Seed dormancy is an ecological adaptation that allows seasonal timing of germination for seeds in a population. Several environmental stimuli can trigger dormancy release, the most important being seed moisture content, light, and temperature. Of these, temperature is arguably the most important. The objective of this brief review is to consider the various ways temperature impacts seed dormancy release. It will cover general aspects of seed dormancy, temperature effects on primary dormancy and considerations for conducting and interpreting seed dormancy research.

Propagators of cultivated plants have long recognized that germination-delaying mechanisms exist in seeds. The first recorded discussion of seed dormancy was written by Theophrastus in ≈300 B.C. (Evenari, 1981). He recognized that germination of most seeds declined during storage (seed deterioration), germination in some seeds increased (dormancy release).

One problem with discussing seed dormancy is that there is no single recognized terminology to describe the many different types of seed dormancy. Crocker (1916) described seven types of dormancy based on treatments used to overcome them. Subsequently, Nikolaeva (1977) defined dormancy based primarily upon physiological controls. More recently, Lang (1987) proposed the terms eco-, para-, and endo-dormancy to simplify terminology. This system is currently used in sufficient American Society for Horticultural Science journals. However, this terminology is not sufficient to adequately describe all the types of dormancy found in seeds. Baskin and Baskin (1998) have developed the most complete set of terms to describe seed dormancy. They have extended the dormancy classifications of Nikolaeva to include additional specialty types. In this review, I will use a system based on the work of Nikolaeva, as modified by Baskin and Baskin (Hartmann et al., 2002). In this review, I will limit each category to a brief description and emphasize dormancy conditions that are affected by temperature.

**Primary exogenous dormancy**

In exogenous dormancy, the tissues enclosing the embryo impact germination by either inhibiting water uptake, modifying gas (O₂) exchange, or possibly contain germination inhibitors (Bewley and Black, 1994).

Seeds of species with exogenous physical dormancy fail to imbibe water because of properties of the seed coverings. This form of seed dormancy occurs only in 15 plant families (Baskin et al., 2000). Of these, most of the species displaying physical dormancy are found in the Malvaceae and Fabaceae. The anatomical structures preventing water uptake can be the seedcoat (testa) or endocarp (Baskin et al., 2000). In most species, there are elongated palisade cells in the outer layer of the seedcoat (exocarp) that prevent imbition. Mechanical abrasion or chemical degradation of the seed coverings and submersion of the seed in hot water are the most common horticultural practices to induce seeds with physical dormancy to imbibe water. Collectively, these treatments are termed scarification. However, in nature, it appears that temperature is the major factor determining water uptake in seeds with physical dormancy.

Temperature impacts dormancy release for seeds with exogenous physical dormancy by affecting the seed coverings. For instance, some seeds require high temperature or daily fluctuations (≥15 °C change) in temperature to allow imbition. This requirement is postulated as a way for seeds to detect whether they are in open or protected areas (Baskin and Baskin, 1998). A higher daily temperature extreme, as well as a greater day/night fluctuation would occur in an open area, indicating less competition from other plants after germination. The coverings of seeds with physical dormancy may also be cracked by temperature fluctuations, alternate freezing and thawing and in some species by fire.

For many seeds with physical dormancy, a specialized location on the seed coverings can act as an “environmental sensor.” In the Fabaceae, it is usually the lens (strophiola) (Manning and van Staden, 1987; Morrison et al., 1998); and in the Malvaceae, it is the chalazal plug (Egley, 1989). These structures are disrupted by temperature and become the site of water entry into the seed. For example, Quinlivan (1968) demonstrated that seeds of Lupinus varius L. became permeable to water at the lens after exposure to fluctuating temperature (i.e., 65 °C day temperatures with night temperatures down to 25 °C).

**Primary endogenous dormancy**

The second major category of primary seed dormancy is endogenous seed dormancy. Seeds with endogenous dormancy fail to germinate because of factors associated with the embryo. There are two types of endogenous dormancy—morphological and physiological.

