# Soil physical conditions and plant growth

## 1. INTRODUCTION

The environment is a complex of so many factors, all interacting with each other, that it is impossible to isolate any one factor that does not influence another. For the study of environmental effects, however, this complex is usually sub-divided into clearly defined units. One of these units is the soil, which is vitally important for plant growth and development. Soil in itself represents a complicated physical, chemical, and biological system by which the plant is supplied with the water, nutrients, and oxygen it requires for its development.

Although over the centuries plants have adapted themselves to various kinds of soil, the adaptation capacity of certain species is limited. This can be clearly seen when soil properties alter. The nature of the soil determines whether a species will thrive and influences its natural distribution. Within small areas, slight local variations in the soil may be sufficient to affect a plant's chances of survival.

The physical properties of soil are known to be of fundamental importance for plant growth, but much of the literature on the subject is qualitative or vague. This is not surprising in view of the difficulty one encounters in attempting to divide the edaphic factors unambiguously into physical, chemical, and biological classes. Most physical phenomena have important effects on the chemical and biological soil properties and processes, and these in turn influence plant growth.

Soil is a physical system and can be described in terms of grain size, apparent density, porosity, moisture content, temperature, and friability. Plant growth is affected by the amount of moisture and air in the soil and by the temperature of the soil. The composition of the soil can impede or foster root development and shoot emergence. It should be mentioned, too, that the physical features of the soil have certain indirect effects on other edaphic factors such as nutrient supply and pH.

Unlike mobile organisms, terrestrial plants are bound to the soil where the seed has fallen. Plants generally have to cope with a hostile environment and may not survive, but in course of time every type of soil, however hostile, becomes covered with vegetation. Since the type of vegetation depends on the prevailing soil conditions, in a sense each particular vegetation is adapted. In nature, however, plant species are rarely found on the soils whose physical

conditions are optimal for their growth and performance. Comparative experiments with various plants show that the general shape of the curve representing the response to the degree of severity of adverse conditions (such as oxygen deficiency, soil compaction, low soil temperature, high sodium chloride concentrations) is very similar to all plants, whether or not they are adapted. Minor differences in a single soil factor are sufficient to cause minute variations in the occurrence of plant species in the field. Comparative experiments have also shown not only that plants have a tremendous plasticity that enables them to survive under adverse conditions but also that species develop different strategies in order to survive. We do not fully understand many plant-soil relationships because we do not have sufficient knowledge about:

a) the physical conditions of the soil in space and time;

b) the differences in a plant's response at various developmental stages;

c) the plant's response to changes in the degree of adversity of conditions;

d) the extent to which a plant's response is determined by the interaction of other factors;

e) methods to assess the effect of minor differences in response over a long period in a plant's life-cycle.

One of the serious drawbacks of ecophysiological experimentation is that we can hardly discern differences amounting to less than 5-10 per cent but in nature even smaller differences may determine discrimination in the long run, especially in interspecific competition.

It is therefore with considerable diffidence that I present this paper, since it cannot solve the two main problems in plant ecology, namely:

1) Why are certain types of vegetation (species) restricted to a certain habitat, whereas others clearly prefer another set of conditions?

2) How can diversity of species in a vegetation be maintained for a relatively long period (measured by human standards) when so many individuals are all dependent on the same resources, i.e., light, water, and minerals?

The second of these problems is the more challenging one, since we know that in contrast to the diversity in nature, competition experiments almost invariably result in survival of only one of the competing species (DE WIT 1960). The niche concept, a separation of interests in time and (or) space, was introduced to reconcile this discrepancy (DE WIT & VAN DEN BERGH 1965; VAN DEN BERGH & BRAAK-HEKKE, this volume), but we shall have to learn much more about the ways in which plants behave before these questions can be adequately answered.

If we want to obtain satisfactory answers we must pay close attention to the complete life-cycle of the species in question, since niche differentiation may show up in only one of the life stages (germination, seedling establishment, vegetative growth, generative growth, and dissemination or seed longevity). Sometimes adaptation to a certain habitat can be due to relatively small differences in a number of aspects (PEGTEL 1976; PONS 1976, 1977), none of which alone would fully explain the species' preference for a particular habitat.

Since the ecophysiological approach is based on experience acquired in the field of crop physiology, possibly essential differences in behaviour between natural vegetations and crops must be taken into account. In both kinds of populations the individual responds to the complex of conditions but agricultural practice has selected for uniformity of response, whereas natural selection has often resulted in the maintenance of a certain degree of diversity and plasticity within a population. Moreover, the external conditions are much less predictable for natural vegetations.


## 2. SEED POPULATION AND SOIL PHYSICAL CONDITIONS

### 2.1. INTRODUCTORY REMARKS

The number of seeds in a population on or in the soil depends on the rate of dissemination and on the rate at which seeds are lost through deterioration, germination, and consumption. Seed consumption will not be considered in this paper. The proceedings of a recent Nottingham Symposium on Seed Ecology (HEYDECKER 1973) have provided a considerable amount of information about the behaviour of seeds in general; the information is useful to both agriculturists and ecologists. The seed population is important not only because it determines the timing of germination but also because in a given locality it may represent a high percentage of the total number of individuals present in that locality (see also the paper by RABOTNOV in this volume). Depending on the type of dispersal, seeds pass from the plant and the place where they have been produced to a place on or in the soil where they will lie until conditions are suitable for germination and for growth into new plants. For the ultimate success of the seeds, both their longevity and their germination behaviour are important.

### 2.2. LONGEVITY OF SEEDS

It is well known that several ambiguous factors such as cool temperatures, low oxygen tension, and a low moisture content, all of which tend to decrease metabolic activity, increase the length of time that seeds can be stored (BARTON 1961; HARRISON 1966; ABDALLA & ROBERTS 1968). This finding is surprising, and makes it difficult to explain why many seeds apparently retain their viability longer when buried in moist soil than when kept in dry storage (VILLIERS 1973) (Fig. 1).

