918) that soaking seeds in excess of water may injure them in some way so that they are subsequently unable to germinate, or do so poorly and readily decay. The degree of dormancy of the embryo, the temperature of soaking and the presence of oxygen or carbon dioxide are important in determining the extent of injury (see Crocker and Barton 1953). Dormant seeds appear not to be damaged excessively by storage in water (Shull 1914, Jones 1958) nor is their dormancy relieved by soaking (Barton 1954). Soaking injury is most pronounced with non-dormant seeds such as peas, beans, wheat and sunflower. Soaking at 10^0 and 30^0 C is more injurious than soaking at 20^0 C (Kidd and West 1919, Eyster 1936) due apparently to a greater exosmosis of protein (Eyster 1939) or (contrary to Barton and McNab 1956) growth promoting substances (Eyster 1940) at the extreme temperatures. Following a report by Albaum *et al.* 1942, that soaking injury to oats was accentuated by bubbling oxygen through the water, Barton (1950, 1952) and Barton and McNab (1956) have shown that many kinds of seeds are injured by soaking them in the presence of oxygen. One is reminded of the similar work of Turner

and QUARTLEY (1956) on the inhibitory effect of high pO_2 on peas (see above, section 2dβ). The biochemical changes, chiefly changes in the amounts of various amino acids during the development of soaking injury accentuated by oxygen, have been studied by BARTON and MCNAB. BARTON (1952) found that soaking injury was accompanied by excessive water uptake which was in proportion to the amount of oxygen supplied. Water uptake and soaking injury could be retarded by polyvinylpyrrolidone or hydrogen peroxide but more easily and efficiently by carbon dioxide. After soaking for 24 hours in the presence of carbon dioxide beans germinated perfectly but not at all after soaking for a similar period in the presence of oxygen. The favourable effect of carbon dioxide is not due simply to the exclusion of oxygen, as a mixture of 25 per cent oxygen and 75 per cent carbon dioxide also caused no soaking injury.

According to ADDICOTT and LYNCH (1955) carbon dioxide, especially over 17 per cent, has been shown by YAMAGUCHI to retard abscission of bean leaflet explants in water, whereas oxygen up to 55 per cent accelerates abscission (CARNS, ADDICOTT and LYNCH 1951). It is further of interest that the water uptake of roots has been shown to be reduced by bubbling carbon dioxide through nutrient solutions (CHANG and LOOMIS 1945). Carbon dioxide not only protects seeds against injury by oxygen, but also against the further injury which can be caused by the presence of mineral nutrients in the water in which they are soaked or to toxicity due to selenium or 2,4-D (BARTON 1952).

e) Effects of carbon dioxide on growth.

Mutants ("CO_2-sensitives") of animals (*e.g. Drosophila*, L'HÉRITIER 1951) are known which are unusually sensitive to increase in the carbon dioxide content of the medium in which they live. No work appears to have been done on such mutants, which are probably not lacking, in plants.

α) Carbon dioxide fertilisation.

The concentration of carbon dioxide in normal air is limiting for photosynthesis except at low light intensities, and increases in growth rates can be obtained by temporarily increasing the concentration to as much as 20 times that of air (BROWN and ESCOMBE 1902). Sustained high concentrations, even as low as 0.1 per cent, are injurious according to BROWN and ESCOMBE, but this is disputed by other authors. A considerable literature has grown around this concept of "carbon dioxide fertilisation" of plants, and it has been reviewed by MILLER (1938) and CROCKER (1948). In recent work MORTIMER (1959) finds that the rate of photosynthesis rises after an abrupt increase of the CO_2 content of the air up to about 2 per cent, but after one minute the rate falls again.

Many workers (*e.g.* BROWN and ESCOMBE) have not observed either the necessity of purifying the gas of carbon monoxide, or the necessity to increase the light intensity, which is in minimum at high carbon dioxide concentrations. In most cases beneficial results have been obtained, with increases in total dry weight, yield of fruit or tubers, nitrogen fixation, earliness of flowering and number of flowers. Some authors find that the leaf area is increased, others that it is decreased. In this connection it is of some interest that REID (1929) found that sunflower plants grown in the light in pots under belljars without carbon dioxide weighed less than control plants grown in the dark, but had larger leaves and cotyledons. REID (see also GESSNER 1959 and 2dη) believes that the assumption of assimilatory activity by the leaf is inhibitory to its own expansion, and she cites CORENWINDER'S (1876) experiments in which leaves enclosed in glass cylinders without carbon dioxide grew more than control leaves allowed access to carbon dioxide.

High concentrations of carbon dioxide, such as are present in certain springs (up to 1.2 gm CO_2/litre) are obligatory for the growth of the blue-green alga, *Oscillatoria carbonicicphila*, which grows in such springs (PRAT 1929).

β) Carbon dioxide effects on root growth.

Errors of method in determining the effect of the gaseous environment on root growth have been dealt with in 2d δ.

Although an increase in pCO_2 in the air to about 7 per cent inhibits the growth of the shoot, roots are often exposed to and will tolerate concentrations of this order or even higher. CHAPIN (1902) found the roots of *Vicia sativa* and *Pisum sativum* to tolerate 40 per cent carbon dioxide for 28 hours if subsequently returned to a lower concentration. On the other hand, growth stops with concentrations about 20 to 30 per cent, according to the species (see review by CLEMENTS 1921). CANNON and FREE (1925) confirmed the short-term tolerance of roots for high pCO_2. Above 25 per cent, the roots of *Covillea* stopped growing immediately, but those of *Krameria* and *Mesembryanthemum* species continued for some hours.

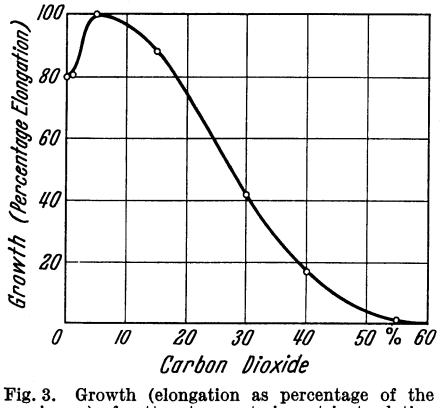


Fig. 3. Growth (elongation as percentage of the maximum) of cotton tap roots in nutrient solution (p_H 4.9) with 21 per cent oxygen and various amounts of carbon dioxide in the aerating gas mixture. (Data from LEONARD and PINCKARD 1946.)