**Morphological dormancy.** Seeds with morphological dormancy have an embryo that is not fully developed at the time of seed dissemination. Seeds where the embryo fills less than half of the seed are considered to have morphological dormancy (Baskin and Baskin, 1998). Enlargement of the embryo occurs after the seeds have imbibed water, but usually before germination begins. The process of embryo enlargement is influenced by temperature. Atwater (1980) distinguished three types of morphological dormancy based on the embryo type found in herbaceous flower crops. These are rudimentary, linear, and undifferentiated embryo types.

Rudimentary embryos are little more than a proembryo embedded in a massive endosperm. These are found in seeds of various families, such as the Ranunculaceae, Papaveraceae, and Araliaceae. Germination-inhibiting chemicals may occur in the endosperm and become active at high temperatures. Methods for inducing germination include: (a) exposure to temperatures of 15 °C or below; (b) exposure to alternating temperatures; and (c) treatment with chemicals such as potassium nitrate or gibberellic acid.

Seeds with linear embryos are torpedo-shaped and up to one-half the size of the seed. Important families and species in this category include the Apiaceae, Eriocaceae, Primulaceae, and Gentianaceae. Conditions such as semipermeability of the inner seedcoats and internal germination inhibitors may be involved. Temperature >20 °C favors germination, as does treatment with gibberellic acid.

Some tropical species have seeds with small embryos that require an extended period at warm temperatures for germination to take place. For example, seeds of some palm species require 1 to 3 months at high temperatures (≥35 °C) to complete germination (Nagao et al., 1980). Other examples include Actinidia sp. and Annona squamosa L., whose seeds require 2 or 3 months at warm temperatures, respectively, to complete germination (Nikolaeva, 1977).
Table 1. Seed dormancy categories (Hartmann et al., 2002).

