Dormancy and Acclimation in Dogwood Clonal Ecotypes

A Thesis Submitted to the College of
Graduate Studies and Research
in Partial Fulfilment of the Requirements
for the Degree of Master of Science
in the Department of Horticulture Science

University of Saskatchewan
Saskatoon

By
Robert Kenneth Stevenson
Saskatoon, Saskatchewan
Spring 1994

© Copyright Robert K. Stevenson. All rights reserved.
In presenting this thesis in partial fulfilment of the requirements for a Postgraduate degree from the University of Saskatchewan, I agree that the Libraries of this University may make it freely available for inspection. I further agree that permission for copying of this thesis in any manner, in whole or in part, for scholarly purposes may be granted by the professor or professors who supervised my thesis work or, in their absence, by the Head of the Department or Dean of the College in which my thesis work was done. It is understood that any copying or publication or use of this thesis or parts thereof for financial gain shall not be allowed without my written permission. It is also understood that due recognition shall be given to me and to the University of Saskatchewan in any scholarly use which may be made of any material in my thesis.

Requests for permission to copy or to make other use of material in this thesis in whole or part should be addressed to:

Head of the Department of Horticulture
University of Saskatchewan
Saskatoon, Saskatchewan S7N 0W0
Timing of vegetative maturity (VM) attainment and cold acclimation/hardiness development were compared in red-osier dogwood (*Cornus sericea* L.) ecotypes under field, shadehouse and controlled environment conditions. Controlled environment studies were also used to evaluate the efficacy of photoperiod/temperature regimes on attainment of VM in these ecotypes. Finally, the influence of turfgrass on VM attainment was examined. Tests made use of dogwood ecotypes from Utah, Massachusetts (Mass), Chalk River (CR), Saskatoon, Northwest Territories (NWT) and Alaska.

Under all systems, the northern ecotypes (Alaska and NWT) attained VM first. Order of VM attainment was consistent between systems. Certain southern ecotypes (Utah and CR) did not attain VM under Saskatoon conditions, however, all plants survived winter temperatures lower than -30°C.

Controlled environment studies indicated that northern ecotypes can be induced to true VM by either short days (8 hr), low night temperatures (5°C), or a combination of both. The more southern ecotypes required short days for VM induction, but low temperatures could enhance earliness of induction. Low temperatures in the absence of short days were not effective for southern ecotypes.

Controlled freezing studies of short day/warm temperature (SD/WT) treated plants indicated that all tested ecotypes acquired a high degree of acclimating ability.
prior to the attainment of VM. Following 4 weeks of acclimation, hardiness levels at bud set (prior to VM) exceeded -22°C.

Planting of dogwoods into established turf led to early growth cessation, but not dormancy induction. Turf-grown dogwoods had stunted growth and winter damage, while control plants exhibited none of these problems.
ACKNOWLEDGEMENTS

Virtually everyone in the Department of Horticulture has helped me in some way with the completion of this thesis work. To all of you I extend my warmest thanks.

I am particularly grateful to my supervisor, Dr. Karen Tanino, for the guidance and support she gave me throughout all my work. Her encouragement to pursue new and varied avenues, regardless of their relevance to my thesis, greatly enriched my studies. For this I am particularly appreciative.

I would also like to thank the Dr. Manjula Bandara for his help with statistical analysis and for taking the time to explain why, as well as how. To Dan Andrews and Satya Miranpuri I owe particular thanks for their help with the propagation and care of my plants.

I wish to thank the members of my committee, Dr. L. Gusta, Dr. G. Simpson, Dr. R. Redmann and Dr. K. Giles for their contributions to the completion of my thesis. Financial support for this research was provided by the Natural Sciences and Engineering Council, Faculty of Graduate Studies and Research, and the College of Agriculture.

To my friends, thank you for your patience and helping me keep things in perspective. Most importantly, thank you Mom and Dad for your constant encouragement and support. If it weren’t for you, I would never have gone this far.
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>ABSTRACT</td>
<td>iii</td>
</tr>
<tr>
<td>ACKNOWLEDGEMENTS</td>
<td>v</td>
</tr>
<tr>
<td>LIST OF TABLES</td>
<td>x</td>
</tr>
<tr>
<td>LIST OF FIGURES</td>
<td>xiii</td>
</tr>
<tr>
<td>LIST OF ABBREVIATIONS</td>
<td>xv</td>
</tr>
<tr>
<td>1.0 INTRODUCTION</td>
<td>1</td>
</tr>
<tr>
<td>2.0 LITERATURE REVIEW</td>
<td>3</td>
</tr>
<tr>
<td>2.1 The Dogwood</td>
<td>3</td>
</tr>
<tr>
<td>2.1.1 General Morphology</td>
<td>3</td>
</tr>
<tr>
<td>2.1.2 Propagation</td>
<td>4</td>
</tr>
<tr>
<td>2.2 Dormancy in Woody Plants</td>
<td>4</td>
</tr>
<tr>
<td>2.2.1 Dormancy Terminology</td>
<td>5</td>
</tr>
<tr>
<td>2.2.2 Induction of Dormancy</td>
<td>12</td>
</tr>
<tr>
<td>2.2.3 Dormancy Release</td>
<td>14</td>
</tr>
<tr>
<td>2.2.4 Factors Influencing Dormancy/Growth Cessation</td>
<td>14</td>
</tr>
<tr>
<td>2.3 Cold Hardiness/Acclimation</td>
<td>16</td>
</tr>
<tr>
<td>2.3.1 Importance of Hardiness Attainment</td>
<td>16</td>
</tr>
<tr>
<td>2.3.2 Terminology</td>
<td>17</td>
</tr>
<tr>
<td>2.3.3 Induction of Cold Acclimation/Hardiness</td>
<td>18</td>
</tr>
<tr>
<td>2.3.4 Factors Affecting Acclimation</td>
<td>20</td>
</tr>
</tbody>
</table>

vi
2.4 Relationship Between Dormancy and Cold Acclimation 21

2.5 Assessment of VM and Cold Acclimation/Hardiness 24

2.5.1 Dormancy Assessment 24

2.5.2 Cold Acclimation/Hardiness Assessment 26

2.6 Chilling Requirement 27

2.6.1 Importance of the Chilling Requirement 27

2.6.2 Factors Behind Satisfaction of the Chilling Requirement 29

2.6.3 Alternative methods for Satisfying the Chilling Requirement 29

2.6.4 Studies in Deciduous Woody Plant Chilling Requirement 30

2.7 Ecotypes 31

2.7.1 Terminology 31

2.7.2 Ecotype Studies 32

3.0 ATTAINMENT OF VEGETATIVE MATURITY (VM) IN DOGWOOD CLONAL ECOTYPES UNDER FIELD, SHADEHOUSE AND CONTROLLED ENVIRONMENT CONDITIONS 35

3.1 INTRODUCTION 35

3.2 MATERIALS AND METHODS 38

3.2.1 Field Studies 38

3.2.2 Shadchouse Studies 42

3.2.3 Controlled Environment Studies 43

3.2.4 Comparison of Field, Shadehouse and Controlled Environment as Systems for Evaluation of Ecotypical Variation in the Attainment
of VM

