1. Introduction

In plants, periods of growth by elongation alternate with periods in which no such growth takes place. This state of outward inactivity has been indicated as 'rest' and as 'dormancy'. There is no agreement as to the use of these terms. Many authors use either term (often without giving an exact definition); some use both as synonyms. CHANDLER (1925) used rest in the general sense, dormancy for cases in which growth is only resumed after a period of chilling; CHOUARD (1951) did the opposite. In the present review only the word dormancy will be used and applied in the widest sense, namely to any case in which a tissue pre-disposed to elongate does not do so.

There are many cases of dormancy; they may be classified into three groups. In the simplest case, growth inactivity is imposed by the environment, i.e. by drought or cold, and disappears as soon as conditions become favorable again. This is the 'gezwungene Unwirksamkeit' of JOHANNSEN (1900) or the 'unfreiwillige Ruhe' of MOLISCH (1909), called in this review imposed dormancy.

[1]
In the other cases the relation between growth and environment is less obvious, as the direct cause of the growth interruption lies within the plant. This cause may be an excess or a lack of substances that reach the dormant tissues from other parts of the plant. Lateral buds usually are inhibited by the growing terminal bud, which in turn often becomes inhibited by the leaves; flower buds may stay dormant because of a lack of organic nutrient matter (see chapter 3). For these cases the general term *summer-dormancy* will be used. This dormancy cannot be broken by a treatment that is limited to the dormant bud.

In the third group of phenomena the cause of dormancy is not systemic, but lies within the dormant tissue itself. This is the *winter-dormancy*. Under natural circumstances it will disappear as a result of a period of low temperature, which is not the case in summer-dormancy.

Many authors do not make a clear distinction between the various types of dormancy. In a bud winter-dormancy is always preceded by summer-dormancy and often followed by imposed dormancy; these phases overlap, and it is difficult to establish just when they begin. Yet at the moment the evidence suggests that they are caused by different physiological processes, so the classification may have more than just practical value. It should be stressed, however, that very little is known about these processes as yet.

In many cases buds become dormant, and sometimes also break again, while environmental conditions remain approximately constant. For such cases Pfeffer (1904) and many after him used the term autonomic or autogenic dormancy, in contrast to aitonomic or aitogenic dormancy, brought about by changes in the environment. KLEBS (1903 cf.) on the other hand maintained that dormancy was caused by the inner conditions of the plant, which came about as the result of an interaction of genetically determined processes within the plant on one hand, and its environment on the other; and that, consequently, dormancy could be prevented if one had complete control of the environment. The space reserved for this controversy in the present review is in no way proportional to the hundreds of pages devoted to its discussion in the German literature of the pre-auxin period. After the discovery of plant hormones and their inhibitors, and the photoperiodic stimulus, the problem appears in a different light and has lost its appeal. KLEBS' opponents were very numerous at the time, yet in his studies on the influence of the environment he was on the verge of discovering photoperiodism, and his discussion of the 'inner conditions' often sounds remarkably modern, although he stressed the importance of nutrient elements and organic matter where the modern author would suggest hormones or inhibitors.

This introduction may be concluded with a few general remarks on the scope of this review. It was compiled as a preparation for experimental work, and published because it appears that reviews of the literature on dormancy of woody plants are either incomplete or out of date. It seems likely that the processes causing dormancy in herbaceous perennials and seeds are largely the same that render the buds of woody plants inactive. However, to include these phenomena would have complicated this review and extended the bibliography to an unmanageable length. In a few cases it was necessary to refer to phenomena in herbaceous plants; in these cases the reader is not referred to the original paper, but to reviews like the book of CROCKER (1948), in order to keep the bibliography as short as possible.
2. IMPOSED DORMANCY

From a physiological point of view the case, in which growth inactivity is induced by the direct action of the environment on the bud, is not of any special interest. Yet it is a very common phenomenon in nature; in the northern temperate zone the majority of the woody plants are in a state of imposed dormancy from January, or even earlier, until the time the buds break in spring. The possibility of inducing dormancy by low temperature has found some application in cases where it was desirable to retard flowering (Molisch 1909). On the whole such cases are rare, as the demand for spring flowering shrubs is limited to the time that they are dormant outside.

Imposing a temporary dormancy by drought seems to have found some practical application in India. Sayed (1937) relates how the roots of certain fruit trees (fig, grape, pomegranate, certain varieties of citrus) are exposed and pruned to enforce a dormant period, which prepares the way for an abundant yield in one season only, instead of the almost continuous production of poor quality fruit that otherwise occurs in this climate. The same practice is followed with the apple (Javaraya 1943); it appears to be possible by imposing two dormant periods to have two crops in one season, although this leads to exhaustion of the tree. It seems that with the apple the period of dormancy imposed by artificial drought prevents the tree from passing into winter-dormancy, which would be hard to break in a climate with warm winters. This state of affairs suggests an intriguing problem; however, more evidence is necessary than has been supplied so far.

It has not yet been demonstrated that imposed dormancy ever leads to another form of dormancy, in other words, that a direct growth prevention causes some growth inhibiting system to form somewhere in the plant that prevents growth when conditions are favorable again.