More recently STOLWIJK and THIMANN (1957) have found inhibition of root growth of *Pisum sativum*, *Vicia faba*, *Phaseolus vulgaris* and *Helianthus annuus* by steady concentrations of 6.5 per cent carbon dioxide in the air in sand cultures. On the other hand, this concentration had no effect on roots of oats or barley. This fits in well with the suggestion (HOWARD 1925) that certain plants may be killed by the development of a dense sward of grass, by reason of the different tolerances of the root systems for carbon dioxide in the soil. Even grass roots are inhibited by suitably high concentrations of carbon dioxide, however, as MICHAEL and BERGMANN (1954) have shown. The growth rate of *Secale cereale* roots could be reduced to one half that of the controls by treating the soil with high concentrations of carbon dioxide either directly, or indirectly by compacting the soil. Absorption of the excess carbon dioxide by activated charcoal reduced these inhibitory effects. (The use of activated charcoal in experiments on carbon dioxide is suspect because BALLARD (1958) finds that it may give off enough carbon dioxide to stimulate dormant *Trifolium* seeds to germinate. The amount given off depends on the provenance of the charcoal.) As might be suspected, in MICHAEL and BERGMANN'S experiments, rice was much less sensitive than rye. Pure carbon dioxide stops the growth of roots, both excised and intact, of rice, barley and tomato (VLAMIS and DAVIS 1944). Cotton roots will tolerate and grow with 15 per cent carbon dioxide and 21 per cent oxygen in nutrient solutions but not with 60 per cent carbon dioxide (Fig. 3) (LEONARD and PINCKARD 1946). ERICKSON (1946) found 6.8 per cent carbon dioxide not injurious to tomato roots in nutrient solutions. Further references to work of this kind are given in BERGMAN (1959).

According to many Russian authors (KURSANOW 1956) roots are able to fix some carbon dioxide from the soil atmosphere and thus contribute to the total of assimilated carbon of the plant. The extent and importance of the contribution is not yet fully established (see also the review by PONTOVICH 1951).

γ) Effects of carbon dioxide on growth of algae and fungi.

Depending on light intensity and p_H, high concentrations (usually less than 10%) of CO_2 narcotise the machinery of photosynthesis in algae (RABINOWITCH

1945). Growth of *Scenedesmus quadricauda* is retarded with 5% CO_2 and photosynthesis in *Chlorella* with 1% CO_2 (STEEMANN NIELSEN 1953, 1955).

There are many difficulties of method in ascertaining the responses of fungi to gases such as oxygen or carbon dioxide. Without adequate aeration growth may be affected by the accumulation of products of anaerobic metabolism (such as methane or carbon dioxide) or of "staling factors", so that the effect of aeration might be quite indirect and consist merely of the physical removal of these substances. Ammonia may accumulate in the medium and relatively high concentrations of carbon dioxide will then be tolerated simply because it helps to lower the p_H (BROWN 1923).

Yeast will grow in an atmosphere consisting entirely of carbon dioxide and water vapour but most fungi will not tolerate much more than 10 per cent carbon dioxide (ROCKWELL and HIGHBERGER 1927). As usual, temperature affects the response, partly at least by its effect on the solubility of the gas (BROWN 1922b), but also indirectly. *Penicillium roquefortii* is partially inhibited at 21° C by 7 per cent carbon dioxide and completely inhibited at 30° and 9° C (GOLDING 1940). The growth rate of certain wood-rotting fungi is increased by carbon dioxide, a concentration of 15 per cent giving double the rate in air (THACKER and GOOD 1952). Some fungi are sensitive to surprisingly small amounts of carbon dioxide. The sporophores of *Agaricus bisporus* are sometimes killed and always distorted in the presence of 5 per cent carbon dioxide, and are somewhat inhibited by even 1 per cent (LAMBERT 1933). Fungal growth in the soil (DURBIN 1959) or on stored fruits, vegetables and meat (MORAN, SMITH and TOMKINS 1932) may be controlled by carbon dioxide. Increasing the pCO_2 in the soil by ploughing-in green manure to stimulate activity of a saprophytic microflora, or by compacting the soil, gives a measure of control of the "take-all" disease of wheat, *Ophiobolus graminis* (GARRETT 1956).

The formation of reproductive structures is usually more sensitive to carbon dioxide than mycelial growth, as for example in *Mucor mucedo* (LOPRIORE 1895), *Pyronema confluens* (ROBINSON 1926), *Choanephora cucurbitarum* (BARNETT and LILLY 1955), and *Collybia velutipes* (PLUNKETT 1956).

f) Morphogenetic effects of carbon dioxide.

α) Effects on higher plants.

(See also 2 d η, p. 760.)

There are few references to specific morphogenetic effects of carbon dioxide. SHIPPY (1930) showed that concentrations of carbon dioxide over 10 per cent, particularly with a restricted oxygen supply, did not allow callus tissue to form over wounds or between grafted surfaces. Other students of regeneration (ZIMMERMAN and HITCHCOCK 1940) have found that adventitious shoots and roots may be induced to form on stem cuttings exposed to high (90 per cent) concentrations of carbon dioxide. *Hibiscus syriacus* cuttings were found to be particularly responsive. REID (1929) obtained adventitious roots on sunflower hypocotyls only in the presence of carbon dioxide. Mention has been made above of the suppression of leaf growth by excess carbon dioxide. FARMER and CHANDLER (1902) observed this, and since they found that the stomatal index (number of stomata per unit area) was considerably increased, either the number of stomatal initials was increased or cell expansion was reduced. They found no alteration of the leaf structure, contrary to MONTEMARTINI (1892) who observed an increase of the thickness of the palisade relative to the spongy mesophyll.

MER and RICHARDS (1950) made the interesting discovery that oat seedlings grown in a tightly closed box developed long mesocotyls and much shorter

coleoptiles than seedlings grown with a free circulation of air. The greater the number of seedlings enclosed in the box the longer were the mesocotyls. The effect was shown to be due to carbon dioxide accumulating from the respiration of the seedlings. When oat seedlings are grown in a continuous stream of air they show the effect with 5 per cent but not with 1 per cent of carbon dioxide in the air. Light inhibits the elongation of the mesocotyl, whether carbon dioxide is present or not. Carbon dioxide reduces the dry weight of the plumules (MER 1957) apparently by reducing the outflow of materials from the endosperm. Cell extension of the coleoptile is reduced but cell division continues in the node meristem, adding to the number of cells in the mesocotyl. It appears that the growth of the coleoptile is inversely correlated with that of the mesocotyl. Since the supply of materials from the endosperm is reduced by carbon dioxide treatment, MER (1959) attempted to supply the coleoptiles with sugar via the roots. The elongation of the mesocotyl was further promoted by 2 per cent sucrose, glucose or mannitol and the coleoptile was made even shorter. Supplies of nitrate, however, allowed the coleoptile to elongate and slightly suppressed the elongation of the mesocotyl, but nitrate had no effect on the coleoptile in air. Since sugar promotes the growth of detached coleoptiles but nitrate does not, the problem of reduced coleoptile growth in the intact seedlings appears to be one of transport, and it is assumed that carbon dioxide affects the transfer of nitrogenous materials from the endosperm to the coleoptile. This does not explain why mesocotyl growth should be stimulated by carbon dioxide at the expense of coleoptile growth. The phenomenon has some biological importance as well as physiological interest, since grass seedlings germinating in the soil at depth may produce long mesocotyls, thus carrying up the shoot apex towards the soil surface (CARR and CARR 1957).