<table>
<thead>
<tr>
<th>Dormancy types</th>
<th>Causes of dormancy</th>
<th>Conditions to break dormancy</th>
<th>Representative genera</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Primary dormancy</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>a. Exogenous dormancy</td>
<td>Imposed by factors outside the embryo</td>
<td>Scarification</td>
<td>Baptisia, Convolvulus, Gleditsia, Lapinus</td>
</tr>
<tr>
<td>Physical</td>
<td>Impermeable seedcoat</td>
<td></td>
<td>Beta, Iris</td>
</tr>
<tr>
<td>Chemical</td>
<td>Inhibitors in seed coverings</td>
<td>Removal of seed coverings (fruits)</td>
<td></td>
</tr>
<tr>
<td>Chemical</td>
<td>Leaching seeds</td>
<td></td>
<td></td>
</tr>
<tr>
<td>b. Endogenous dormancy</td>
<td>Imposed by factors in the embryo</td>
<td>Warm or cold stratification</td>
<td></td>
</tr>
<tr>
<td>Morphological</td>
<td>The embryo is not fully developed</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rudimentary</td>
<td>Small undifferentiated embryo</td>
<td>Cold stratification and potassium nitrate</td>
<td></td>
</tr>
<tr>
<td>Linear</td>
<td>Small differentiated embryo &lt;1/2 size of seed</td>
<td>Warm stratification and gibberellic acid</td>
<td></td>
</tr>
<tr>
<td>Physiological</td>
<td>Factors within embryo inhibits germination</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nondeep</td>
<td>Positively photodormant (requires light)</td>
<td>Red light</td>
<td>Lactuca, Primula</td>
</tr>
<tr>
<td></td>
<td>Negatively photodormant (inhibited by light)</td>
<td>Darkness</td>
<td>Cyclamen, Nigella</td>
</tr>
<tr>
<td>Intermediate</td>
<td>Embryo germinates if separated from the seedcoat</td>
<td>Moderate period (up to 8 weeks) of cold stratification</td>
<td>Cucumis, Impatiens</td>
</tr>
<tr>
<td></td>
<td>Often responds to gibberellic acid</td>
<td></td>
<td>Aconitum, Cornus, Pinus</td>
</tr>
<tr>
<td>Deep</td>
<td>Embryo does not germinate when removed from seedcoat or will form a physiological dwarf</td>
<td>Long periods (&gt;8 weeks) of cold stratification</td>
<td>Dictamnus, Euonymus, Prunus, Rhodotypos</td>
</tr>
<tr>
<td>c. Combinational</td>
<td>Combinations of different dormancy</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Morphophysiological</td>
<td>Combination of underdeveloped or rudimentary embryo and physiological dormancy</td>
<td>Cycles of warm and cold stratification</td>
<td></td>
</tr>
<tr>
<td>Epicotyl</td>
<td>Radicle begins growth when temperature and water permit, but epicotyl is dormant</td>
<td>Warm followed by cold stratification</td>
<td></td>
</tr>
<tr>
<td>Epicotyl and radicle</td>
<td>Radicle and epicotyl require chilling stratification, but radicle is released during first year and then</td>
<td>Cold stratification followed by warm followed by a second cold stratification</td>
<td>Convallaria, Trillium</td>
</tr>
<tr>
<td>(double dormancy)</td>
<td>After-ripening</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Exo-endormancy</td>
<td>Combinations of exogenous and endogenous dormancy conditions: physical (hard seedcoat) plus intermediate physiological dormancy</td>
<td>Sequential combinations of dormancy releasing treatments. Example: scarification followed by cold stratification</td>
<td>Cercis, Tilia</td>
</tr>
<tr>
<td>2. Secondary dormancy</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>a. Thermodormancy</td>
<td>After primary dormancy is relieved, high temperature induces dormancy</td>
<td>Growth regulators or cold stratification</td>
<td>Apium, Lactuca, Viola</td>
</tr>
<tr>
<td>b. Conditional dormancy</td>
<td>Change in ability to germinate related to time of the year</td>
<td>Chilling stratification</td>
<td>Many species with endogenous dormancy display conditional dormancy</td>
</tr>
</tbody>
</table>
temperatures above 14 to 16 °C are generally not effective for relieving dormancy (Seeley, 1997). This observation has led to the concept of stratification degree hours for predicting the time required to relieve dormancy (Seeley and Damavandy, 1985). One hour at optimum stratification temperature (4 °C) is equal to one “stratification degree hour.” Partial stratification degree hour values are assigned to warmer or cooler temperatures, but temperatures below freezing and above 16 °C have no effect toward dormancy release. In addition, time above 16 °C can negate previous chilling.

Some species have seed lots where some seeds may not require stratification to germinate but the rate of seedling emergence is improved for all seeds by brief exposure to chilling temperatures. This phenomenon has been referred to as a facultative form of physiological dormancy (Geneve, 1998). Genera in this group include Antirrhinum, Eustoma, and Impatiens (Ecker et al., 1994; Montero et al., 1990; Simmonds, 1980) and various conifers (Jones and Gosling, 1994). For example, in purple coneflower [Echinacea purpurea (L.) Moench.] germination percentage and rate of emergence were improved in five of six seed lots by a 10-d treatment of either 5 or 10 °C (Wardlinghshen and Geneve, 1994).

Primary combinational dormancy

Combinational dormancy combines two or more kinds of dormancy, such as morphophysiological dormancy, where there is an underdeveloped embryo and physiological dormancy (Ilex) or exo-endormancy that combines seedcoat dormancy and endogenous physiological dormancy (Cercis canadensis L.). To induce germination, all blocking conditions must be eliminated in proper sequence.

Morphophysiological dormancy. The most common form of combinational dormancy is morphophysiological dormancy. Currently, eight different types of morphophysiological dormancy are recognized (Baskin and Baskin, 1998; Nikolaeva, 1977). Those with horticultural interest include simple and epicotyl types.