3. SUMMER-DORMANCY

3.1 Terminal buds

One might expect that under favorable conditions elongation would be continuous, at least in young plants; however, studies of trees and shrubs in the tropics have revealed that only in a small percentage of species this is the case. Volkens (1912) mentioned Albizia moluccana, Artocarpus incisa and Morinda citrifolia as plants that show this type of growth; Klebs (1912) and Coster (1927) gave a few additional examples. Among woody evergreens of the temperate zone continuous growth seems to be even more uncommon. So far, only Calluna vulgaris has been mentioned as a plant in which growth is only interrupted during unfavorable environmental conditions (Chouard 1951). Other examples may be Alnus maritima, Sambucus canadensis and Rosa ssp., which show continuous growth when planted in the tropics (Coster 1927). Generally, species of temperate climates keep their periodicity in the tropics, but show the remarkable phenomenon that the branches become independent of each other in this respect (Wright 1907, Dingler 1911, Coster 1926, '27).

In certain species continuous growth may be brought about by artificial conditioning of the environment: some woody plants show uninterrupted growth in long day or continuous light. More details about this will be given later. In herbaceous perennials continuous growth is not uncommon; annuals apparently only show imposed dormancy (Klebs 1903, Chouard 1951).
Much more common than continuous elongation is intermittent growth: under constant conditions a period of growth is followed by a period of outward inactivity, then elongation is resumed, and so on. This was first described from the tropics, where it is the most common type of growth. The plants may either be evergreen, or periodically lose their leaves; in climates with a dry season they are often leafless during this period (SCHIMPER 1898, HUBER 1898, VOLKENS 1912, KLEBS 1912–26, SIMON 1914, COSTER 1927). In temperate climates intermittent growth is common in vigorously growing young plants, especially seedlings, through spring and summer. Fully grown trees usually show one period of growth; several, however, show two or occasionally more periods (KLEBS 1914). This second period of growth, usually starting towards the end of June, causes the so-called lammas shoots (German: Johannistriebe, Dutch: St Jansloten), that are characteristic of beech and oak (SPAETH 1912, MAGNUS 1913, DOSTÁL 1927). In some plants, e.g. _Acer platanoides_, the elongation does not come to a complete standstill, and the interruption between two periods of rapid growth only shows as a few very short internodes with smaller leaves (TAMMÉ 1903, SPAETH 1912).

An explanation of intermittent growth may be that during the sudden rapid elongation of the young shoots the initiation of new organs does not take place, at least not fast enough; another possibility, which does not exclude the first, is that elongation does not begin until the terminal meristem has initiated a certain minimum number of primordia. From the phenomenon of intermittent growth the notion of an autonomic dormancy developed (SCHIMPER 1898). Yet there is considerable influence of the environment.

Considering the evidence, it appears that two influences determine what has been called here intermittent growth: an inhibition of elongation exercised by the leaves, and a stimulation by the roots. The inhibitory influence of the leaves may be demonstrated by defoliation, which has been shown again and again to cause the terminal bud to resume growth (i.e. GOEBEL 1880). This inhibition may be so strong that the terminal buds dies; this commonly occurs in plants with sympodial growth like _Ailanthus_ and _Robinia_ (KLEBS 1911) and several plants with decussate buds, e.g. _Syringa_ (LUYTEN and VERSLUYS 1921). Experiments of KLEBS (1914) and others (to be discussed) suggest that in some plants the inhibitory system develops in the dark; in others, e.g. the oak (SPAETH 1912) it seems to be favored by the light.

Stimulation of elongation by the roots was pointed out by KLEBS (1911) who showed that an abundant supply of nutrient elements will prolong growth considerably. He even thought this to be the most important environmental factor, and suggested that the influence of defoliation was due to the fact that nutrient elements, no longer used by the leaves, all stream to the terminal bud. A modern hypothesis is that of WENT (1938) who suggested that a hormone, ‘caulocaline’, necessary for stem formation, is synthesised in the roots. The rapid elongation after the buds break exhausts the supply of caulocaline and stem formation has to stop; a period of assimilatory activity follows in which the roots restore the equilibrium with the parts above ground and synthesise more caulocaline; then elongation starts afresh, and so on. According to this theory the beneficial effect of nutritional supply to the roots is not due to the ions themselves but to the indirect effect on the production of caulocaline through the stimulation of root growth. Shoots in a favorable position in regard to supply from the roots continue growth for a long time, often far into autumn;
so do the shoots that develop after heavy pruning has upset the balance between root system and the upper parts of the plant.

So far no explanation has been offered for the very sudden and rapid development of the young shoot. Another unexplained phenomenon is that the second growth of some varieties (clones) of oak is morphologically different from the first. In *Quercus robur 'Fürst Schwarzenberg'* the leaves of the lammas shoots are mottled with white, while in *Q. petraea laciniata* the leaves of the second shoot are more or less normal, whereas those on the first growth are filiform (Spaeth 1912).