For reviews of the role of carbon dioxide in photoperiodism see DOORENBOS and WELLENSIEK (1959) and LIVERMAN (1955).

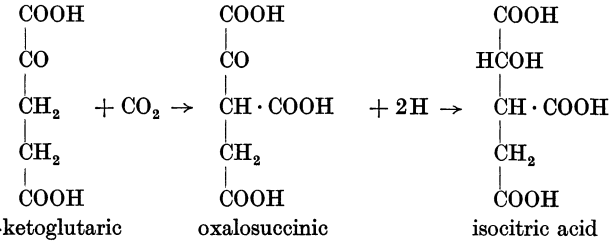
β) Effects of carbon dioxide on morphogenesis in *Blastocladiales*.

The thallus of *Blastocladia* species is a branched structure bearing both thin-walled zoosporangia and brown, pitted, resistant sporangia. The thallus of *Blastocladiella* is unbranched and consists of two cells, a rhizoid cell and a terminal cell. For more than half the life of the plant the future nature of the terminal cell is undecided, but certain factors eventually determine that it shall be either a thin-walled, colourless zoosporangium, or a thick-walled resting sporangium. It was discovered that this step in determination in *Blastocladia pringsheimii* may be controlled by carbon dioxide. A very high concentration (99.5 per cent at p_H 5.5) of carbon dioxide will cause resting sporangia to form in cultures of this fungus (CANTINO 1949). *Blastocladiella emersonii* plants will virtually all produce resting sporangia following addition of 0.01 M bicarbonate to the medium. However plants which are more than three-fifths through their generation time are not affected by bicarbonate addition, and continue to develop towards the production of zoosporangia.

Biochemically, there are considerable differences between the two kinds of sporangia. For instance, the resting sporangia have few or no enzymes of the tricarboxylic acid cycle, and contain much more ketoglutaric acid and lipoidal material than the ordinary, colourless ("OC") cells, which develop into zoosporangia [see review by CANTINO and TURIAN (1959) and the article by CANTINO in Vol. XV]. Even in the OC cells, the tricarboxylic acid cycle is a comparatively weak system of respiration, but the enzymes present may be involved in the fixation of carbon dioxide.

As a mechanism for the action of bicarbonate CANTINO suggests that it interferes with, and finally stops, the functioning of the tricarboxylic acid cycle. The specific step is held to be the reductive carboxylation of ketoglutarate to oxalosuccinate and then to isocitrate,

by a TPN-specific isocitric dehydrogenase, which remains functional during the formation of the resting sporangia, unlike the other enzymes of the Krebs' cycle.



α-ketoglutaric oxalosuccinic isocitric acid

Since very many changes in proteins and enzymes are known to follow the initiation of the first steps in determination, the immediate step following addition of bicarbonate triggers-off a number of subsidiary changes, some of which (*e.g.* the formation of melanin) can be interrupted without affecting the main changes.

γ) Reversible transformation in fungi.

The reversible transformation of certain dermatophyte fungi from mycelial growth to yeast-like budding (M—Y transformation) is brought about by increasing the CO_2 concentration of the medium (references in NICKERSON 1953). *Sporotrichum schenckii* requires about 5% CO_2 at 37° C for M—Y transformation (DROUHET and MARIAT 1952). Other fungi in which M—Y transformation is brought about by excess carbon dioxide are *Mucor rouxii* (NICKERSON 1958) and *Histoplasma farciminosum* (BULLEN 1949). As in the *Blastocladiales* there are biochemical differences between the two forms of the dermatophytes (for details and references see CANTINO, Vol. XV, and NICKERSON 1958). These differences concern the mechanism of cell division. The cell wall of yeasts and yeast-like forms contains a protein which, by its high sulphur content, resembles keratin. The protein chains are cross-linked by S—S bridges and are complexed with mannan. Budding in yeasts is initiated by a localised plasticization of the cell wall under the action of an enzyme which reduces the S—S groups in the protein—mannan complex. This disulphide reductase enzyme can be obtained from mitochondria of baker's yeast and of *Candida albicans*, but not from a mutant (M) strain of *Candida* which is permanently mycelial and incapable of M→Y transformation. Reduction of S—S groups is carried out by hydrogen transferred by the disulphide reductase from a reduced metallo-flavoprotein. This flavoprotein is supposed to lose its metallic component by mutation, by exhaustion of the medium or by the addition of a chelating agent to it. The capacity for cell division is thereby lost and the Y→M transformation takes place. Y→M transformation is inhibited by adding compounds containing thiol groups (cystein, glutathione) to the medium and M→Y transformation can also be induced in the M-mutant of *Candida* by these compounds.

δ) Zoospore formation in *Oedogonium*.

Oedogonium forms zoospores in standing water, especially in the summer, but not in running water. GUSSEWA (1930) has shown that zoospore formation is controlled by the carbon dioxide content of the water and believes that the dissolved gas, not its hydrated forms, is responsible. With 50 mg/litre of carbon dioxide (3 per cent in the gas phase) in the culture solution, so many zoospores form that the filaments fall to pieces. However, the zoospores themselves are somewhat damaged by this level of carbon dioxide, for they are rather amoeboid. The influence of carbon dioxide is not affected by light or p_H. The response seems to

involve temperature as well as carbon dioxide, for zoospores are not formed in nature in the autumn despite the greater solubility of carbon dioxide at the lower temperatures then prevailing. GUSSEWA thinks that at higher temperatures the carbon dioxide of respiration does not go into solution in the water of the habitat, but is retained in the cells, and that it is the rise in internal concentration of carbon dioxide which normally initiates zoospore formation. This phenomenon should be investigated further in the light of the work on the *Blastocladiales*, outlined above.

LOOMIS (1957) has summarized work which has conclusively shown that the gonads are initiated in *Hydra* when the CO_2 content of the medium rises, either as a result of overcrowding or by the experimental upply of excess CO_2. He and NICKERSON (1958) have drawn attention to the general neglect of carbon dioxide tension as a factor in morphogenesis. LOOMIS has suggested that CO_2 gradients in a bulky tissue may constitute a morphogenetic field and be involved in differentiation. He also suggests that the volatile, lipoid-soluble substance produced by eggs of *Fucus*-species, which chemotactically attracts the spermatozoids to the eggs may be carbon dioxide (COOK and ELVIDGE 1951). WHITAKER (1940) has proposed that the "group effect" in fertilized *Fucus* eggs (determination of the axis of polarity along radii from the centre of the group of eggs) depends on a common action of hydrogen ions and CO_2. This is denied by JAFFE (1958). Removal of CO_2 from the air completely stops development in the *Acrasiales* (COHEN 1953). In *Dictyostelium discoides* both culmination and general development are affected.

4. Injurious gases with formative effects.

a) Ozone.