Seeds with simple morphophysiological dormancy usually require warm (>15 °C) followed by cold (1 to 10 °C) conditions during which time the embryo develops during the warm temperature cycle and then breaks physiological dormancy during the chilling cycle. Various temperate zone herbaceous and woody plants fall into this category, including windflower (Anemone), twinleaf (Jeffersonia), ash (Fraxinus), yew (Taxus), and holly (Ilex) (Nikolaeva, 1977). In nature, these seeds are usually shed from the plant with an undeveloped (linear) embryo that requires a warm period to initiate growth inside the seed coverings. Once the embryo reaches a certain size, it can respond to chilling temperature, which releases the seed from physiological dormancy.

In some species, cultivated and wild forms differ with respect to morphophysiological dormancy. For example, in Anemone coronaria L., cultivated ‘de Caen’ seeds showed only morphological dormancy (requiring only warm treatment), while wild populations of Anemone displayed morphophysiological dormancy and required warm followed by cold stratification (Horovitz et al., 1975).

An interesting species with morphophysiological dormancy is North American pawpaw [Asimina triloba (L.) Dunal.] (Finneseth et al., 1998). This species requires 88 weeks of chilling temperatures to relieve endogenous physiological dormancy followed by warm temperatures to satisfy morphological dormancy prior to germination. This sequence is a reversal of the more common warm followed by cold temperature to relieve morphophysiological dormancy.

Seeds with epicotyl dormancy display the most fascinating dormancy patterns found in seeds. These seeds have separate dormancy conditions for the radicle and epicotyl (Barton, 1944; Baskin and Baskin, 1998; Crocker, 1948). These species fall into two subgroups. In one group, seeds initially germinate during a warm period of 1 to 3 months to produce root and hypocotyl growth beyond the seed coverings, but then require 1 to 3 months of subsequent chilling to enable the epicotyl to grow (simple epicotyl dormancy). This group includes various species of lily (Lilium), viburnum, peony (Paeonia), as well as black cohosh [Cimicifuga racemosa (L.) Nutt.] and liverwort (Hepatica acutiloba DC.). The response of the epicotyl to chilling varies with the size of the radicle (Barton and Chandler, 1957). For peony, 85% of the epicytols exposed to 7 weeks of chilling grew if the radicle had reached 4 cm in length. In contrast, only 40% of the epicytols were released from dormancy under the same conditions with smaller 2–3 cm radicles.

In the second group, both the epicytol and the radicle require chilling, but are released from dormancy at different times. Seeds in this group require a chilling period to relieve radicle dormancy, followed by a warm period to allow the radicle to grow, then a second cold period to release the epicotyl from dormancy. In nature, such seeds require at least two full growing seasons to complete germination. These are the seeds for which the term “double dormancy” was first coined. Examples include bloodroot (Sanguinaria canadensis L.), Trillium sp., and lily-of-the-valley (Convallaria majalis L.). There are also seed population differences in this group. Barton (1944) showed that in both bloodroot and Solomon’s seal (Polygonatum multiflorum L.) about half the seeds showed simple epicotyl dormancy while the other half showed double dormancy.

Secondary dormancy

Under natural conditions, seeds released from primary dormancy often experience secondary dormancy when environmental conditions are not favorable for germination (Bewley and Black, 1994; Crocker, 1916; Karssen et al., 1983; Khan, 1981). These conditions can include unfavorable temperature, prolonged light or darkness, water stress, and anoxia. These conditions are particularly involved in the seasonal rhythms (dormancy cycling) and prolonged survival of weed seeds in soil (Baskin and Baskin, 1998; Egley, 1995). Chilling temperatures can induce secondary dormancy in nondormant seeds. Coreopsis lanceolata L. seeds were relieved of nondeep physiological dormancy by dry storage for 6 to 18 months. The stored seeds germinated at high percentages at 15 and 25 °C, but entered secondary dormancy if held at 5 °C (Banovetz and Scheiner, 1994).