3.3 RESULTS

3.3.1 Field Studies

3.3.2 Shadehouse Studies

3.3.3 Controlled Environment Studies

3.3.4 Field, Shadehouse and Controlled Environment System Comparison

3.4 DISCUSSION

3.4.1 Systems Comparison

3.4.2 VM Attainment

3.4.3 Satisfaction of the Chilling Requirement

3.5 CONCLUSION

4.0 INFLUENCE OF PHOTOPERIOD, TEMPERATURE AND CULTURAL PRACTICES ON VM INDUCTION

4.1 INTRODUCTION

4.2 MATERIALS AND METHODS

4.2.1 Photoperiod and Temperature Studies

4.2.2 Turfgrass Studies

4.3 RESULTS

4.3.1 Photoperiod and Temperature Studies

4.3.2 Cultural Practices: Enhanced Dormancy Induction by Turfgrass

4.4 DISCUSSION

4.4.1 Effective VM-Inducing Regimes
4.4.2 Ecotype Comparison
4.4.3 Diurnal Temperature Fluctuation
4.4.4 Cultural Practices: Enhanced Dormancy Induction by Turfgrass

4.5 CONCLUSION

5.0 DORMANCY DEVELOPMENTAL AND COLD ACCLIMATION

5.1 INTRODUCTION

5.2 MATERIALS AND METHODS
  5.2.1 Plant Propagation and Preparation
  5.2.2 Acclimation and Freezing Tests

5.3 RESULTS

5.4 DISCUSSION

5.5 CONCLUSION

6.0 SUMMARY AND CONCLUSIONS

7.0 LITERATURE CITED

APPENDIX 1
LIST OF TABLES

Table 3.1 Attainment of vegetative maturity (VM) under field conditions (Saskatoon, SK) for five dogwood (Cornus sericea L.) clonal ecotypes. 47

Table 3.2 Satisfaction of the chilling requirement under field conditions (Saskatoon, SK) for five dogwood (Cornus sericea L.) clonal ecotypes. 47

Table 3.3 Attainment of vegetative maturity (VM) under shadehouse conditions (Saskatoon, SK) for five dogwood (Cornus sericea L.) clonal ecotypes. 55

Table 3.4 Satisfaction of the chilling requirement under shadehouse conditions (Saskatoon, SK) for five dogwood (Cornus sericea L.) clonal ecotypes. 55

Table 3.5 Vegetative maturity (VM) attainment of four dogwood (Cornus sericea L.) clonal ecotypes under a controlled environment short day/warm temperature (SD/WT) regime. 58

Table 3.6 Comparison of satisfaction of the chilling requirement for four dogwood (Cornus sericea L.) clonal ecotypes under field and shadehouse conditions (Saskatoon, SK). 58

Table 3.7 Comparison of vegetative maturity (VM) attainment date for four dogwood (Cornus sericea L.) clonal ecotypes under field and shadehouse conditions (Saskatoon, SK). 61

Table 4.1 NWT ecotype vegetative maturity (VM) attainment under different controlled environment photoperiod/temperature regimes. 88

Table 4.2 Alaska ecotype vegetative maturity (VM) attainment under different controlled environment photoperiod/temperature regimes. 88

Table 4.3 Mass ecotype vegetative maturity (VM) attainment under different controlled environment photoperiod/temperature regimes. 92

Table 4.4 Utah ecotype vegetative maturity (VM) attainment under different controlled environment photoperiod/temperature regimes. 92

Table 4.5 Dogwood (Cornus sericea L.) ecotype vegetative maturity (VM) attainment under a short day/warm temperature (SD/WT) controlled environment regime. 96
Table 4.6 Dogwood (*Cornus sericea* L.) ecotype vegetative maturity (VM) attainment under a short day/low temperature (SD/LT) controlled environment regime.

Table 4.7 Dogwood (*Cornus sericea* L.) ecotype vegetative maturity (VM) attainment under a long day/low temperature - modified (LD/LT-mod) controlled environment regime.

Table 4.8 Dogwood (*Cornus sericea* L.) ecotype vegetative maturity (VM) attainment under long day/low temperature (LD/LT) & long day/warm temperature (LD/WT) controlled environment regimes.

Table 4.9 Dogwood (*Cornus sericea* L.) ecotype satisfaction of a chilling requirement under the short day/low temperature (SD/LT) controlled environment regime.

Table 4.10 Dogwood (*Cornus sericea* L.) ecotype satisfaction of a chilling requirement under the long day/low temperature - modified (LD/LT-mod) controlled environment regime.

Table 4.11 Effective vegetative maturity (VM) inductive regimes for four dogwood (*Cornus sericea* L.) clonal ecotypes from the photoperiod/temperature study and the diurnal temperature fluctuation study.

Table 5.1 0 days short day/warm temperature (SD/WT) stage hardiness of three dogwood clonal ecotypes following 0 and 4 weeks of acclimation at 5°C.

Table 5.2 20 days short day/warm temperature (SD/WT) stage hardiness of three dogwood clonal ecotypes following 0, 2 and 4 weeks of acclimation at 5°C.

Table 5.3 Budset (BS) stage hardiness of three dogwood clonal ecotypes following 0, 2 and 4 weeks of acclimation at 5°C.

Table 5.4 Vegetative maturity (VM) and NVM (intermediate 20 days short day/warm temperature and budset) stages hardiness of three dogwood clonal ecotypes following 0, 2 and 4 weeks of acclimation at 5°C.

Table 5.5 Post Budset (PBS) stage hardiness of three dogwood clonal ecotypes following 0, 2 and 4 weeks of acclimation at 5°C.

Table 5.6 Hardiness changes of three dogwood clonal ecotypes at 0 weeks acclimation (5°C) over all developmental stages.
Table 5.7  Hardiness changes of three dogwood clonal ecotypes at 2 weeks acclimation (5°C) over all developmental stages.

Table 5.8  Hardiness changes of three dogwood clonal ecotypes at 4 weeks acclimation (5°C) over all developmental stages.
LIST OF FIGURES

Figure 3.1 Geographical distribution of dogwood (Cornus sericea L.) clonal ecotypes 39

Figure 3.2 Dormancy induction and satisfaction of the chilling requirement of field planted dogwood (Cornus sericea L.) clonal ecotypes 48

Figure 3.3 Daylength in Saskatoon, SK, Canada plotted on a mid-monthly basis (latitude: 52.07N, 106.38W). Supplied by Environment Canada. 49

Figure 3.4 Saskatoon, SK, Canada max/min temperatures - 1992 (supplied by Environment Canada) 50

Figure 3.5 Dormancy induction and satisfaction of the chilling requirement of shadehouse-grown dogwood (Cornus sericea L.) clonal ecotypes 54

Figure 3.6 Controlled environment vegetative maturity (VM) induction under short day/warm temperature (SD/WT) conditions. 57

Figure 3.7 Chilling requirement of two growth chamber induced vegetatively mature dogwood (Cornus sericea L.) clonal ecotypes 60

Figure 4.1 Photoperiod and temperature studies on vegetative maturity (VM) induction in dogwood clonal ecotypes: greenhouse regime (25C, 22h day) 85

Figure 4.2 Controlled environment photoperiod and temperature studies on vegetative maturity (VM) induction in dogwood clonal ecotypes: NWT ecotype 89

Figure 4.3 Controlled environment photoperiod and temperature studies on vegetative maturity (VM) induction in dogwood clonal ecotypes: Alaska ecotype 90

