**INFLUENCE OF TEMPERATURE ON GROWTH AND
FLOWERING OF FOUR *MECONOPSIS* GENOTYPES**

by

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ABSTRACT

INFLUENCE OF TEMPERATURE ON GROWTH AND FLOWERING OF FOUR *MECONOPSIS* GENOTYPES

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Meconopsis betonicifolia Franch. and *M. grandis* Prain are members of the *Papaveraceae* L. native to the Himalayan mountains. These species and the hybrids derived from them are especially prized as ornamentals for their intense blue flowers and gardenesque habit. Longwood Gardens, a horticultural display garden in eastern Pennsylvania, USA, has identified these plants as having good conservatory display qualities. However, empirical observations indicate these species are intolerant of the hot summers that occur in this geographic region. The experiments performed in this study were designed to identify how temperature would affect plant characteristics critical to display for blue flowered *Meconopsis* as well as the red flowering *M. punicea* Maxim. *Meconopsis betonicifolia*, *M.* 'Lingholm', a variety from the *M.*

George Sherriff Group, and *M. punicea* plants were forced in the greenhouse at minimum night/day temperatures of 7.2°C /10°C, 12.8°C /15.6°C, and 18.3°C /21.1°C between December 2000 and May 2001. All plants grown in the 7.2°C /10°C and 12.8°C /15.6°C temperatures had larger canopy widths when starting to flower than those plants in 18.3°C /21.1°C environment. Plants grown in the two cooler temperature ranges also had taller flower stems, at 64.27cm and 54.44cm, for the coolest and medium environment, respectively, compared to the warmest environment at 46.27cm. The stem diameter was greatest on plants in the warmest environment at .691cm compared to the intermediate and warm temperatures at .526cm and .438cm for the medium and warmest environment, respectively. Plant dry weight was also inversely related to temperature. Plants grown at 7.2°C /10°C, at 41.8g, were 33% heavier than those grown at 12.8°C /15.6°C, at 31.4g, and 100% heavier than the plants in the 18.3°C/21.1°C, at 20.6g, at harvesting.

This study demonstrated forcing temperature regulated net photosynthesis and dry weight gain of *Meconopsis* species and hybrids. It also showed that display quality plants with tall, strong flower stems and good foliage could be grown when temperatures were monitored and maintained at 7.2°C /10°C or 12.8°C /15.6°C and proper genotypes were selected.

INTRODUCTION

Meconopsis Vig. is a broad genus in the family Papaveraceae L. containing 43 species that vary in height from 25cm to 200cm and colors including white, yellow, red, and blue. The most well known species are *Meconopsis betonicifolia* Franch., *M. grandis* Prain, *M. horridula* Hook.f. and Thoms., *M. x sheldonii* G. Tayl., which is an interspecific hybrid of *M. betonicifolia* and *M. grandis*. These are popularly known as the blue poppies that have clear blue flowers. Blue poppies have been in continuous cultivation for over 100 years. These are popular garden plants in few parts of the world, restricted mainly to the British Isles where they are found in residential landscapes and horticulture display gardens.

Longwood Gardens is a world renowned horticulture display garden located in the Delaware Valley region of the eastern United States. Longwood Gardens, since its inception, has displayed ordinary and unusual plants in unique ways. *Meconopsis* is considered a plant that would add to Longwood Gardens' long tradition of using uncommon plants to create extraordinary displays. The tall upright habit, robust foliage, and large blue flowers make *Meconopsis* a desirable plant for conservatory display.

Meconopsis is not widely cultivated in the United States because of poor performance in most parts of the country. Empirical observations suggest the factor limiting cultivation of these plants is high temperatures during the growing season. Cool summer temperatures are only found in the northern parts of the northeast and Pacific Northwest where *Meconopsis* is

occasionally grown as a garden plant. Summer temperatures may be the cause for *Meconopsis*' inability to survive year-round in the Delaware Valley. Longwood has tried to grow *Meconopsis* for many years, unsuccessfully, for indoor floral displays (Loving, personal communication). Installation of new production greenhouses with improved summer cooling has renewed interest in trying to grow *Meconopsis* (Harbage, personal communication).

Meconopsis betonicifolia and *M. grandis* are believed to be the two blue flowered species most commonly grown in the United States. Interspecific hybrids between these species are also listed in the trade. The hybrids between the two species offer the opportunity to determine if interspecific hybrids are better suited to higher temperatures than the parent species due to hybrid vigor. To successfully cultivate *Meconopsis*, it is necessary to determine, quantitatively, how they perform under defined temperature conditions.

There are temperature control limitations of growing plants for display. Due to high summer temperatures, field growing is not a practical option for producing a crop of *Meconopsis*. Greenhouse production of *Meconopsis* is a viable option. Summer production of *Meconopsis* may be difficult because the solar temperature gain in the greenhouse often exceeds the cooling capability. *Meconopsis* winter production is promising because temperature control is more reliable when outside temperatures are cooler.

Many processes involved in plant growth are influenced by temperature, especially photosynthesis and respiration. Plant growth is dependent on positive net photosynthesis. This means, that to survive and grow, a plant must take in more carbon through total photosynthesis than it loses through respiration. Therefore, influence of temperature on net photosynthesis (total

photosynthesis minus respiration) may explain differences in general plant performance at different temperatures.

The objectives of this study are to determine the effect of temperature on the flowering, growth, and net photosynthetic response of selected *Meconopsis* species and hybrids and to use this information to define conditions suitable for production of these plants. These genotypes could then be used for ornamental display at Longwood Gardens, other public gardens, and in the field of horticulture.

LITERATURE REVIEW

***Meconopsis* Vig. classification**

Meconopsis Vig. is in the family Papaveraceae L. and is derived from the Greek words *mekon*, meaning poppy, and *-opsis*, indicating a resemblance (Coombes, 1997). The genus was first established by L.A.G. Viguier, in 1814, based upon Linnaeus' *Papaver cambricum* L., which was transferred to the new genus as *Meconopsis cambrica* (L.) Vig. (Grey-Wilson, 2001).

Meconopsis is one of 32 genera in the Papaveraceae, which includes approximately 650 species (Baumgardt, 1982). There is a dispute as to how many *Meconopsis* species exist. Kaderiet *et al.* (1997) and Norton *et al.* (1986) list 47 and 49 species, respectively, while others list 43 species (Sulaiman and Babu 1996, Grey-Wilson 2001, and Jermyn 2001).

The genus *Meconopsis* is divided into two subgenera and there are several subsections in each subgenus (Taylor, 1934). The subgenera are *Dioscogyne* G. Tayl. and *Eumeconopsis* (Prain) Fedde (Grey-Wilson 2001). Keys have been made to differentiate the species and are available to the average gardener in books such as *Poppies* written by Grey-Wilson (2001).

Some taxonomists feel *M. cambrica* should be placed into a different genus than the other species of *Meconopsis*. However, since *M. cambrica* is the type-species for the genus, separating *M. cambrica* would require reassigning all other *Meconopsis* species to a new genus.

***Meconopsis* nativity and habitat**

The native habitat in which *Meconopsis* grows can provide information necessary for successful cultivation of these plants. All species, except *M. cambrica*, are native to the Himalayas between 2100m and 5800m altitude (Sulaiman and Babu, 1996). They grow in screes, scrub, on moraines, cliffs, gentle slopes, in alpine meadows, or woodlands (Grey-Wilson, 2001). Plants may grow in temperate, sub-alpine, or alpine zones (Jermyn, 2001).

One feature consistently found in areas with healthy native populations is a rich source of mineral nutrients (Sulaiman and Babu, 1996; Cobb, 1989). *Meconopsis* grows best in a high organic matter-containing, acid soil (Cobb, 1989). *Meconopsis* can grow in alkaline soil but flowers are less vibrant.

The average maximum temperature where *Meconopsis* occurs in the wild is 22 °C and the average maximum humidity is 82% (Sulaiman and Babu, 1996). This gives a general guide to temperature and humidity levels allowing successful *Meconopsis* cultivation.

***Meconopsis* chromosome numbers**

Cytological observations of *Meconopsis* have identified chromosome number and ploidy levels for some species. The chromosome number varies among species and within at least one species. For example, *M. cambrica* has been identified with both $n=11$ and $n=14$, where n is the haploid chromosome number (Norton, *et al.* 1986). Chromosome number of *M. betonicifolia* is $n=40$ and *M. quintuplinervia* Regel is $n=42$. The species also have variable ploidy levels where *M. cambrica* and *M. villosa* (Hook.f.) G. Tayl. are tetraploids while *M. quintuplinervia* and *M. betonicifolia* are nearly duodecaploids. Variability of chromosome numbers of inter-specific hybrids suggests that aneuploidy has occurred.

Differing levels of chromosomes and ploidy levels limit the ability of species to cross pollinate. Norton *et al.* (1986) studied this effect in several of the species mentioned above. They crossed *M. cambrica*, *M. villosa*, *M. betonicifolia*, *M. horridula* Hook.f. & T. Thoms, *M. quintuplinervia*, and *M. aculeate* Royle. Results indicated that large differences in ploidy level reduced ability of species to successfully hybridize. In their research, crosses between parents with ploidy levels differing by eight produced little or no viable seed. Crosses between parents with no difference in ploidy level produced many viable seed. Crosses between parents with ploidy levels differing by four produced some viable seeds but not as many as the crosses with no difference in ploidy level. So, the degree of ploidy level difference between parents was inversely related to the amount of seed produced.

Low seed set may also result from problems with pollen incompatibility. In the research by Norton *et al.* (1986), pollen viability based on staining was above ninety percent for all of the species tested but none of the species had seed germination rates above 40 percent. Three of the species had below 20 percent pollen germination and one had no germination. It is difficult to judge chromosome combining ability based upon ploidy level if plants cannot self-pollinate. This may be the reason for the low germination rates reported by authors that discuss *Meconopsis*.

Allelic frequencies of *M. paniculata* (D. Don) Prain, *M. simplicifolia* (D. Don) Walp., and *M. sinuata* Prain are more or less similar at most loci (Sulairman and Babu, 1996) but there is some variation. This variation in allelic frequency within a species may be due to the fact that the natural populations are small and separated by geographical barriers. Therefore, the absence

of gene flow between different populations of the same species may lead to low genetic diversity when plants in the trade are descendents from just one population.

***Meconopsis* appearance**

Meconopsis species vary in flower color, foliage, size, and habitat. Flower color varies from white to yellow, red, blue, violet, and purple (Straley, 1987); however, the flower color that makes this genus most attractive as an ornamental is blue.

The color of the blue poppies is determined by anthocyanins, chemical pigments that reside in the vacuoles (Geneve, 1996). Anthocyanins usually appear as red, pink, purple, or blue. Anthocyanins are formed when a sugar, usually glucose, is added to a group of compounds called anthocyanidins. The anthocyanidin that provides the blue color is delphinidin. Unlike *Borago* L., *Mertensia* Roth, and many other blue flowers, *Meconopsis* does not change color from blue to pink as the vacuole pH changes. The flowers are also not pink in bud as are some of the weaker blue flowers of other genera.

The flowers of the blue poppies are of value because the blue color is clear. There is little or no red mixed with the blue color. Many blue flowers are slightly violet because red pigment is also present. True blue is uncommon in plants and highly sought after for ornamental horticulture.

Flowers are not the only attractive aspect of *Meconopsis*. Foliage can be diverse in shape, form, and color. The growth habit of *Meconopsis* varies widely. Most species produce large basal rosettes of leaves that develop over many months or years. These rosettes eventually produce flower stems ranging from 25cm tall, with one flower, to 200cm tall, with 50 flowers

(Thomas, 1990). Height is an asset for plants used in the garden, the landscape, and for cut flowers.

Flowering of all *Meconopsis* is determinate, beginning at the top of the flower scape and proceeding downward (Straley, 1987). The flowers can be held drooping or outward-facing. The height, upright habit, and blue flower color provide a unique display form for gardens or conservatories.

Meconopsis is typically described as a hardy perennial, although often it is short-lived (Hinkley, 1999). Many species in the genus are considered to be monocarpic. Monocarpic refers to plants producing fruit once and then dying. Some *Meconopsis* are polycarpic. Polycarpic plants are those bearing fruit many times, or year after year (Still, personal communication). Sometimes polycarpic species die after flowering in the first season of growth. The reason for the death of these polycarpic plants is still unclear but may be due to resource demands from heavy fruit loads in the first year of growth. To avoid this problem, some nursery professionals often recommend removing flower buds in the first year so that the plants will live longer (Hinkley, 1999).

***Meconopsis* garden culture**

Meconopsis is common in gardens in northern parts of the United Kingdom and occasionally is seen in gardens in the northern coastal regions of the United States. Adequate summer moisture and preferably drier winters is essential for successful cultivation (Cobb, 1989). In Scotland, where *Meconopsis* is most commonly grown, the temperature rarely exceeds 27°C. These are critical issues to remember when attempting to cultivate *Meconopsis* in a greenhouse setting.

Gerald Straley (1987) writes that one-half of the species can be seen in North American gardens most of which are grown only by plant collectors. *Meconopsis* species vary in popularity or degree of cultivation. Hybrids between *M. betonicifolia* and *M. grandis* Prain are considered to be the finest species for the garden. Other species are less often cultivated.