A great many woody plants of the temperate zone show only one period of growth per summer; in some species this period is long, in others it is very short (lists of various cases are given by Klebs 1914 and Wareing 1949). Plants which stop growing very early, before June 21, are those in which no more leaves unfold than were laid down the previous year, or the year before (Büsgen and Münch 1939, Wareing 1949, 1950b). One wonders, why growth is not resumed as soon as new leaf primordia have been formed. The explanation may be, in analogy to that proposed for intermittent growth, that the inhibitory influence of the leaves is too strong, that the roots take too long a time to produce the necessary caulocaline, or both.

In cases where growth is continued until after the longest day, another factor comes into play. In 1923 Garner and Allard found that long day, as compared to short day, prolonged growth and retarded leaf-fall in several woody species. Matzke (1936) studied these photoperiodic responses in the 'field' and saw that street lamps retarded leaf-fall in *Platanus, Populus* and *Salix*. Some species do not go dormant at all when the day is long and other conditions are favorable; thus far the following examples are known: *Liriodendron tulipifera* (Garner and Allard 1923), *Robinia pseudacacia, Pinus taeda* (Kramer 1936), *Populus* spp. (van der Veen 1950a, b), *Salix repens* (Chouard 1951). Other species show uninterrupted growth when illumination is continuous: *Fagus sylvatica* (Klebs 1914), *Liquidambar styraciflua* (Kram er 1936), *Fagus grandifolia, Acer rubrum*, various *Pinus* species (Jester and Kramer 1939) and the species mentioned above that grow continuously in long day. It appears that in all these species growth is uninterrupted when the daily photoperiod exceeds a certain critical length; they are, in this respect, 'long day plants'. The question arises whether there are 'short day plants' and 'neutral plants' too. This indeed seems to be the case. Garner and Allard (1923) found that grafts of apple grew better in a 12 hour photoperiod than in the natural long summer day; Moshkov (1935) found that *Salix babylonica* and *Pyrus ussuriensis* showed a longer growing period in a 14 hour day than in a long day. Wareing (1950a) demonstrated that in first year seedlings of *Pinus sylvestris* dormancy is delayed and more leaves are formed in long days up to 20 hours; when illumination is extended to over 20 hours there is a sharp fall in leaf number. He explained this by (a) a growth promoting substance (perhaps auxin or an auxin precursor) formed during the preceding light phase and active during the first four hours of darkness, and (b) a growth inhibiting system (perhaps an auxin inhibitor) which becomes active after four hours of darkness. In older plants the number of nodes is predetermined by the number of initials laid down in the bud the previous year, and only the length of internodes and leaves is affected by the photoperiod (Wareing 1950b). Comparatively few plants are 'neutral' and show no or only a very slight response to daylength. So far, species of *Fraxinus* and *Quercus* have been shown to belong to this category (Kramer 1936, Jester and Kramer 1939).
Little is known about the perception of the photoperiodic stimulus. PHILIPS (1941) demonstrated that in seedlings of *Thuja occidentalis*, *Pinus taeda* and *Robinia* red supplementary light was more effective than white light, which in turn had a much stronger effect than (weak) blue light. In analogy to the processes which take place in the photoperiodic induction of flowering it seems plausible to suppose that the perception of the photoperiodic stimulus leading to growth inhibition takes place in the leaves. However, light may have a marked effect on naked branches where one has to suppose that perception takes place in the buds (chapter 4).

Cessation of growth of the terminal bud is very important in climates with a severe winter season, as only when growth is coming to a standstill, can the shoot 'ripen', that is, prepare itself for the winter cold. This process consists of the surrounding of the terminal growing tip by bud scales, thickening of cell walls along the whole length of the twig, and the accumulation of organic substances, especially starch. The interest of Russian workers in photoperiodic growth responses stems mainly from this relation between growth stop and winter hardiness (GEVORKIANTZ and ROЕ 1935, MOSHKOV 1935, ELENEV 1938, GULISASVILI 1948).

A more extensive review of photoperiodism in woody species is given by WAREING (1949).

### 3.2 Lateral buds

Lateral buds do not develop in the season during which they are initiated, except in rare cases like some species of *Ulmus* where the oldest lateral growing points elongate immediately, often without forming bud scales, giving rise to what SPAETH (1912) has called sylleptic shoots. Normally the lateral buds are prevented from sprouting by a strong inhibitory influence exercised by the terminal growing tip (GOEBEL 1880) and a similar influence, although much weaker, from the leaf in axil of which the bud is situated (DOSTÀL 1909). Since THIMANN and SKOOG discovered in 1934 that auxin descending from the terminal bud is of crucial importance in this inhibition, the phenomenon has been widely studied, and various explanations have been proposed. They will only be mentioned briefly here as they have been reviewed recently by SÖDING (1952) and the experimental work has been done with herbaceous plants, especially peas.

THIMANN and SKOOG originally suggested that the quantity of auxin descending from the tip was such that the concentration in the lateral buds would pass the maximum for growth and consequently inhibit elongation. VAN OVERBEEK thought that the descending auxin would block the transport to the lateral buds of nutrient substances necessary for growth. WENT suggested that the auxin would attract other substances necessary for growth; as the terminal bud has a far higher auxin content than the lateral buds it would leave too little of these substances to the latter. There are several other theories (i.e. BORGSTRÖM 1939b). According to SÖDING (1952) the most plausible theory so far is that of SNOW, who thinks that the auxin causes the formation of an inhibitor, which is transported in all directions, while auxin only travels basipetally. Consequently, the auxin stream from the terminal growing tip does not enter the lateral buds, but the inhibitor, formed as a result of auxin activity, passes into the buds and prevents their growth.