There have been relatively few reports of the effects of ozone on the physiology of higher plants. Ozone is used as a fungicide and bactericide, especially in the preservation of meat. It is toxic to plants at a concentration of about 1.0 ppm, but there have been reports of stimulating effects on the development and growth of plants. BRINER, CHODAT and PAILLARD (1935) reported that maize and oat seedlings, treated for a short time with ozone in air at concentrations between 10 and 0.01 ppm, eventually gave rise to plants which were 10 to 15 per cent heavier than controls. RICHARD (1949) claims that ozone will make many different kinds of fungi sporulate, but that the gas is somewhat toxic to the spores themselves.

Ozone is sometimes transiently present at a concentration of as much as 0.5 ppm in the air. It is produced by irradiation of oxygen in the ultra-violet, for oxygen strongly absorbs the wavelengths in the region 1849 Å. The ozone produced by a mercury vapour lamp may have a fairly short life, since the reversion to oxygen is catalysed by humidity, light, surface adsorption and radiation at 2537 Å (ultraviolet). Nevertheless, sufficient ozone may be produced to account for many of the reported injurious effects of ultra-violet light, when mercury vapour lamps have been used as the source (see POPP and BROWN 1936). WANGERMANN and LACEY (1952), endeavouring to substantiate an earlier report (see POPP and BROWN 1933) that ultra-violet irradiation would stimulate flowering of *Lemna* species, found that under the conditions of their experiments ozone was produced in sufficient quantities to kill the plants with a 30-second exposure. The chlorophyll was bleached by the ozone, which also affected plants elsewhere in the room, not directly exposed to the ultra-violet. ERICKSON and WEDDING (1956) have also studied the effects of ozone on *Lemna*, and TODD, MIDDLETON and BREWER (1956) find that 24 hours exposure to 1 ppm. reduces the chlorophyll content by about 40 per cent, and that the rate of photosynthesis is also reduced by this amount. Ozone treatment (1.2 ppm for 15 hours) caused an increase in the rate of respiration and a loss of pigment in green lemons. The rate of respiration of *Lemna* and of beans was similarly affected. No effects were observed on the growth of Kentia palms or of avocado. MIDDLETON (1955) finds that the upper leaf surfaces of Pinto beans are damaged by four hours exposure to 0.1 ppm ozone or 10 minutes to 0.5 ppm. TODD (1958) and TODD and GARBER (1958) and

WEDDING and ERICKSON (1955) have found similar depressant effects on the photosynthesis and growth of peas and beans. Ozone is present in abnormally high concentrations in the air in the Los Angeles and San Francisco Bay areas of California, but according to MIDDLETON (1956) it is not directly responsible for much damage to crops. TODD, MIDDLETON and BREWER (1956) find the toxicity of ozone to be considerably less than that of ozonised hexene ("artificial smog").

b) Carbon monoxide.

Carbon monoxide is very toxic to many animals, but not particularly so to plants. PFEFFER's words (1903) "carbon monoxide acts as a violent poison only to those organisms which contain haemoglobin and in all other cases it behaves almost as a neutral gas so that it is very much less poisonous to plants than the dioxide" are still fairly near the truth, although we know of effects of carbon monoxide on plants at levels of concentration which are also toxic to animals. The toxic effects are due to the formation of carbonyl compounds with enzymes and proteins containing iron. Animals with haemoglobin are poisoned when the air contains 0.1 per cent of carbon monoxide, at which concentration half their haemoglobin is combined with carbon monoxide. Much lower concentrations, however, are distressful because of the reduction in oxygen-carrying capacity of the blood. According to MEETHAM (1952) the carbon monoxide content of the air in London is negligible in the parks but rises to 50 or 80 ppm above the pavements in the streets. For those more sensitive to the gas, these levels may not be innocuous. Plants are sensitive to 500 ppm of carbon monoxide, a concentration which would rapidly kill mammals, but not insects (ZIMMERMAN 1935).

Owing to the fairly large amounts (15 to 20 per cent) of carbon monoxide in smoke and illuminating gas the effects of these mixtures were attributed, in much of the early work, to their carbon monoxide content. KNIGHT and CROCKER (1913) (who have admirably reviewed the earlier work of such authors as MOLISCH, NELJUBOV and RICHTER) called attention to the much more effective unsaturated hydrocarbons (ethylene, acetylene, propylene etc.) present in quite small amounts (often below the level of chemical estimation) in these mixtures, and showed that the effects of smoke and illuminating gas were probably due more to these hydrocarbons than to carbon monoxide. In some of their experiments the unsaturated hydrocarbons were scrupulously removed from the carbon monoxide (obtained from three different chemical reactions) by scrubbing through bromine and then through caustic soda. Smoke was thus found to be ten times as effective as pure carbon monoxide in eliciting the "triple response" of etiolated pea seedlings (see article by EVENARI, this Volume). Carbon monoxide brings about the triple response at approximately 1 per cent in air, but ethylene is effective at 0.2 ppm. WEHMER (1925) has also criticized some of the earlier work, in which the effects of illuminating gas were ascribed to its carbon monoxide content. Not all authors have been as careful as KNIGHT and CROCKER, and ZIMMERMAN, CROCKER and HITCHCOCK (1933) in eliminating effects due to other gases, and few even mention the source of the carbon monoxide they used. BOTTOMLEY and JACKSON (1903) claimed that young *Tropaeolum* seedlings grew quite well with 10 per cent carbon monoxide, but no carbon dioxide in the air around them. RABINOWITCH (1945) suggests that some carbon dioxide was probably present in the gas they used. Nevertheless many plants seem to be very tolerant of even such large concentrations of carbon monoxide (RICHARDS and MACDOUGAL 1904). Green plants illuminated in a closed system liberate small quantities of carbon monoxide. Plant powders and chlorophyll extracts also produce carbon monoxide when illuminated in the presence of oxygen and water (WILKS 1959). Larger quantities, rising, in a closed system, to 800 ppm., are produced by the alga *Anacystis nidulans* (GAFFORD, cited by WILKS 1959). LANGDON (1917) and LANGDON and GAILEY (1920) found carbon monoxide to be a major constituent of the gas in the bladders of *Nereocystis*, one of the larger brown algae, and they believe it to be a product of respiration in that plant. In fact, certain organisms, which according to their morphology may be described as bacteria or