Gardeners have tried growing *Meconopsis* in a variety of situations. Some recognize the limited range of the species but often have misconceptions regarding the growing conditions. Dan Hinkley (1999) stated that the genus needs cool summer climates. It appears that *Meconopsis* can tolerate quite variable soil conditions but must have a cool and moist environment. One Scottish expert on the genus suggested that *Meconopsis* could be grown at 35° C if it is misted and has a continually moist soil (Christie, personal communication).

Currently, commercial propagation of *Meconopsis* is most commonly done from seed. Seed germination can be erratic and of low percentage (Qu and Norton, 1986). Because of these germination problems, propagation of *Meconopsis* can be difficult. However, seed propagation is still the most common, and economically feasible, form of production. Propagation by crown division is sometimes used. In fact, some hybrids are sterile and are propagated exclusively by division but multiplication of *Meconopsis* by crown division is very slow. Other propagation methods, such as in vitro culture are being researched (Qu and Norton, 1986) but are not yet reliable.

Seed viability is dependent on species and length of time in storage. Seeds of the species that remain viable for long periods may be collected in the fall and sown in the spring (North American Rock Garden Society, <http://www.nargs.org/>). It is recommended that seeds be

germinated in low temperatures, 5 to 15 °C, in a peat based, soilless compost. Recommendations for germination temperature and media are generally consistent but may not be correct.

Species that lose seed viability quickly, such as *Meconopsis punicea* Maxim., should be sown outdoors immediately upon harvest for germination in the spring. Other species can be sown up to one year after collection without detriment to viability (Appendix C).

While recommendations suggest sowing at 5-15°C (North American Rock Garden Society, <http://www.nargs.org/>; Thomson and Morgan Web Site, <http://www.thompson-morgan.com/seeds>), this author has found 85 to 90% of *Meconopsis* seed germinated when incubated at 21.1°C for one month (Appendix C). This is contrary to the often cited belief that the temperature must be cooler for optimum germination.

Genotypes for research

Meconopsis genotypes used in this study were chosen based on their availability and reported taxonomic identity in relation to the goals of this study. The four genotypes were *Meconopsis betonicifolia*, two hybrids derived from *M. betonicifolia* and *M. grandis*, and *M. punicea*. Three of the genotypes, *Meconopsis betonicifolia*, a cultivar from the *M. George Sherriff* Group (Stevens and Brickell, 2001b), and *M. 'Lingholm'* are the famous true blue poppies while *M. punicea* has brilliant red, pendant flowers.

Originally, it was intended to focus on *M. betonicifolia*, *M. grandis*, *M. ×sheldonii*, and *M. punicea* in this study. Plants were purchased with these taxonomic names in November 2000. Recently, it became clear that the true taxonomic identity of the plants (and many of the hybrids and some of the species commonly available in the trade) were inaccurate due to mislabeling. New information provided by the *Meconopsis* Group (Stevens and Brickell, 2001b)

has indicated that plants used in this study listed as *M. grandis* were probably a cultivar in the newly formed George Sherriff Group and *M. ×sheldonii* are *M. 'Lingholm'*.

The Meconopsis Group, a group of plantspeople interested in improving the base of knowledge for the blue poppies, is currently sorting out the names of species and cultivars and has a trial of *Meconopsis* at the Royal Botanic Garden, Edinburgh, Scotland. More information on the new classification system for *Meconopsis* can be found in articles in *The New Plantsman* from both March and June 2001 (Stevens and Brickell, 2001a, 2001b).

Meconopsis betonicifolia, discovered in 1886 and originally named *M. baileyi* Prain, can vary in both form and color. This species is the best-known Himalayan poppy and certainly the easiest blue form to grow. *Meconopsis betonicifolia* emerges fairly early in spring. The perfect sky-blue flowers, composed of four to six petals, can be up to 8 cm or more across (Cobb, 1989). This species can grow to a height of 1.2 m and a width of 46 cm (Thomas, 1990).

The cultivar from the *Meconopsis* George Sherriff Group, which will be referred to as *Meconopsis* George Sherriff Group, or G. S. Group, is a hybrid with unknown identity. The unidentified cultivar in the G. S. Group is sold by The Blue Poppy Nursery in Palmer, Alaska. The hybrid has some characteristics of both *M. betonicifolia* and *M. grandis*.

Meconopsis 'Lingholm' is a good blue form named for Lingholm Garden in Scotland. *Meconopsis* 'Lingholm' may be the most commonly grown cultivar in the United States because the plant is easily propagated from seed; however, it is commonly mislabeled as *M. ×sheldonii*. Over the years that *M. ×sheldonii* has been cultivated, there has been backcrossing resulting in confusion in the trade (Thomas, 2000). True *M. ×sheldonii* are sterile.

Meconopsis punicea is a blood-red species from China and is a difficult plant that is doubtfully perennial (Cobb, 1989). The long red petals remind some of banners streaming in the wind. The large plants of *Meconopsis punicea* measure 30cm across and may have up to 20 separate flowering crowns with up to 50 separate blooms, on 60cm stems, at the end of June. Unfortunately, the plants are rarely perennial and this fact, combined with low germination rates, has led to the species being lost in cultivation several times over the last century. *Meconopsis punicea* is often considered monocarpic and this may relate to the occasional loss of the plant in cultivation.

Temperature effects on growth

Temperature is one of the critical factors controlling plant developmental processes (Yuan *et al.*, 1998). The researcher was unable to find research describing the effects of temperature on growth and flowering of *Meconopsis*. Research on the effects of temperature on the growth and flowering of other Papaveraceae genera is also scarce. Considerable research is available describing the effects of temperature on the growth and flowering of other perennials genera. Research on other perennials may serve as a guide to studying the effect of temperature on *Meconopsis*.

Research on other perennials has shown that as growing temperature increases, flower number usually decreases within a species specific range, therefore, flower number is affected by the temperature in which a plant is grown. At 14°C, *Oxypetalum* had three to five flowers per cyme with only a few aborted flowers (Armitage *et al.*, 1990). At 30°C, the plants had only one to two flowers per cyme and the percentage of aborted flowers increased. There was also an accompanying decrease in number of flowering cymes at 30°C. The number of flower buds on

Coreopsis grandiflora (Hogg ex Sweet.) 'Sunray', *Rudbeckia fulgida* (Ait.) 'Goldsturm', and *Leucanthemum superbum* (Bergman ex J. Ingram) 'Snowcap' decreased $\approx 80\%$, 75% , and 55% , respectively, as temperature increased from 16°C to 26°C (Yuan, *et al.*, 1998). Flower bud number also decreased in *Dahlia pinnata* Cav. 'Royal Dahlietta Yellow' as temperature increased (Brondum and Heins, 1993). The Dahlia had 10 buds per plant at 15°C , two buds per plant at 25°C , and all flower buds were aborted at 30°C .

Flower diameter is also affected by temperature. *Dahlia* 'Royal Dahlietta Yellow' flower diameter decreased as average daily temperature increased from 11°C to 30°C (Brondum and Heins, 1993). The mean flower diameter decreased from 7 cm at 11°C to 4.5 cm at 30°C . In research by Yuan *et al.* (1998), plants grown at cooler temperatures had more and larger flowers and were taller but took longer to reach visible flower.

Temperature influences not only flowering characteristics, but also plant appearance. Plant height, stem length, stem diameter, leaf number, crown width, and dry weight can be affected by temperature. Temperature has often been reported to affect stem/height length positively. Stem length of *Oxypetalum caeruleum* was greater at 30°C than at 14°C (Armitage *et al.*, 1990). Cultivars of *Arachis hypogaea* L. grew taller in $35/30^{\circ}\text{C}$, day/night respectively, than in $25/25^{\circ}\text{C}$ (Talwar *et al.*, 1999). Plant height of *Cucumis sativus* 'Corona' increased linearly as mean temperature increased from 18°C to 24°C (Papadopoulos and Hao, 2000). Stem length of *Capsicum annuum* L. 'Resistant Giant #4' increased as average daily temperature increased from 14°C to 26°C (Si and Heins, 1996).

Temperature has also been shown to have a negative affect on height and stem length. Height of *Rudbeckia* decreased 50% when temperature increased, and *Leucanthemum* 'Snowcap'

and *Coreopsis* 'Sunray' decreased with increase in temperature from 16 to 26°C (Yuan *et al.*, 1998). Primary shoot length decreased in *Dahlia* 'Royal Dahlietta Yellow' as the temperature increased from 20°C to 30°C (Brondum and Heins, 1993).

There may be two explanations for the variety of reactions to temperature on shoot length. The first one may be that different plants have a different temperature at which they switch from vegetative growth to flowering, thus ceasing the growth of the shoot. The second explanation may be that the different genera react differently to high temperatures and some genera or species stop stem extension when flowering while some continue to grow while flowering.

A possible reason for different responses from different genera is that the plants come from different regions of the world with diverse environments. Plants adapted to different temperatures in these diverse environments and optimum growth takes place at a variety of temperatures.

Research generally shows an inverse relationship of temperature on stem diameter. Stem diameter decreased linearly with an increase in temperature for *Oxypetalum caeruleum* (Armitage *et al.*, 1990). As temperature increased above 22°C, the stem diameter decreased in *Chamaecyparis thyoides* (L.) B. S. P. (Jull *et al.*, 1999).

There is a positive relationship of temperature on number of leaves. Leaf count increased in *Cucumis sativum* as mean day temperature increased from 18°C to 25°C (Papadopoulos and Hao, 2000). Leaf number of *Capsicum annuum* L. 'Resistant Giant # 4' increased as average daily temperature increased from 14°C to 26°C (Si and Heins, 1996).

Research has shown an inverse relationship of temperature on crown width. The crown width of *Chamaecyparis thyoides* decreased as temperature increased from 22°C to 30°C (Jull *et al.*, 1999).

An optimum temperature range has been correlated with larger dry weight in plants. Shoot dry weight of *Capsicum annuum* increased as the temperature increased from 14°C to 26°C (Si and Heins, 1996). Shoot dry weight for *Chamaecyparis thyoides* increased from 14°C to 26°C but then decreased as temperatures increased to 30°C (Jull *et al.*, 1999).

Dry weight is composed primarily of carbon. Plant carbon is accumulated through photosynthesis. Plant carbon is lost during respiration. Therefore, for a plant to gain dry weight or grow, it must take in more carbon through photosynthesis than it loses through respiration. The term net photosynthesis is used to describe the difference between total photosynthesis and respiration. Temperature has been shown to have a strong affect on net photosynthesis.

In research by Armitage *et al.*, (1990), net photosynthesis in *Oxypetalum caeruleum* (D. Don.) Decne., at high light levels, rose from 9 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (μmol refers to $\mu\text{mol CO}_2$ assimilated) to 12 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ between 14°C and 22°C, but then decreased to 11 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ as temperature rose further to 30°C. A plant that has a lower tolerance of high temperatures is *Eucalyptus nitens* (Deane and Maiden) Maiden (Battaglia, 1996). *Eucalyptus nitens* had a net photosynthesis of 15 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at 10°C and the net photosynthesis dropped to 8 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at 35°C. Leaf net photosynthesis rates of two cultivars of *Cucumis sativus* decreased with increased day temperatures (Papadopoulos and Hao, 2000); however, there was no variation in rate of net photosynthesis between 15 to 34°C when plants were under saturating light

conditions. Plant growth in young cucumber plants happened mainly through increases in leaf area ratios rather than increases in net assimilation rates (Papadopoulos and Hao, 2000).

The optimal temperature for carbon dioxide assimilation is usually correlated with the optimal temperature for plant growth under a given set of environmental conditions and can reflect a plant's native (evolutionary origin) habitat (Ranney and Ruter, 1997). There is also considerable variation in the thermotolerance among different plants not only between genera, but also within genera, species, and in some cases, ecotypes and provenances (Ranney and Ruter, 1997). Therefore, it is important to test the thermotolerance of the different species of *Meconopsis* that are of display importance.

The environmental conditions found in the native habitat of *Meconopsis*, such as temperature, are different than plants found in other parts of the world. It would be rational to assume that *Meconopsis* needs a cooler environment than plants that are native to warmer regions of the world, such as *Gaillardia × grandiflora*, of which one parent of the hybrid is native to Mexico.

The optimum temperature for flowering is probably related to the growing conditions of the native area. For crops such as *Meconopsis* and *Campanula* L., native to temperate alpine regions, the optimum temperature for growing and flowering the plants will be different than those plants from warmer climates, such as groundnut or cucumber.

Justification for Meconopsis research

To successfully cultivate *Meconopsis*, it is necessary to determine, quantitatively, how they perform under defined temperature conditions. It is possible that species and hybrids vary in their optimum growing temperatures.

One objective of this study was to determine the effect of temperature on the growth, flowering and net photosynthetic response of selected *Meconopsis* species and hybrids and to use this information to define conditions suitable for production of these plants. These genotypes could then be used for ornamental display at Longwood Gardens, other public gardens, and in the field of horticulture.

There are temperature control limitations of growing plants for display. Due to high summer temperatures, field growing does not appear to be a practical option for producing a crop of *Meconopsis*. Greenhouse production of *Meconopsis* is a viable option if cool temperatures can be maintained. Greenhouses are designed to enhance crop productivity of out-of-season crops by maintaining a plant growth environment favorable to the plant (Papadopoulos and Hao, 1999). Maintaining a favorable growth environment can be difficult during some periods of the year.