In some cases, seeds that did not require chilling stratification to satisfy primary dormancy may require it for release from secondary dormancy. For example, Nemophila insigis Doug. ex Benth. seeds require darkness to germinate. If these seeds are exposed to light for a period of time, they enter secondary dormancy and will no longer germinate in the dark without a chilling treatment (Chen, 1968).
A high-temperature environment for germination can induce a common form of secondary dormancy termed thermodormancy. Thermodormancy can develop in species such as apple (Malus), lettuce (Lactuca), celery (Aptum), Schizanthes, and pansy (Viola) if the germination temperature is too high (>25 °C). This phenomenon should not be confused with the thermal inhibition most seeds experience when the temperature exceeds the maximum temperature for germination. Seeds experiencing thermodormancy will not germinate when the temperature returns to near optimum temperatures, while thermally inhibited seeds will germinate when temperatures are lowered.

Seeds of some species of ash (Fraxinus) display morphophysiological dormancy that requires extended time (10 to 18 weeks) of warm stratification followed by additional time at 5 °C (=12 weeks) to relieve primary dormancy (Young and Young, 1992). Strati- fied seeds showed considerable secondary dormancy when germinated at constant 20 °C or alternating 20/30 °C (Piotto, 1994). Interestingly, there was no secondary dormancy seen in a widely fluctuating 25/5 °C germination environment. This and other studies suggest that caution should be taken when interpreting laboratory experiments where germination temperatures are held constant or day/night temperature fluctuations are minimized compared to the outside environment (Baskin and Baskin, 1998; Hilhorst, 1998).

Apple seeds require chilling stratification to relieve primary endogenous dormancy. Following release from dormancy, they are sensitive to induction into secondary dormancy at germination temperatures above 30 °C (Visser, 1954). Ozga and Dennis (1991) determined that abscisic acid content was not well correlated with induction of secondary dormancy. Hillhorst (1998) presents a convincing case for considering temperature-associated changes in membranes being responsible for release from dormancy, especially in seeds displaying secondary dormancy. Membranes adjust to varying temperature to maintain their fluidity, which directly impacts integral membrane proteins. These changes in the membrane may be related to release from primary dormancy or induction into secondary dormancy.

Germination models

A number of attempts have been made to develop mathematical models that predict seedling emergence from dormant seeds (Bradford, 1996; Christensen et al., 1996; Forcella, 1998; Kebreab and Murdoch, 1999; Pritchard et al., 1996; Seeley and Damavandy, 1995). Some models that consider only temperature effects on dormancy release have been remarkably effective. For example, Bauwmeester and Karssen (1992) were able to predict seedling emergence in the field for a number of weed species using a “germination temperature window” based on the previous exposure of these seeds to various temperatures. Although temperature is implicated in most aspects of seed dormancy release, it is apparent that ad- ditional features such as population effects, seed moisture, light, and nitrate levels must be considered when developing an effective model for dormancy release under field conditions (Hilhorst, 1998).

Genetic and environmental (primarily temperature) factors affect seed dormancy release. The genetic component can influence entire populations of seeds or individual seeds within a seed lot. An example where entire populations of seeds show different depths of dormancy is illustrated in Prunus serotina L. Ehrh. seeds collected from different climatic zones (Farmer and Barnett, 1972). Seeds from ecotypes collected from higher altitudes required longer periods of chilling stratification to relieve dormancy and were slower to germinate at permissive germination temperatures following stratification compared to seeds collected from lower altitudes.

Genotype differences need to be considered when applying models that may have been generated using only one ecotype. Perez (1997) compared stratification requirements between low bud chilling peach accessions from subtropical regions with those of high-chilling accessions. Low-chilling genotypes showed dormancy release at temperatures as high as 14 °C, whereas this temperature had no impact on germination in high-chilling genotypes.

There are also differences in the depth of dormancy observed for seeds within a seed lot. The complexity of this genetic component becomes apparent when considering the correlation between seed-chilling requirements and bud-chilling requirements of plants (Powell, 1987). In studies with almond (Prunus dulcis L.), a high quantitative correlation was observed between the mean time for bud and seed dormancy release in seedling populations and the mean for both the seed and pollen parents (Kester, 1969). However, there was a low correlation between the time required to release dormancy in each individual seed and the subsequent chilling requirements for buds of the new plant developing from that embryo (Kester et al., 1977). This difference suggests that dormancy involves both a genetic component within the embryo and a maternal component from the seed parent. As a result, a great deal of variability can exist in the time to dormancy release in individual seeds within a given seed lot and between different seed lots of the same species collected in different years and different locations.