Figure 4.4 Controlled environment photoperiod and temperature studies on vegetative maturity (VM) induction in dogwood clonal ecotypes: Mass ecotype 91

Figure 4.5 Controlled environment photoperiod and temperature studies on vegetative maturity (VM) induction in dogwood clonal ecotypes: Utah ecotype 94

Figure 4.6 Photoperiod and temperature studies on vegetative maturity (VM) induction in dogwood clonal ecotypes: SD/WT (short day/warm temperature) controlled environment regime 95
Figure 4.7 Photoperiod and temperature studies on vegetative maturity (VM) induction in dogwood clonal ecotypes: SD/LT (short day/low temperature) controlled environment regime 98

Figure 4.8 Photoperiod and temperature studies on vegetative maturity (VM) induction in dogwood clonal ecotypes: LD/LT-mod (long day/low temperature-modified) controlled environment regime 99

Figure 4.9 Photoperiod and temperature studies on vegetative maturity (VM) induction in dogwood clonal ecotypes: LD/LT (long day/low temperature) controlled environment regime 101

Figure 4.10 Photoperiod and temperature studies on vegetative maturity (VM) induction in dogwood clonal ecotypes: LD/WT (long day/warm temperature) controlled environment regime 102

Figure 4.11 Influence of diurnal temperature fluctuation on efficacy of controlled environment vegetative maturity (VM) induction: Mass ecotype 106

Figure 4.12 Influence of diurnal temperature fluctuation on efficacy of controlled environment vegetative maturity (VM) induction: Utah ecotype 107

Figure 4.13 Effect of turfgrass on vegetative maturity (VM) attainment of Mass ecotype dogwood (Cornus sericea L.) under Saskatoon, SK field conditions 108

Figure 5.1 Controlled environment studies on the influence of developmental stage (0 - 0 days vegetative maturity (VM) inductive conditions, 20 - 20 days of VM inductive conditions, NVM - intermediate of 20 days and budset (BS) stage, BS - budset, VM - vegetative maturity, PBS post budset) on hardiness and acclimation ability in 3 Dogwood (Cornus sericea L.) clonal ecotypes following 0, 2 and 4 weeks of acclimation at 5°C 132

Figure 5.2.1 Damage rating 1 of controlled freeze tests 128

Figure 5.2.2 Damage rating 2 of controlled freeze tests 129

Figure 5.2.3 Damage rating 3 of controlled freeze tests 130

Figure 5.2.4 Damage rating 4 of controlled freeze tests 131
LIST OF ABBREVIATIONS

SD/WT - Short days (8/16 h day/night) with warm temperatures (20°C day 15°C night)

SD/LT - Short days (8/16 h day/night) with low temperatures (15°C day 5°C night)

LD/WT - Long days (22/2 h day/night) with warm temperatures (20°C day 15°C night)

LD/LT - Long days (22/2 h day/night) with low temperatures (15°C day 5°C night)

LD/LT-mod - Long days (22/2 h day/night) with low temperatures (8 hours of 15°C beginning with the day period, 16 hours of 5°C)

g.h. - greenhouse regime (approx. 22 h days with 25 ± 5°C)

Mass - Massachusetts dogwood ecotype

NWT - Northwest Territories dogwood ecotype

CR - Chalk River dogwood ecotype

S'toon - Saskatoon dogwood ecotype

Utah - Utah dogwood ecotype

Alaska - Alaska dogwood ecotype

VM - Vegetative Maturity
1.0 INTRODUCTION

Low temperature is a major limiting factor to plant distribution. Ability of plants to tolerate low temperatures is essential to survival. To withstand freezing conditions, plants must be able to acclimate and attain levels of hardiness exceeding lowest winter temperatures. Equally important to maximum hardiness is timing and maintenance of hardiness attainment. Previous studies have shown temperature, daylength and plant dormancy status to be particularly important to acclimation (Fuchigami et al. 1982, Howell and Weiser 1970, Van Huystee et al. 1967).

Previous studies suggest that attainment of certain dormancy states is critical to cold acclimation (Fuchigami et al. 1982, Nissila and Fuchigami 1978, Friesen and Stushnoff 1989). Attainment of vegetative maturity (VM) may be particularly critical, since before this stage, plants cannot cold acclimate to any appreciative level (Friesen and Stushnoff 1989, Fuchigami et al. 1982). At VM, plants will not begin to grow if placed under ideal conditions (Fuchigami et al. 1982, Kobayashi et al. 1982). A chilling requirement must be satisfied before plants will begin to grow (Weiser 1970, Fuchigami et al. 1982, Lavender and Stafford 1984). By contrast, growth cessation (rather than VM/dormancy attainment) has been inferred to be sufficient to allow cold acclimation (Howell and Weiser 1970, Weiser 1970, Juntilla and Kaurin 1985, Chen and Li 1978). Short days are considered to be ideal for the
induction of VM or fall growth cessation (Weiser 1970, Smithberg and Weiser 1968, Juntilla and Kaurin 1985), most often accompanied by warm temperatures.

While the above conditions are considered necessary for the induction of dormancy and cold acclimation in deciduous woody plants, these ideas are largely based on studies of plants from temperate regions. Studies of ecotypes from a large latitudinal range are few, and fewer still are those experiments which test species whose range extends into the extreme climates of the sub-arctic. The only large-scale study of dogwood ecotypes (Smithberg and Weiser 1968) investigated ecotypical variation in acclimation levels and timing. While growth cessation was noted, tests of dormancy induction were not undertaken. Results indicated that northern ecotypes cold harden earlier, but eventually ecotypes attained the same degree of ultimate hardiness.

The dogwood clonal ecotype system is an attractive method to study dormancy and hardiness. Ecotypes of the same species from a range of latitudes will be used to determine if there is ecotypical variation in timing of dormancy attainment in dogwood ecotypes. No such system presently exists to evaluate dormancy induction. Tests will also determine effective photoperiod/temperature regimes for the induction of growth cessation and VM for each ecotype. In addition, the importance of VM attainment as a pre-requisite to significant cold acclimation will be evaluated. Finally, field, shadehouse and controlled environment systems will be compared for dormancy induction.
2.0 LITERATURE REVIEW

2.1 The Dogwood

Dogwood is a general name for many of the members of the genus *Cornus* in the family Cornaceae. The genus consists of approximately 45 species of deciduous trees and shrubs, and is native to all continents with the exception of Australia (Stimart 1986). In North America there are many species within this genus, but this literature review will concentrate on *Cornus sericea* L. (or *Cornus stolonifera* Michx.), also known by the familiar name red-osier dogwood (Bailey and Bailey, 1976). This species was used for all tests in the thesis.

2.1.1 General Morphology

Generally, *C. sericea* has a shrub like growth habit, although specific morphology can vary depending on ecotype (personal observation). Dogwoods are generally deciduous, and the *C. sericea* species has opposite, parallel veined leaves which are centrally attached (Stimart 1986). Leaf shape and stem pubescence vary considerably among ecotypes (personal observation).