There is some evidence that this kind of correlative inhibition may lead to
a non-reversible inhibition; CHANDLER et al. (1937) showed that winter dormancy may develop in the lower lateral buds while the terminal bud is still growing.

3.3 Flower buds

Previously, the possibility was suggested that no elongation will take place in a bud before a certain number of primordia has been laid down by the meristem. For flower buds this seems to be a rule: flowers rarely stretch before they are complete. This points to another, as yet completely unknown inhibiting system.

In many spring flowering woody plants, flower initiation is complete before autumn; obviously, inhibitory influences prevent their immediate development. To what extent these are identical with those that cause vegetative buds to stay dormant is not clear. Defoliation may cause the terminal flower buds of the horse chestnut to open (KLEBS 1914). There do not seem to be experimental data on the effect of defoliation or the cutting away of the terminal bud on lateral flower buds in general. In Forsythia neither has any effect, but during August and September flower buds may be induced to open by 'ringing' the bark at the base of the twig so that assimilatory products may accumulate. If the twig is defoliated simultaneously, there is no such accumulation and the flower buds remain dormant (DOORENBOS 1953).

In the Philippines, flower buds of the mango are forced to open by smoke from bonfires, a treatment known as ‘smudging’ (GONZALEZ 1923, BORJA and BAUTISTA, 1932, GALANG and AGATI 1936). The effect appears to be due to heat (GONZALEZ 1933).

4. WINTER-DORMANCY

4.1 Occurrence of winter-dormancy

Winter-dormancy may be looked upon as an adaptation to a cold season. It does not occur in the tropics, but is almost universal in woody plants of the cold temperate zone; here, however, it varies in intensity from species to species. Winter-dormancy is extremely deep, that is, hard to break, in Fagus, Quercus and Fraxinus, and light in the lilac and the apricot. Not all buds on the plant are in the same state of dormancy. Flower buds are often easily aroused; striking examples are plants like Hamamelis ssp. and Prunus subhirtella pendula that will flower from October onwards whenever temperature permits. In shrubs like Forsythia and certain trees, e.g. several species of elm and ash, the difference is not so pronounced, but flowers develop well in advance of the leaves. There are also differences between the vegetative buds of one plant. In Syringa vulgaris small buds develop more easily than large ones (DOSTÁL 1942). SIMON (1906) held the opinion that the small buds over a year old, at the basis of shoots of the lilac have no winter-dormancy at all. In the beech, however, such buds are dormant (KLEBS 1914). Buds on strongly developed one year old shoots have a deeper winter-dormancy than other buds on the plant – a phenomenon to be considered when pruning deciduous trees in mild climates where the danger of prolonged dormancy exists (CHANDLER et al. 1937).

That a suitable treatment of one bud on a plant in winter-dormancy will cause only that bud to develop, has been demonstrated a number of times (MOLISCH 1909, HOWARD 1915, COVILLE 1920, DENNY and STANTON 1928b). Apart from the fact, that winter-dormancy is not transported through the plant, this shows that a developing shoot on a dormant branch is supplied with water and
nutrition. This led to the belief that winter-dormancy is limited to the buds; however, GOUWENTAK (1941) demonstrated that not only the buds are dormant, but the cambial meristem as well. The roots probably never go dormant (SIMON 1906, LADEFOGED 1946). When shrubs are brought into the greenhouse during autumn, roots will develop while the buds stay dormant. The formation of adventitious roots on cuttings is another matter. No roots will develop on cuttings of *Salix* during winter-dormancy (MOSHKOV and KOCHERZHENKO 1939). VAN DER LEK (1934) showed that elongation of root primordia in cuttings of *Populus canadensis* is inhibited by the buds during winter-dormancy; the root primordia themselves are not dormant. As soon as the buds start to develop they stimulate root formation. The situation in plants that have no root primordia is not clear.

Buds pass into winter-dormancy only after some correlative inhibition (primarily that exercised by the leaves, it seems) has brought growth to an end. This state of affairs was already known to KLEBS (1911). He suggested that when the terminal bud stops growing, the products of the assimilatory activity of the leaves would accumulate. This would render the hydrolysing enzymes inactive, and this enzyme inactivity would constitute the essence of winter-dormancy. KLEBS' hypothesis was supported by work of LAKON (1916, '17) with *Acer negundo* and its mottled and white leaved forms. The less chlorophyll the leaves on a branch contain, the later the buds go dormant and the easier they are to force. LAKON considered this to be due to the fact that mottled leaves have a smaller assimilatory activity so that insufficient organic material is formed to accumulate. Twigs with completely white leaves hardly go dormant at all and are killed by frost in winter. Similarly, the fact that buds on witches brooms show little or no winter-dormancy (SCHELLENBERG 1915) has been considered to be due to the fact that the parasites causing these abnormal growths consume the reserves of organic material.