In an attempt to reconcile these different types of seed behaviour, VILLIERS (1973) showed that longevity is high at low water content (depending on the species, 5-8 per cent) and at high water content when the seed has fully imbibed. He assumed that ageing phenomena occurred at all levels of water content. These ageing processes are assumed to result in cross-linkage of macromolecules, which render enzymes and membranes non-functional, and in a gradually increasing number of somatic mutations, many of which may cause the production of defective proteins.
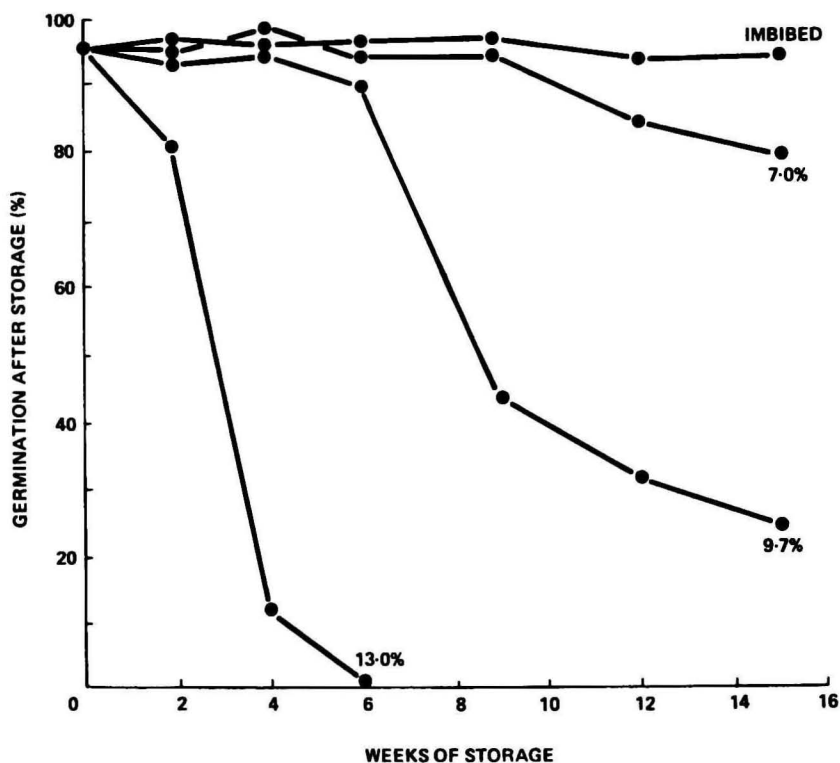
GERMINATION AFTER STORAGE (%)

100

80

60

40

20

0   2   4   6   8   10   12   14   16

WEEKS OF STORAGE

IMBIBED

7·0%

9·7%

13·0%

FIG. 1.    *Influence of the water content of seeds during storage on longevity* (VILLIERS 1973)

By comparing the results of germination experiments with those of electron-microscopical studies on the embryos, Villiers concluded that the functioning of macromolecule and organelle repair mechanisms was seriously impaired during air-dry storage at intermediate relative humidities of the air. In practice, the degree of ageing can be related to the amounts and kinds of substances lost by leaching from the seeds during soaking. According to SIMON (1974), when dried seeds were moistened again the initial leakage of electrolytes which normally decreased rapidly when the seeds reached a water content of about 15 per cent persisted due to the globular state of the plasma membrane of these dry seeds. This globular state is ineffective in maintaining gradients of ions and charge across the membrane. After rewetting, the normal non-leaky bilayer structure is restored, a process which would take more time in aged seeds. In imbibed seeds stored in the soil, leakage will not occur while the seed remains viable, provided the membranes remain in good condition. Repeated alternation of drying and wetting, which often occurs in the upper soil layers, could ultimately lead to the complete exhaustion of accumulated solutes and

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could therefore prove very harmful. In this respect it is interesting to note that the reverse response has been reported more frequently. A number of authors (e.g. KOLLER et al. 1962; HEGARTY 1970; PEGTEL 1976) demonstrated that both germination and establishment improved after seeds of various species were repeatedly wetted and dried. After studying the effects of the duration and number of the drying-wetting cycles, BERRIE & DRENNAN (1971) concluded that germination was more rapid when the seeds were redried after short periods of inbibition. A prolonged wet period before redrying resulted in embryo damage and poor germination, the critical factor being whether or not active cell division had begun in the imbibed embryo. The duration of the periods of imbibition that seeds can withstand depends on the species (CARCELLOR & SORIANO 1972) and the stage of development of the embryo (WOODRUFF 1969). Since these periods cannot be controlled under field conditions, repeated drying will result in a reduction of the seed population.

It may be concluded that seeds lying in or on the soil are subject to deterioration as a consequence of ageing. The rate of deterioration increases with increasing temperature and decreasing water content. Reiterated drying-wetting cycles are especially harmful. In fully imbibed seeds deterioration and ultimate death are postponed by the continuous repair of damaged structures. Although seeds have a fairly efficient repair mechanism, their ability to produce vigorous seedlings gradually declines during the ageing process.

## 2.3. DORMANCY

The fate of a seed after dissemination depends largely on external conditions and its internal features. In many cases seeds are not able to germinate immediately after dissemination, even when conditions seem to be favourable. These seeds are "dormant" (GORDON 1973). The function of dormancy in determining the timing of growth resumption whenever external conditions become suitable is quite clear, but the phenomenon itself is very complex. For instance, dormancy may depend on a variety of internal features. The seed coat may be highly resistant to the diffusion of oxygen from the environment to the embryo. Furthermore, the seeds coatings may contain substances that inhibit embryo growth and have to be broken down or rinsed out before germination can start. Dormancy may also be governed by an internal hormonal balance between growth-inhibiting and growth-promoting substances in the embryo itself, i.e., a balance which is inadequate for growth initiation (HEMBERG 1949; WAREING 1965; WAREING et al. 1973).

In some cases the degree of dormancy of the seeds depends on the conditions to which the mother plant was exposed during fruit development. Very often, the inability to germinate directly after dissemination disappears for no apparent reason in a few weeks (after ripering). There is also a kind of dormancy that can be induced in normally non-dormant seeds by the application of special treatments such as high temperatures (thermo-dormancy) or osmotic stress.

The breaking of dormancy requires a specific sequence of external factors. The literature on dormancy and termination of dormancy is very extensive, and at first gives the impression that each case forms a separate problem. Only recently has some progress been made in formulating more unifying concepts (ROBERTS 1973); these new theories are mainly based on what the various dormancy-breaking agents have in common; some of the latter play a role in the ecological situation, whereas others are in use only in laboratory experiments. In a series of papers Roberts and co-workers (for references see ROBERTS 1973) developed the hypothesis that stimulation of the activity of the pentose phosphate (PP) pathway leads to loss of dormancy. These authors classified the dormancy-breaking agents into a number of categories, and found a very close resemblance between the stimulation of germination and the possible stimulation of the PP pathway, which for the relevant ecological factors can be summarized as follows:

nitrate     is known to break seed dormancy in a large number of species
            (TOOLE et al. 1956; STEINBAUER & GRIGSBY 1957; WILLIAMS & HARPER
            1965) and stimulates hydrogen acceptance by intermediates of the
            PP pathway; it shares this property with agents such as nitrite,
            oxygen, and methylene blue, which have been shown to stimulate
            germination in certain cases;