In order to produce a good crop of *Meconopsis*, it is important to consider when plants would grow best in the greenhouse environment. Empirical observations have shown that *Meconopsis* grows best when temperatures are cooler than 27°C, as in Scotland. Therefore, summer production of *Meconopsis* may be difficult because the solar temperature gain in a greenhouse often exceeds the cooling capability. *Meconopsis* winter production is promising because temperature control is more reliable when outside temperatures are cooler. Initially, this project focused on growth of plants in the greenhouse during winter months because this period offered the highest degree of temperature control.

Another objective of this research was to enhance the knowledge of the genus *Meconopsis* for the field of horticulture. It was important to produce a quality flowering crop in

a greenhouse from established plants. The information discovered or confirmed during these experiments would help produce a crop of *Meconopsis* that horticultural display gardens, such as Longwood Gardens, would be able to use.

There are cost limitations to producing crops out of season. There are structural costs of greenhouses that must be built and maintained to have environmental control during growing periods. There are also energy costs to maintain greenhouses at the optimal temperature for plant growth. Both factors can prohibit production for some crops. Although associated costs may be relatively high, many crops are grown in a greenhouse environment.

Greenhouse technology and growing capabilities have increased substantially in the past fifteen years. Because of the increased environmental controls in the greenhouse, many climate-sensitive plants that used to be considered too difficult to force are now being grown. Many public gardens have increasingly sophisticated greenhouses and now have the capabilities to force these plants with equal or better quality than the industry.

Longwood Gardens recently finished work on a greenhouse facility that makes it possible to grow climate sensitive crops to a very high degree of accuracy. Other public gardens have been improving their growing facilities as well. Atlanta Botanical Garden is in the process of upgrading facilities and the Chicago Botanic Garden has been in a constant state of greenhouse renovation. The reason for the renovations at Chicago Botanic Garden has simply been to improve the environmental controls (Ault, personal communication).

Although the horticultural industry currently has the resources to force difficult crops, such as *Meconopsis*, this research may be most important to public horticultural facilities. Due to the high cost of forcing some of the more difficult plants, it may not be economically viable

for the industry to pursue forcing crops like *Meconopsis*. Public gardens, because they are not profit driven, may be able to grow these plants for display in order to fulfill their mission to the public.

While there are possible costs associated with the production of *Meconopsis*, there is a possible cost savings by growing *Meconopsis* over other plants for display in a conservatory. Because *Meconopsis* can tolerate, and actually may grow better in, lower temperatures, then these plants can be grown in the winter with little to no temperature augmentation. This can be a large energy savings to gardens growing and displaying *Meconopsis*.

MATERIALS AND METHODS

Experiment 1: Influence of greenhouse temperature on growth of *Meconopsis* during winter

Experiment 1 was conducted from December 15, 2000 to May 15, 2001. Sixty one-year-old plants of *M. betonicifolia*, *M. George Sherriff Group* (G.S. Group), *M. 'Lingholm'*, and *M. punicea* were purchased from The Blue Poppy Nursery (Palmer, Alaska). Plants had been grown in 3.8 liter containers, then shipped to Longwood Gardens, Inc. on November 1, 2000, with most of the soil removed.

Plant Culture

On November 1, 2000, the plants were potted into 7.3 cm square by 22.9 cm tall black plastic tree band pots open at the bottom (Anderson Die and Manufacturing Co., Portland, OR) using Sunshine Aggregate Mix #4 (Sun Gro Horticulture, Bellevue, Washington). A paper towel was placed at the bottom of each pot to prevent soil loss. Plants were then placed in a cooler at 1°C and were watered as needed for six weeks for vernalization. Most plants of all genotypes had basal rosette foliage and some *M. punicea* had flower buds when received.

All plants were removed from the cooler and potted into 19 cm wide by 17.8 cm tall, round, fiber, 4 liter 3R77 nursery pots (Kord Products Inc, Brantford, Ontario, Canada) on December 15, 2000. Potting medium was Sunshine Aggregate Mix #4. Each pot was top dressed with 6 grams 15.0N-3.9P-10.0K Osmocote Plus 5-6 Month slow release fertilizer (The

Scotts Co, Marysville, OH). Plants were grown in glass greenhouses under natural photoperiodic conditions and hand watered as needed to keep uniformly moist. Plants were initially placed pot-to-pot and then spaced on 45cm centers on February 11, 2001 to prevent interplant shading.

Insects and diseases were observed on some plants during the experiment. Triflumizole (50%) (Terraguard 50 WP©, Uniroyal Chemical Co., Middlebury, CT), at a rate of .66g product per .625 liter water, or triadimefon (25%) (Strike©, Olympic, Harleysville, Pennsylvania), at a rate of 1.25 mg product per 2.5 liter water, or a combination of trifloxystrobin (50%) (Compass©, Bayer, City, State), at a rate of .284 g product per 1.25 liter, water plus an organosilicon surfactant (Capsil 30©, Aquatrols, Cherry Hill, NJ), at rate of .296 ml product per 1.25 liter water, were used to control powdery mildew (*Erysiphe* sp.).

Bifenzanate (50%) (Floramite©, Uniroyal Chemical Co., Middlebury, CT), at a rate of 1.8 ml product per 3.75 liter water, or Ovation© (Ovation©, Scotts, Marysville, Ohio), at a rate of .3 ml product per 1.25 liter water, were used to control two-spotted spider mite (*Tetranychus urticae* (Koch)).

Avid© (Avid©, Syngenta, Basel, Switzerland), at a rate of .6 ml product per 1.25 liter water, or pymetrozine (25%) (Endeavor©, Syngenta, Basel, Switzerland), at a rate of 2.25 ml product per 3.75 liter water, or imidacloprid (1% granular) (Marathon II©, Olympic, Harleysville, Pennsylvania), at a rate of .6g product per 1.25 liter water, were used to control foxglove aphids (*Aulacorthum solani* (Kaltenback)) and greenhouse whiteflies (*Trialeurodes vaporariorum* (Westwood)).

Some plants died during the course of the experiment. These plants were removed to prevent possible spread of insects or disease. These plants were not included in the statistical analysis unless data were taken before they died.

Temperature treatments

Plants of all four genotypes were placed into three temperature regimes in six separate greenhouse compartments with two compartments for each temperature regime. Three temperature treatments were established by setting heat to turn on when temperatures fell to: 10°C/7.2°C, 15.6°C/12.8°C, and 21.1°C/18.3°C day/night, respectively. Ventilation for cooling was activated when temperatures rose to 12.8°C/10°C, 18.3°C/15.6°C, and 23.9°C/21.1°C day/night, respectively, for the same three treatments.

The temperature regime with a heating set-point of 10°C/7.2°C and a cooling set-point of 12.8°C/10°C, day/night, is referred to as the cool temperature regime. The temperature regime with a heating set-point of 15.6°C/12.8°C and a cooling set-point of 18.3°C/15.6°C, day/night, is referred to as the intermediate temperature regime. The temperature regime with a heating set-point of 21.1°C/18.3°C and a cooling set-point of 23.9°C/21.1°C, day/night, is referred to as the warm temperature regime.

Temperatures in each compartment were monitored every 15 minutes with an Argus Environmental Control System (Argus Controls, White Rock, BC, Canada).

Data measurements

Data were collected from onset of bloom through completion of the experiment on May 15, 2001 on plant attributes related to flowers and to general plant growth.

Flowering data collected included:

- *Total flower number:* The sum of flowers opened on a plant.
- *Flower width:* The width of each flower was measured, in cm, on the day of flower opening.

General plant growing data collected included:

- *Flower height:* Height of the flower center above the root medium surface was measured, in cm, on the day of flower opening.
- *Flower stem diameter:* Stem diameter was measured, in cm, at a point one half of the distance from the root medium surface to the center of each flower. The measurement was made with a Fowler Max-Cal Caliper (Fred V. Fowler Co Inc., Newton, MA).
- *Canopy width at first flower:* The distance across the widest point of the canopy was measured, in cm, from tips of opposing leaves. The distance across the canopy perpendicular within the horizontal plane to the preceding width, measured in cm from tip to tip of opposing leaves when the first flower opened on a plant, was also measured. The average of these two measurements was recorded as the canopy width at first flower.
- *Basal leaves at first flower:* The number of basal leaves was counted when the first flower opened on a plant.
- *Raceme leaves at first flower:* The number of raceme leaves was counted when the first flower opened on a plant.

- *Total leaf number at first flower:* The sum of basal and raceme leaves when the first flower opened on a plant.
- *Canopy width at harvest:* The distance across the widest point of the canopy was measured, in cm, from tips of opposing leaves. The distance across the canopy perpendicular within the horizontal plane to the preceding width, measured in cm from tip to tip of opposing leaves at harvest, was also measured. The average of these two measurements was recorded as the canopy width at harvest.
- *Basal leaves at harvest:* The number of basal leaves was counted at harvest.
- *Raceme leaves at harvest:* The number of raceme leaves was counted at harvest.
- *Total leaf number at harvest:* The sum of basal and raceme leaves at harvest.
- *Fresh weight:* The fresh weight of the non-root portion of five randomly selected plants from each treatment block was measured immediately after harvesting on May 15, 2001.
- *Dry weight:* The dry weight of the non-root portion of five randomly selected plants from each treatment block was measured after drying in an oven at 49°C for two weeks following harvesting on May 15, 2001.

Photosynthetic response

- *February photosynthesis:* February net photosynthesis rates were measured as $\mu\text{mol CO}_2$ taken up per m^2 of leaf surface area per second ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). Photosynthesis measurements for one group of replicates (blocks) were made on February 16, 2001 while measurements for the other group of replicates were made on February 17, 2001. The largest healthy leaf, if large enough to cover the area of the cuvette, on

each living plant was measured using a Li-Cor 6400 Portable Photosynthesis System (Li-Cor Inc, Lincoln, Nebraska). All measurements were made with a constant light level of $2000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and $500 \mu\text{mol}\cdot\text{s}^{-1}$ air flow. If a leaf was not at least 7 cm long and 4 cm wide, then it was unable to be measured and the photosynthesis rate was not taken.

▪ *March photosynthesis:* Photosynthesis measurements (as previously discussed) for one block were made on March 30, 2001 while measurements for the other block were made on March 31, 2001.

Statistical analysis

The experiment was organized as a nested factorial design. Ten plants from each genotype were randomly assigned, to each of the two compartments, within each of the three temperature regimes. The plants were assigned randomly to positions on benches within each growing compartment. The data was analyzed with the Analysis of Variance (ANOVA) procedure from Statistical Analysis Systems (SAS, Cary, NC) using the mixed procedure (Littell *et al.*, 1996). The Tukey-Kramer adjustment was used for the Differences of Least Square Means (Kramer, 1956). The Satterthwaite Method was used for testing P values (Satterthwaite, 1946).

Experiment 2: Influence of temperature on summer forcing of *Meconopsis*

Experiment 2 was conducted from July 13, 2001 to December 13, 2001. Ninety three-month-old plants of *M. betonicifolia*, *M. G. S. Group*, and *M. 'Lingholm'* were purchased from The Blue Poppy Nursery. *Meconopsis punicea* was not available for the experiment. Plants had

been grown in one-liter containers, then shipped to Longwood Gardens, Inc. on July 10, 2001, with most of the soil removed.

Plant Culture

On July 13, 2001, plants were potted into 15 cm wide by 15 cm tall, square, fiber, 2 liter 3R66 nursery pots (Kord Products Inc, Brantford, Ontario, Canada) as previously described. Each pot was top dressed with 2 grams 15.0N-3.9P-10.0K Osmocote Plus 5-6 Month slow release fertilizer. Plants were grown in glass greenhouses under natural photoperiodic conditions. Pad-and-fan cooling was used to keep the temperature cooler in the greenhouses. Plants were hand watered as needed to keep uniformly moist. Plants were placed on 20cm centers. Some plants died during the course of the experiment. These plants were removed to prevent possible spread of insects or disease.

Temperature treatments

Plants of all four genotypes were placed into two temperature regimes in separate greenhouse compartments. There were two compartments for each temperature regime. Temperature treatments were established by setting heat to turn on when temperatures fell to 21.1°C/18.3°C and 26.7°C/23.9°C day/night, respectively. Ventilation for cooling was activated when temperatures rose to 23.9°C/21.1°C and 29.5°C/26.7°C day/night, respectively, for the same two treatments.

The temperature regime with a heating set-point of 21.1°C/18.3°C and a cooling set-point of 23.9°C/21.1°C, day/night, is referred to as the cool temperature regime. The temperature regime with a heating set-point of 26.7°C/23.9°C and a cooling set-point of 29.5°C/26.7°C, day/night, is referred to as the warm temperature regime.

Temperatures in each compartment were monitored every 15 minutes with an Argus Environmental Control System (Argus Controls, White Rock, BC, Canada).

Data collected

The number of plants surviving 41 and 55 days after the experiment began was recorded.

Statistical Analysis

The experiment was organized as a nested factorial design. Fifteen plants from each genotype were randomly assigned to each of the two compartments for each of the two temperature regimes. Within each growing compartment the plants were assigned randomly to positions on a bench.