As most authors do not distinguish between the various forms of dormancy, little evidence has been presented to show when winter-dormancy starts. Perhaps the first sign of its onset is that the terminal buds do not break after the branches are defoliated. In an experiment of JOST (1891) this was the case in the ash as early as May 5; in many plants defoliation is effective till July or later, occasionally until autumn. After this first onset, dormancy gradually becomes deeper. The buds are now in the stage which has been indicated as 'Vorruhe' (preliminary rest) by JOHANNSEN (1900). The term has little significance however, as it indicates two phenomena: correlative inhibition and the early stages of non-correlative dormancy. When the leaves fall, their inhibitory action ceases, but now winter-dormancy is at its deepest point. The buds have entered the 'Mittelruhe' (main rest). Little change takes place until the winter cold begins gradually to break dormancy, and it becomes easier to force the buds; JOHANNSEN's 'Nachruhe' (afterrest). The difference between the last two stages is only quantitative; originally this was how JOHANNSEN meant it, but later (1906) he suggested that during the 'Mittelruhe' growth itself was impossible, while in the 'Vorruhe' and the 'Nachruhe' growth was possible, but prevented by some inhibitive influence. However, as WEBER (1916) was the first to point out, there are forcing agents that will break dormancy at any time, so growth is always possible.

4.2 The breaking of winter-dormancy

In nature, winter-dormancy is broken by a period of cold. So far it has not been demonstrated where the optimal temperature of this process lies. It need
not necessarily be below 0° (LAMB 1948). At 12 to 20° the rate is very slow, but the process does take place, and consequently it is probably impossible to keep a bud permanently both alive and dormant, although it may be kept in that state for a year or more (WEBER 1916b, COVILLE 1920). High temperatures have some forcing action, as every nurseryman knows; the effect of very low temperatures is not known. In relation to the problem of delayed foliation the cold requirement of several deciduous fruit trees has been calculated. It varies much, not only for different species but also for varieties; moreover, there seems to be a large influence of the environment in which the tree grows. The cold requirement of fruit trees is usually expressed as the number of hours of 7° C necessary to break dormancy; as an example the work of WEINBERGER (1950a) with peach varieties may be cited.

That cold is necessary to break winter-dormancy seems to have been discovered by KNIGHT in 1801 (PFEFFER 1904). The first scientific experiments were those of MÜLLER-THURGAU with potatoes in 1882. Experiments with woody plants were done by PFEFFER (1904), HOWARD (1906) and others; a review of this work is given by GARDNER (1926). In 1907 Aalsmeer growers did a practical experiment with shrubs; the results were promising but as the method was found to be too costly it was continued with lily-of-the-valley only (DE VRIES 1913).

A sufficiently long period of cold causes the buds to pass from winter-dormancy into a state of imposed dormancy; they do not break before they are transferred to the warmth. This shows that the effect of chilling is not reversed in subsequent high temperature. Nevertheless BENNETT (1950) demonstrated experimentally that the low temperature treatment required to break the dormancy of pear buds is less effective when interrupted by periods of a moderately high temperature.

That a moderate degree of desiccation has a forcing effect was shown by HOWARD (1906, '10), mainly with cut branches of the horse chestnut. After a dry summer some plants have a tendency to show new growth; this is sometimes thought to be the same effect (LAKON 1915), but more likely it is a breaking of summer-dormancy as a result of premature death of the leaves (KLEBS 1914).

The influence of light on the winter-dormancy of Fagus sylvatica was discovered by JOST (1894) who showed that buds remain dormant in the dark. KLEBS (1914) demonstrated that they may be forced by continuous artificial light of low intensity. Whether this treatment has the same effect on any plant in which it prevents dormancy in autumn, is not yet known. Continuous illumination does break dormancy in Populus (VAN DER VEEEN 1951a, b), but not in Quercus (KLEBS 1914, '17) which shows little influence of daylength in autumn. KRAMER (1936) found a forcing action of long day in some leafless seedlings. GUSTAFSSON (1938) could break dormancy in young plants of Pinus resinosa, which had been insufficiently chilled and failed to develop in spring, by a 16-hour day. On the other hand, MATZKE (1938) saw no effect of street lamps on the opening of buds in spring; VAN DER VEEEN (1951a, b) showed that long day does not suffice to force the poplar.

As the action of light does not appear to be universal, it probably is not the key to the problem of winter-dormancy that it otherwise might well be. However, not many have agreed with WEBER (1916c), who after having succeeded in forcing the beech with acetylene, concluded that the influence of continuous light was a stimulus ('ein bloszer Reiz') wholly comparable to the effect of acetylene or any other forcing agent.
Injury of buds or neighbouring tissue has a distinct, but rarely strong dormancy breaking effect (Jost 1893, Simon 1906, Howard 1910, Weber 1911, '22, Jesenko 1912b, Portheim and Kühn 1914, La Marca 1916, Coville 1920, Dostál 1942). Probably the effect of radium emanation (Molisch 1912) and of X rays (Weber 1922b), and perhaps also that of an electric current (Bos 1907) is due to injury.

A useful forcing method is the warm water bath, invented by Molisch (1909a, b), which consists of dipping leafless shrubs or cut branches into water of 30–40° C for about 12 hours. Steam of the same temperature has a similar action (Boresch 1924). The effect of cold water is slight or nil (Jesenko 1912, Wittmack 1918).