temperature has a number of quite different effects on dormancy, depending on
            whether the seed is "dry" or "wet" (ROBERTS 1973); freshly shed
            seeds that have been kept dry show a rapid loss of dormancy at
            high temperatures (after ripening); when kept imbibed immediately
            after harvesting they germinate only within a small temperature
            range that is sometimes high (35-45°C) and in other cases low
            (3-7°C) (VEGIS 1964); another well known way of breaking dormancy
            is to keep the imbibed seeds for a certain time at low temperatures
            (3-5°C) (stratification treatment); in some cases fluctuating
            temperatures are required to stimulate germination. According to
            ROBERTS (1973), in all these treatments a stimulation of the PP
            pathway seemed to lead to a concomitant increase in the seed's
            ability to germinate;

light       has effects on dormancy breaking, invariably via the phytochrome
            system; light-sensitive seeds respond to red light and their
            germination is promoted, whereas far red counteracts this
            stimulation; there does not seem to be enough evidence yet to
            prove that the PP pathway is involved, but there are indications
            that this may be the case, e.g. the changes in respiration seen
            after exposure to light (EVENARI 1961) and the involvement of
            phytochrome in the stimulation of gibberellic acid synthesis
            (LOVEYS & WAREING 1971).

Although we still do not know the exact role of the PP pathway, the above-mentioned working hypothesis is rather attractive and may help to reconcile a number of experimental results from various sources. Nevertheless, differences between species and within species between populations will have to be quantitatively specified if we want to understand their behaviour in the field. As an example of such a detailed approach, mention should be made of the studies done on the germination pattern of winter annuals by JANSSEN (1973a, 1973b, 1974), who analyzed the effects of light and temperature on seed behaviour in combined laboratory and field experiments. These investigations included alleviation of dormancy, shifts in optimum and maximum temperatures from dissemination onward, and the interaction between light and temperature. By applying experimentally obtained parameters to the physical conditions of the microsites, the author was able to use computer simulation to predict the behaviour of the seeds. The different behaviour of representatives of two microsites on dry sandy soils in the coastal dunes near Oostvoorne (The Netherlands) was clarified in this way. Seeds of *Veronica arvensis* and *Myosotis ramosissima* appeared to be well adapted to their respective habitats.

PEGTEL (1976), who compared the ecological behaviour of two varieties of *Sonchus arvensis,* one a coastal and the other an arable type, demonstrated a difference between their germination responses to soil temperature and soil moisture regimes, the response fitting the situation in the respective habitats. Germination trials in the field confirmed the results obtained from laboratory experiments. Nevertheless, under natural conditions only a few seedlings were found,mainly because of the limited life-span of the achenes. Adaptation was assumed to be of little ecological value in this case, particularly since field tests showed that sown seeds of both varieties ultimately germinated in both habitats.

## 2.4. GERMINATION

Viable, non-dormant seeds germinate if the environment is suitable. The essential environmental factors are an adequate supply of water, a suitable temperature, an adequate supply of oxygen, and in some species either the presence or absence of light. According to most definitions, a seed may be considered to have germinated when the radicle breaks through the seed coat. Seedlings germinating on the ground become fixed in the soil by subsequent root growth. It is obviously important for this process to occur quickly, particularly at sites where conditions are subject to rapid changes. Seeds germinating within the soil must complete emergence before their reserves are exhausted. In any case, the germination process represents a risky period in the life-cycle of plants in the field.

Hence a seed's germination rate should be high in order to ensure rapid attachment to the soil and to diminish the risk. In most of the literature on germination the percentage of germinated seeds is plotted against time. A

hundred per cent germination can be reached within one or two days or may take much longer even though the germination rate of each individual seed is still fast. In this way the germination rate of the population is indicated and the curves show seed polymorphism (RORISON 1973). A steep slope means that everything is staked on one throw ("gamblers") and is therefore rather risky (JANSSEN 1973b). The risks are mainly determined by changes in water availability, since the most sensitive tissue, the growing root-tip, is confined to the upper soil layer which is bound to follow changing weather conditions quite rapidly. In bare soil changes in temperature and water content are much more pronounced than when there is a cover, particularly at high levels of irradiance.

Young root parts of various species do not differ according to their function, which means that differences in sensitivity between species are mainly determined by either the rate of root differentiation or the capability of the root to resume growth upon alleviation of stress. These predominantly morphogenetic properties determine the changes of survival in environments with changing degrees of adversity (MILTHORPE & MOORBY 1974).

Both the temperature and the water content of the soil are important in determining the rate of germination and the germination percentage ultimately reached. At constant temperatures the proportion of seeds that germinate tends to increase with rising temperature up to an optimum and then decreases at higher temperatures. The rate of germination follows the same pattern, but the optima frequently occur at slightly different temperatures (Fig. 2, GULLIVER & HEYDECKER 1973). In the ascending part of the curve the rate of germination appears to be almost linearly related to temperature. HEGARTY (1973) showed that diurnal fluctuations within this temperature range can be simply handled by using the average value. Complications are encountered when non-linear parts of the curve have to be included.

GULLIVER & HEYDECKER (1973) also reviewed the effects of water supply on germination. The response pattern to an increase in water supply is rather similar to the pattern for temperature (Fig. 3), despite the obvious dissimilarity of these factors.