*C. sericea* produces small, four part, bisexual flowers with a green calyx and a white corolla (Stimart 1986, Gunatilleke and Gunatilleke 1984). Flower organization is typically in compound cymes, with approximately 75 flowers per
inflorescence. It produces white fruit which measure approximately 8X8 mm at maturity (Gunatilleke and Gunatilleke 1984). The fruit is considered to be a drupe with a two-celled stone (Stimart 1986). Flowering generally occurs once per year in spring or early summer, and plants are considered to be self-incompatible (Gunatilleke and Gunatilleke 1984, Stimart 1986).

2.1.2 Propagation

Propagation is typically by seed, cutting, or grafting (Stimart 1986). Dogwoods require adequate moisture for growth and do poorly in excessive heat. Plants have few pests. Propagation by cutting is an effective form of multiplication for *Cornus sericea*. Plants will root readily in a moist medium with some drainage. Use of a rooting compound will enhance establishment. Verkade et al. (1988) found establishment of cuttings could be enhanced through mycorrhizae inoculation during propagation. The effects of such a treatment were long term and affected later developmental stages. Application to pre-rooted seedlings was ineffective.

2.2 Dormancy in Woody Plants

The topic of dormancy is extensive, including among the more common forms: seed dormancy, tuber dormancy and vegetative dormancy. This review of literature will pertain primarily to vegetative organ dormancy in woody plants. For the purposes of this thesis, woody plant vegetative dormancy will be referred to as dormancy.
2.2.1 Dormancy Terminology

Dormancy is an intricate part of woody plant life cycle. In most plants, this state of non-growth will be achieved at some period during its existence, typically annually if not more frequently. Dormancy tends to be a state allowing survival during adverse environmental conditions, since plants that are dormant are more tolerant of environmental stresses (Murakami et al. 1990). Proper attainment of this state can be crucial to plant survival. The results of many years of investigation and discovery have led to a plethora of terms to describe various dormancy states (see Lang et al. 1985). To date there has been little agreement with respect to a universal naming and description of each state.

General Description of Dormancy

Dormancy in woody plants is not limited to a single form. Many forms and stages of dormancy are exhibited at different times within the same organ. Various stimuli have been shown to induce each different form. This diversity of dormant states and stimuli has led to countless definitions. The definitions range from the simple and succinct, to the comprehensive and detailed. The following is a summary of some of the existing definitions which generally describe the dormant state.

Fuchigami et al. (1982) very simply describe dormancy as the state of not growing. They use the example that when a bud stops growing, the bud is dormant. When all the buds on a plant stop growing, then the plant is dormant. In a general
sense Lang et al. (1985) describe dormancy as any rest period or reversible interruption of the phenotypic development of an organism. With more reference to site of growth cessation, Lang et al. (1985) describe dormancy as a state where there is no visible growth of any structure containing a meristem. In a later paper, Lang (1987) qualifies the time frame of this state by modifying the definition to be a temporary suspension of visible growth of any plant structure containing a meristem. Salisbury and Marinos (1985) make reference to the fact that dormancy is not total growth cessation, but that the term implies a complete "shut-down" of all energy requiring processes except those that are essential for the maintenance of the living state. The essence of these descriptions is that growth is ceased in plants, except for those processes essential to life.

Specific Dormancy State Terminology

Two of the recent and most commonly referred to papers on dormancy terminology are those by Fuchigami et al. (1982) and Lang et al. (1985). These two papers will be reviewed in detail, followed by an overview of descriptions of dormancy states.

The Fuchigami et al. (1985) paper describes different dormancy events throughout a growing season, complete with names for and definitions of observed states. The model, which is based on perennial woody species such as dogwood, is called the "° Growth Stage Model" (degree growth stage model). The purpose of the model was to allow numerical description and prediction of the annual growth
cycle and hardiness attainment of vegetative buds. As the group indicates, "(the model) provides a quantitative means of describing distinct physiological stages in plant growth and development". Fuchigami et al. (1985) felt there was a need to relate environmental factors to identifiable growth stages. The model has met with general acceptance, as indicated by the frequency of its citation. For the purposes of this thesis, the ° Growth Stage Model (°GS) will serve as the basis for most terminology.

The model identifies 5 major stages in dormancy development. They are Spring Bud Flush, Maturity Induction Point (MIP), Vegetative Maturity (VM), Maximum Rest (MR), and End of Rest (ER). Spring bud flush (0°), as the name implies, is the period of rapid growth that most plants experience in spring. This growth continues, apparently uninhibited by most environmental factors, until a plant attains the next developmental stage; the Maturity Induction Point (MIP). Acclimation capabilities at the spring bud flush stage are minimal to none.

On attainment of MIP (90°), plants become sensitive to shortening daylengths. Growth begins to slow and buds will set under these conditions. Cold acclimation cannot begin before the attainment of this stage. At the MIP stage, a plant requires the fewest number of short days with warm temperatures (SD/WT) to attain the next stage - Vegetative Maturity (VM - 180° stage).

The transition to the 180 °GS is triggered by a short day stimulus. The rate of development is further influenced by other environmental factors, of which temperature appears to be important. At VM, unlike MIP, leaf removal no longer
stimulates resting buds to resume growth. This defines VM (Kobayashi et al. 1982). However, care must be taken not to get lost in changing definitions. For instance, Smithberg and Weiser (1968) describe the state where newly formed buds do not grow on exposure to favourable environment (we refer to it as VM), as rest. Seibel and Fuchigami (1978) call the same state winter dormancy, while rest refers to the deepest stage of winter dormancy. With the attainment of VM also comes completion of the first stage of acclimation. It is only at this point that plants become competent to respond to acclimating temperatures. Although plants can acclimatize before this point, they will not do so as effectively. Injury can result from failure to achieve VM and the first stage of cold acclimation before the first lethal freezing conditions. It has also been suggested (Kobayashi et al. 1982) that in dogwood, rest development only occurs after the attainment of VM.

Rest becomes deeper as plants progress from VM to maximum rest (MR). Kobayashi et al. (1982) suggest that this development is low temperature-mediated. At maximum rest, a plant requires the longest period of active growth conditions (nearly 200 days in the case of Massachusetts ecotype), or the greatest concentration of gibberellic acid before growth will resume. From maximum rest, dormancy is slowly released by chilling temperatures until End of Rest (ER) is attained.

End of Rest (ER) occurs when further exposure to inductive chilling temperatures no longer shortens the time for buds to begin growing in a warm environment favourable for growth. This is the dormancy stage at which plant growth becomes inhibited only by unfavourable growth conditions. A plant at the
end of rest stage will begin to grow within 5 to 8 days on exposure to active growth conditions.

While the °GS model of Fuchigami et al. (1982) has been accepted by many, the terminology of Lang et al. (1985) has been embraced by others. Unlike the Fuchigami et al. (1982) model which was based on experimental tests meant to quantify dormancy development, the terminology of Lang et al. (1985) is a description of events without quantification. They do not attempt to describe stages of dormancy development, but rather describe dormancy states.

Lang et al. (1985) state that there are really two general phenomena that can be classified as dormancy: Rest and Quiescence. They describe the rest event as a "plant organ condition characterized by an internal (innate) inhibition of growth resulting from physiological factors having certain distinct features such as onset intensity and duration, thus a plant cannot be induced to grow even if suitable conditions prevail." Quiescence is described as the condition in a "plant organ wherein development is delayed because of unfavourable chemical or physical conditions in the environment." Based on their general description of dormancy phenomena, they attempt to re-define some of the dormancy states.

