Dormancy and Magnolias: an Engaging Mystery

Manus A.G. Kanellos

Dormancy in deciduous woody plants is a phenomenon not very well understood, and, indeed not much is known about the physiology of magnolias. Here, I describe my doctorate studies that consisted of a series of experiments designed to increase our understanding of this phenomenon.

Dormancy is a much-misused term often defined as rest and after-rest, quiescence, summer and winter dormancy, and others. In this study, dormancy is defined as *the temporary suspension of visible growth by any plant structure containing a meristem.* The words making up this definition were chosen deliberately. The word *temporary* is used because dormancy is always reversible, and the word *visible* is used since there are invisible processes continuing inside the structure. Finally, *...by any plant structure* describes an assortment of similar phenomena occurring in a variety of plant structures like seeds, roots, corms and rhizomes, buds, and cambia.

The majority of woody plants show a well-marked period of dormancy during their annual growth cycle. In the Temperate Zone, trees usually suspend their growth in late summer to early autumn, gloriously drop their leaves, and enter dormancy. This is an important survival strategy, since it enables the plant to withstand unfavorable growing conditions—a dormant structure is invariably more resistant to adverse conditions such as frost, drought, and heat.

Why Study Magnolias?

E. H. Wilson, the great plant explorer, stated "no other group of trees and shrubs is more favorably known or more highly appreciated in gardens than magnolias, and no group produces larger or more abundant blossoms." His statement is even more relevant today with over 30 species and numerous cultivars and hybrids in cultivation.

The simplicity and beauty of the magnolia flower are difficult to describe on paper, perhaps because fragrance is one of their most appealing characteristics. In their quest to lure pollinators (beetles of all things!) magnolia flowers are very fragrant indeed.

Magnolias are thought to be among the earliest angiosperms in evolutionary history and they are a very diverse and fascinating genus of plants.

One of the most popular of all is the deciduous *Magnolia* × *soulangeana* Soul., a cross between *M. denudata* and *M. liliiflora* made in France over 150

years ago, by Etienne Soulange-Bodin. Nowadays, there are more than 100 cultivars of *Magnolia* × *soulangeana*. Most deciduous magnolias are precocious, which means they flower before the leaves appear. In fact, precocious magnolias are closely related and are classified by taxonomists as a separate subgenus, *Yulania*.

Whilst dormant, the *Yulania* magnolias are wind and cold resistant and some species are able to tolerate soil temperatures of 23 °F (–5 °C) without serious damage. Unfortunately, their flowers and new growth are vulnerable to frost damage as they then may come into flower as early as late February. Ordinarily, *Yulania* flowers are produced from terminal buds, whereas the axillary buds are usually vegetative (containing only leaves). However, flower buds are also occasionally produced from axillary buds. Although magnolias have been in cultivation for thousands of years, little is known about their physiology and the events that govern their dormancy.

Because of this combination of factors, we selected *Magnolia* × *soulangeana* to be the model species for our study. Some of the questions we asked were:

- What induces dormancy?
- What type of dormancy is induced?
- What causes plants to break dormancy?
- Can we change anything?
- Could we manipulate the flowering time of the plant or is species selection and luck the best way to avoid frost damaged displays?

We decided to look closely at the effects that photoperiod and temperature have on *M.* × *soulangeana*.

Effects of Photoperiod

Photoperiod (the number of hours of light each day) alone is responsible for the initiation of dormancy in a number of species of temperate woody plants. These fall within two categories: plants that are sensitive to photoperiod, and plants that are insensitive to photoperiod.

For photoperiod-sensitive plants like sycamore (*Acer pseudoplatanus*), horse chestnut (*Aesculus hippocastanum*), *Larix* spp., camellia (*Camellia japonica*), and oak (*Quercus robur*), short days (less than 12 hours of light) initiate or accelerate the onset of dormancy, whereas long days delay or even prevent the onset of dormancy. For plants that are insensitive to photoperiod, such as lilac (*Syringa vulgaris*), apple (*Malus* spp.), olive trees (*Olea europea*), and roses (*Rosa* spp.), the inductive factor remains a mystery. Low temperatures, the progression of time, and other factors such as nutrient levels, light intensity, and drought are thought to be involved.

Methods and Results

To investigate the role of photoperiod we worked with young plants raised from rooted cuttings that we treated with different lengths of photoperiod, ranging from 8 to 17 hours per day. The young *M.* × *soulangeana* plants were 60cm in height, and had an average of 25 leaves each. The plants were still actively growing when we received them.