An optimum curve has generally been demonstrated when the percentage germination was plotted against the water status of the substrate. High levels of water supply may eliminate some of the seeds, thus reducing the percentage germinated although still favouring the rate of germination of the surviving seeds. The most likely assumption is that an excessive water supply affects the emergence of seedlings by reducing oxygen availability. Due to subsequent crusting of the soil under field conditions, this situation may even continue for a certain time after a return to a lower water level.
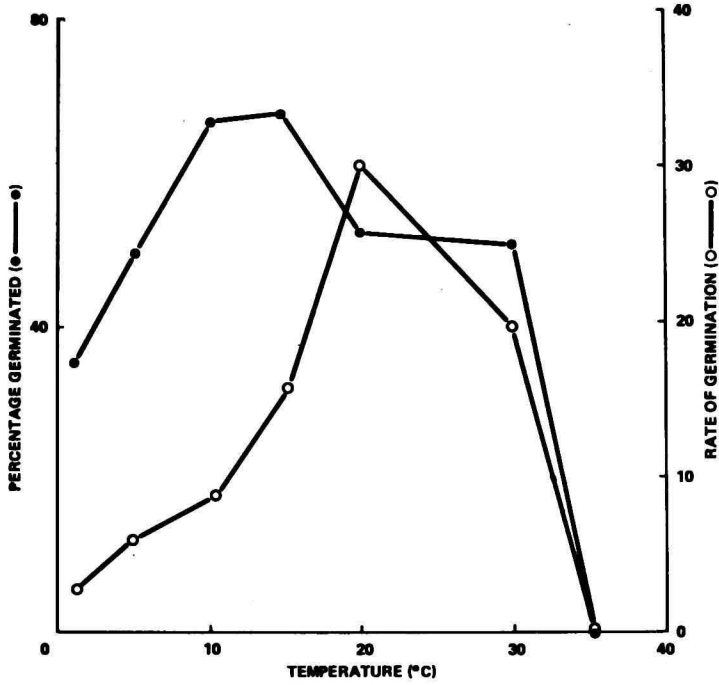
FIG. 2.    *Influence of temperature on the rate of germination and on the percentage of seeds ultimately germinating* (GULLIVER & HEYDECKER 1973)
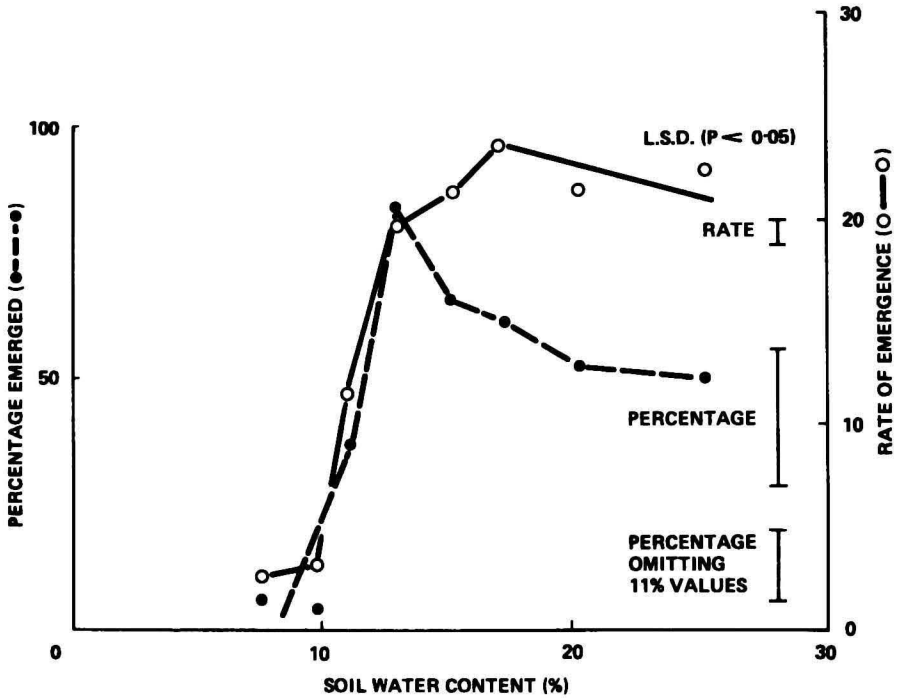


FIG. 3.    *Effect of the water content of the soil on the rate of emergence and percentage of seedlings ultimately emerging* (GULLIVER & HEYDECKER 1973)

## 2.5. ESTABLISHMENT OF SEEDLINGS

Reserves present in the seed are limited. Hence, the seedling has in due course to supply itself with all the essentials for growth. Soil factors affect seedling growth via their influence on root growth and root activities. The latter can be divided into two categories, *viz.* absorption of water and minerals, on the one hand, and, on the other, the synthesis of substances which are essential for shoot performance and are not (or insufficiently) synthesized in the shoot itself. In the past, most attention was paid to the meaning of the absorptive capacities of the roots for the performance of the whole plant, but more recently the emphasis has shifted to the role of root-borne growth essentials (e.g. hormones) in determining such processes like shoot growth, green leaf area duration, chlorophyll formation, and even the rates of photosynthesis and transpiration. The relative importance of these control systems may alter from case to case. As a whole, however, all these activities will depend on the supply of energy from the shoot. It has been shown repeatedly that there is an accurate control mechanism which regulates the feed back between root and shoot activities (BROUWER 1963; BROUWER & KLEINENDORST 1967).

Since the basic problem of the young seedling is the energy supply, its success will depend on illumination conditions. If it is situated in a standing crop that absorbs most of the light, the energy supply will be poor. Consequently, the over-all performance of the seedling will be bad and root growth will be more restricted than shoot growth. However, seedlings can perhaps survive for a rather long time in such a situation, because, to a certain extent, respiration losses are coupled to the available reserve of carbohydrate (McCREE 1970; PENNING DE VRIES 1975). Nevertheless, some maintenance respiration will go on and the seedlings will require light intensities for themselves well above the compensation point. As shown by LAZENBY (1955) for *Juncus effusus,* the surrounding vegetation can seriously limit seedling survival. Slow growth may also affect the incidence of pathogens (HARPER *et al.* 1955).


## 3. VEGETATIVE GROWTH

Within a vegetation much depends on the morphological characters and spatial distribution of shoot parts. A rosette plant is deemed to have fewer chances to reach the required level of illumination than tall species or plants with more vertically directed leaves. VAN DOBBEN (1967) and HARPER (1965) discussed the strategical implications on the basis of detailed comparison of the density-dependent mortality of broad-leaved horizontally developed plants and narrow-leaved upright plants.

When leaves reach a more exposed position, the energy supply improves but

at the same time there is a greater need for root activities. In fact, the seedlings are now in the same situation as those growing from the very beginning on exposed areas. Freely growing plants and plants partially exposed in a vegetation are both affected by physical soil conditions, so it is not necessary to distinguish between the growth response in early and more mature phases of vegetative development: in free-growing plants the growth distribution follows a quite regular pattern from seedling emergence until flowering (VAN DOBBEN 1962; TROUGHTON 1974). Complications may occur if, in the course of the plant's development, the nature of the processes that limit whole-plant growth changes as a result of interactions between individual plants (interspecific as well as intraspecific competition). Hence, in any study of the effects of physical soil factors on the vegetative development attention should be paid to: (a) differences in response between freely growing plants and plants in dense vegetations; and (b) differences in response due to interactions with other factors in the environment.

The influence of the soil temperature on bean plants in successive developmental stages may serve as example here. During germination the optimum temperature is quite high, the rate of germination being determined mainly by the biochemical reactions by which the reserves in the seeds are converted into structural tissues in the seedlings.

Once the shoots have emerged, there is a distinct drop in optimum temperature. In this phase the absorption processes determine the growth rate. The temperature curve is a reflection of the root activities and is determined by both the quantity of roots present and the absorption per gram of roots.