Ecodormancy refers to dormancy having to do with the habitat or environment. It is regulated by factors external to the plant (Lang et al. 1985). It can be thought of as cessation of growth due to unfavourable environmental factors (drought, extreme temperatures, nutrient deficiencies, air pollution, etc.). Growth will resume when environmental conditions return to normal. Ectodormancy is
dormancy having to do with an external organ factor (similar to correlative inhibition or summer dormancy). This describes dormancy regulated by factors that are within the plant, but are external to the dormant structure. Lang et al. (1985) cite a subtending leaf or apex correlating with a lateral bud’s inactivity as an example of ectodormancy. The last state is endodormancy, or dormancy having to do with factors inside the affected structure. Only when perception of the environmental condition is by the organ that becomes dormant do they consider the structure to be endodormant.

In a subsequent paper (1987), Lang refines the 1985 dormancy terminology to universally apply to seeds, bulbs and other potentially dormant structures. Dormancy is re-defined as the temporary suspension of visible growth of any plant structure containing a meristem. Ecto, eco and endodormancy are also re-defined. Endodormancy occurs when the initial reaction leading to growth control is a specific perception of an environmental or endogenous signal in the affected structure alone. Ectodormancy was renamed paradormancy. This new state refers to the condition when the initial reaction leading to growth control involves a specific signal originating in, or initially perceived in, a different structure from the one in which dormancy is manifested. Ecodormancy now refers to the response when one or more factors in the basic growth environment are unsuitable for overall growth metabolism. Lang states that this is not so much a biochemically inductive process, as a growth limitation associated with inadequate basic environmental factors (i.e. temperature extremes, water or nutrient deficiency).
While the Fuchigami et al. (1985) and Lang et al. (1985) terminologies of dormancy states are frequently referenced, there are other descriptions and terminologies in existence. An earlier paper by the Fuchigami group (Seibel and Fuchigami 1978b) describes a state referred to as winter dormancy. It is the point at which defoliation no longer induces bud break (a seeming predecessor to vegetative maturity of Fuchigami et al. (1982)). However, in the same paper, VM is described as the point at which no visible injury occurs as a result of defoliation (Seibel and Fuchigami 1978b). Changes in word definition can make reading of older papers somewhat confusing. In a preceding paper Seibel and Fuchigami (1978a), describe deepest winter dormancy in dogwood as the longest period of time required for bud burst when placed in LD environment. This seems to correspond to what is now referred to as maximum rest. The paper by Lang et al. (1985) is a good reference for the many other descriptions of dormancy states that exist in the literature.

Despite the large body of work that identifies and describes dormancy states and the environmental and physiological factors behind them, other researchers consider that dormancy states may not accurately represent the dormancy process. Carter and Brenner (1985) agree with Levitt, that the dormancy process is a gradual transition beginning with the first slight slowing of growth (due to temperature, daylength or water stress change) to the complete cessation of growth. (Kaurin et al. 1984) suggest that dormancy attainment is often the culmination of a gradual transition from a state of inhibition (i.e. apical dominance or state of leaf-imposed correlative dormancy).
2.2.2 Induction of Dormancy

The induction of dormancy is largely considered to be environmentally stimulated. Induction of growth cessation, vegetative maturity/rest will be examined in this section.

Growth Cessation

Growth cessation normally precedes true dormancy acquisition. Attainment of growth cessation is mostly attributed to changes in temperature and photoperiod. Leaves as a photoperiod receptor site are important to dormancy induction. Fuchigami et al. (1977) showed leaves are important for rest induction and subsequent cold acclimation in dogwood. Defoliation of plants before the attainment of VM resulted in varying degrees of stem dieback. Renquist et al. (1978) also found defoliation of plants prior to the attainment of VM led to winter injury.

Qamaruddin et al. (1993) believe night length controls budset and growth cessation in Picea abies. Under 16 hours, the northern ecotype responded quickly, slowing growth and setting buds earlier than the southern ecotype. Weiser (1970) supports the photoperiod concept. He indicates that decreasing photoperiod causes growth cessation in many northern deciduous species. Smithberg and Weiser (1968) determined photoperiod to be the main factor triggering autumn phenomena in dogwoods. Similarly, in the northern species, Salix pentandra, Juntilla and Kaurin (1985) observed that photoperiod is the primary environmental factor controlling growth cessation in seedlings. Their results also indicate that plants are adapted to
changes in irradiance and spectral energy distribution. Higher irradiance and more far red light are needed to induce growth cessation in northern ecotypes than in southern ecotypes. Bjornseth (1985) poses an interesting hypothesis that induction of growth cessation may be an on/off switch that is triggered by the attainment of a critical night length. Further, it may be that the critical night length needs to be attained several times, with longer nights becoming more effective. In this manner, the process would be more gradual. Bjornseth refers to this as exposure to photoperiodic pulses. These would build up potential, or as he puts it, breakdown the potential for growth.

Contrary to these previous studies Powell (1987) states that the short days of late summer or autumn are often not the causal reason behind growth cessation. He refers to the formation of terminal buds in late spring or early summer. It is his perception that growth cessation is due to competition of numerous sinks for essential metabolites. Kobayashi and Fuchigami (1983) consider phytohormones to be responsible for induction of buds. They are of the opinion that the balance of promoters and inhibitors, rather than the absence of inhibitors, is critical for bud development.

Vegetative Maturity/Rest

Photoperiod has long been recognized to be important in the induction of VM and the rest period. Seibel and Fuchigami (1978) induced winter dormancy in Massachusetts dogwoods using 10 hour days. In another study, Renquist et al.
(1978) determined a constant 20°C to be the optimal temperature for the induction of VM in dogwood under 10 hr days. Their computer model further refined the critical photoperiod to be 14.2 hours.

Kobayashi (1982) found that rest development in dogwoods was promoted by chilling temperatures following the attainment of VM. The most effective temperatures were those above freezing. Further, the rate of development from VM to rest was also a function of growth stage. As rest became deeper, the influence of the cool temperatures became greater.

2.2.3 Dormancy Release

Following the attainment of maximum rest (Fuchigami et al. 1982) plants gradually lose dormancy and enter the quiescent stage. The attainment of the quiescent stage is closely linked with the satisfaction of a chilling requirement. Until rest is overcome, via satisfaction of the chilling requirement, quiescence will not be attained and plants cannot be induced to grow (Fuchigami et al. 1982). The mechanism and variation behind satisfaction of the chilling requirement will be dealt with in the chilling requirement section of the Literature Review.

2.2.4 Factors Influencing Dormancy/Growth Cessation

Daylength, temperature, hormone balance and rhythmic cycles may be responsible for dormancy induction, however, there are other factors which may
influence growth cessation and promote VM (Fuchigami et al. 1982) while not actually causing them.

Age can be an important factor influencing dormancy induction. Young plants that are vigorously growing may enter dormancy later than more mature plants. Powell (1987) observes that some temperate zone woody plants, particularly those that are young and vigorous may grow late into autumn without forming terminal buds. Plants may also become less receptive to certain dormancy induction stimuli with age. Juntilla and Kaurin (1985) note that physiological age of *Salix pentandra* species will affect response to growth cessation inductive photoperiods.