As the nutrient elements strongly affect growth in summer (Klebs 1911 etc.), Lakon (1912) studied their influence on winter-dormancy. He placed cut branches in the greenhouse in a nutrient solution and found a strong forcing action; however, Kühn (1916) in similar experiments found only a weak effect.

A great many other chemical substances have been tried; those that had some effect are summarized in Table I.

**TABLE I**

*Chemicals that have been shown to have some dormancy breaking action in buds of woody plants*

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<th>Acetylene</th>
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<th>Amyl alcohol</th>
<th>Camphor</th>
<th>Chloral hydrate</th>
<th>Chloroform</th>
<th>Ether</th>
<th>Ethyl alcohol</th>
<th>Ethyl bromide</th>
<th>Ethyl chloride</th>
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acetaldehyde  
acetone  
adine dihydro-  
chloride  
adine sulfate  
aesculin  
chlorophyll  
dimethyl hydro-  
resorcin  
ether  
elcohol  
formaldehyde  
glucose  

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<td>indole butyric acid</td>
<td>AMLONG &amp; NAUNDORF 1938</td>
<td></td>
<td>HOWARD 1917</td>
</tr>
<tr>
<td>a-nitronaphtalene</td>
<td>GUTHRIE 1941a</td>
<td>AVERY &amp; JOHNSON '47</td>
<td>AMLONG &amp; NAUNDORF</td>
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<td>2-4 D</td>
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<td>CHANDLER et al. 1937</td>
<td>HERBERT 1924</td>
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<td>dinitro-o-cyclohexyl</td>
<td>Weinberger 1939</td>
<td></td>
<td>DUTTON 1924</td>
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<td>phenol</td>
<td>van Horn 1942</td>
<td></td>
<td>de Ong 1926</td>
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<td>dinitro-cresol</td>
<td>Samisch 1945</td>
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<td>MALLY 1934</td>
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<td>Jeffery 1951</td>
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<td>BLACK 1936, '52</td>
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<td></td>
<td>Black 1952</td>
<td></td>
<td>Newton 1923</td>
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<tr>
<td>chloro-o-phenyl-</td>
<td>GUTHRIE 1941a</td>
<td></td>
<td>GUTHRIE 1941a</td>
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Three of the methods mentioned have found practical application in the forcing of spring-flowering shrubs for the florist trade. The first of these was also the first chemical forcing method to be discovered, namely ether (JOHANSSON 1900–06, LEDIN 1901, HAM 1902, LEMOINE 1903, MAUMÉNÉ 1903, AYMARD 1904, and many articles in almost any horticultural periodical of the day). It was superseded by the warm water bath of MOLISCH (1909), which is easier to apply. More recently, ethylene chlorhydrin, discovered by Denny (1928) has found practical application (CROCKER 1948).

None of these methods is of any use in combating winter-dormancy in the field, which is necessary where deciduous trees are grown in climates with a mild winter where their cold requirement is not met with, giving prolonged dormancy or ‘delayed foliation’ as a result. This phenomenon occurs in Israel (LACEY 1944, SAMISCH 1945), and elsewhere in the Mediterranean area (REBOUR 1936), in the Black Sea region of Russia (RAJNOVA 1950), in East Africa (JACKSON 1947, LAMBERT 1948), in South Africa, in California and the southern United States, and in Argentina (BURGOS 1943, LEDESMA 1951). The literature about delayed foliation in America and South Africa is so numerous that the reader is referred to the reviews of CHANDLER et al. (1937), HILL and CAMPBELL (1949), and BLACK (1952), and to the bibliography. The peach in particular has been closely studied, as prolonged dormancy causes the death of floral organs or flowers within the bud, which in turn leads to the shedding of flower buds (CHANDLER and TUFTS 1934, WEINBERGER 1950a, b).

More or less by chance it was discovered that winter oil sprays against certain
pests have a dormancy breaking action, especially when substances like dinitro-o-cyclohexyl phenol (DNO) or dinitro-ortho-cresol (DNC) have been added (literature, see Table I). However, authors agree that by far the best method to prevent delayed foliation is to breed varieties that require but little cold.

4.3 Physiological causes of winter-dormancy

Recently, two Russian workers claimed that during winter-dormancy the plasmodesmata are absent, appearing again as soon as dormancy is broken (Genkelj and Oknina 1948, Oknina 1948). Straussbaugh (1921) showed that the moisture retaining capacity of the bud is higher when the bud is dormant. He suggested that winter-dormancy involves protoplasmatic changes, one of which is a change in colloidal properties, creating an increased imbibition, which may account for the marked retention of water against the forces of dehydration. This state of affairs leads to a marked relation between dormancy and frost resistance, which has also been noted by several other authors (Levitt, 1945). On of the most important papers emphasizing this point is one by Kessler (1935), who shows that during winter-dormancy there is a higher viscosity and perhaps also a greater density of the protoplasm. He worked with Hedera helix and two herbaceous plants.

The biochemical approach has been also used. Fischer (1891), Leclerc du Sablon (1904) and many others showed that in autumn when winter-dormancy is at its deepest point, the plant has a high reserve of organic substances, while the moisture content is low. When dormancy is broken, changes in these reserves occur. This will be briefly dealt with presently.