Actinomycetes (THIMANN 1955), are known which normally utilize carbon monoxide as a carbon source, and others catalyze the oxidation of the gas to carbon dioxide. According to ZIMMERMAN, CROCKER and HITCHCOCK (1933 b) *Nephrolepis* plants are unaffected by 10 per cent of carbon monoxide, but most species lose their leaves when exposed continuously to 1 per cent. Flower buds and ripe fruits may absciss very rapidly, but the stems and shoot buds are very resistant and new buds may be produced during continuous treatment with carbon monoxide. Lenticels become hypertrophied, abnormally small leaves may be produced and the rate of stem growth is considerably reduced, by continuous exposure for a few days to 1 per cent carbon monoxide. There is practically no retardation in growth with 0.01 per cent, but there are considerable differences in tolerance between species. Dahlias and tomatoes were little affected by 1 per cent. With concentrations of the order 0.01 per cent, 45 of 108 species gave epinastic responses of the leaves, 4 gave hyponastic responses and the rest gave no response. Of 80 species of plants, 27 were found to form roots on the stems under the influence of carbon monoxide (ZIMMERMAN, CROCKER and HITCHCOCK 1933 a). In the most sensitive plants (tobacco, *Tagetes* spp., *Galinsoga*, *Balsaminea*, *Hydrangea*) stimulation of root initiation and growth was obtained with exposure to 0.05 per cent for a period up to 15 days (or until stem growth ceased), but the best results were obtained with 1 per cent. With 50 per cent, root growth was still stimulated but the plants aged rapidly. The absence of root formation in RICHARDS' and MACDOUGAL'S experiments (1904) with seedlings is attributed to the fact that they used too high a concentration of the gas, of the order of 70 per cent, which is then inhibitory to root growth. The effects of carbon monoxide on the chemical composition and respiration of seedlings is dealt with by GRAFE and RICHTER (1911) and TANG (1932).

As the specific inhibition of cytochrome oxidase by carbon monoxide is reversed partially, or completely, by light, the gas has been found to have much larger effects on plants kept in the dark, or on parts of plants which normally grow in the dark, than on plants or parts of plants in the light. One of the most sensitive reactions is that which produces the triple response of etiolated pea seedlings. Carbon monoxide inhibits the respiration and chloride uptake of wheat roots (SUTTER 1950), but has no effect on nitrate assimilation (NANCE 1950) which, as has already been stated, is but little affected by aerobic respiration. HACKETT and SCHNEIDERMANN (1953) have used carbon monoxide as a specific inhibitor to demonstrate that the terminal oxidase mediating the action of auxin in the elongation of the cells of *Avena*-coleoptiles and pea stems is very probably cytochrome oxidase. TANG and BONNER (1947) found that the indoleacetic acid oxidase of pea seedlings is sensitive under certain conditions to carbon monoxide, and HESLOP-HARRISON and HESLOP-HARRISON (1957 a) suggest that this might be one reason for its apparently auxin-like effects.

Following a report by MININA and TYLKINA (1947) the HESLOP-HARRISONS (1957 a and b) have examined the effect of 1 per cent carbon monoxide on the determination of the sex of the flowers in *Mercurialis ambigua* and *Cannabis sativa*. Fewer male flowers were produced and more female flowers were formed. Since the same "feminisation" of the plants can be induced by spraying them with dilute auxin solutions, HESLOP-HARRISON (1957) suggests that the gas treatment raises the auxin levels in the plant at the moment when the sex of the flower primordia is being determined. However, no difference in auxin content between the plants treated with carbon monoxide and untreated control plants could be detected.

DUBROVINA (1958) claims that plants with a greater leaf area and a more rapid rate of growth result from seeds pre-treated with carbon monoxide before planting,

than from untreated seeds. The treatment is said also to increase the life of the plants.

No thoroughly satisfactory explanation has been given for the auxin-like action of carbon monoxide. In fact, its effects are rather more like those of ethylene than of auxin (*e.g.* effects on abscission) and it seems not wildly improbable that, in interfering with aerobic metabolism, carbon monoxide treatment might result in the formation by the plant of very small amounts of ethylene. The effects such as abscission, ageing, root initiation on stems are very like those which can be induced by concentrations of ethylene of the order of 0.2 to 1 ppm in the atmosphere around the plant. Perhaps studies using isotopically-labelled carbon monoxide might reveal that it is in fact metabolized by higher plants. Whether any small amounts of ethylene which might be produced could be detected is a matter more for experiment than for controversy.

c) Ethylene and other unsaturated hydrocarbons.

The effects of ethylene as a product of plants have been dealt with by EVENARI in the preceding article. Together with other unsaturated hydrocarbons, acetylene, propylene, butylene etc., it is a component of illuminating gas (about 3 to 4 per cent) and smoke, and it is a common contaminant of the air of laboratories with faulty gas-taps or habitual smokers. Of the unsaturated olefines, ethylene is by far the most effective in producing responses in plants. In the induction of the triple-response in etiolated peas it is 500 times as active as acetylene and 2000 times as active as propylene. Most of the morphogenetic and growth effects of ethylene have been covered in EVENARI'S article, but flower-induction is dealt with here.

Some varieties (*e.g. Cabezona*, grown in Puerto Rico) of pineapple sometimes take as long as 5 years to flower. It was discovered by accident that smoke will force the plants to flower and at one time it was common practice among growers to erect a tent over the plants and to light a fire under it (TRAUB, COOPER and REECE 1939). The same effect can be induced by the unsaturated hydrocarbons which are present in the smoke, particularly ethylene (RODRIGUEZ 1932) and acetylene (LEWCOCK 1934). The practice of using either smoke or these gases to induce flowering has been superseded by the technique of spraying with solutions of naphthalene-acetic acid, which also will induce pineapples to flower (reviewed by OVERBEEK 1951). The plants of many species of *Xanthorrhea*, another genus of the *Liliales*, widespread in Australia, are commonly observed to flower profusely after the bush has been burnt near them, and by inference they probably do so in response to the ethylene in the smoke. SÖDING (1952), in an amusing footnote (p. 2), refers to the difficulties of carrying out sensitive auxin-assay tests when smoking is allowed in laboratories. The cause of the difficulty is probably ethylene. *Avena*-coleoptiles are also very sensitive to ozonated hexene or natural smog (HULL, WENT and YAMADA 1954).

5. Atmospheric pollution.

(See also the article by BAUMEISTER, Vol. IV, p 502 for a discussion of damage to plants caused by sulphur dioxide).

The effects of atmospheric pollution by sulphur dioxide, fluorine, hydrogen fluoride, chlorine, hydrogen chloride, nitric acid, smog and "ozonated hexene" on plants have been studied in the more industrialised countries for over a hundred years, firstly in Germany and Great Britain, Austria and France, and since the last fifty years in Canada and the United States. Most of the earlier research arose from public or private concern over the disastrous effects of the effluent gases from industries burning large amounts of coal (steelworks, copper smelters,

potteries etc.) on the surrounding vegetation. Attention was given to the large amounts of sulphur dioxide in the polluted air. In more recent work stress has been laid on the hydrocarbons resulting from incomplete combustion of fuels such as petroleum, and on fluorine and fluorides which may be emitted, for instance, during the manufacture of superphosphates. An enormous literature has accumulated as a result of work sponsored by industry, and in many countries government departments have been set up to deal with the problems arising from atmospheric pollution and to conduct investigations on the hazards to health and to plants due to it. Even as early as 1903, HASELHOFF and LINDAU listed 125 of the "more important references" and there have been many subsequent reviews. THOMAS (1952) discussed the whole subject of gas damage to plants and DAVENPORT and MORGIS (1954) issued abstracts of nearly 4000 references to atmospheric pollution. These cover the nature and origin, chemistry, effects on health and vegetation, techniques for estimation and control, and legal and economic aspects of atmospheric pollution. Recent reviews of the effects on plants have been published by WENT (1955), ADAMS (1956), MIDDLETON and PAULUS (1956), DAS-GUPTA (1957) and BLEASDALE (1957).