Powell (1987) alluded to competition by various sinks for metabolites leading to growth cessation in dogwoods. Competition for resources can also occur beyond the plant. Studies by Walker and Williams (1988), while not directly investigating dormancy, show that grass competition in container-grown dogwoods (Bailey’s red-osier dogwood) reduced growth. In another test investigating the effects of cover crops, Calkins and Swanson (1993) found that bare soil treatments reduced the cold hardiness of the six tree species tested compared to the cover crop treatments. They conclude that companion crops and mulches can reduce plant losses to winter injury through enhancing cold acclimation. Although not stated, it is likely that water and nutrient competition by cover crops, similar to Walker and Williams (1988), led to earlier growth cessation and earlier acclimation. However, such treatments may not be appropriate for all species, as Murakami et al. (1990) suggest that plants prone to desiccation may also lack the ability to develop a high degree of rest.
2.3 Cold Hardiness/Acclimation

2.3.1 Importance of Hardiness Attainment

Quite simply, plants that do not become adequately hardy will not survive. While levels of dogwood hardiness can exceed -196°C (Hurst et al., 1967), the timing of hardiness attainment and release is equally important. Late hardiness attainment or early spring deacclimation can lead to injury. Dickinson, N.D. dogwoods (stem sections) taken from the field in January, were able to survive -196 and -269°C provided they were first held at -40°C overnight (Guy et al. 1986). However, if plants were deacclimated for 2 weeks under 22°C greenhouse conditions prior to freezing tests, hardiness levels fell to -10°C or warmer.

Hardy woody species that cold acclimate too slowly in the fall are often injured by early autumn frosts (Fuchigami et al. 1971). Weiser (1970) echoes this idea and points out that relatively minor modifications in hardiness regulation could reduce losses substantially. For example, delay of spring bloom in peaches and apricots, or induction of hardiness a week or two earlier in autumn on woody ornamentals, or prolongment of dormancy in plants that begin to grow too early in the spring would be tremendously beneficial (Weiser 1970). Weiser feels that it is likely that many species possess the ability to resist severe freezing stress, but lack proper timing of acclimation to survive. Fuchigami et al. (1982) agree with this concept. Some plants (i.e. introduced or man-made hybrids) are injured as they fail to attain 180 °GS (VM) and the first stage of acclimation before lethal freezing conditions occur (Fuchigami et al. 1982).
2.3.2 Terminology

Hardiness generally refers to instantaneous plant cold tolerance or resistance. It is a measure of the lowest temperature that the plant can survive at a given moment. Cold acclimation refers to the natural development of hardiness attainment in autumn and early winter (Fuchigami et al. 1982). This thesis describes cold acclimation potential as plant ability to acclimate on exposure to acclimating temperatures.

Cold acclimation can be divided into three stages. The first stage of cold acclimation is typically induced by the SD/WT conditions of fall (Howell and Weiser 1970, Fuchigami et al. 1982, Nissila and Fuchigami 1978), and imparts a moderate degree of acclimation potential. However, Howell and Weiser (1970) indicate that rhythmic growth cycles or perhaps light quality may also play a role. Weiser (1970) concurs with the idea that plants may have hardiness rhythms.

The second stage of acclimation is dependent on the attainment of the first stage. It is achieved through exposure to cool temperatures that are stimulatory following the attainment of VM (Fuchigami et al. 1982). At this point, rate of acclimation becomes a function of temperature with maximum acclimation rate occurring at maximum rest.

Valkonen et al. (1990) report that the third stage of acclimation is induced by prolonged exposure to temperatures below -30°C. It is during this third stage of cold acclimation that hardiness can be driven down to -196°C and lower. This
degree of hardiness and stage of acclimation is lost rapidly as temperatures increase above the induction level.

2.3.3 Induction of Cold Acclimation/Hardiness

It is well acknowledged that freezing resistance changes dramatically throughout the year (Weiser 1970). Hardiness in dogwoods is typically low during the active growth phase of spring and early summer. Growth chamber studies determined non-dormant dogwood hardiness to be -4°C (Chen and Li 1978), while Van Huystee et al. (1967) observed hardiness in dogwoods to be at least -5°C at all times of the year. Van Huystee et al. (1967) also observed distinct changes in hardiness of dogwoods throughout the fall. They observed that the first stage of acclimation occurred before freezing temperatures (middle of September). In late October and early November, the bark progressed from a first to a second stage of acclimation. Acclimation increased from -18°C to below -87°C in 2-3 weeks. This last change in acclimation always occurred within a few days of the first fall frosts. Fuchigami et al. (1982) indicate that while frosts will enhance acclimation, low temperatures are effective. In fact, at this stage even temperatures as high as 20°C will induce acclimation. Smithberg and Weiser (1968) observed that cold weather was not necessary for acclimation, as dogwoods began to acclimate well in advance of cold conditions.

Under more controlled conditions, Bray and Brenner (1981) observed that dogwoods treated with SD (8 or 10 hours) to be hardier than those treated with LD
While SD or LT are typical regimes for the induction of cold acclimation potential and hardiness, other studies have investigated alternative induction stimuli. Chen and Li (1978) tested low temperature, water stress, short days, and combinations of these treatments for their influence on acclimation induction. Each of the various treatments appeared to trigger independent frost hardiness mechanisms, resulting in some synergistic effects from multiple factor treatments. Hardiness levels ranged from -4°C in the controls, to -25.5°C under low temperature treatment.

Acclimation stages have been observed in other species. Howell and Weiser (1970) found apple had two stages of acclimation - one induced by short days, and one by frost or low temperature. In the first stage, leaves were stimulated by SD to produce a translocatable promoter of cold acclimation. LT could also effectively promote the first stage of acclimation, even in the presence of long days. Still, LT was not necessarily required for the attainment of the first stage of acclimation. During the first stage of acclimation, plants could be driven to hardiness levels of -30°C. Frost was required to drive hardiness lower than this level. Howell and Weiser found acclimation to be most rapid when plants first received SD and then received frosts, however, low temperature alone could induce acclimation. Weiser (1970) made similar observations about deciduous species in general. Interestingly, Howell and Weiser (1970) also observed that SD plants in the greenhouse acclimated to -25°C in the absence of LT. They suggest that this indicates other factors may be involved in the first stage of acclimation (i.e. rhythmic cycles, light quality).
2.3.4 Factors Affecting Acclimation

Many factors, including age, affect induction of hardiness (Howell and Weiser 1970). Chen and Li (1978) observed that low temperature treatment over 21 days induced hardiness to -15.5°C in 2 month dogwood plants, compared to -25.5°C in 4 month plants. Interestingly, this age effect was not seen in plants treated with SD or water stress or a combination of these factors. Water status is important as Li and Weiser (1971) report that dehydration could impart a greater freezing tolerance of non-acclimated plants through supercooling.

Plant origin can influence hardening. Qamaruddin et al. (1993) found northern ecotypes of Picea abies hardened faster than southern ecotypes under inductive conditions. They suggested fast response following the initiation of the growth cessation process, was an advantage to the northern population. In a classic ecotype experiment, Smithberg and Weiser (1968) observed similar results with dogwoods. Comparing 21 ecotypes grown in St. Paul, Minnesota, they observed that cold hardening began at different times in autumn, yet all ecotypes attained the same degree of ultimate hardiness by midwinter. The southern ecotypes (Mass and Seattle) were late to develop winter buds and acclimate. These ecotypes also grew rapidly, and late into the fall.