RESULTS

The general appearance of plants at the time of first flowering was best in the cool and intermediate temperature regimes and worst in the warm temperature regime (personal observation). Plants flowered earlier as temperature increased from the warm, to the intermediate, to the cool regime (personal observation).

Experiment 1

During the months of December, January, February, and March, the average temperature remained within 1.1°C of the cooling target temperatures for all three temperature regimes (Table 1). During April, the average temperature of the cool temperature regime rose 4.1°C above the cooling target, the average temperature of the intermediate temperature regime rose 1.8°C above the cooling target, and the average temperature in the warm regime did not rise above the cooling target (Table 1).

During May, the average temperature of the cool temperature regime rose up to 6.9°C, the average temperature of the intermediate temperature regime rose 6.3°C above the cooling target, and the average temperature in the warm regime rose 5.3°C above the cooling target.

The average daily light level was 772 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in December, 823 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in January, 888 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in February, 1256 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in March 1521 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in April, and 2037 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in May (Table 2).

Flowering Data

The number of flowers produced by a plant was significantly affected by temperature, genotype, and the temperature $\times$ genotype interaction (Fig. 1, Table 2). In general, there were fewer flowers in the warm temperature regime compared to the intermediate and cool temperature regimes. The temperature $\times$ genotype interaction for flower number was because *M. punicea* reacted to temperature differently than the other genotypes (Fig. 1). *Meconopsis punicea* had more flowers in the cool temperature regime than in the warm temperature regime. All other genotypes had similar number of flowers in all three temperature regimes.

Flower width was significantly affected by genotype and there was a genotype $\times$ temperature interaction (Fig. 2, Table 3). *Meconopsis punicea* had the widest flowers, *M. betonicifolia* and *M. 'Lingholm'* were intermediate, and *M. G. S. Group* had the smallest flower width (Table 3). Width did not vary across the three temperature regimes within the genotypes *M. betonicifolia* and *M. G. S. Group* (Fig. 2). Flower width of *M. punicea* varied within the three temperature regimes; it was greater in the cool temperature regime less in the intermediate and warm temperature regimes (Fig. 2).

General plant growth data

Flower stem diameter was significantly affected by temperature and genotype (Table 4). Stem diameter was greatest in the cool temperature regime. The hybrid *M. 'Lingholm'* and *M. betonicifolia* had the greatest flower stem diameter, *M. G. S. Group* was intermediate in diameter thickness, and *M. punicea* had the smallest flower stem diameter.

Flower height was significantly affected by temperature and genotype (Table 4). Plants grown at the cool temperature regime were taller than plants grown at the warm temperature

regime (Table 4). Height of the flower was greatest for *M. betonicifolia*, intermediate for *M. G. S. Group* and *M. 'Lingholm'*, and least in *M. punicea*.

Canopy width at first flower was significantly affected by genotype (Table 5). *Meconopsis betonicifolia* and *M. 'Lingholm'* had the largest canopies followed by *M. G.S. Group*. *Meconopsis punicea* had the smallest canopy.

Canopy width at harvest was affected by genotype (Table 5). *Meconopsis 'Lingholm'* and *M. betonicifolia* had the largest canopies at harvest; however, *M. betonicifolia* canopy was not larger than *M. G. S. Group* (Table 5). *Meconopsis punicea* had the smallest canopy width at harvest (Table 5).

Basal leaf number at first flower was significantly affected by genotype and the temperature $\times$ genotype interaction (Table 6). *Meconopsis betonicifolia* had more basal leaves than *M. G.S. Group* or *M. 'Lingholm'*. The temperature $\times$ genotype interaction was due to *M. betonicifolia* and *M. punicea* having a greater number of basal leaves in the cool temperature regime while *M. G.S. Group* or *M. 'Lingholm'* were not affected by temperature (Fig. 3).

Number of raceme leaves at first flower was significantly affected by genotype (Table 6). *Meconopsis betonicifolia* had the greatest number of raceme leaves compared to *M. G.S. Group* which was intermediate and *M. 'Lingholm'* which had the fewest number of raceme leaves. *Meconopsis punicea* does not produce raceme leaves (Table 6, Table 7).

The number of total leaves at first flower was significantly affected by temperature and genotype (Table 6). Plants grown in the cool temperature regime had more total leaves at first flower than plants grown at the warmest temperature regime. *Meconopsis betonicifolia* had more total leaves than the other three genotypes.

Number of basal leaf number at harvest was significantly affected by genotype (Table 7). *Meconopsis* G.S. Group had fewer basal leaves compared to the other three genotypes.

Number of raceme leaves at harvest was significantly affected by temperature and genotype (Table 7). Number of raceme leaves at harvest greatest in the cool and intermediate temperature regimes. Number of raceme leaves at harvest was greatest in *M. betonicifolia* and *M. G.S. Group*.

Number of total leaves at harvest was significantly affected by genotype (Table 7). *Meconopsis betonicifolia* and *M. 'Lingholm'* had a greater number of total leaves than *M. G.S. Group*. *Meconopsis punicea* produced an intermediate number of total leaves at harvest.

Fresh weight at harvest was significantly affected by genotype (Table 8). *Meconopsis betonicifolia* and *M. 'Lingholm'* had a higher dry weight at harvest. Dry weight at harvest was significantly affected by temperature and genotype. Dry weight was greater for plants grown under the cool temperature regime compared to the warm temperature regime. *Meconopsis 'Lingholm'* dry weight was larger than *M. G.S. Group* and *M. punicea*. *Meconopsis G.S. Group* a similar dry weight to both *M. betonicifolia* and *M. punicea*.

Net photosynthetic response

Net photosynthesis during February 2001 was affected by the temperature, the genotype, and the genotype $\times$ temperature interaction (Fig. 3, Table 9). Plants grown in the cool temperature regime had a higher mean rate of net photosynthesis compared to plants in the intermediate and warm temperature regimes. The net photosynthesis rate for *M. punicea* during February was lowest in the warm temperature regime.

Net photosynthesis readings for March 2001 were affected by genotype (Fig. 4, Table 10). The net photosynthetic response for the three genotypes *M. betonicifolia*, *M. G. S. Group*, and *M. 'Lingholm'* were highest in the cool temperature regime, intermediate in the intermediate temperature regime and lowest in the warm temperature regime. In general, net photosynthetic rates in March appeared to be lower than the net photosynthetic rates in February. *Meconopsis* 'Lingholm' had a higher net photosynthesis compared to the other three genotypes.

Experiment 2

The average daily light level was $772 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in July, was $823 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in August, and was $888 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in September (Table 11).

Plant survival was 18% after 41 days (August 23) and 8% after 55 days (September 7) when grown in the cool temperature regime (Table 12). All plants placed in the warm temperature regime were dead after five weeks.

Fig. 1. Influence of temperature by genotype interaction on mean number of flowers produced on *Meconopsis*.

Means with the same letter are not significantly different according to Tukey-Kramer Adjusted P for multiple means, $P=0.05$.

Table 2: Influence of temperature and genotype on mean number of flowers produced on *Meconopsis*

Variable	n ^y	Number of flowers
Temperature regime		
Cool	67	7.2a ^z
Intermediate	73	7.3a
Warm	55	5.5b
Genotype		
<i>M. betonicifolia</i>	54	6.3ab
<i>M. G. S. Group</i>	56	7.6a
<i>M. 'Lingholm'</i>	42	4.7b
<i>M. punicea</i>	43	8.3a
ANOVA		
sources of variation	df	F value
Temperature (T)	2	7.67 ^{***}
Genotype (G)	3	8.41 ^{***}
T × G	6	4.54 ^{***}

^zMean separation within columns by Tukey-Kramer Adjusted P, $P < .05$.

^yn=number of plants in treatment.

^{***}Significant at $P < .001$.

Fig. 2. Influence of temperature by genotype interaction on mean width of *Meconopsis* flowers.

Means with the same letter are not significantly different according to Tukey-Kramer Adjusted P for multiple means, $P=0.05$.

Table 3: Influence of temperature and genotype on mean flower width of *Meconopsis*.

Variable	<i>n</i> ^y	Flower width (cm)
Temperature regime		
Cool	67	11.2a ^z
Intermediate	73	10.4a
Warm	55	9.7a
Genotype		
<i>M. betonicifolia</i>	54	10.8b
<i>M. G. S. Group</i>	56	9.0c
<i>M. 'Lingholm'</i>	42	10.6b
<i>M. punicea</i>	43	12.1a
ANOVA		
sources of variation	df	F value
Temperature (T)	2	5.92 ^{NS}
Genotype (G)	3	37.32 ^{***}
T × G	6	5.82 ^{***}

^zMean separation within columns by Tukey-Kramer Adjusted P, *P*<.05.

^ynumber of plants in treatment

^{NS, ***}Non-significant and significant at *P*<.001, respectively.

Table 4: Influence of temperature and genotype on mean flower stem diameter and mean flower height of *Meconopsis*.

Variable	<i>n</i> ^y	Flower stem diameter (cm)	Flower height (cm)
Temperature regime			
Cool	67	0.66a ^z	65.4a
Intermediate	73	0.54b	55.5ab
Warm	57	0.46b	48.2b
Genotype			
<i>M. betonicifolia</i>	54	0.67a	74.9a
<i>M. G. S. Group</i>	56	0.56b	55.4b
<i>M. 'Lingholm'</i>	43	0.71a	53.8b
<i>M. punicea</i>	44	0.29c	39.0c
ANOVA			
sources of variation	df	F value	F value
Temperature (T)	2	22.4 [*]	22.8 [*]
Genotype (G)	3	52.4 ^{***}	87.3 ^{***}
T × G	6	1.1 ^{NS}	.9 ^{NS}

^zMean separation within columns by Tukey-Kramer Adjusted P, *P*<.05.

^ynumber of plants in treatment

NS, *, ***Non-significant and significant at *P*<.05 and *P*<.001, respectively.

Table 5: Influence of temperature and genotype on mean canopy width for *Meconopsis* at first flower and harvest

Flower and harvest				
Variable	n ^y	Canopy width		Harvest (cm)
		First flower (cm)	n	
Temperature regime				
Cool	67	38.1a ^z	74	39.0a
Intermediate	73	38.2a	60	36.6a
Warm	56	34.1a	27	29.1a
Genotype				
<i>M. betonicifolia</i>	54	45.2a	47	39.7ab
<i>M. G. S. Group</i>	55	36.7b	40	35.3b
<i>M. 'Lingholm'</i>	43	42.4a	47	41.6a
<i>M. punicea</i>	44	22.0c	27	23.5c
ANOVA				
sources of variation	df	F value		F value
Temperature (T)	2	3.9 ^{NS}		2.9 ^{NS}
Genotype (G)	3	72.8 ^{***}		17.2 ^{***}
T × G	6	.23 ^{NS}		1.6 ^{NS}

^zMean separation within columns by Tukey-Kramer Adjusted P, *P*<.05.

^ynumber of plants in treatment

NS, ***Non-significant and significant at *P*<.001, respectively

Fig. 3: Influence of temperature by genotype interaction on number of basal leaves produced on *Meconopsis* at first flower.
Means with the same letter are not significantly different according to Tukey-Kramer Adjusted P for multiple means, $P=0.05$.

Table 6: Influence of temperature and genotype on number of basal, stem, and total leaves produced on *Meconopsis* at first flower

Number of leaves at first flower				
Variable	n ^y	Basal	Raceme	Total
Temperature regime				
Cool	67	39.2a ^z	7.8a	46.9a
Intermediate	73	35.0a	8.5a	43.5ab
Warm	57	29.6a	8.4a	38.0b
Genotype				
<i>M. betonicifolia</i>	54	40.9a	12.9a	53.8a
<i>M. G. S. Group</i>	56	28.5b	10.9b	39.4b
<i>M. 'Lingholm'</i>	43	32.6b	7.2c	39.9b
<i>M. punicea</i>	44	37.8ab	NA ^x	37.9b
ANOVA				
sources of variation	df	F value		
Temperature (T)	2	4.01 ^{NS}	.81 ^{NS}	4.64 ^{NS}
Genotype (G)	3	7.45 ^{***}	139.9 ^{***}	13.14 ^{***}
T × G	6	4.37 ^{***}	.66 ^{NS}	3.38 [*]

^zMean separation within columns by Tukey-Kramer Adjusted P, $P < .05$.

^ynumber of plants in treatment

^x*M. punicea* does not produce raceme leaves.

^{NS, *, ***} Non-significant and significant at $P < .05$, $P < .001$, respectively

Table 7: Influence of temperature and genotype on number of basal, stem, and total leaves produced on *Meconopsis* at harvest

Variable	n	Number of leaves at harvest		
		Basal	Raceme	Total
Temperature regime				
Cool	76	79.1a ^z	6.6a	85.8a
Intermediate	60	89.6a	7.5a	97.1a
Warm	28	74.6a	4.0b	78.5a
Genotype				
<i>M. betonicifolia</i>	47	85.0a	9.9a	94.8a
<i>M. G. S. Group</i>	42	58.0b	9.5a	67.4b
<i>M. 'Lingholm'</i>	49	93.6a	4.9b	98.3a
<i>M. punicea</i>	26	87.9a	NA ^y	87.9ab
ANOVA				
sources of variation	df	F value		
Temperature (T)	2	2.0 ^{NS}	5.8 ^{NS}	2.9 ^{NS}
Genotype (G)	3	7.9 ^{***}	30.3 ^{***}	6.4 ^{***}
T × G	6	1.4 ^{NS}	1.2 ^{NS}	1.5 ^{NS}

^zMean separation within columns by Tukey-Kramer Adjusted P, $P < 0.05$.