At a later stage, when the plants have developed a closed-crop surface, the rate of dry-matter production is the same over a large part of the temperature range. Only at very low temperatures at which the leaves are partly wilted does root temperature cause a measurable reduction in dry-matter production.

The dotted line in the top part of Fig. 4 shows the effect of the root temperature on plant height. The course of this line is also indicative of leaf area development. In such situations taller plants are favoured in that they overshadow smaller plants. The results presented in Fig. 4 suggest the following interpretation. Root-zone temperatures primarily affect root growth and development. In addition, they determine the water permeability of the root tissue (KRAMER 1949). As a consequence of the latter, the water supply to the shoot will be affected and this in turn will cause differences in leaf water potential and hence leaf-area development.

At very low root temperatures (5 and 10°C) there is hardly any extension growth, because leaf water potentials are very low. Despite the markedly reduced increase in leaf area, the photosynthetic activity is much less affected (GROBBELAAR 1963). This leads to an accumulation in the plants of reserves that remain partially available for growth resumption as soon as conditions improve. The relative insensitivity of the photosynthetic process
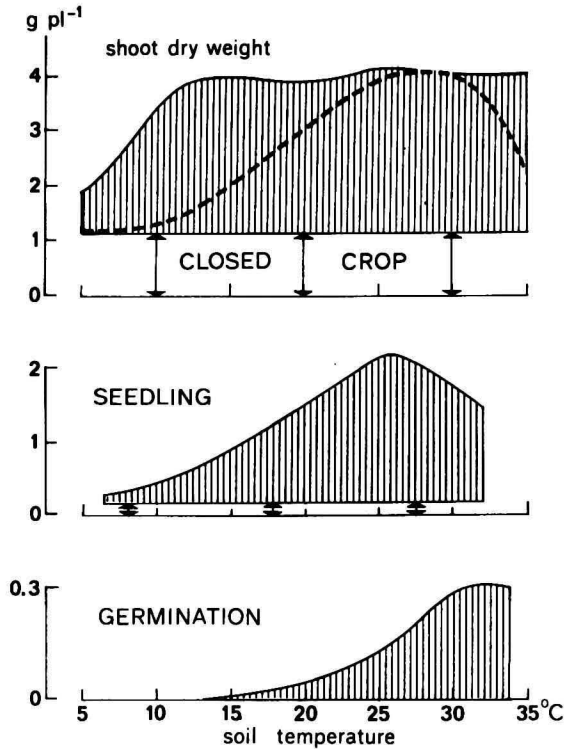
FIG. 4.   Effect of soil temperature on growth of bean seedlings in
          various stages of development.
          Bottom: germination during the first 10 days after sowing.
          Middle: weight increase during 8 days after the start of
                  treatment of plants pregrown uniformly until they
                  reached the weight indicated by the arrows.
          Top   : weight increase during 8 days after the start of
                  treatment of plants pregrown uniformly until they
                  reached the weight indicated by the arrows
                  (closed green-leaf surface)

explains why the effects of adverse soil conditions are less harmful once a
closed-crop surface has been attained. All light is then captured and diverted
into dry matter. This course of events illustrates a phenomenon known from
agricultural experience, namely that deficiencies in the root medium cause a
reduction in yield mainly by reduction in leaf growth, thus reducing leaf area
(WATSON 1947).

     This also means that the degree of adversity of a given soil factor depends
largely on the density of the vegetation. In a dense vegetation, light is the
limiting factor and thus diminishes the importance of soil factors. In open
vegetations soil factors are more important. This might partly explain why
annuals or biennials may occur in a relatively open vegetation whereas dense
vegetations are almost completely composed of perennials with different growth
forms (PEGTEL, personal communication).

The responses of bean plants to soil temperature, as discussed above, are representative for those plants in which the growing points of the shoot are situated well above ground level. In rosette plants and in grasses in the vegetative stage these growing points are located in or near the soil surface, and are therefore influenced by the soil temperature. As a result, the growth of such plants is more profoundly affected by soil temperature (Fig. 5), since not only root growth and root activity but also shoot development, e.g. leaf appearance (BROUWER et al. 1973), are directly controlled by this factor.
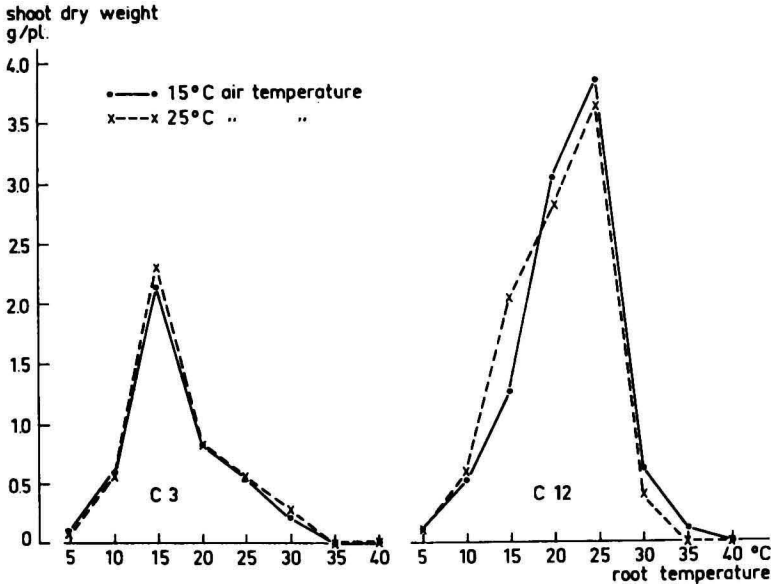


FIG. 5.    *Dry weights of shoots of two ryegrass* (Lolium perenne) *clones grown for 9 weeks on nutrient solutions kept at the indicated root temperatures and two different air temperatures* (KLEINENDORST & BROUWER 1965)