It seems reasonable to expect that a study of the forcing methods will give some insight in the nature of winter-dormancy; however, at first sight one is confronted by a baffling variety of methods, that does more to complicate than to clarify the problem. It seems hardly possible that cold, heat, light, injury, anaesthetics, toxic substances, acids and salts can all have the same effect. Yet several authors have tried to embrace all actions in one comprehensive theory. One may pass over vague notions like ‘shock’ or ‘stimulus’, and the easily refuted theory that the effect of all forcing agents is due to dehydration (Aymard 1904, Stuart 1910). Weber (1922a, 1924b) suggested that necro-hormones were the general dormancy-breaking agent. This hypothesis, revived by Dostáš (1942) is founded on the forcing effect of injury; however, there is no evidence that every forcing agent damages the tissues, nor that necro-hormones stimulate elongation.

Other more important theories have their starting point in the classical experiments of Müller-Thurgau who showed that as a result of low temperature both sugar content and respiration rate of dormant potato tubers show a marked increase. This rise in respiration occurs in woody species also, not only as a result of a cold treatment (Simon 1906), but also after the action of ether, a warm water bath, ethylene chlorhydrin and the lesser forcing agents (Johannsen 1896, Müller-Thurgau and Schneider-Orelli 1912, Iraklionow 1912, Howard 1917, Denny and Miller 1932). Similarly in woody plants cold or other forcing agents increase the sugar content at the cost of starch (Fischer 1891, Niklewski 1906, Gardner 1926). Müller-Thurgau supposed, that this increase in sugar is the cause of the rise in respiration. However, Miller showed that in potatoes treated with ethylene chlorhydrin, the increase in sucrose comes later and has no relation to the rise in respiration rate (Crocker 1948). In woody
plants where the starch reserve is much more limited, all starch may be converted into sugar without breaking of dormancy (Johannsen 1900); when such plants are forced with ethylene chlorhydrin the treatment causes the sugar content to fall as a result of increased respiration (Denny and Miller 1932). Consequently, the increase in sugar does not seem to be of much importance in the process of the breaking of dormancy, either as a respiration stimulus, or as an agent that increases osmotic pressure in the cells and so forces the buds into growth, as Coviile (1920) thought.

Meanwhile, the marked conversion of starch into sugar points to an increase in amylase activity, and as there is also a rise in soluble nitrogenous substances (Denny and Miller 1932), it seems that the forcing agent stimulates enzymatic activity. This effect, suggested by Klebs (1911) was demonstrated by Howard (1917) who found that in dormant apple twigs the oxidase and the various hydrolases were stimulated into greater activity by injury, warm water bath, ether, alcohol and other treatments. Coviile (1920) concluded that as a result of chilling, certain membranes became permeable, thus permitting the amylase to come into contact with the starch. Denny and Miller (1932) however, found no extensive increase in amylase activity in dormant lilac buds treated with ethylene chlorhydrin, but a large increase in catalase and a moderate increase in invertase.

In work on potato tubers the effect of various dormancy breaking agents on the physiological processes mentioned has been compared with their forcing action. It appears that in none of the cases there is an obvious relation. The increase in respiration does not seem to be of crucial importance: methyl, ethyl and isopropyl alcohols decrease respiration but show some forcing action. Enzyme activity is not stimulated by the thiocyanates and thiourea to an extent commensurate with their bud forcing action. Nor is the action of certain chemicals proportional to the rate in which they increase the permeability of slices of dormant tubers to electrolytes (Crocker 1948). It does not seem probable that there is a different state of affairs in woody plants.

Another theory was outlined for the first time by Weber (1916b, '18). He suggested that either during narcosis easily oxidizable material accumulated, causing a sudden increase in respiration at the end of narcosis which would stimulate other processes and lead to new growth, or, that intramolecular respiration during narcosis would lead to the formation of substances which stimulate growth activity. In support of this theory Weber could point to the forcing action of a vacuum (Stuart 1910), a N₂ or H₂ atmosphere (Weber 1916a), and the warm water bath, which increases respiration while simultaneously cutting off the oxygen supply. Later, the strong bud forcing effect of HCN, which poisons the respiratory process, was discovered (Gassner 1925). Boresch (1926) was a strong supporter of Weber's theory; he showed that the products of intramolecular respiration like acetaldehyde, acetone, formaldehyde, ethyl alcohol and methyl glyoxal are dormancy breaking agents.

In 1935 a new era in the research on winter-dormancy began when BoySEN Jensen suggested that it was due to a lack of auxin. Indeed, Zimmerman (1936) could ascertain auxin only in sprouting buds, while Avery et al. (1937) found no auxin in dormant buds of Aesculus and Malus. Similar results were obtained by Bennett and Skoog (1938) and by Söding (1952). BoySEN Jensen put dormant lilac twigs in an indole acetic acid (IAA) solution, but got no effect whatsoever, although the substance was taken up readily. However, Amlong and
NAUNDORF (1938) by applying IAA and other compounds directly to the buds by brushing and spraying got a forcing action that was even stronger than that of a warm water bath. BENNETT and SKOOG (1938) got similar, but weak effects; BORGSTROM (1939b, p. 120) showed a bud forcing action of an IAA solution on Betula, Fagus and Quercus from the middle of December till the end of March. NIETHAMMER (1940) applied with success the filtered culture fluids of a yeast and a Penicillium, which were rich in growth substances. However, GOUWENTAK (1941) demonstrated that IAA or its sodium salt can only activate the cambium when it is no longer dormant; in her opinion, IAA has no dormancy breaking effect.