This maternal vs. paternal inheritance fac- tor can be illustrated in reciprocal crosses of petunia (Girard, 1990). Seed coverings (ma- ternal tissue) have an important influence on dormancy release (Hartmann et al., 2002) and these tissues are ostensibly maternal tissue. In petunia (Petunia hybrida Hort. Vilm.-Andr.), the requirement for light was maternally inherited, while endogenous dormancy within the embryo was under paternal control.

Whether controlled by environmental fac- tors during development or by genetic factors within the embryo or seed coverings, the time required for dormancy release in individual seeds within a given seed lot is about normally distributed (Fig. 2). This suggests that release from seed dormancy could be described using a population-based thermal time model similar to well-characterized thermal time models for germination in nondormant seeds (Bradford, 1996). Accordingly, Pritchard et al. (1996) used thermal time to describe dormancy loss in horsechestnut (Aesculus hippocastanum L.) seeds. A negative linear relationship was observed between dormancy release with chilling over a range of stratification temperatures.

A second factor affecting predictive models for seed dormancy release is the interaction between temperature and seed moisture content. Chilling stratification is not effective unless seeds are hydrated. In nature, the degree of seed hydration varies depending on the environment. Therefore, there is a critical moisture content below which seeds would not be positively affected by chilling for dormancy release. In several conifer species, the critical moisture content appears to be Ï‰25% moisture on a fresh weight basis (Gosling and Rigg, 1990). About 35% seed moisture allows dormancy release to proceed without
allowing a germination during prolonged storage (Jones and Gosling, 1994). Downie et al. (1998) also observed that dormancy release in spruce [*Picea glauca* (Moench.) Voss.] seeds was achieved at a moisture content starting at \( \pm 25\% \). At this moisture content, seeds were at the boundary between water binding regions 3 and 4 as determined by moisture sorption isotherms (Vertucci and Farrant, 1995). In this condition, cellular components are hydrated, but not sufficiently to support turgor-driven cell expansion. Based on cellular properties in these moisture ranges, they suggested that protein hydration and possibly synthesis was required for release from dormancy in seeds requiring chilling stratification (Downie et al., 1998). Interestingly, freshly harvested seeds that require after-ripening (nondeep physiological dormancy) are released from dormancy in water binding region 2 (for example, wild oats, Foley, 1994). This example indicates that the internal processes responsible for dormancy release are probably different for seeds with endogenous physiological dormancy that experience dormancy loss due to dry storage compared to those requiring chilling stratification.

Finally, the most interesting problem with models that attempt to describe the time required for dormancy release at a given temperature is conditional dormancy. This problem goes directly to the question “what constitutes dormancy release?”. Dormancy cycling, as observed in many species, is a function of conditional dormancy (Baskin and Baskin, 1998). It is a transitional state between the dormant and nondormant seed condition. This transition can be observed by evaluating germination over a range of germination temperatures. Nondormant seeds germinate rapidly over a wide range of temperatures, while conditionally dormant seeds germinate only within restrictive (optimum) temperatures (Vegis, 1964). In most laboratory studies, seeds are exposed to a dormancy releasing treatment (e.g., chilling temperatures) and the time to dormancy loss as indicated by germination at an optimal temperature is recorded. In reality, this measurement is an indication of the time required to move from a dormant to conditionally dormant state. The time required to achieve a fully nondormant state would be indicated by the ability to germinate over a range of temperatures (Baskin and Baskin, 1998). In nature, seeds can go through years of dormancy cycling, each cycle containing periods of dormancy, nondormancy and conditional dormancy. When other factors (such as light) are not limiting, germination occurs only when the degree of dormancy release corresponds to an appropriate germination temperature range. Therefore, models that attempt to predict germination in dormant seeds in nature must consider the impact of temperature on the degree of dormancy release (conditional dormancy) and adjust the model to account for corresponding permissive germination temperatures.