^ynumber of plants in treatment

^x*M. punicea* does not produce raceme leaves.

^{NS}, ^{*}, ^{***} Non-significant and significant at $P < 0.05$, $P < 0.001$, respectively

Table 8: Influence of temperature and genotype on mean fresh and dry weight for *Meconopsis* at harvest

Temperature	<i>n</i> ^y	Fresh weight (g)	Dry weight (g)
Cool	40	193.1a ^z	41.8a
Intermediate	36	148.2a	31.4ab
Warm	26	80.3a	20.6b
Genotype			
<i>M. betonicifolia</i>	29	172.8a	38.9ab
<i>M. G. S. Group</i>	26	111.5b	27.6bc
<i>M. 'Lingholm'</i>	29	222.7a	41.6a
<i>M. punicea</i>	18	55.1b	16.9c
ANOVA			
sources of variation	df	F value	
Temperature (T)	2	5.07 ^{NS}	7.93 ^{***}
Genotype (G)	3	19.36 ^{***}	6.10 ^{***}
T × G	6	2.20 ^{NS}	.81 ^{NS}

^zMean separation within columns by Tukey-Kramer Adjusted P, $P < .05$.

^ynumber of plants in treatment

NS, *** Non-significant and significant at $P < .001$

Table 9: Influence of temperature and genotype on mean net photosynthesis of *Meconopsis* in February 2001

Variable	n^y	$\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1x}$
Temperature regime		
Cool	73	19.8a ^z
Intermediate	72	17.0ab
Warm	63	12.0b
Genotype		
<i>M. betonicifolia</i>	59	16.2ab
<i>M. G. S. Group</i>	56	16.5ab
<i>M. 'Lingholm'</i>	55	17.3a
<i>M. punicea</i>	38	15.1b
ANOVA		
sources of variation	df	F value
Temperature (T)	2	10.74*
Genotype (G)	3	3.75*
T × G	6	4.29***

^zMean separation within columns by Tukey-Kramer Adjusted P, $P < .05$.

^ynumber of plants in treatment

^xPhotosynthesis measured as $\mu\text{mol CO}_2$ taken up per m^2 of leaf area per sec

*, *** Significant at $P < .05$ and $P < .001$, respectively.

Fig. 4- Influence of temperature by genotype interaction on mean net photosynthesis rate (P_n), measured in $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, for *Meconopsis* plants in February 2001. Means with the same letter are not significantly different according to Tukey-Kramer Adjusted P for multiple means, $P=0.05$.

Table 10: Influence of temperature and genotype on mean net photosynthesis of *Meconopsis* in March 2001.

Variable	<i>n</i> ^y	$\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1x}$
Temperature regime		
Cool	75	13.4a
Intermediate	66	10.1a
Warm	53	10.2a
Genotype		
<i>M. betonicifolia</i>	57	10.3b
<i>M. G. S. Group</i>	55	10.3b
<i>M. 'Lingholm'</i>	56	13.6a
<i>M. punicea</i>	26	10.8b
ANOVA		
sources of variation	df	F value
Temperature (T)	2	1.00 ^{NS}
Genotype (G)	3	15.12 ^{***}
T × G	6	1.50 ^{NS}

^aMean separation within columns by Tukey-Kramer Adjusted P, *P*<.05.

^yNumber of plants in treatment

^xPhotosynthesis measured as $\mu\text{mol CO}_2$ taken up per m^2 of leaf area per sec

^{NS}, ^{***}Non-significant and significant at *P*<.001, respectively.

Fig. 5- Influence of temperature by genotype interaction on mean net photosynthesis rate (P_n), measured in $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, for *Meconopsis* in March 2001.
Columns with the same letter are not significantly different according to Tukey-Kramer Adjusted P for multiple means, $P=0.05$.

Table 11: Average day and night temperatures outdoors and in each temperature regime during Experiment 2.

Temperature regime	Greenhouse compartments	Temperature (°C)					
		July		August		September	
		day	night	day	night	day	night
Outdoors		25.3 ^z	20.1	27.2	22.9	18.5	16.9
Cool	1	23.7	19.1	25.2	21.0	18.7	16.7
	2	23.1	18.4	24.9	20.8	18.5	16.2
Warm	1	28.2	21.8	28.9	23.2	20.6	18.0
	2	23.7	18.6	25.5	20.8	19.1	16.6

^zTemperatures are averages of measurements taken at 15 min intervals. Day measurements were taken during hours of recordable light.

Table 12: Mean number of *Meconopsis* plants surviving 41 and 55 days after placement in cool or warm greenhouse compartments on July 13, 2001.

Genotype ^z	Temperature regime	August 23	September 7
<i>M. betonicifolia</i>	Cool	6 ^z (2) ^y	4 (4)
	Warm	0 (0)	0 (0)
<i>M. G. S. Group</i>	Cool	4.5 (.5)	2.5 (2.5)
	Warm	0 (0)	0 (0)
<i>M. 'Lingholm'</i>	Cool	6 (0)	1 (1)
	Warm	0 (0)	0 (0)

^zMeans of 30 plants divided equally into two compartments for each treatment/ genotype combination.

^yNumbers in parenthesis equal standard error of the means.

DISCUSSION

This research showed that flowering, growth, and photosynthetic activity of *Meconopsis* genotypes were dependent on temperature with some responses genotype dependent.

Temperature effects on flowering

Flower number of *Meconopsis* was greater in the cool and intermediate temperature regimes than in the warm temperature regime (Fig. 1, Table 2) which was similar to studies by Maginnes and Langhans (1961) and Yuan *et al.* (1998). These studies demonstrated with both a tender perennial, *Antirrhinum majus* 'Jackpot', from 10 to 21°C (Maginnes and Langhans, 1961), and with a number of perennials, *Coreopsis*, *Rudbeckia*, and *Leucanthemum* (Yuan *et al.*, 1998), that cooler temperatures increased flower number.

Identification of an optimal temperature resulted in increased number of flowers in several studies and that for some plants, it has been shown that increasing heat, to a threshold temperature, may increase flower number (Yuan *et al.* 1998; Whitman *et al.*, 1997). While an increase in the forcing temperature to an optimal temperature in each of the previously mentioned studies resulted in an increased number of flowers, the number of flowers decreased as the temperature surpassed the threshold temperature. This may be due to genetic differences in the species studied.

Flower width of *Meconopsis* was not affected by temperature (Table 3). This is contrary to research by Bronden and Heins (1993), working with *Dahlia*, and Yuan *et al.* (1998), working

with a number of perennials, *Coreopsis*, *Rudbeckia*, and *Leucanthemum*, where flowers grown in cooler temperatures were larger than flowers grown in warmer temperatures. However, research by Durso and DeHertogh (1977), working with *Campanula*, showed flower diameter not being influenced by temperature. The optimum temperature for flowering is probably related to the growing conditions of the native area. For crops such as *Meconopsis* and *Campanula*, native to temperate alpine regions, the optimum temperature for growing and flowering the plants will be different than those plants from warmer climes, such as groundnut (*Arachis*) or cucumber (*Cucumis*).

Temperature effects on growth

This study showed *Meconopsis* flower stem height decreased as temperature increased from the cool to the warm temperature regime (Table 1). Similar results were found with length of the flowering spike in *Antirrhinum majus* L. 'Jackpot' which decreased as temperature increased from 10 to 21°C (Maginnes and Langhans, 1961). *Rudbeckia* flower height also decreased 50 percent with an increase in temperature as did *Leucanthemum* 'Snowcap' and *Coreopsis* 'Sunray' (Yuan *et al.*, 1998). Shoot length of *Dahlia* 'Royal Dahlietta Yellow' also decreased as temperature increased from 20 to 30°C (Bronden and Heins 1993).

Conversely, some plants show an increased stem height or length in reaction to increased temperature, as in *Oxypetalum* (Armitage *et al.* 1990), *Arachis* (Talwar *et al.* 1999) and *Cucumis sativus* 'Corona' (Papadopolous and Hao 2000). These plants are from warmer climates with a relatively long growing season. *Meconopsis* is native to a cooler climate with a shorter growing season. *Meconopsis* may have evolved to fit the cooler temperatures of their native habitat.

Stem diameter of plants is an important aspect of display. Strong flowering stems allow the plants to be supported without staking. Staking increases labor costs, decreases aesthetic appeal, and creates safety hazards and should be avoided when possible. Stem diameter of *Meconopsis* was greatest in the coolest temperature regime (Table 2). Armitage *et al.* (1990), working with *Oxypetalum caeruleum*, and Jull *et al.* (1999), working with *Chamaecyparis* also showed increased stem diameter at cooler temperatures.

While *Meconopsis* had more total leaves at first flower in the cool temperature regime than in the warm temperature regime (Table 6) the number of leaves at harvest was not different at the different temperature regimes (Table 7). The general body of research on the subject of leaf number in relation to temperature shows that leaf count increased as temperature increased, as with *Cucumis sativus* 'Corona', as day temperature increased from 18 to 25°C (Papadopolous and Hao, 2000), and *Capsicum annuum* 'Resistant Giant #4', as average daily temperature increased from 14 to 26°C (Si and Heins, 1996). Both *Cucumis* and *Capsicum* are heat loving plants native to growing regions with long growing seasons. *Meconopsis* is native to alpine regions with a short growing season and cool growing temperatures which could explain why the plants had a different reaction to temperature.

Plant fresh weight of *Meconopsis* showed no effect from temperature while plant dry weight was temperature dependent, being greatest in the cool temperature regime (Table 8). Fresh weight may have been more variable than dry weight because as much as 90 percent of fresh weight is water and water fluctuates in plants during the course of a day. If the plants were not at full saturation at the time of harvest, fresh weights would have varied. Previous research on the influence of temperature on dry weight has been variable. In some instances, an increase

in temperature has been shown to result in an increase in dry weight as with *Capsicum annuum* 'Resistant Giant #4' (Si and Heins, 1996). In another study with *Chamaecyparis*, shoot dry weight increased as temperature increased from 14 to 26°C but decreased as the temperature rose further to 30°C (Jull *et al.* 1999). *Meconopsis* may behave in the same manner as *Chamaecyparis* where dry weight increases as temperatures rise to an optimal level but decreases when temperatures rise higher.

Temperature effects on net photosynthetic response

Net photosynthesis in *Meconopsis* was highest in the cool temperature regime during February but showed no difference during March (Table 9 and Table 10). *Oxypetalum caeruleum* P_n rates increased as temperature increased from 14 to 22°C and then decreased as temperature increased further (Armitage *et al.* 1990). *Eucalyptus nitens* tolerated less heat because P_n rate at 10°C was $15 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, nearly double that at 35°C with a P_n rate of $8 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Battaglia, 1996). Two cultivars of *Cucumis sativus* had decreased leaf P_n rates as day temperatures increased (Papadopolous and Hao, 2000).

Lack of differences in P_n rates in March may have resulted from temperatures in the greenhouses that were not as close to the optimal setting. The temperatures in the greenhouses after February were difficult to maintain due to heat buildup from increasing light intensity, longer days, and higher outside temperatures. As the season progressed the temperature in the cool temperature regime greenhouses gravitated closer to the temperatures in the other two temperature regimes (Table 1).

In March the plants in all three temperature regimes were also developmentally similar. During February, the plants in the cooler temperature regimes were less developed and flowering

was just beginning compared to those in the warm temperature regime which were almost finished flowering. During March, all plants were flowering or past flower. This could explain the reduced P_n rates during March because all plants were in a similar developmental stage.

Two possible reasons for the P_n rate to be low in the warmer temperature regime during February 2001 are: first, that gross photosynthesis (P_g) in the cool temperature regime was high and respiration was low while the gross P_g in the warm temperature regime was low while respiration was low, or second, that gross P_g in the cool temperature regime was high and respiration was low while the gross P_g in the warm temperature regime was high while respiration was high. Both reasons would cause the P_n rate to be higher in the lower temperature regime. Research has shown that respiration rate increases exponentially as temperature increases within range within a range (Jiao *et al.*, 1997). These findings help explain the reason for higher rates of P_n in the cooler temperature regimes.

Reduced P_n at higher temperatures might be offset by increased light levels. Net photosynthesis measurements in this study were not taken at saturated light levels. The light source in the Li-Cor 6400, used for measuring P_n , was capable of emitting up to $2000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. In preliminary work, it appeared that the light saturation point for *M. 'Lingholm'* was close to $2500 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. The P_n rate at saturating light could not be measured. The light level inside the greenhouse was considerably lower with an average daily light level of $1170 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. P_n response might be larger at higher temperatures if the plants had more light and an adequate source of nutrients, CO_2 , and water.

Light levels above the light saturation point can provide excess light that cannot be processed by the photosynthetic system and cause a breakdown in the photosynthetic apparatus,

thus reducing P_n and lowering the quantum efficiency of the plant (Raghavendra, 1998). High light levels can cause heat stress when the plant does not have the ability to cope with the excess light which becomes heat. The plant does not cope well with the heat that is associated with the high light levels. Heat stress plays a significant role in the ability of a plant to photosynthesize.