For the first experiment, the plants were divided into two groups. From late August to March, one group was maintained under short day lengths (8 hours) and the second group was maintained under long day lengths (17 hours). The results showed that long days could delay, but not prevent, the inevitable onset of dormancy. Plants under long days entered dormancy 30–40 days later than normal. Additionally, the plants subjected to long day lengths came to budbreak on average ten days earlier than plants maintained under the short day lengths. Thus, plants under long days showed a 40- to 50-day reduction in dormancy period.

In a second experiment, we looked at the effect of the photoperiod on the time to budbreak in more detail. To do this, we maintained plants outside so they could enter dormancy naturally. In January, we moved plants inside and forced them under four different photoperiods (8, 11, 14, and 17 hours). We found that photoperiod had a small effect on the initial time that the plants started to budbreak, but the rate of budbreak was much faster under longer photoperiods. A month after initial budbreak, 85% of the buds of plants grown under long day length were opened compared with 65% of those under short day length. When we repeated the experiment, the following year the results were very similar.

Effects of Temperature

From the start, our hypothesis was that since the flowering time of magnolias varies from year to year, temperature may play an important role. So although we had good reason to believe that temperature was important, we were uncertain of its exact role. Do magnolias have a chilling requirement, and if so, how much?

The Time Effect

We were interested to see if higher than normal temperatures throughout the winter would make any difference on the duration of dormancy. Would chilled plants (plants that had experienced low temperatures) come to budbreak any earlier than unchilled ones? We were also interested to see whether chilling at various times throughout dormancy had any effect. That is, are magnolias equally sensitive to low temperatures throughout their dormancy period?

Methods and Results

Again, the plants were divided into two groups. One group was grown in a heated greenhouse (62.6 °F, 17 °C), and the other group was grown in an unheated poly tunnel (mean 44.6 °F, 7 °C). Starting in October, every six weeks we chilled some of each group of plants for three to six weeks at 39.2 °F (4 °C). We then forced them at a high constant temperature of 71.6 °F (22 °C) with 16 hours of supplementary lighting each day. (This is a standard method to determine how dormant a plant is.)

To our surprise, both groups of plants showed very similar lengths of dormancy (measured by the amount of time to budbreak) even though they were growing at very different temperatures. It did not seem to matter whether the plants had experienced low temperatures. However, it did seem to matter *when* the forcing conditions were applied. The later we forced the plants, the faster they came to budbreak. For example, plants forced in October came to budbreak within 45 days, whereas plants forced in February came to budbreak within a week. Thus, the progression of time itself is an important component for satisfying the dormancy requirement for *Magnolia* × *soulangeana* and probably other *Yulania* magnolias.

We also discovered that plants from the poly tunnel broke more buds than those maintained in the heated greenhouse. Plants forced in October broke relatively few buds (15-20%) with plants from the poly tunnel breaking more than those maintained in the greenhouse. At later forcings, plants from the greenhouse broke on average 50% of their buds compared with 75% of the buds for plants maintained in the poly tunnel.

Effects of Temperature Revisited

In the second year, we looked into whether the temperature at which we chilled the plants was important, so we partly repeated the experiment of the first year since the results were so unexpected.

Once again, the plants were divided into two groups: one group to be grown in the heated greenhouse, and the other group to be grown in the unheated poly tunnel. Every six weeks, we chilled some plants for various durations (up to six weeks) and at various temperatures from 39 to 66 °F (4 to 19 °C). Thereafter the plants were forced in a manner similar to the first year.

Under forcing conditions, we found that the temperature at which the magnolia plants were chilled was not as important as for other species in terms of time to budbreak. Again, the most crucial factor in determining the time to budbreak was the time that the plants were forced. However, we

did note that lower temperatures (below 50 °F, 10 °C) were more effective in releasing the plants from dormancy. In fact, the lower the temperature, the more buds broke.

How Dormancy Development and Flowering Were Affected

In another experiment that we carried out that year, we grew 40 sexually mature magnolias in six greenhouse compartments, each having a different set temperature ranging from 50 to 81 °F (10 to 27 °C). In September, the plants were moved to the greenhouse where they remained for eight months. Every six weeks, five plants from each of the six greenhouses were moved to another greenhouse under forcing conditions (high temperature of 72 °F (22 °C), and 16 hours of light each day). This practice was followed to see how dormant a plant was by measuring the time to budbreak.