Plant organs are important to the acclimation process. Hurst et al. (1967) note that while leaves of deciduous species do not become hardy, they may be important for the reception of a light stimulus to initiate acclimation processes. Renquist et al. (1978) agree with this concept. Hurst et al. (1967) found removal of
leaves (Minnesota dogwood ecotype), or covering with tinfoil, retarded acclimation. If even one pair of leaves was exposed to inductive photoperiods, acclimation to -40°C was possible. To produce acclimation, the leaves had to be present on the plant for at least 7 to 14 days following exposure to the critical photoperiod for effective hardening. Leaves were also a factor in the survival of dogwoods (Fuchigami et al. 1977). Plants defoliated before the attainment of vegetative maturity suffered varying degrees of stem dieback. Those defoliated following VM suffered no injury.

2.4 Relationship Between Dormancy and Cold Acclimation

There is a close relationship between dormancy and cold acclimation (Howell and Weiser 1970, Nissila and Fuchigami 1978). However, many studies have only been able to correlate the two states. Nonetheless, there are a large number of these studies which lend strong evidence to the relationship of cold acclimation and dormancy.

Of the dormancy states, VM appears to be particularly important. Friesen and Stushnoff (1989) found dogwood hardness under field conditions was minimal before the attainment of VM. After the attainment of VM, plants could acclimate to levels of -20°C. Nissila and Fuchigami (1978) observed in dogwood, the first stage of acclimation occurred just after the attainment of VM on exposure to low temperatures, but before rest. In 1982, Fuchigami et al. reported the second stage of cold acclimation occurs following exposure to low temperatures after the
attainment of VM, while the first stage of acclimation is normally induced by SD/WT after the MIP. The first evidence of acclimation appears at VM. These tests report observations of plants under natural conditions, and do not attempt to determine if attainment of VM or rest is a pre-requisite to acclimation.

Christersson (1978) investigated the influence of various growth chamber regimes on the cold acclimation of *Picea abies* and *Pinus sylvestris*. Short days (SD - 8/16 hrs) combined with low temperatures (LT)(2°C) was the most effective regime for hardening. Plants treated with 1/2 SD with warm temperatures (WT) (20°C), the traditional dormancy induction regime, and 1/2 SD/LT, hardened just as effectively as the same total length of SD/LT. Unfortunately the dormancy status was not measured in these tests. Still, the results demonstrate pre-treatment with a dormancy inducing regime (SD/WT) can reduce the length of SD/LT needed to elicit the same degree of hardiness as SD/LT alone. Similarly, Fuchigami *et al.* (1982) indicate plants can acclimate under LT, but not as effectively as they could if previously induced into competency. Howell and Weiser (1970) also found exposure to SD and then to low temperatures were very effective for acclimation induction.

Early studies by Van Huystee *et al.* (1967) concluded cold acclimation capacity is dependent on growth phase, and rest appears necessary for attainment of maximum cold acclimation. However, other controlled environment studies indicate only attainment of growth cessation was necessary. For instance, another interesting component of the Christersson (1978) study observed the development of frost
hardiness is possible in the absence of a dormancy stage. The long day (LD - 20/4 hrs) with LT treatment ceased growth (but there was no dormancy) and permitted acclimation. This result indicates the key to acclimation is growth cessation rather than dormancy induction. With reference to the stages of acclimation, Valkonen et al. (1990) suggest the start of the first stage of cold acclimation coincides with growth cessation, while the second stage coincides with rest. Howell and Weiser (1970) and Weiser (1970) suggest, although growth cessation appears to be pre-requisite to acclimation in woody plants, this does not imply plants must be physiologically dormant. Juntilla and Kaurin (1985) state apical growth cessation is a pre-requisite for frost hardening in many woody plants, while Chen and Li (1978) observed acclimation increases in dogwood, despite plants do not cease growth under various growth chamber photoperiod, water stress and temperature treatments.

While there appears to be correlations or relationships between dormancy induction and cold acclimation induction, relationships beyond this point are less certain. Van Huystee (1967) notes rest was attained before maximum cold resistance, and rest often could be broken as early as late November. Fuchigami et al. (1982) state following 180 °GS (VM), the rate of acclimation becomes a function of temperature (not dormancy state).
2.5 Assessment of VM and Cold Acclimation/Hardiness

As with any treatment and response tests, a study must include a suitable evaluation of response to treatment. Selecting the proper assessment technique is critical to the attainment of accurate results.

2.5.1 Dormancy Assessment

Some of the more common methods for evaluating dormancy status include measuring percent bud break, days to bud break and concentration of GA required to break dormancy (Kobayashi et al. 1982). While all of these techniques are considered accurate, they have one major drawback. It can take weeks to months to obtain results using these techniques (Kobayashi et al. 1982, Renquist et al. 1978). For instance, Fuchigami et al. (1977) found dogwood in maximum rest required 180 days under ideal conditions before growth (bud break) resumed. Frequently this is an unacceptable length of time to wait for results. At the moment however, tests which have been proven reliable, time efficient, and cost effective are virtually non-existent (Murakami et al. 1990).

The defoliation test is commonly used to assess attainment of VM (Fuchigami et al. 1982). This procedure involves the removal of leaves, and frequently the apical bud, followed by exposure to active growth conditions. Under these conditions removal of the leaves will stimulate re-foliation if the plant has not attained VM. The number of days that it takes a plant to break bud and leaf out is
an indication of the degree of dormancy. The greater number of days to bud break, the more dormant the plant is.

As indicated by Kobayashi et al. (1982), conventional methods of dormancy assessment are a slow. Some researchers have proposed new methods which could reduce the assessment time. Faust et al. (1991) found differences in the water status of buds at different stages of dormancy. Magnetic Resonance Imaging (MRI) showed endodormant buds have no free water, whereas paradormant buds did. If changes in bud water status can be effectively correlated to different states of bud dormancy, MRI would permit a fast method of determining dormancy status. While the method is quicker than conventional techniques, it has the disadvantage of being expensive. To circumvent the need to wait for bud burst before original dormancy state can be determined, Renquist et al. (1978) developed a computer model to predict VM attainment. The model was based on the assumption that temperature and photoperiod were the most important parameters for VM attainment. Results indicated 14.2 hours was the critical photoperiod for initiation of VM in dogwood. In another study, Murakami et al. (1990), proposes the concept that water potential may be an indicator of rest status as a strong correlation between mid-day water status and days to bud break was found.

As a final note, within plant variation should always be considered when testing for dormancy status. Different organs or tissues within an organ can exhibit varying degrees of dormancy development (Fuchigami et al. 1982). Heide (1985) refers to his earlier work (1974a) where he observed cambial tissues require a
shorter critical photoperiod than needed for apical growth cessation. In a review of bud and seed dormancy, Powell (1987) refers to Chandler (1960) who observed that rest in buds occurs acropetally beginning at the base of the current year's growth.

2.5.2 Cold Acclimation/Hardiness Assessment

The number of cold acclimation/hardiness assessment techniques are as diverse as those for testing dormancy. Some of the more popular methods of assessing hardiness are tissue specific visual browning, conductivity measurements, viability (vital stains) tests and re-growth tests. As with dormancy studies, the assessment techniques selected for acclimation/hardiness studies must be suited for the test. Hardiness level within a plant can vary (Weiser 1970). For example, he notes that roots are less cold resistant than stems, but they can attain similar levels on exposure to cold temperatures.