In England at least three books (THRING 1957, MEETHAM 1952, and D.S.I.R. 1955) have appeared in recent years dealing with the subject and conferences are held regularly by the National Smoke Abatement Society. In America, where there are special and peculiar problems in California, regular reports are issued by the Air Pollution Foundation, annual symposia are held and the proceedings published; articles appear regularly in the Archives of Industrial Health, and in 1950 a specialist journal (Journal of Air Pollution Control) was started.

So many recent reviews are available that it seems unnecessary to add to their number. Moreover, since the pollutants appear to have no special morphogenetic effects and none but depressant effects on growth (except where sulphur dioxide relieves sulphur deficiency) the main mass of data descriptive of symptoms of injury is of little interest to plant physiologists interested in problems of development and growth however important it may be to the vegetable grower in a polluted area, or to the plant pathologist. WENT (1957) has given due warning that the plant physiologist working in urban areas should be aware of the influence of atmospheric pollutants on physiological processes in plants, and should guard against it. He finds evidence of damage to plants, presumed to be due to atmospheric pollution, in most cities of over a million inhabitants. The studies of stomatal physiology made by LOFTFIELD (1921) and of photosynthesis under field conditions (THOMAS and HILL 1949) are examples of fundamental work undertaken as a result of interest in pollution problems and supported by funds made available for their investigation by industries suspected of causing atmospheric pollution.

There are important differences between plants in their tolerance of atmospheric pollution. Among the most sensitive plants are the lichens, and the centres of cities have been called "lichen deserts" (VARESCHI 1936). Conifers are also extremely sensitive. The longevity of their leaves is reduced so that the foliage of affected trees is sparse and the trees have an unthrifty appearance. On the other hand, certain evergreens *(Rhododendron, Buxus, Ilex)* are very tolerant of atmospheric pollution. Some varieties of *Gladiolus* are extremely susceptible to leaf damage by fluorine or hydrogen fluoride (JOHNSON *et al.* 1950; HENDRIX and HALL 1958) and might be used as indicators of pollution by these gases (MILLER 1952). According to ADAMS (1956) and ZIMMERMAN (1952) fluorine is the most toxic pollutant, damage being caused by one part in 10^8. On the other hand, mercury vapour is also extremely toxic, since it may be accumulated by plants from the air in which it is present at a dilution of 1 in 10^8. Mercury vapour from paints used in greenhouses has been shown to cause damage to plants (DIMOND and STODDARD 1955).

BOBROV (1952, 1955a, b) has shown that *Poa annua* is very sensitive to damage by "smog", whether natural or artificial. Natural smog is a mixture of about 70 different chemicals, including hydrocarbons and oxidants, which causes irritation to the eyes and damage to crops, shortens the life of articles made from rubber (*e.g.* car tyres) and reduces visibility. Artificial smog is produced by passing ozone through olefines, generally hexene ("ozonised hexene").

Most pollutant gases damage the leaves more when the stomata are open (*i.e.* during the daytime) than when they are closed (KONITZ and WENT 1953). Often the immature and senescent leaves are less susceptible than the leaves of intermediate age. Of the damaged leaves, the youngest is damaged at its tip (its oldest part) and the oldest at its base (the part which has just ceased growing). The pattern of damage thus indicates the pattern of maturation of the leaf. One of the most interesting observations on the pattern of damage is that rust-infected parts of bean leaves show no injury by smog, while the rest of the leaves might be severely damaged (YARWOOD and MIDDLETON 1954). Maximum protection was afforded when the lesions of the fungus (*Uromyces phaseoli* or *Puccinia helianthi*) were seven days old. Apparently the protection is given by some change in the leaf metabolism or some chemical which diffuses beyond the limits of the fungal infection.

Hydrogen sulphide acts like cyanide on the terminal oxidases and inhibits aerobic respiration. There is some evidence that plants can reduce elemental sulphur to hydrogen sulphide and this is held to account for the fungicidal effects of sulphur (MCCALLAN 1948, COCHRANE 1958). Mercury vapour reacts with sulphydryl groups of enzymes and proteins (BARRON 1951). No mechanism has been suggested to explain the toxic action of fluorine.

6. Toxic gases of the soil atmosphere.

In conditions of poor aeration and in the presence of organic matter soil organisms may produce methane and hydrogen as well as carbon dioxide. Flooded soils under rice may have a methane content of the soil air as high as 2.8 per cent and a hydrogen content of 6.5 per cent (WAKSMAN 1932). Methane is also familiar as the "marsh gas" of swamps. Nitrous oxide may be formed by reduction of nitrate under anaerobic conditions. Hydrogen sulphide may be produced either from the breakdown of proteins or from the reduction of sulphates. In estuarine muds the hydrogen sulphide combines with iron to form black FeS and other iron sulphides.

It is not known how far the effects of anaerobic conditions on the growth of the roots of higher plants are due to the presence of these gases in the soil air. Hydrogen sulphide is said to be very toxic to most roots, even in low concentrations (RUSSELL 1950). Methane has little effect on barley and appears actually to be utilised by rice roots as a carbon source (VLAMIS and DAVIS 1944). Hydrogen in low concentrations is not very toxic to plant roots, although it depresses symbiotic nitrogen fixation. PERSIDSKY and WILDE (1954) have shown that volatile substances released from soil humus of forest soils and from sawdust affect the growth of roots (see also CHOLODNY 1948, 1951). The importance of these volatile compounds in soils is difficult to assess. According to MCNEW (1953) anaerobic respiration in soils may result in the accumulation of salicylic aldehyde to a concentration as great as 50 ppm. Although such a concentration does not affect root growth of wheat or sugar cane, it increases the susceptibility of the roots to attack by a root-rot fungus, *Pythium arrhenomanes*.

III. Effects of solutions.

The toxic effects of distilled water on organisms have already been dealt with by FISCHER (Vol. II, p. 734).

1. Common salt, calcium and other mineral elements.

The effects of salt on germination and morphogenesis have been dealt with by ADRIANI (Vol. IV, 730—731, and 723—726). Apart from the purely osmotic effects (see WANGERMANN, this Volume) there are specific ion effects due to the separate action of the chloride and the sodium ions. The extensive literature on the utilisation of salt-affected soils and "alkali soils" has been reviewed in detail by HAYWARD and BERNSTEIN (1958) and by RICHARDS (1953). GIBOR (1956) and RITCHIE (1957) have studied the relative tolerance of brine algae and marine fungi to different concentrations of sea water. Some fungi (*e.g. Phoma* sp., *Curvularia* sp.) from tropical marine habitats grow faster in high than in low concentrations of salt, so long as a relatively high temperature is maintained. The same behaviour is also found in a modified form with a tropical terrestrial fungus, *Aspergillus flavus* (RITCHIE 1959). Some of the marine organisms will withstand very high concentrations of salt water. One of the species of *Dunaliella (D. salina)* will multiply in brines eight times as concentrated as sea-water.