The optimal temperature for maximal leaf P_n in *Alstroemeria* L. was around 20°C while the optimal temperature for whole plant growth was around 10-12°C (Jiao *et al.*, 1997). Root-zone cooling is one way to provide the proper cultural conditions to for flowering of *Alstroemeria*. The culture of *Alstroemeria* may be a good model for growing *Meconopsis* in the future because *Meconopsis* has a foliage basal rosette and the cool temperatures provided by root zone cooling may be beneficial to growth and flowering of *Meconopsis*.

Genotype effects

Meconopsis punicea was dramatically different than the other genotypes in this study, primarily due to the single flowering stems, smaller canopy, and red, drooping flowers. The *M. punicea* in this study conformed to the described habits of the species. These differences provided for some of the genotypic differences in the study.

The flower width of *M. punicea* varied across the temperature regimes but was greatest in the cool temperature regime. This provided for the temperature by genotype by temperature interaction for flower width because the other species did not vary across temperature regimes.

The P_n rates for *M. punicea* were similar to *M. betonicifolia* and *M. G.S.* Group but less than *M. 'Lingholm'* (Table 9 and Table 10). *Meconopsis punicea* reacted to temperature differently than the other genotypes providing for the temperature by genotype interaction that

occurred. *Meconopsis punicea* had an equally high P_n rate in the cool temperature regime as the other genotypes but had the lowest P_n rate in the warm temperature regime.

Meconopsis G.S. Group had the smallest flowers of genotypes studied (Table 3). Flower width of the three blue-flowered genotypes was consistent across the three temperature regimes. *Meconopsis* 'Lingholm' and *M. betonicifolia* had greater stem diameter than *M. G.S.* Group (Table 4). *Meconopsis betonicifolia* were taller than the other genotypes (Table 4). Many genera have one species that is taller than the others and *Meconopsis* is no exception. Many times cultivars are chosen for their height.

Meconopsis betonicifolia and *M. 'Lingholm'* had the largest canopy at first flower (Table 5); however, at harvest, *M. betonicifolia* was not larger than *M. G.S.* Group. *Meconopsis betonicifolia* was similar to *M. G.S.* Group at harvest and not at first flower because *M. G.S.* Group canopy shrank slightly from first flower to harvest while *M. betonicifolia* shrank considerably more. The shrinking of leaf canopy occurs due to the drying down of the lower leaves that were measured during first flower.

Meconopsis betonicifolia had more basal, raceme, and total leaves at first flower than the other blue-flowered genotypes (Table 6). At harvest, *M. G.S.* Group had considerably fewer basal leaves than the other three genotypes (Table 7). *Meconopsis betonicifolia* and *M. 'Lingholm'* had more raceme and total leaves at harvest than *M. G.S.* Group. *Meconopsis 'Lingholm'* and *M. betonicifolia* had larger dry weights than the other genotypes indicating the plants are genetically larger or that they are best adapted to the environment tested (Table 8).

In February 2001, *M. 'Lingholm'* had similar P_n rates to both *M. betonicifolia* and *M. G.S.* Group (Table 9). In March 2001, *M. 'Lingholm'* had higher P_n rate than the other three

genotypes, which were similar in P_n rate (Table 10). *Meconopsis betonicifolia* and *M. G.S.* Group had similar P_n rates across all three temperature regimes while *M. 'Lingholm'* was had the greatest P_n rates in the cool temperature regime and the least P_n rates in the warm temperature regime.

Meconopsis 'Lingholm' was the best genotype for winter forcing in this study. The combined characteristics of thick stems, wide flowers, tall stems, and wide canopy made this genotype favorable to *M. betonicifolia* and *M. G.S.* Group. *Meconopsis betonicifolia* was a strong genotype due to the height, flower width, number of flowers, and canopy width; however, the flower stems were not as thick as *M. 'Lingholm'* and, although *M. betonicifolia* had more flowers than *M. 'Lingholm'*, the display was not more effective. *Meconopsis G.S.* Group was not a strong genotype because the genotype was inferior in most traits to *M. 'Lingholm'* and *M. betonicifolia*.

Experiment 2

In the second experiment, the growing conditions were simply too warm for *Meconopsis* which proved that *Meconopsis* cannot handle the summer heat associated with the Delaware Valley. Temperatures exceeded 30°C regularly and this killed the plants.

One nursery person in Scotland claims that *Meconopsis* can be grown in 95°F (35°C) if humidity is high as well (Christie, 2001). Strybing Arboretum, located in San Francisco's Golden Gate Park, is able to grow *Meconopsis* as a foliage plant in a relatively warm climate. This may be because the fog and cool nights provide a favorable climate for growing. Further research could be done on exactly how much shade and moisture is needed to grow *Meconopsis* in a warm climate such as is common in the Mid-Atlantic region.

CONCLUSION AND RECOMMENDATIONS

The results collectively indicate that 1) *Meconopsis* requires a relatively narrow set of conditions for good flowering, with good defined as many flower buds and satisfactory plant height, 2) *Meconopsis* can be grown under conditions that can be maintained in a greenhouse environment (at least during winter months), and 3) that the resultant *Meconopsis* plants are of display quality.

Unless a garden is able to keep a consistently cool temperature in the summer it would be best to force *Meconopsis* for winter display in the Delaware Valley and any region with a similar climate. The plants in the study were given six weeks of vernalization to assure flowering. Future studies should investigate the necessity of vernalization.

In order to produce conservatory display-quality plants these steps must be followed: Purchase plants that are at least one year of age in the autumn and then cool them at 4 to 6°C for at least six weeks for vernalization. Transplant into 3.8 liter containers in December and place them in either the cool or intermediate temperature regimes as defined above. The potting medium should drain well and the medium should be kept moist. The plants should start to bloom by early February under these conditions.

There are strengths and weaknesses of all the genotypes that were tested. Based on number of flowers and flower width, *M. punicea* appears to be one of the stronger genotypes. However, the drooping form of the flowers and short stature prevented *M. punicea* from

consideration as one of the stronger plants for display. *Meconopsis punicea* also had smaller stem diameter, fragile petals that often dropped the day of opening, and the red flower color is not as coveted in a garden plant.

Meconopsis betonicifolia had a large stature but the flower stem was thinner than *M. 'Lingholm'*. The flower color of *M. betonicifolia* seemed more variable (personal observation) than *M. 'Lingholm'*. While *M. betonicifolia* had more flowers than *M. 'Lingholm'*, the floral display was not more effective.

Meconopsis G.S. Group was the weakest of the three blue genotypes. The plants were smaller and the floral effect was poor. There was considerable variation in the *M. G.S.* Group plants and this can be traced to their unsure past where the parentage of the plants is inconclusive.

Based upon all factors of plant growth, especially stem diameter and canopy width, and blue flower color, *M. 'Lingholm'* was the most desirable genotype for display. The higher photosynthesis, fresh weight, and dry weight of *M. 'Lingholm'* appear to be indicators of improved performance under the cool temperature regime. *Meconopsis 'Lingholm'* also appeared to have a more intense blue flower color than the other blue-flowered genotypes (personal observation).

Meconopsis could make an impact as a forced display crop in a public garden, as a spring bedding plant, or as a cut flower in the Delaware Valley. Increased research could dispel some of the rumors about the difficulty of growing plants in the genus. These plants could have quite an impact on the world of horticulture with their size, habit, and wonderful blue color.

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APPENDIX A: A SELECTION OF SPECIES, CULTIVARS, AND VARIETIES OF *MECONOPSIS*

The following is a list containing photographs of *Meconopsis* the author has seen in cultivation.

Meconopsis betonicifolia

Meconopsis betonicifolia 'Hensol Violet'

Meconopsis betonicifolia var. *alba*

Meconopsis delavayi

Meconopsis grandis

Meconopsis horridula

Meconopsis nepaulensis

Meconopsis quintuplinervia

Meconopsis superba

Fertile Blue Group

Meconopsis 'Lingholm'

often mislabeled as *xsheldonii*, synonymous with *M.* 'Blue Ice', *M.* 'Corrennie'

Meconopsis 'Ormswell'

Meconopsis 'Slieve Donard'

initially known as *M. grandis* 'Prain's Variety'

Crawdson Hybrids

Meconopsis Crawdson Hybrids

Meconopsis 'Miss Jebb'

George Sherriff Group

Meconopsis 'Jimmy Bayne'

Meconopsis 'GS600'

Other hybrids and cultivars

Meconopsis 'Ascreavie'

Meconopsis 'Houndswood'

Meconopsis 'Willy Duncan'

APPENDIX B: A BREEDING STRATEGY FOR THE GENUS *MECONOPSIS* (VIG.)

A breeding strategy for the genus *Meconopsis* (Vig.)

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Rationale

There are thousands of species of ornamental plants available for the garden in the United States. One could argue that we have an adequate supply of plant varieties to accommodate any landscape situation or need. Based on this promise, why would it be beneficial to grow *Meconopsis* for the garden? Why would one more plant benefit the industry and home-owner? Why would the world of horticulture want to breed another variety of plant when there are so many other options currently available? The answer is that *Meconopsis* offer improvements in flower and form over plants currently available to the gardener.

Meconopsis betonicifolia was first introduced in 1924 by Frank Kingdon Ward. "Ward knew that the blue poppy, the most famous garden plant from south-east Tibet, was really a significant plant, with enormous potential for the garden" (Cox 2001). From the first introduction until today *Meconopsis* has remained an extremely popular plant. In fact, as early as 1937 the blue poppy had garnered international attention. In 1937 the hybrid *Meconopsis xsheldonii* won the Award of Merit from the Royal Horticulture Society (Jermyn 2001). Christopher Grey-Wilson may have best summed the genus with the comment "Of all the varied members of the poppy family, none has created such excitement and intrigue as the famous blue poppies. No other genus in the Papaveraceae has plants with blue flowers and, for this alone, they have long stolen the hearts of gardeners" (Grey-Wilson 2001).

It is evident that *Meconopsis* is important as a genus because in 1998 the *Meconopsis* Group was formed to try to clarify the identity and nomenclature of the perennial blue *Meconopsis* currently being grown in gardens (Jermyn 2001). Attention of this magnitude justifies further study into the breeding of this wonderful plant.

Some feel fortunate simply to be able to grow the blue poppies and their relatives. George Straley stated that “in the Pacific Northwest we are fortunate to grow the blue poppies and their relatives—some of the world’s most spectacular flowers” (Straley 1987).

The difficulty in growing plants in the genus *Meconopsis* has led to claims that *Meconopsis betonicifolia* is “among the most beautiful and frustrating of all plants” (Malitz 1996). Breeding *Meconopsis* to tolerate a wider regime of environments would lead to much joy and relief among plant lovers in many places- especially in places with warmer summer climates not adequate for growing *Meconopsis*.

“Although the world germplasm potential is immense, relatively little concentrated effort is being made to develop superior landscape plant materials” (Pellett 1983). Most of the focus of plant breeding is toward flower color or size. Discovering how to adapt the blue poppy to different environments could help the plant breeding field progress. “It is the primary goal in improvement of landscape plant materials to combine desirable aesthetic and utilitarian qualities with ability to tolerate environmental stresses” (Pellett 1983). This is especially true for *Meconopsis*.

About *Meconopsis*

Meconopsis (Viguiet) is the family Papaveraceae and is named for the Greek words *mekon*, meaning a poppy, and *-opsis*, indicating a resemblance (Coombes 1997). The genus was first established by L.A.G. Viguiet, Montpellier, in 1814, based upon Linnaeus’ *Papaver cambricum*, which was transferred to the new genus (now *Meconopsis cambricum*) (Grey-Wilson 2001). “The species most easily raised from seed and most widely available is

Meconopsis betonicifolia, Kingdon Ward's introduction from Tumbatse in south-eastern Tibet in 1924" (Jermyn 2001). *Meconopsis* is considered to have at least 15 species in the subfamily *Papaveroideae* (Kaderiet *et al.* 1997).

There is a dispute as to how many species there are in the family: either 43 or close to 50. Kaderiet *et al.* (1997), and Norton *et al.* (Norton *et al.* 1986) list 47 to 49 species while others list 43 (Sulaiman and Babu 1996, Grey-Wilson 2001, and Jermyn 2001). The finest species for the garden is considered to be *M. xsheldonii* (Jermyn 2001) which is a cross between *M. grandis* and *M. betonicifolia* made in 1934 by W. G. Sheldon of England (Jermyn 2001). Gerald Straley states that only half are seen in the garden in the North America (Straley 1987).

The genus *Meconopsis* is divided into two sub-genera and several subsections of the subgenera. The subgenera are the Subgenus *Dioscogyne* G. Taylor and the Subgenus *Eumeconopsis* (Prain) Fedde (Grey-Wilson 2001). Keys have been made to differentiate the species and are available to the average gardener in books such as *Poppies* by Grey-Wilson (2001).

There are also many cultivars of *Meconopsis*. The most well known hybrid is *M. xsheldonii* but there are many other good cultivars available. The Appendix lists some of the cultivars and their characteristics.