Firstly, the results showed that the rate of leaf fall was very sensitive to temperature. The lower the temperature, the sooner the leaves fell. That explains our observations of late leaf fall in the warmer autumns. Surprisingly, at the end of the experiment in April, the plants that were maintained in a higher than 68 °F (20 °C) temperature had retained half of their leaves.

From the standpoint of dormancy, however, such higher temperatures were not able to keep the plants growing. All plants, regardless of the temperature at which they were maintained, entered dormancy after about 6 weeks. We also observed that temperatures higher than 64 °F (18 °C)—even in late September—resulted in a sporadic flowering, as is commonly observed in natural populations of *M.* × *soulangeana* in a warm, late summer.

Temperature also had a tremendous effect on the dormancy completion of magnolias and on the type of the subsequent flowering. The plants that were maintained at temperatures higher than 68 °F (20 °C) never broke dormancy—that is, they did not break any significant amount of vegetative buds. However, plants kept at 64 °F (18 °C) broke dormancy first. Interestingly, flower buds had a different dormancy mechanism compared to the vegetative buds of the tree. Whereas only plants that experienced significant periods at temperatures below 68 °F (20 °C) showed significant vegetative growth afterwards, all plants eventually flowered. Plants maintained at temperatures higher than 68 °F (20 °C) partially flowered (less than 50%) but failed to resume normal vegetative growth, at least until the end of observations in late June. Interestingly, the vegetative buds originally enclosed within the flower buds produced a few chlorotic leaves after the flower senesced but this was not considered dormancy breaking.

As mentioned previously, *Yulania* magnolias, for the most part, are precocious; that is, the flowers appear before the leaves. Our experiment showed

that the period between flowering and leafing is influenced largely by temperature. We found that when flower buds were subjected to extremely low temperatures, such as constant 50 °F (10 °C) for the duration of the experiment, the plants produced flowers after the leaves had appeared! From another experiment we concluded that it was largely the temperature during the budbreak period that determines the time span between flowering and leafing.

Percentage of budbreak was also directly responsive to temperature. Similar to the previous experiments with young plants, the lower the temperature the more buds broke and the more bushier the plant. As the temperature increased from 50 to 68 °F (10 to 20 °C) the number of buds that opened decreased from nearly 90% to 50%, whereas when the temperature was increased further, the number of opened buds dropped dramatically to less than 3% (which was not considered dormancy breaking).

Additionally, this study revealed that many of the quality characteristics of the *M.* × *soulangeana* flower such as overall size, tepal length, color, and color distribution in the flowers are largely dependent on the temperature that the flower buds have experienced since they were formed. It seems that the colder the winter, the more likely we will enjoy large, long, but less colorful flowers. In fact, the optimum temperature, for the most colorful flowers (purple) was around 68 °F (20 °C).(See photograph on next page.)

Overall Conclusions and Discussion

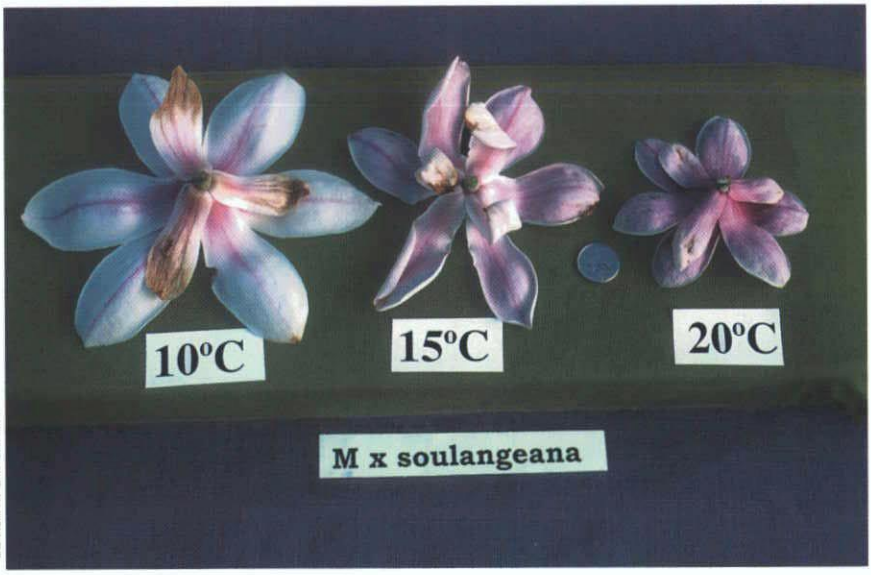
Both photoperiod and temperature were shown to influence autumn growth in terms of leaf production, the progression of leaf fall, flowering and dormancy induction. So, what exactly induces dormancy? The results from the experiments described here showed that although environmental conditions may delay or advance the onset of dormancy, the progression of time is the key factor.