The morphogenetic effects of excess calcium, including those of "lime-induced chlorosis" and the relative tolerances of different species to calcium in the environment have been mentioned in many of the articles in Vol. IV (*e.g.* BAUMEISTER, p. 523—524). The "chemomorphoses" caused by heavy metals such as nickel, chromium and cobalt, which are responsible for the toxicity of selenium soils, are mentioned by KRAUSE (p. 753—802, Vol. IV) Selenium replaces sulphur in plant proteins and its effects may be antagonized by additional supplies of sulphate. Selenium has been found to be incorporated into proteins by the fungus, *Candida albicans*, the habit of which is changed thereby from that of a filamentous fungus to that of a budding, single-celled yeast (NICKERSON, TABOR and FALCONE 1956) Since selenium has no extra effect on isolates of *Candida* which are already yeast-like, it is held to promote cell-division, but not to affect cell extension. The SeH group is not readily oxidised and since a reduced state of the thiol groups of the cell wall is held to be a pre-requisite for budding, the effects of selenium on *Candida* are readily explained in terms of the hypothesis outlined in 3 f γ. Other effects of selenium are dealt with by SHRIFT (1958) and by VERGNANO (1958a and b).

2. Chemicals in the marine environment.

A considerable body of information has accumulated during the last twenty years, largely as a result of the activities of ZOBELL, BAAS BECKING and his colleagues, and WOOD, on the chemical changes in estuaries and in the sea (WOOD 1958). Most of these changes involve transformations of inorganic and organic materials by bacteria. The organic materials are either provided by the decay brought about partly by bacteria, partly by marine fungi and flagellates, of algae and marine animals, or are carried down to the sea as dissolved organic matter in rivers. The main chemical changes involve sulphur, phosphate, iron and nitrogen.

Sulphur is a constituent of the cell walls of brown and red algae and rapidly-decaying algae provide materials for the activity of sulphur bacteria. Sulphates are also present in solution in sea-water. They can be reduced to hydrogen sulphide by *Desulphovibrio desulphuricans*:

$$H_2SO_4 + 8(H) = 4\ H_2O + H_2S.$$

The ability to reduce sulphate is a property common to many fungi and all algae and green plants, but *Desulphovibrio* is remarkable in that it may utilise hydrogen gas, or a wide variety of organic compounds including lactic acid, various alcohols, glucose and some amino acids as hydrogen donors, and also in the wide range of environmental conditions in which it will multiply and reduce sulphates. The hydrogen sulphide which is formed is removed from the environment either as ferrous sulphydryl (hydrotriolite) (Baas Becking and Kaplan 1956) or by re-oxidation by other organisms. Thus is set up a "sulphur cycle" comparable with the "nitrogen cycle" of soils. The reduction of sulphate by *Desulphovibrio* is a function of salinity, and is curtailed in the absence of sodium chloride. The bacterium will not grow at p_H above 9.4 because of the limitation imposed by the HCO_3^- ion at that p_H (Baas Becking and Wood 1955). Below p_H 5.8 iron sulphide is not produced. Iron is available in sea-water or muds very largely as the relatively insoluble ferric phosphate, but as this is more soluble than the hydrotriolite, the latter is precipitated and the phosphoric acid goes into solution. Thus the reduction of sulphate releases phosphate (Baas Becking and MacKay 1956) and is therefore accompanied not only by a low oxygen content but also by a high phosphate content of the sea-water. The "sulphur cycle" is completed by the abiological oxidation of sulphides to sulphur on the sea-bed or in deep muds. The subsequent oxidation to sulphate is carried out by marine thiobacilli. In shallow water the filamentous forms, *Thiothrix* and *Beggiatoa* oxidise sulphides or thiosulphates, as well as sulphur, to sulphates. Where photosynthesis is possible the green and purple sulphur bacteria may also be involved in the sulphur cycle. Organic sulphur compounds may also be broken down or synthesized and released into the environment. Methionine, cysteine, cystine, and dimethyl sulphide are formed by bacteria, algae and the sea-grasses (Wood 1953).

It is believed that the productivity of the sea is limited more by phosphorus than by nitrogen supply (Harvey 1955). Since the fecal pellets of marine animals contain ferric phosphate (Cooper 1948) this could be a drain on the phosphate of the system if it were not liberated during the reduction of sulphates. Phosphate may also be solubilized by the weak acids which result from the decomposition of carbohydrates from the cell walls of algae.

The nitrogen cycle of the sea is essentially the same as that of the land but is less well-known (Waksman *et al.* 1933). Nitrogen fixation by anaerobes *(Clostridium pasteurianum)* or, in the absence of oxygen, by purple sulphur bacteria may be of considerable importance in maintaining the nitrogen balance of the organic system in estuaries and in the depths of the sea where the redox potential is sufficiently low. Blue-green algae of the littoral zone may also be important contributors (Baas Becking 1951). Certain diatoms (*Fragillaria* spp.) form algal "blooms" where nitrate is abundant and when the nitrate has been used up the blue-green alga, *Anabaena*, or certain *Chlorophyceae*, which utilise ammonia, succeed the diatoms and form a "bloom" (Hutchinson 1944, Ryther 1954).

The complex interrelationship between different organisms in the marine and estuarine environment, in which the chemical activities of one type of organism provide the environment for the development of another, and it for a third and so on, have been termed "metabiosis" (Baas Becking and Wood 1955). However violently the redox potential, p_H or hydrogen sulphide content may fluctuate, some organisms of each kind, whether chemolithotropic, chemoautotrophic or photosynthetic, survive to enable the system to maintain reversibility. Diatoms have been found which are viable at p_H 1.2, at low oxygen tensions and in the p_H-Eh range controlled by *Thiobacillus thiooxidans*. With changes in these

conditions different organisms may multiply rapidly ("bloom") and disappear leaving little permanent change in the environment. Many marine organisms produce organic materials into the environment including antibiotics, and these may play a part in regulating the periodicity of algal and bacterial blooms (FOGG 1957, LUCAS 1955, STEEMANN-NIELSEN 1956, RICE 1954).