The environment where *Meconopsis* grow can give a great deal of information as to the requirements of the plants in cultivation. The native habitat is variable for the type of *Meconopsis* one is attempting to cultivate or breed. All but one species, *M. cambrica*, are restricted to the Himalayas between 2100 and 5800 m altitude (Sulaiman and Babu 1996). Plants from the genus grow in screes, in scrub, on moraines or cliffs, on gentle slopes, in alpine

meadows, or in woodlands (Grey-Wilson 2001). Plants may grow in temperate zones, sub-alpine zones, or alpine zones (Jermyn 2001). Most species, though not exclusively, prefer soil with an acidic pH, high organic matter and NPK concentrations (Sulaiman and Babu 1996).

Gardeners have tried growing *Meconopsis* in a variety of situations as well. They recognize the limited regime of the species but often have misconceptions of the growing conditions. Dan Hinkley states correctly that the genus needs “cool summer climates only in zones 3-8” (Hinkley 1999). I have found *Meconopsis* to tolerate quite variable soil conditions but must have a cool and moist environment. One Scottish expert on the genus suggests that *Meconopsis* could be grown in 95° F if it has mist and continually moist soil (Christie 2001). As fickle as the genus can be there are many more misconceptions as to what they can tolerate, especially for germinating seeds.

Insects can be a problem and white flies and aphids are a common parasite. Slugs are damaging or even deadly to the young seedlings (Straley 1987). A clue to the pollination of the genus falls on the large brightly colored flowers which suggest insect pollination (Norton *et al.* 1986).

Many of the plants in the genus are considered to be monocarpic, which means that they flower only once, set seed, and die after flowering. The other plants in the genus are considered perennials although some remark that some of those perennial are short-lived (Straley 1987).

The habit of *Meconopsis* varies widely. Most species produce large basal rosettes of leaves that develop over many months or years. These rosettes eventually produce flower stems ranging from several inches tall with one flower to six feet tall with many flowers. With all

Meconopsis the flowering begins at the top of the flower scape and proceeds toward the bottom of the scape (Straley 1987).

The true benefit of the genus is that *Meconopsis* flower color covers all the colors of the rainbow. The flowers, held drooping or outward-facing, range in color from white to yellow, red, blue, violet, and purple (Straley 1987). However, the flowers that give the genus its reputation are blue in color.

What gives plants the blue color are the chemical pigments anthocyanins that reside in the vacuoles (Geneve 1996). Anthocyanins usually appear as red, pink, purple, and blue. Anthocyanins are formed when a sugar (usually glucose) is added to a group of compounds called anthocyanidins. The anthocyanidin that provides the blue color is delphinidin (Geneve 1996). Unlike borage, *Mertensia*, or some of the other blue flowers, *Meconopsis* do not change color from blue to pink as the pH of the vacuole changes. The flowers are also not pink in bud as some of the weaker blue flowers are.

There are genetic considerations for breeding *Meconopsis*. Some work has been done on the chromosome and ploidy levels for some of the species of *Meconopsis*. The chromosome count is variable between species and within at least one species. For example, *M. cambrica* has been identified with both $n=11$ and $n=14$ chromosome levels (Norton *et al.* 1986). *M. betonicifolia* shows the variability of chromosomes in the genus with $n=40$ (Norton *et al.* 1986). *M. quintuplinervia* has approximately 42 chromosomes (Norton *et al.* 1986). The species also have variable ploidy levels where *M. cambrica* and *M. villosa* are tetraploids while *M. quintuplinervia* and *M. betonicifolia* are nearly duodecaploids (Norton *et al.* 1986). The variability of inter-specific chromosomes suggests that aneuploidy has occurred.

The differing levels of chromosomes and ploidy levels affect the ability for the species to intercross. Norton and Yong studied this effect in a few of the species mentioned above (Norton *et al.* 1986). Norton *et al.* crossed the species *cambrica*, *villosa*, *betonicifolia*, *horridula*, *quintuplinervia*, and *aculeate*. What was discovered is that the greater the difference in chromosome ploidy level the less compatible the species are for crossing (Norton *et al.* 1986). In the research, a difference of ploidy level of 8 led to little viable seed. However, no difference in ploidy level produced much more viable seed. A ploidy difference of 4 produced some viable seed but not as much as the crosses with no difference in ploidy level (Norton *et al.* 1986). Norton and Yong claim that pollen type does not have an effect on compatibility (Norton *et al.* 1986).

The low seed set occurring from the crossing of species with a ploidy difference may not be due to a problem with chromosome incompatibility, but rather may be a problem with the pollen. In the research by Norton *et al.*, the pollen stainability rates are above ninety percent for all of the species tested but none of the species had germination rates above 40 percent (1986). Three of the species had below 20 percent germination and one had no germination. It is difficult to judge combining ability based upon ploidy level if plants cannot even self-pollinate.

Allelic frequencies of *M. paniculata*, *M. simplicifolia*, and *M. sinuate* are more or less similar at most loci (Sulaiman and Babu 1996). This is probably due to the fact that the natural populations are small and separated by geographical barriers (Sulaiman and Babu 1996). Therefore, the absence of gene flow between populations leads to low genetic diversity. While there are many species of *Meconopsis*, the populations of individual species are homogeneous. This isolation could also explain the difference in chromosome level within a species.

Ideotype

When defining a breeding strategy for a plant the breeder always has an ideotype in mind. This model plant type, which may never be attainable, should be specified as a goal for the breeder to work toward. Ideotype depends upon the situation for which the plant is being bred. This may be different for the parties involved and the breeder should be willing to change or adjust goals as situations change. What traits should a breeder set as a goal for *Meconopsis*?

The following is an ideotype for most ornamental species, as outlined in *Genetics and Breeding of Ornamental Species* (Harding *et al.* 1991). The common ideotype for ornamental plants is:

- Rapid rooting potential- to reduce propagation time
- Large, horizontally arranged leaves- to give maximum ground cover during the early stages of growth
- A high leaf initiation rate in long days- to reduce the length of the leaf initiation phase prior to flowering
- Good internode extension- to reduce the number of leaves required before flower induction can begin
- A low minimum leaf number- so that flower induction can begin immediately short days start, with little or no further leaf production
- Rapid flower bud development in short days and, ideally, in long days- to reduce overall cropping time

- Little or no flower delay at temperatures above and below optimum- to improve predictability of cropping
- Low competitive ability- to reduce crop variability
- Strong apical dominance, but with rapid and uniform release of lateral meristems from dominance after removal of the vegetative growing point or after initiation of a terminal flower
- High maximum leaf number in long days- to reduce the frequency of low value, prematurely budded compound sprays
- Moderate peduncle extension- to improve visual appeal
- Strong peduncles and stems, able to take up water after a period boxed- to enhance retailer and customer satisfaction
- Pink blooms- to facilitate the development of color sports; all colors can be derived from pink

Not mentioned but also a concern to the industry is pest and disease resistance.

The ideotype for *Meconopsis* is more specific than the ideotype for plants in the field of horticulture in general. While the field of horticulture may have different ideotypes for individual species of *Meconopsis*, there are common ideotypes between the species such as:

- a variety of true colors, especially blue
- heat tolerance for perenniality in a warm summer from zone 3 to zone 8 climates
- more floriferous plants
- earlier flowering season

- longer flowering season
- consistency in size, habit, and foliage color
- sturdier stalks
- quick production and reproduction
- tall size
- good foliage color
- evergreen foliage
- more/less leaf hairs depending on the effect or purpose
- insect and disease resistance

Longwood Gardens has a certain ideotype for *Meconopsis* that is close to the industry ideotype. Longwood would like a *Meconopsis* with the following characteristics:

- rich, true blue color- some plants do not have as rich of a blue color as others
- heat tolerance for perenniality in a warm summer zone 6 climate- *Meconopsis* will currently not tolerate the summer heat in the Delaware Valley
- more floriferous plants- Longwood would like plants that have many flowers to have a larger floral effect
- longer flowering season- Longwood would like to use plants for a long period of time in display
- consistency in size, habit, and foliage color- Longwood uses plants that are uniform in size, habit, and color of foliage
- consistency in growth- consistent, uniform plants are easy to predict for cropping

- sturdier stalks- plants that do not need staking are good for display
- quick production and reproduction- long growing times lead to higher costs for labor and production, this would be good to avoid
- tall size- Longwood prefers plants with a tall stature so that they do not appear dwarfed in the immense size of the conservatories
- good foliage color- foliage color that properly complements the flower color is critical for a proper floral effect
- insect and disease resistance- Longwood would prefer to avoid spraying or using chemicals for disease and pest control

The ideotype has been defined. It is time to examine the ways to achieve the ideotype.

How to achieve these goals

Ornamental plant breeding has occurred around the world for centuries but it has often not been as effective as possible. In China, plant breeding has such problems as the aim of breeding, selection of appropriate original materials for breeding, the criteria for evaluating new cultivars, and regional testing before release of a new cultivar (Chen *et al.* 1995). These problems happen in the United States as well.

The ideotypes for *Meconopsis* have been defined. How would a breeder achieve these ideotype with the limitations that occur in the genus? The breeder must use the available gene pool.

It is important for a breeder to have a wide variety of genetic resources from which to draw. There are three main gene pools from which a *Meconopsis* breeder could realistically use to breed. The first is to breed within the species by selecting for favorable traits and then crossing to favorable phenotypes that have the wanted characteristics. This could mean growing large numbers of intra-specific hybrids to select for traits such as intensity of flower color, hairiness, leaf color, or sturdy stalks. The Appendix provides a list of cultivars that could provide positive traits.

The second method is to breed inter-specifically within the genus to select favorable traits from other species of *Meconopsis*. This method could work for variations in height, ability to propagate by seed or by division, adding flower color to a species that does not normally produce that color, heat tolerance, and foliage color. A small number of the genus has been crossed together and the specific and general combining ability for those species has been determined. This should happen with all the species of ornamental importance, or species that can offer novel traits for *Meconopsis* such as heat tolerance in *M. cambrica*. Plants with similar ploidy level are more likely to be compatible crosses but it is not impossible for crossing plants with different ploidy levels- especially with the technology to rescue fertilized embryos.

The third method for breeding is to breed make inter-generic crosses between the genera in the family Papaveraceae. This may include Papaveraceae that can offer heat tolerance such as *Roemeria*, *Argemone*, *Papaver*, or *Eshscholtzia*. By making the crosses by hand and then excising fertile embryos, this method could work. Breeders should also be aware of the chromosome and ploidy level of the genus and species to which the *Meconopsis* is bred.

There are a myriad of opportunities for this genus that has such a large gene pool. The methods that could be used for creating the *Meconopsis* ideotype are hybrid breeding, backcrossing, cell fusion, cell suspension, mutation, haploid breeding, embryo rescue use of chimeras, and gene transfer.

It is important for a *Meconopsis* breeder to determine broad and narrow based heritability. In other ornamental crops, there are certain traits that show high heritability. These characteristics are days to flower, flowers per plant, maximum leaf number, internode length, and cut flower yield (Harding *et al.* 1991).

Another factor affecting breeding is heterosis. Heterosis has been shown to occur in *Papaver somniferum*, a member of the Papaveraceae (Singh *et al.* 1999). IN this case the researchers identified the best general combiners and most heterotic hybrids with low inbreeding depression (Singh *et al.* 1999). This is a good model for *Meconopsis* to follow. As stated earlier, it would be good for a *Meconopsis* breeder to cross species that might be of value to other species of value to see what characteristics may emerge. Crosses that appear to be of value, or have favorable characteristics, should be inbred to fix good characteristics. Then these inbred lines can be crossed to combine favorable traits.

This is a possible solution for improving both between inter- and intra-specific breeding. Intra-specific breeding may not be effective because often the species are homozygous due to their aforementioned geographic isolation. If intra-specific crosses are made then the breeder should attempt to cross plants that originated from separate geographic areas.

The breeder can also complete a *line x tester* analysis to determine the species that provide the most benefit to hybrids. However, this may not provide much benefit because there are not many hybrids available.

Backcrossing is a method of breeding that could work extremely well. If a *Meconopsis* species or phenotype has higher heat tolerance, than the breeder can make a cross between a species with heat tolerance and one with favorable aesthetic characteristics, and the continually cross back to the recurrent parent with favorable aesthetic features. Eventually, the line will become close in appearance to the aesthetic qualities with the addition to heat tolerance. This will work for intra- and inter-specific hybrids but may even work with inter-generic hybrids. However, effort may have to be made to rescue embryos in situations where the plant has been pollinated but the zygote fails to form.

Embryo rescue operations consist of excising only the embryo, or the ovary containing the embryo, and growing that small segment of the plant to a full size plant (Malitz 1996).

The use of haploidy from anther, ovary, or ovule center may be a possible way to overcome genetic differences in or between *Meconopsis* or other genera. If an octoploid *Meconopsis* species is grown as a haploid then it might have a better chance to cross to a regular tetraploid species because they would both, theoretically, have the same number of chromosomes. Haploidy can also help identify the actual genes for a plant. There are no recessive genes for a plant to express in further breeding (Malitz 1996).

It would be possible to attempt to create a chimera from a species of *Meconopsis* and another plant in Papaveraceae, or any other genus for that matter. A chimera is formed when the somatic cells of two separate genera or species fuse (Malitz 1996). This is often how variegation

occurs. Chimeras can arise when a somatic cell mutates and all ensuing clones bear the chimera. Another way that *Meconopsis* could produce a chimera is to grow a plant in vitro with another species or genus. With prodding, these plants may fuse and form a new variety or hybrid (Malitz 1996).