KLEINENDORST & BROUWER (1967) showed in climate-room experiments that air temperature was of negligible importance in perennial ryegrass, the growth rate being governed solely the the temperature of the root medium (Fig. 6). PEACOCK (personal communication) found that the temperature at a height of 0.5 cm above the soil surface determined the growth of perennial ryegrass in the field. In addition to leaf-area development, soil factors -including soil temperature- may affect leaf orientation. This further complicates a quantitative evaluation of the significance of soil temperature when plants are grown in competition. The results of these studies suggest that the degree of adversity is also dependent on other external conditions to which the plants are exposed (interaction). This seems to be supported by the results
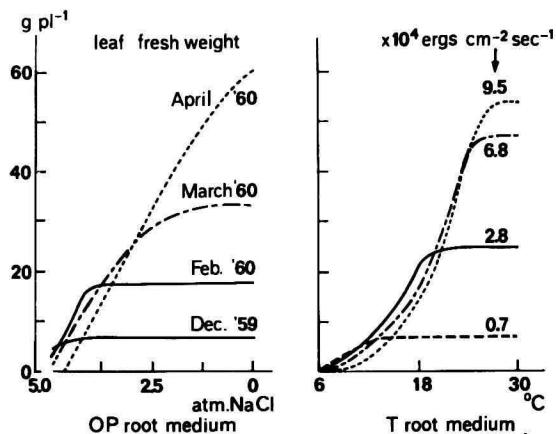
FIG. 6.   *Effects on the growth of bean plants of light intensity interacting with osmotic concentration and temperature of the root medium*

shown in Fig. 6 concerning the interaction between light level and the osmotic concentration as well as the temperature of the root medium. The response to a reduced water supply induced by either an enhanced osmotic concentration or by low root temperatures is of minor importance at low light intensities. The effects of a lower water potential, which persists under such conditions of low light supply, are completely obscured. At increasing light intensities the growth rate of the controls increased correspondingly, and the effect of the adverse factor became manifest at decreasing levels. It is interesting to see that in the range of maximally tolerable adversity a shift also occurred. Plants which had survived the stress treatments at low light intensities died when treated in the same way at high light intensities. Under low root temperatures this mortality was due to the low water potential which developed as a consequence of the high irradiance. At high NaCl concentrations the death of the plants might have been caused by the toxic effects of ion accumulation in the tissue. An analysis of the components responsible for these growth responses showed that both morphological (or phenotypical) adaptations (leaf area ratio) and physiological processes (net assimilation rate) are involved (Fig. 7).

A comparison of the effects of temperature and osmotic potential has shown that the physiology of the response is rather similar. Both factors influence shoot growth through their effect on the water balance of the plant. The interaction with light intensity can be explained on this basis. However, the water balance is only one of the several possible ways in which adverse root treatments can influence plant performance (BROUWER 1973). Other root activities, for instance mineral absorption or hormone production, might have
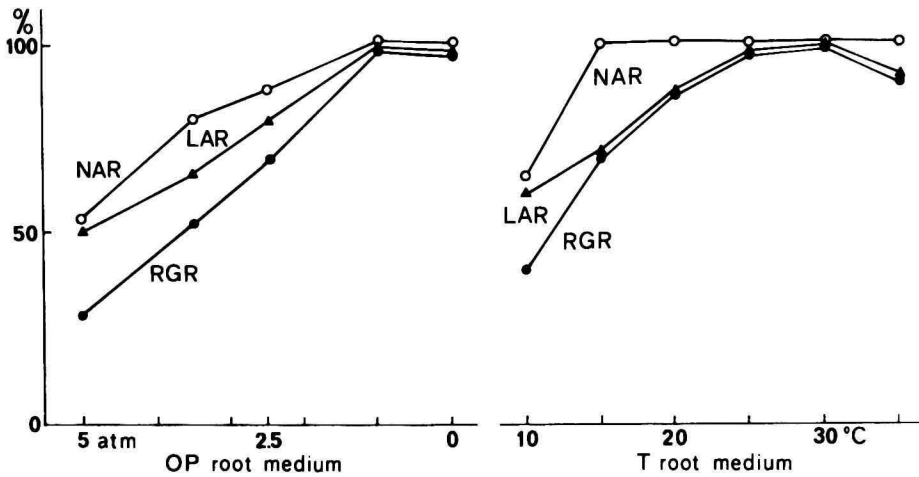
FIG. 7. *Effects of osmotic concentrations and suboptimal temperatures of the root medium on the relative growth rate of bean plants, exerted via morphological (leaf area ratio) and physiological (net assimilation) characters*

been reduced too. Roots have been reported (LIVNE & VAADIA 1972; WIEDENROTH 1974) to produce gibberellic acid and cytokinin-like substances contributing to leaf elongation, stomatal control, chlorophyll formation, etc. It has been shown that this aspect was not critical in the experiments in question (BROUWER & KLEINENDORST 1967). Under other conditions, however, these aspects may become growth limiting. The same holds for possible changes in biochemical pathways in the roots, i.e., changes whose effects on the overall plant performance are overshadowed by the effects of the water potential.

We find a different situation when we consider another factor in the root environment, namely gas-exchange restrictions. Much research has been done on the effects of poorly aerated soil on plant growth and performance (ARMSTRONG 1974). Comparison of plants grown in well-aerated soils (well supplied with oxygen, no accumulation of $CO_2$) with plants grown in soils with reduced gas exchange invariably shows reduced root growth. Quantitatively, considerable differences between species occur (Fig. 8). The penetration of roots into anaerobic layers depends on a number of internal and external factors. A high level of metabolism, high temperatures, and high organic nitrogen content all reduce maximum penetration considerably, e.g. in our experiments with water-logged sandy soils, maize roots penetrated to a depth of 75 cm below the ground-water table at 15°C and low nitrogen nutrition. The depth of penetration was reduced to 20-25 cm at 25°C and a higher nitrogen nutrition level.

In their response to anaerobiosis, maize plants occupy an intermediate position between plant species whose roots hardly penetrate the anaerobic
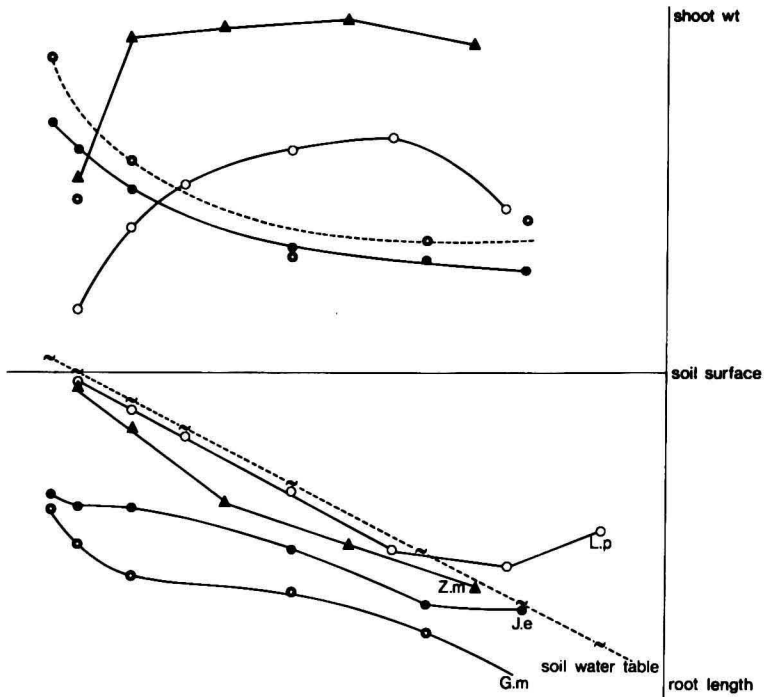
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shoot wt