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Many of the numerous geophytic plant species are commercially important floriculture crops, including Gladiolus L., Hyacinthus L., Iris L., Lilium L., Narcissus L., and Tulipa L. Lilium and Tulipa are two of the world’s major floriculture crops with hundreds of cultivars being grown as potted flower plants, fresh cut flowers, and garden ornamentals. Geophytes are especially suitable for commercial floriculture production because the storage organs can be harvested, stored, and forced into flowering (programmed). Production time required for forcing is often short because the storage organ provides stored photosynthates for rapid growth. Unfortunately, only a few genera have been extensively studied, including Gladiolus L., Hyacinthus L., Iris L., Lilium L., Narcissus L., and Tulipa L. Hundreds of other species may also have high commercial potential but remain unstudied. One key factor in the cultivation and possible commercialization of new geophytes is that many species have cold requirements that must be characterized (Hartsema, 1961). Procedures for breaking dormancy are often complex and cannot be transferred from one species to the next. However, a number of basic patterns have emerged.

Terminology

Geophytes are plants in which the perennial buds are situated below ground on a storage organ such as a rhizome, tuber, corm, or bulb. Rhizomes, such as with Alstroemeria L. are modified, elongated, underground stems which grow horizontally with well-defined nodes. Tubers have nodes marked only by small buds and are separable into three types: root and stem tubers and enlarged hypocotyls. Root tubers, e.g., Dahlia Cav., have vegetative buds only at the apex of the storage organ and the primary storage tissue is the root. Stem tubers, such as with Solanum tuberosum L., have buds distributed over the entire surface and the primary storage tissue is the stem. Enlarged hypocotyls, such as with Cyclamen L., are similar to stem tubers but the primary storage tissue has been derived from the hypocotyl. Corms, e.g., Gladiolus, are modified stems with well-defined nodes and can be differentiated from rhizomes in that they are typically round, have a vertical axis of growth and form on top of the previously planted and senescing corm. In bulbs the primary storage organ is the swollen leaf bases and/or scales (modified leaves), which are positioned atop a compressed short stem (basal plate). Hippeastrum Herb. is an example of a bulb composed of compressed leaf bases and Tulipa and Lilium exemplify bulbs with scales. In addition, bulbs can be either tunicate, enclosed in dry leaf bases, e.g., Tulipa and Hyacinthus, or nontunicate, without a covering, e.g., Fritillaria L. and Lilium. Other plant materials are occasionally lumped into the term geophyte, such as woody crowns and pseudobulbs. Woody crowns, in particular, can be difficult to differentiate from geophytes and are often cold stored and forced. However, geophytes will be defined in the strictest sense for this discussion.

Role of storage organs

Storage organs permit plants to survive periods of unfavorable weather conditions, such as high or low temperatures, drought, or improper light levels. Consequently, the success of a geophytic species depends on growing rapidly when environmental conditions are favorable. The growth period is often brief and plants become dormant when the conditions are not favorable. Geophytic species respond to many environmental signals that determine when to become dormant and when conditions are unfavorable. Growth unless they have been exposed to 0 to 10 °C for 6 weeks (Konishi and Inaba, 1967; Moser and Hess, 1968). Geophytes are found in a range of climates from tropical to arctic and, therefore, differ greatly in response to temperature. Species such as Tulipa require exposure to temperatures averaging 5 °C for

Received for publication 4 Apr. 2002. Accepted for publication 4 Sept. 2002. Approved for publication by the Director, North Carolina Agricultural Experiment Station.

*E-mail: john_dole@ncsu.edu.

Research Approaches for Determining Cold Requirements for Forcing and Flowering of Geophytes

John M. Dole¹

Department of Horticultural Science, Campus Box 7609, North Carolina State University, Raleigh, NC 27695-7609