Cell suspensions may be a promising solution to heat tolerance in *Meconopsis*. This technique has worked for cold-tolerance and involves scattering cells through a growth medium suspension in vitro (Malitz 1996). The in vitro vessel is subjected to high temperatures and any surviving cells have the possibility to form a complete, heat tolerant plant.

The same theory is behind the technique of exposing pollen to high heat levels. If the traits of the plant are expressed in the pollen, then this is a way to select for heat tolerance.

A common method for creating variations is to mutate seeds, pollen, or plant material. Mutation can occur from radiation, a sharp temperature transition, presence of chemicals, or an electrical charge (Malitz 1996). The mutations can affect individual or multiple genes or the entire chromosome. The process does not have to great expense. A common method of mutation is to irradiate pollen or seed in a microwave.

Colchicine can also induce polyploidy. Polyploidy can lead to larger flowers, double petals, and more robust plants. In general, polyploidy is thought to lead to gigantism- especially in ornamentals (Malitz 1996). This has occurred in crops such as petunia and *Hibiscus* (Malitz 1996).

Gene transfer is the last method of improving the genetic quality of *Meconopsis*. Gene transfer in the process of introducing new genes into the chromosome of the plant (Malitz 1996). Inserted genes have already been used in many plants but typically only those of agronomic

importance. The Bt gene would be an obvious candidate for pest resistance in *Meconopsis*.

There also may be a gene transfer that could instill heat tolerance in *Meconopsis*.

There are other ways methods for breeding but the above methods seem to have the most promise for *Meconopsis*. The idea is to provide a plant that is adaptable to a wider range of environments. This is why environmental stresses have been the focus of the breeding methods.

A Model for the future

The key to breeding *Meconopsis* in the future is to work together. The first step is to identify all possible information about the genus. All plants should have their chromosomes identified, their ploidy levels identified, and heritability should be known. The *Meconopsis* Group should identify institutions and individuals that would be interested in working on a breeding program. The different institutions should then share the tasks of identifying genetics, breeding the plants, and testing the progeny. Several institutions can already be identified as having an interest in improved cultivars. Longwood Gardens, University of British Columbia Botanic Gardens, Edinburgh Botanic Garden, and Strybing Arboretum are a few examples of institutions that are already growing *Meconopsis* but may use improved plant varieties.

The genome of *Meconopsis* has much to offer the field of horticulture. The potential of the genus has not been tapped. The next few years should add much knowledge to the genus and plant breeding in general. As researchers discover more about genes and their interaction, then breeders on either the basic or biotech level may be able to improve the stress tolerance of the genus. It is a promising future for this plant that has stolen the hearts of so many gardeners.

Appendix

Cultivated Hybrids and Varieties of *Meconopsis*

The Meconopsis Group has grouped and renamed cultivars to clear confusion of mislabeled plants.

Fertile Blue Group

xsheldonii [Ryovan]- cultivar sold by Herronswood Nursery, probably 'Lingholm'

'Aberchalder Form'-

'Lingholm'- often labeled *xsheldonii*, syn. 'Blue Ice', 'Corrennie'

'Miss Dickson'

'Ormswell'

'Slieve Donard'- initially called *M. grandis* 'Prain's Variety'

Crewdson Hybrids

'Miss Jebb'

Kingsbarn Hybrids

Infertile Blue Group

'Bobby Masterson'- syn. 'Betty Dream Poppy', 'Betty Sherriff'

'Cruikshank'-

'Maggie Sharp'- unusually pale blue flowers

George Sherriff Group

'Jimmy Bayne'-

'Branklyn'-

'GS600'-

Other hybrids and cultivars

xharleyana- (*M. simplicifolia* X *M. integrifolia*)

xhybrida- (*M. simplicifolia* X *M. grandis*)

xsheldonii- (*M. betonicifolia* X *M. grandis*) Sterile hybrid.

M. betonicifolia 'Hensol Violet'

‘Harlow Carr Strain’
var. *alba*

M. cambrica var. *aurantica*- a form with orange flowers

‘Flore Plena Aurantica’- the orange counterpart to ‘Flore Plena’

‘Flore Plena’- a form with semi-double yellow flowers

‘Frances Perry’- single flower variant with deep orange-crimson flowers

‘Muriel Brown’- semi-double red flowers

‘Rubra’- probably syn. to ‘Francis Perry’

M. grandis ‘Alba’- white form

‘Keillour Crimson’- dark purple flowers

‘Nepal Form’- bluish purple flower, vigorous

‘Sikkim Form’- pale leaves and small purpleish-blue flowers

M. quintuplinervia ‘Kaye’s Compact Form’- compact, close rosettes

‘Ascreavie’-

‘Dawyck’-

‘Willy Duncan’- taller form with larger, almost cupped flowers

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APPENDIX C: INFLUENCE OF *MECONOPSIS* SEED AGE ON FINAL PERCENT OF SEEDS WITH EMERGED RADICALS AND FINAL PERCENT OF SEEDS GERMINATED 28 DAYS AFTER SOWING

INTRODUCTION

Empirical evidence suggests *Meconopsis* seed is short-lived, meaning viability decreases rapidly after maturity (Cobb, 1990). However, data is not available indicating the actual timeframe over which viability is lost. This experiment evaluated the three blue-flowering genotypes of *Meconopsis*, *M. betonicifolia*, *M. George Sherriff Group*, and *M. 'Lingholm'* for viability four, six, and eight months after seed maturity.

MATERIALS AND METHODS

The seed was gathered from plants at the Blue Poppy Nursery in Palmer, Alaska in July 2000. The seed was stored at 1°C in a cooler beginning at harvest excepting shipping to Longwood Gardens. The seed was placed onto wetted blotter paper in seed germination boxes. Seeds were checked daily for moisture and the blotter paper was rewetted when it dried. The temperature of the germination chamber was 21°C.

For the seed sown after four months, there were 25 seeds in each replicate, with four replicates. For the seed sown after six and eight months, there were 50 seeds in each replicate. Number of emerging radicals and seeds germinating was counted after 7, 14, 17, 19, 21, 24, 26, and 28 days. Germinated seeds were removed from the experiment when counted.

RESULTS

Seed of the three genotypes of *Meconopsis* showed a decreased rate of radical emergence and germination as the seed aged (Fig. 1). Radical emergence and seed germination also occurred more slowly as seed aged. Radical emergence appeared to be similar for all three

genotypes for each month tested except for *M. 'Lingholm'* after 6 months, which appeared higher than the other genotypes. Radical emergence was reduced 10 to 30% between 4 and 8 months.

Meconopsis betonicifolia lost 45 to 50% germination between 4 and 6 months while *M. G.S.* Group germination dropped 30%. Germination appeared to be similar for all three genotypes for each month tested except for *M. 'Lingholm'* after 6 months, which appeared higher than the other genotypes. *Meconopsis 'Lingholm'* appeared to have the highest rate of germination and appeared to be less affected by seed age between 4 and 6 months. However, after 8 months the seed germination rates of *M. 'Lingholm'* were similar to the other genotypes.

DISCUSSION

As expected, seed germination rates decreased as the seed aged. The germination rates are higher than reported by some of the literature. The germination temperature is also higher than in previously reported literature on the subject. It may be that the temperature at which individuals were reporting poor germination was too low for optimum germination. It is also likely that the seed was not fresh and may have been more than 8 months old.

BIBLIOGRAPHY

Cobb, J. 1989. The genus *Meconopsis*. Timber Press, Portland.

Fig. 1. Influence of *Meconopsis* seed age on final percent of seeds with emerged radicals and final percent of seeds germinated 28 days after sowing.

APPENDIX D: A *MECONOPSIS* TISSUE CULTURE MEDIA TRIAL

INTRODUCTION

The hybrids and cultivars of blue-flowering *Meconopsis* are extremely confused in the trade. For this reason, many of the *Meconopsis* that are in the horticultural trade are incorrectly identified. Also, some cultivars of *Meconopsis* are sterile. While the Meconopsis Group is working to sort out the problems of the big, perennial blue poppies, plants are still circulated in the United States with incorrect identification.

Due to the problems with cultivar identification and sterility, it would be good for the horticultural industry to have a method of tissue culture for *Meconopsis*. In order to reproduce some of the favorable cultivars, these sterile cultivars must be reproduced asexually. Division of *Meconopsis* is possible but the process may take several years to produce just a few additional plants. Tissue culture of *Meconopsis* is a possible solution to the problems with sterility and slow asexual reproduction.

A study was completed in India that examined the possibility of reproducing some species of *Meconopsis* in vitro in order to conserve germplasm (Sulaiman and Babu, 1993). The experiment showed success and it would be good to follow the procedure set forth by that study.

MATERIALS AND METHODS

During the course of the experiment two separate tissue culture media were used. One medium used IBA (Table 1) as the hormone while the other medium used GA₃ (Table 2). 500 ml of both media were made.

Apical meristems of the genotypes *M. betonicifolia*, *M. G.S. Group*, and *M. 'Linholm'* were all isolated for tissue culture. The meristem tissue was sterilized in a bleach solution for 20 minutes after harvesting. The

The plants were started on the IBA medium on November 17, 2001. 6 *M. betonicifolia*, 4 *M. G.S. Group*, and 3 *M. 'Linholm'* were transferred on December 18, 2001 onto the IBA medium. The remaining cultures were contaminated or rotting and were discarded. 3 *M. betonicifolia*, 4 *M. G.S. Group*, and 1 *M. 'Linholm'* were transferred on December 18, 2001 onto the GA₃ medium. The remaining cultures were contaminated or rotting and were discarded.

BIBLIOGRAPHY

Sulaiman, I. M., and C. R. Babu. 1996. Enzyme polymorphism analyses in three endangered species of Himalayan poppy, *Meconopsis* (Papaveraceae). Genetic Resources and Crop Evaluation. 43: 351-356.

Table 1: Meconopsis multiplication medium using IBA as the auxin

Major salts	Amount used in 1 L of 10X stock	Amount of stock used in 1 L of medium	Amount used ²
NH ₄ NO ₃	16.5 g		
KNO ₃	19.0 g		
CaCl ₂ 2H ₂ O	4.4 g	100 ml	50 ml
MgSO ₄ 7H ₂ O	3.7 g		
KH ₂ PO ₄	1.7 g		
Minor salts	Amount used in 1 L of 100X stock	Amount of stock used in 1 L of medium	
MnSO ₄ H ₂ O	1.69 g		
ZnSO ₄ 7H ₂ O	.86 g		
H ₃ BO ₃	.62 g		
CoCl ₂ 6H ₂ O	2.5 mg	10 ml	5 ml
CuSO ₄ 5H ₂ O	2.5 mg		
Na ₂ MoO ₄ 2H ₂ O	.025 mg		
KI	.083 mg		
Organics			
myo-inositol dissolved in H ₂ O		100 mg	50 mg
Fe EDTA dissolved in H ₂ O		64 mg	32 mg
Glycine	2.0 g/L	1.0 ml	0.5 ml
Nicotinic acid	5.0 g/L	1.0 ml	0.5 ml
Pyridoxine	0.5 g/L	1.0 ml	0.5 ml
thiamine HCL dissolved in H ₂ O	0.5 g/L	1.0 ml	0.5 ml
IBA dissolved in 95% EtOH	10 mg/ 100 ml	20.0 ml	10 ml
BA dissolved in KOH	10 mg/ 100 ml	10.0 ml	5 ml
Sucrose		30.0 g	15 g
PH		5.8	5.8
Bacto-Agar		7.0 g	3.5 g

²500 ml of media made on November 7, 2001. 12 ml used in each tube.

Table 2: Meconopsis multiplication medium using GA₃ as the auxin

Major salts	Amount used in 1 L of 10X stock	Amount of stock used in 1 L of medium	Amount used ^z
NH ₄ NO ₃	16.5 g		
KNO ₃	19.0 g		
CaCl ₂ 2H ₂ O	4.4 g	100 ml	50 ml
MgSO ₄ 7H ₂ O	3.7 g		
KH ₂ PO ₄	1.7 g		
Minor salts	Amount used in 1 L of 100X stock	Amount of stock used in 1 L of medium	
MnSO ₄ H ₂ O	1.69 g		
ZnSO ₄ 7H ₂ O	.86 g		
H ₃ BO ₃	.62 g		
CoCl ₂ 6H ₂ O	2.5 mg	10 ml	5 ml
CuSO ₄ 5H ₂ O	2.5 mg		
Na ₂ MoO ₄ 2H ₂ O	.025 mg		
KI	.083 mg		
Organics			
myo-inositol dissolved in H ₂ O		100 mg	50 mg
Fe EDTA dissolved in H ₂ O		32 mg	16 mg
thiamine HCL dissolved in H ₂ O	0.5 g/L	1.0 ml	0.5 ml
BA dissolved in KOH	10 mg/ 100 ml	5.0 ml	2.5 ml
GA ₃ Dissolved in 95% EtOH	10 mg/ 100 ml	35 ml	17.5 ml
Sucrose		30.0 g	15 g
PH		5.8	5.8
Bacto-Agar®		7.0 g	3.5 g

^z500 ml of media made on January 16, 2002. 12 ml used in each tube.