How can we explain the role of time? One has to consider that a tree has many growing points including developing fruits (*M.* × *soulangeana* fruits prolifically), all supplied by a limited input of resources. During budbreak at the start of the growing season, organogenesis, internode elongation, and leaf production all start from the same point. However, over the course of time, increased competition between organs will occur, which in turn may lead to growth limitation. Fruit growers for example, commonly find it necessary to remove large numbers of fruits from temperate fruit trees to obtain optimum fruit size. Thus, dormancy induction may also occur in response to limited assimilates within the plants, i.e. during high sink demand and low source availability. If this were the case, dormancy would confer a second ecological advantage to plants (in addition to winter

survival). Canopy renewal (the ability to form a new canopy in the spring) enables the plant to grow at a rapid rate when conditions are mostly favourable. The longer growing season for seedlings (smaller size and fewer meristems in competition) when compared with mature plants also supports this hypothesis.

What happens once plants are dormant? The results from these experiments were used to construct a hypothetical model to interpret the effects of temperature, photoperiod, and the role of time progression on dormancy completion. The proposed model suggests that dormancy can be divided into two phases. In phase 1, after a period of time, low temperatures enable plants to eventually respond to warm temperatures. Development of this phase proceeds over a wide range of temperatures up to 21°C (69 °F). During phase 2, time to budbreak is jointly influenced by the progression of time and the extent of the warm temperatures. The end result in either case is that magnolias are likely to break bud early, which causes them to be susceptible to late frosts.

With regard to budbreak, the model also suggested that long days might be a substitute for low temperatures as in other plant species. The amount of low temperature that plants experienced during dormancy largely determined budbreak percentage, whereas temperature during budbreak also



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influenced the number of open buds, flower quality (size and color) and the degree of precociousness. So, although we do not know the "substance" that releases plants from dormancy we now know that the essential ingredients are time and warm temperatures.

The information provided by this study may also be very useful in the horticultural industry. By advancing time to budbreak or delaying the dormancy onset by manipulating the photoperiod and temperature to extend the growing season, horticulturists may find that they can shorten the juvenile period of young trees and thus, improve profit margin.

Implications for Gardeners

Although a complete manipulation of dormancy and time to budbreak is difficult to achieve; the findings of this study can be used to provide guidelines for the magnolia grower to minimize the risk of frost damage for *M.* × *soulangeana*.

Regarding the site of planting, the results suggest that sites which are prone to high autumn temperatures should be avoided to reduce the risk of autumn flowering, although some gardeners may find flowering in autumn of *M.* × *soulangeana* desirable.

The results further suggest that as time progresses, *M.* × *soulangeana* plants become increasingly prone to early flowering even under fairly low temperatures. However, there are a number of cultural practices that can be used to delay flowering through preventing the accumulation of heat units. Scientists working on frost protection in Utah, USA pioneered the use of evaporative cooling by sprinkling apple trees with water whenever air temperatures exceeded 45 °F (7 °C) to reduce bud temperature and slow down bud development. They achieved a 17-day bloom delay, which greatly reduced the likelihood of severe frost damage. Scientists in the UK, also found that sprinkling apple buds with water caused evaporative cooling which slowed the rate of bud development and delayed flowering.

Spraying fruit trees with whitewash was recommended more than a century ago to reflect sunlight and slow bud development in late winter. Painting trunk and major branches white to reflect sunlight and reduce winter injury has become a common practice in the management of some deciduous fruit trees and olive orchards in the Mediterranean region. Whitewashing in midwinter with white latex paint delayed pistil elongation in 'quiescent' peach buds and provided 1-2 day bloom delays. Freeze injury of flower buds, which was measured by fruit set, was also reduced. Other cultural practices that were proposed to delay flowering in temperate zone fruit trees but may also be applied to delay flowering in *M.* × *soulangeana*, include