soil surface

L.p

Z.m

J.e

soil water table

G.m

root length

FIG. 8.   *Rooting depth and shoot weight of various species
as affected by the height of the soil water-table
(constantly maintained at levels between +5 and
−80 cm relative to the soil surface).*
G.m. = Glyceria maxima, J.e. = Juncus effusus,
L.p. = Lolium perenne,  Z.m. = Zea mays

regions in the soil *(Phaseolus vulgaris)* and others whose roots are much less
affected than maize roots *(Oryza sativa, Phragmites australis).* The marked
divergency of the responses alone suggests that at least in some species there
has been a considerable degree of adaptation to the reduced gas exchange
properties of the soil. With respect to the physiological aspects of this
adaptation, various plant properties are involved because anaerobiosis is
generally accompanied by changes in other soil properties, *viz.*: low partial
pressures of oxygen, accumulation of carbon dioxide, a lowered oxidation-
reduction (redox) potential, and the accumulation of reduced forms of carbon,
nitrogen, sulphur, iron, and manganese, some of which may reach toxic levels.
ARMSTRONG (1975) discussed the degree to which tolerance is achieved on the
basis of the following plant properties: (a) the ability to exclude or tolerate
soil-borne toxins, (b) the development of air-space tissue, (c) the ability to
metabolize anaerobically and tolerate an accumulation of anaerobic metabolites,
and (d) the ability to respond successfully to periodic inundation.

It has long been known that roots of intact plants can oxidize reduced substances in the root medium (MOLISCH 1888). FUKUI (1953) associated this ability to oxidize the rhizosphere with the ability to penetrate reduced paddy soils. The oxygen diffuses from the atmosphere, via intercellular spaces in shoots and roots, to the root surface. The limited size of the normally present intercellular cavities, cannot even satisfy the oxygen demands of normal root metabolism, let alone provide sufficient rhizosphere oxygenation to avoid intoxication by reduced soil-borne substances. Most plants respond to reduced oxygen tension by enhancing the porosity of the cortical tissue: values of about 5 per cent in well-aerated soils can increase to between 15 and 85 per cent, depending on the species (Fig. 9) and the degree of anaerobiosis. It is evident that such large cavities could considerably reduce
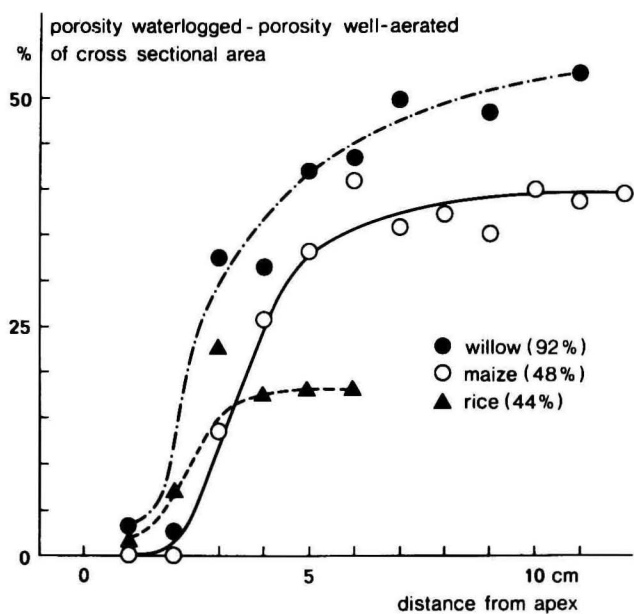


FIG. 9.    *Increase in porosity (expressed as percentage of cross-sectional area) of the roots of willow, rice, and maize plants in waterlogged soil and soil at field capacity. (Numbers between parentheses represent the highest porosity values found in waterlogged soils)*

diffusion resistance, but whether this completely explains their existence is still an open question (WILLIAMS & BARBER 1961; ARMSTRONG 1971). Perhaps plants adapt more readily when less tissue has to be maintained. In this respect it is noteworthy that the development of similar cavities in the root cortex is induced by a deficiency of various mineral elements.

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The adequacy of the oxygen supply to the active sites determines whether or not normal aerobic respiration can proceed. If it cannot, most plants shift over to anaerobic dissimilation processes, and this leads to the accumulation in the plant root of toxic products such as ethanol and lactic acid. Adapted species have been shown to accumulate less toxic substances instead, for instance shikimic acid and malic acid (ARMSTRONG 1974). In addition to bio-chemical and anatomical adaptations, mention should be made of adaptations of the morphology of the root system. In wet soils an $O_2$ gradient will generally be maintained from the soil surface to the lower soil layers. Strongly reduced root growth in deeper soil layers leads to enhanced induction and growth of (adventitious) roots at the stem base, where conditions are less adverse.

It is generally rather difficult to decide which factor limits root development in a particular case. As already mentioned, radial oxygen losses enable some plants at least to improve conditions in the direct vicinity of the roots. Differences between plant species include differences in sensitivity to a number of factors acting at the same time (SHEIKH 1970). Whereas root growth responses of various species to waterlogging tend qualitatively in the same direction although they differ greatly, the concomitant shoot responses show even greater deviations quantitatively. Fig. 8 shows two typical response patterns. In *Glyceria maxima* and *Juncus effusus* the shoot weights are highest at very high ground-water levels, and decrease at lower water tables. *Zea mays* and *Lolium perenne* show distinct optima. In our case the experiment was started with established seedlings. LAZENBY (1955), who worked with variations in water level immediately after sowing, found a similar descending curve for *Juncus effusus*. Water levels lying more than 15 cm below the surface dit not stop growth of the pregrown plants, but germination did not occur at water tables deeper than 10 cm. KLEINENDORST & BROUWER (1967) found that aeration of the nutrient solution affected rooting and subsequent growth of various clones of perennial ryegrass in a quite different way, since aeration proved to be more essential for root initiation than for root elongation. They also observed distinct clonal differences.