On the other hand, Russian workers have maintained that there are dormancy breaking hormones. RICHTER and KRASNOSSELSKAYA (1942) and K. and R. (1945) showed that a pulp of developing buds injected under the bark of dormant twigs of Tilia and Fraxinus had a forcing effect. DANILOV (1946) showed that in Fraxinus also extracts of unfolding buds of oak and birch, as well as of Avena-coleoptiles, were effective. The action was weaker than that of a warm water bath, but not due to injury. A remarkable feature of these experiments is that the stimulus appears to be transported. However, they do not prove that hormones are concerned in the breaking of dormancy, as water was injected in the controls and the pulp obviously contains a great many substances besides hormones.

The most recent theory of winter-dormancy was developed by HEMBERG (1949) who showed that dormant Fraxinus buds are very rich in elongation inhibiting substances, which disappear when dormancy is broken by the natural winter cold, or by a treatment with ethylene chlorhydrin. According to this author the amount of these inhibitors is such that the auxin content of dormant buds of trees cannot be established by the Avena-test. Later, HEMBERG (1952) found that the dormant potato tuber contains neutral and acid inhibiting substances; when dormancy is broken, only the latter disappear.

Previously, HEMBERG had shown that glutathione leads to the destruction of the inhibiting substances in the dormant potato tuber; and as GUTHRIE has shown that ethylene chlorhydrin treatment of potatoes causes a rise in the glutathione content, probably because it is synthesised, this tripeptide may well be of crucial importance in the breaking of winter-dormancy (CROCKER 1948). However, when injected into the stem of woody plants, it shows only a weak forcing action (GUTHRIE 1941b). Yeast extract, which is rich in glutathione, when injected into the bark of trees has a distinct dormancy breaking effect (BENNETT and SKOOG 1938, GUTHRIE 1940). But the most active component is not glutathione, but some other compound (BENNETT et al. 1940); according to GUTHRIE (1941b) it is not unlikely that the activity stems from adenine or adenine-containing nucleotides.

5. CHEMICALLY INDUCED DORMANCY

Inducing dormancy by an overdose of growth promoting substances has become a regular practice with potato tubers in storage. The substances that have so far proved to be the most satisfactory for this purpose are naphthalene acetic acid and its derivatives (see CROCKER 1948 for a review). The same substances have been successfully used on rose bushes in storage (MARTH 1942, '43).

This treatment has also been applied to deciduous fruit trees in the field to
prevent frost damage in spring by delaying bud development. Hitchcock and Zimmerman (1943) had some results with sprays during the previous summer. Sell et al. (1942, ’44) treated buds of tung trees in February and March with NAA, IAA and other compounds with subsequent delay in bud opening but extensive damage to the buds. They found that lanoline emulsion in itself has some retarding influence. This can also be said of oil sprays; if these are applied early, they have a dormancy breaking effect, applied too late, they tend to prolong dormancy (Hill and Campbell 1949).

The influence of growth regulating substances has been reviewed by Avery and Johnson in 1947. Since then very little seems to have been published on the subject (Harris 1950).

To which extent the physiological effect of the substances mentioned may be compared with summer- and winter-dormancy as they occur under more natural circumstances, is completely unknown. The fact that in potatoes a dormant state induced by NAA may be broken by ethylene chlorhydrin (Crocker 1948) might point to some relation with winter-dormancy.

6. SUMMARY

In this review the term dormancy is applied to all cases where a living tissue predisposed to elongate does not do so. Dormancy phenomena in buds of woody plants are classified under three headings:

imposed dormancy: external causes, directly and reversibly imposed by the environmental conditions;

summer-dormancy: internal causes, namely physiological processes inside the plant, but outside the bud; influence of the environment only indirect;

winter-dormancy: internal causes, namely an inhibitive system inside the bud; influence of the environment indirect.

Summer-dormancy in terminal buds appears to be caused by (a) lack of a stimulus from the roots and (b) inhibitory influence from the leaves. The former has been called ‘caulocaline’ by Went; the latter appears to be formed in certain species only when the night surpasses a certain length. Nothing is known about the nature of either the stimulatory or the inhibitory influence. Summer-dormancy in lateral buds is caused by an inhibition descending from the terminal bud. Here auxin plays an important rôle, but little more is known, as demonstrated by the great number of theories on the subject. In flower buds it seems that there are additional causes for summer-dormancy.

A striking fact about winter-dormancy is the variety of means to break it. However, the study of these forcing methods and their physiological effects has done little to clarify the problem of winter-dormancy as a physiological phenomenon. In this respect the most promising approach appears to be that of Hemberg, who recently demonstrated that winter-dormancy is caused by elongation inhibiting substances.

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