3. Dissolved organic matter.

Surprisingly large amounts of organic matter occur in solution, either as colloidal particles or true solutes, together with some organic debris, in natural waters. The amounts in fresh waters range from 15 to 300 ppm. In the sea, about 40 per cent of the total dispersed organic matter is in solution [PLUNKETT and RAKESTRAW (1955)]. This material is derived from breakdown of organisms, secretion or excretion by organisms, from sediments or in the run-off water from the land. A very large number of different compounds, including vitamins, sugars, amino acids, carotenoids and chlorophyll-like pigments have been isolated from natural waters and lake sediments (SAUNDERS 1957). The organic compounds may be

(1) utilised as carbon sources in the nutrition of algae, flagellates and other organisms,

(2) the source of accessory factors required for growth,

(3) toxic substances,

(4) chelating or complexing agents which, by forming complexes with trace metals may detoxicate them when they are present in excess, or render harmless the chelating or complexing agents (WARIS 1953).

SAUNDERS (1957) has discussed these possible roles of organic matter in the growth of algae. He points out that many algae will utilise quite complex organic substrates for growth, and that many also require certain vitamins or other compounds for growth. For instance, the *Euglenophyta* require thiamin and vitamin B_{12} for growth, and the requirements for many of the *Chrysophyta* are extremely complex. The ability of many of the organic compounds present in solution in natural waters to chelate metals such as iron, and so prevent them from precipitating and becoming unavailable to plants is also of considerable importance (PROVASOLI and PINTNER 1953).

The toxicity of some of the organic compounds in solution is a topic which belongs properly to Section VII A of this Volume, since these "antibiotics" are produced by certain organisms and are toxic for others. Among the most potent and important are those produced by the organisms of the "red tides" at sea, *Gonyaulax* and *Gymnodinium*. The toxins produced by these organisms, and those produced by many blue-green algae in fresh-water, are sufficiently potent to kill higher animals, and are responsible for the death on a large scale of fish or livestock. Sea water is quite lethal for "land bacteria", chiefly bacteria of the intestinal tract of animals. This is, of course, of extreme importance in the disposal of sewage of coastal cities and towns, which, when discharged into the sea, would otherwise be a major hazard to health (ZOBELL 1946). The toxicity of sea water to these bacteria appears to be due to antibiotics contained in it (ROSENFELD and ZOBELL 1947, KETCHUM 1953).

The fact that growth hormones are known to have quite large effects on the growth of algae (BENTLEY 1958) leads to speculation on the possibility that natural waters may contain small quantities of such hormones and that these may stimulate, or even inhibit, growth.

4. Pollution of natural waters.

The discharge into a river or lake of chemicals or sewage causes considerable changes in the environment which disturb its natural biological balance. The nature of the pollutants may range from fresh water (which may sufficiently lower the salinity of a brackish stream to kill halophytic organisms) to organic compounds such as detergents and antibiotics. If continually discharged, hot water (as at the Reddish Canal, near Manchester) may allow of the establishment of an exotic, thermophilic flora and fauna. The normal fauna and flora of an unpolluted stream are referred to by limnologists as "katharobic". With gross organic pollution the increase in the number of microorganisms may result in the development of completely anaerobic conditions and a "saprobic" flora. Such a flora, consisting of a number of fungi dominated by *Sphaerotilus natans* ("sewage fungus", BUTCHER 1958), develops on the silt which finally deposits on the bed of the stream. As a result of the breakdown of the organic matter, the environment gradually becomes less anaerobic again and the fauna changes from one of tubificid worms and *Chiromonid* larvae through the stages of isopods and molluscs to caddis-fly larvae, ephemerids and fresh-water shrimps, restoring the original katharobic fauna (LIEBMAN 1951). If the degree of organic pollution is less, the silt will carry a flora of diatoms (for example, *Nitzschia palea*).

Some pollutants are extremely poisonous to aquatic organisms. Copper is very toxic to many algae, and is used as a poison for filamentous algae. Detergents and the waste products of factories may affect organisms directly by their surfactant or antoxidant properties. Water plants are very sensitive to chlorine in chlorinated water, a concentration of 5 ppm being lethal to *Cabomba* and *Elodea* in four days (ZIMMERMAN and BERG 1934). Zinc and boron are also very toxic for many plants even in very small doses. Ammonia, nitrates, sulphides and phosphate are among the other agents of pollution which find access to natural waters. As a result of the accession of nitrate and phosphate to lakes in the vicinity of cultivated fields and towns, the character of these lakes changes. Originally oligotrophic, that is with few littoral plants and a poor development of plankton, with relatively uniform oxygen content from surface to bottom and a rich bottom fauna, these lakes tend to become eutrophic, with large quantities of suspended matter, abundant littoral plants, a rich development of plankton and a very poor bottom fauna on the anaerobic mud. The smaller the lake the more rapidly this process of eutrophication proceeds (WELCH 1935).

IV. Effects of solids.

There are relatively few ways in which solids can exert chemical effects. One of the most important is that of acting as adsorption surfaces. Solutes which are present in limiting concentration in the body of a solution will become adsorbed on suitable surfaces and there theoretically reach a concentration of 100 per cent. This effect is of considerable importance, for instance, in the sea. FOGG (1958) has discussed the well-known fact that many microorganisms which are present in small numbers in sea water will multiply rapidly when an increased surface is presented to them, *e.g.* by enclosing the sea water in a bottle. Bacteria in sea or lake water occur mainly on the surfaces of particles in suspension. The solid surface available in sea-water is about 10 mm^2/litre, about 10^{-5} that of the surface of a litre bottle, to which the bacteria would have access when it is filled with sea-water. When sea-water is filtered and enclosed in glass containers "as much as half of the organic matter in solution is decomposed within two weeks

and after five or six months storage in the dark as little as 5 per cent of the original amount may remain".

WOOD (1956) discovered that diatoms living heterotrophically at great depths in the sea were "epontic", i.e. attached to living and non-living substrates. According to VISHNIAC (1956) marine fungi resemble marine bacteria in being associated with surfaces. Many more isolations of fungi could be made from small pieces of algal thalli than from the sea-water itself. Only rarely were algal surfaces not found to be contaminated with fungi. It is well-known also that fungi will grow on the surface of optical glass, especially in the humid tropics. OHTSUKI (1959) finds that such a fungus, which he calls *Aspergillus glaucotonophilus*, requires relatively high concentrations of solutes for growth and can only be grown if the medium contains more than 5 per cent or up to 22 per cent NaCl, or an equivalent amount of sugar to obtain the same osmotic pressure. This peculiar fungus will not grow in a saturated atmosphere. Some strains will grow only at a relative humidity between 60 and 80 per cent. OHTSUKI refers to it as an "obligate tonophilic organism". Its ability to grow on glass surfaces is thus connected with the maintenance of a locally high concentration of osmotically active substances in small amounts on such surfaces.

Solids may also act as ion-exchange media. Glass is a particularly suitable medium for ion exchange and it has been used as a carrier to provide a steady, small supply of relatively insoluble ions (*e.g.* ferric ions) to media.

Solids may play a role in the environment by adsorbing toxic organic compounds. SIMINOFF and GOTTLIEB (1951) find that negatively charged soil particles (*e.g.* bentonite) absorb streptomycin very strongly and thus render it innocuous to soil organisms. Other references to phenomena of this kind are given by DIMOND and HORSFALL (1959).

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