The effect of a transition from favourable to adverse conditions depends on the nature of adaptive differences. The time required by plants to adapt them-selves to the new situation determines their chances of survival (BROUWER & WIERSUM 1977). Rapid responses are required to meet a suddenly inadequate water supply or increased transpiration rate, because water in the tissue has to be replaced continuously. With respect to the mineral supply, much greater variation is acceptable. The same holds for the carbohydrate supply, since a rather efficient feedback between photosynthesis and respiration is thought to exist. These characteristics vary according to the species.

The differences in response determine whether one species will win or hold its ground at one place and others will not. The responses of beans (*Phaseolus* )

and willow cuttings (*Salix* spec.) to flooding may be mentioned as examples of such differential behaviour. After a period of growth in well-aerated soil, root elongation in both species is stopped by flooding. Shoot growth, however, is affected only in beans, which indicates that root functioning is reduced more in beans than in willows. This is confirmed by the time course of transpiration before and after flooding. Both species respond with an enhanced root growth in the soil layer near the surface (less adverse). After some time this leads in bean plants to a partial recovery of transpiration and growth. Coincident with the reduction in transpiration of the *Phaseolus* plants, their leaves show chlorophyll breakdown as well as other symptoms of ageing, which can be ascribed to a decreased synthesis of cytokinins by the treated roots (REID 1976).

Initiation of the recovery of such bean plants requires the growth of adventitious roots near the soil surface, the induction of which takes some time. If climatic conditions favour high transpiration rates, the plants will die before they reach this stage. When the plants are in a growth stage during which new root initiation normally does not occur (generative stage), recovery is almost impossible. Here again, the response depends strongly on the prevailing conditions and the stage in the life-cycle.

The local situation also determines whether reduced root growth affects shoot growth via the hormone balance, via the water requirements, or via the mineral absorption. BANNISTER (1964) demonstrated that waterlogging affected the distribution of *Calluna vulgaris* and *Erica cinerea* and *E. tetralix* via differences in its effect on the water balance of these species. In other cases unfavourable aeration conditions in the soil could be compensated for an additional supply of fertilizer (HAMMOND *et al.* 1955; SIEBEN 1963; BROUWER 1977).

It should be mentioned again that the response depends to a great extent on the situation in the vegetation. The relative importance of a given soil factor for growth is greater for individuals in open vegetations than for those in a closed vegetation, since in the latter light is more likely to be the ultimate limiting factor. In such a situation, however, rather small differences in root response may have important consequences for the whole plant, since being a little ahead in the beginning will have considerable advantages in the competition for light as well as in the exploration of soil-bound resources (ELLERN *et al.* 1970).


## 4. GENERATIVE STAGE

Despite considerable differences in the reproduction pattern (GRUBB 1977) of various species, some general remarks can be made. In plants in which the life-cycle is completed with flowering and subsequent seed formation, conditions during the vegetative stage determine both the size of the machinery for photosynthesis and the number of "sites" (seeds) that will be filled.

Usually there is a good correlation between the size of the plant and the

number of seeds initiated, since both are mainly determined by the amount of light energy that has been captured (a certain degree of phenotypic plasticity can be observed here). High fertility levels tend to favour vegetative growth rather than seed initiation; low radiation levels frequently tend to postpone the onset of flowering and, even more so, seed setting. Both phenomena can be ascribed to the low carbohydrate level prevailing under these conditions. Therefore, in determinate plants, which complete their life-cycle with seed ripeness, the amount of light intercepted before flowering determines the number of seeds, whereas the amount of light intercepted after flowering determines the total ultimate seed weight, provided no calamities occur in the interval. Such calamities may cause serious disturbance of the normally rather precise correspondence between the number of flowers and viable seeds. Pollination is a particularly sensitive stage of the life-cycle, and is adversely affected by soil drought or by other soil conditions, such as flooding, which induce internal water deficits.

High air temperatures tend to have adverse effects as well. The success of seed-setting depends mainly on the balance between the levels of reserve carbohydrates and hormones produced by the developing fruits. Thus, in fertile soils or at low light intensities moderate drought may be favourable, since it tends to enhance the carbohydrate content. In determinate plants, after the onset of flowering, almost the entire dry-matter production is drained into the inflorescences. The first sign that this has started is that root growth is considerably reduced and fairly soon afterwards stops completely. This means that the roots produce less cytokinins and less of these substances is transported to the shoot. The resulting low cytokinin level in the leaves is the main reason for their senescence, which in turn is accentuated by unfavourable soil conditions (LIVNE & VAADIA 1972). It is clear that the maintenance of a green, light-absorbing surface (leaf-area duration; WATSON 1947) after seed-setting will determine the mass and possibly also the quality of seeds. Very little is known, however, about the effect of physical soil conditions on seed quality.

Although an appreciable number of herb species reach the end of their life-cycle very soon after flowering, many species flower in successive waves, and in these species vegetative growth and reproduction to on simultaneously for a considerable time. In a sense this behaviour tends to spread the risk of complete failure. Reduction of seed-setting due to adverse soil conditions during one wave may be at least partially compensated for by the next wave. Evidence concerning this phenomenon is, however, very scarce in the ecological literature.

Spreading of the production of viable seeds has also been observed as a year-to-year variation in perennial species (GRUBB 1977), but very little is known about the external factors that determine either failure or abundance.

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## 6. DISCUSSION

On the question of the physical condition resulting in yellowing of shoots, BROUWER pointed out that this effect could be caused by low temperature as well as by oxygen deficiency. The process of yellowing associated with ageing could be stopped by a relatively rapid change in the stress situation if the air humidity is not too low.

ROZEMA (Amsterdam) then asked about the causal background of the increase in biomass production of flooding-tolerant plants under anaerobic conditions. BROUWER thought that the effect may be due to an unaffected assimilation rate, an enhancement of the leaf area, or a reduced respiration.

WENT (Nevada) drew attention to the ecological importance of the experiments with varying levels of the water-table, because they will explain the distribution of plants in the field. BROUWER commented that his experiments have already been started with established plants or tillers, whereas the critical ecological point may be the germination stage. As LAZENBY (1955) has demonstrated for *Juncus effusus,* the germination of this species is quite sensitive to lowering of the water-table, whereas the established plants can also thrive well at rather low water-tables.

CHAPHEKAR (Bangor) asked about the influence of a high water-table or soil compactness on the acceleration of flowering. BROUWER replied that most of his experiments were restricted to the vegetative state, but due to a correlation between the size of plants and the possibility for flowering and seed production he believed that the response will be the same as for vegetative growth.

VAN DER MEIJDEN (Leiden) asked about the ecological advantage of a high temperature demand for germination and the lower temperature optimum for

growth. BROUWER confirmed the more general phenomenon of the need for high temperature at the early growth stages. At the moment, however, the ecological importance remains uncertain.