While whole plant studies are frequently most desirable, hardiness evaluation often focuses on regenerative tissues of the cambium and adjacent phloem in the living bark (Weiser 1970). Guy et al. (1986) based their results primarily on measurements taken of the cortical cells, while Smithberg and Weiser (1968) conducted cold resistance tests on bark. Van Huystee et al. (1967) also looked primarily at the bark in dogwoods (Minn) for hardiness assessment.

Whole plant tests of re-growth are probably the most accurate and representative assessments of natural condition freezing tolerance, but assessment can be time consuming, often taking weeks to months. Despite the time
considerations, this method is considered the most accurate assessment of freezing survival (Christersson 1978). Visual assessment such as the correlation between red stem pigmentation and cold tolerance of bark in dogwoods is quick, but is subjective and general. Finally, evaluation of tissue tolerance is often reasonably rapid (days). These techniques include visual browning, which is somewhat subjective; use of vital stains (Guy et al. 1986), although they may indicate only survival or death; and conductivity measurement to determine cell leakage due to membrane damage (Dexter, 1932).

2.6 Chilling Requirement

Rest is maintained by internal factors which prevent plant growth, even when plants are placed under ideal growing conditions. To overcome this state and be competent for spring growth, plants usually have to satisfy a chilling requirement (Weiser 1970, Fuchigami et al. 1982). This involves prolonged exposure to temperatures a few degrees above 0°C (Weiser 1970, Fuchigami et al. 1982). The optimal temperature range is likely to vary slightly among species and ecotypes.

2.6.1 Importance of the Chilling Requirement

While it is necessary to satisfy a chilling requirement to overcome rest, it is still unclear what role the chilling requirement plays in plant winter survival. Litzow and Pellett (1980) observed that rest (chilling requirement) must be satisfied before deacclimation of dogwoods would occur, when brought indoors into a
greenhouse. This suggests that chilling requirement serves to prevent deacclimation during the winter until rest is satisfied. Similarly, others have also suggested that chilling requirements prevent active growth during unseasonably warm winter weather (Lavender and Stafford 1984). Qamaruddin et al. (1993) suggest this may be the case in populations where there is frequent fluctuation around 0°C. Here a large chilling requirement and heat requirement would be needed to initiate flushing. Conversely, northern ecotypes may satisfy their chilling requirement quickly and break bud early, to take advantage of warm spring temperatures and maximize the growing season.

However, all are not in agreement about chilling requirement purpose. Some research indicates that chilling requirement does not necessarily play a significant role in the prevention of hardiness loss or growth stimulation during unseasonably warm winter weather (Weiser 1970). This is based on observations that plants from cold areas in the northern hemisphere often satisfy their chilling requirements by early to mid-winter (Powell 1987). However, Powell (1987) points out that growth will still not occur in winter, despite satisfaction of the chilling requirement, as ambient air temperatures are too low for active growth.

While the importance of chilling requirement in winter survival is uncertain, its satisfaction is most certainly important for vigorous spring growth (Lavender and Stafford 1984).
2.6.2 Factors Behind Satisfaction of the Chilling Requirement

Researchers have tried to correlate the chilling requirement with stages of dormancy. Weiser (1970) feels that the length of time and the temperature required for satisfaction of the chilling requirement is dependent on the stage of plant dormancy, as well as the ecotype. Fuchigami et al. (1982) also suggest that the genotype has an influence on the duration of chilling required to overcome rest.

2.6.3 Alternative Methods for Satisfying the Chilling Requirement

Exposure to chilling temperatures, as the name implies, is the common means of overcoming the chilling requirement. However, studies have shown that other treatments can lead to satisfaction of the chilling requirement. Physical and hormonal alternatives have been suggested. Tanino et al. (1989) found dogwoods exposed to sublethal stresses (i.e. HCN₂ and hot water) overcame rest (hence bypassing normal chilling requirement satisfaction) and lost their hardiness within 3 weeks.

Although probably not a common or practical method of overcoming the chilling requirement, wounding can induce buds in rest to burst. Litzow and Pellett (1980) observed this phenomenon on dogwood buds near the basal cut following pruning. The effect is localized, as wounding has to occur near the bud to cause a release of rest. Results from freezing tests in this thesis indicated that relatively rapid exposure to low temperature released dormancy in dogwoods under controlled freezing experiments. Kobayashi (1982) lists treatment of plants with gibberellic
acid as another method of overcoming rest for the purposes of determining dormancy state.

Plants not exposed to chilling temperatures will eventually overcome rest and begin to grow, however, this can take many months, and growth will be weak and slow. It is unlikely that a plant could survive another winter following this treatment.

2.6.4 Studies in Deciduous Woody Plant Chilling Requirement

The length of time required to satisfy the chilling requirement and the optimal temperatures required vary considerably between species. Some species require relatively short periods to satisfy the chilling requirement, such as Saskatoon berry (24-29 days depending on cultivar)(Kaurin et al. 1984) and red-osier dogwood ecotypes (less than 60 days in thesis studies). Others satisfy their chilling requirements much later or over a much longer period. Douglas-firs usually enter a dormant state beginning in mid-July and often do not satisfy a chilling requirement before February (Lavender and Stafford 1984).

Not only is there variation in timing between species, but there is often variation within species. Holloway et al. (1983) observed this in lingonberries, and Donselman and Flint (1982) in eastern redbud. Holloway et al. (1983) found that an arctic montane ecotype of lingonberry satisfied its chilling requirement earlier than a northern lowland ecotype. Donselman and Flint (1982) observed chilling requirement increase in Eastern redbud directly related to increasing latitude. The
Florida ecotype of this species did not require the satisfaction of a chilling requirement.

2.7 Ecotypes

2.7.1 Terminology

Generally, plants of the same species have similar morphologies and metabolic systems. However, members of a species that are spatially separated must adapt to local environments, which may lead to variations in plant growth, morphology and environmental response. It is at this point that geographical groups within a species begin to be called ecotypes. That is they are genetically distinct. The individuals of each group are "especially adapted to a specific environmental niche" (Stebbins 1942 from Heide 1985).

While the term ecotype is a widely used environmental term to describe genetic variants of a species, a further distinction was made by some of the earliest researchers in this field. Donselman and Flint (1982) refer to Turesson (1922, 1925) who distinguished between clinal (continuous) and ecotypic (discontinuous) morphological and physiological variation. Heide (1985) also refers to the early studies of ecotypes by Turesson (1922). Turesson gathered individuals of the same species from throughout the species range and observed them in one location. He found many persistent differences among what he called ecological races or ecotypes. According to him, they represented a "genotypic response to the various environments where the species is found".
Florida ecotype of this species did not require the satisfaction of a chilling requirement.

2.7 Ecotypes

2.7.1 Terminology

Generally, plants of the same species have similar morphologies and metabolic systems. However, members of a species that are spatially separated must adapt to local environments, which may lead to variations in plant growth, morphology and environmental response. It is at this point that geographical groups within a species begin to be called ecotypes. That is they are genetically distinct. The individuals of each group are "especially adapted to a specific environmental niche" (Stebbins 1942 from Heide 1985).

While the term ecotype is a widely used environmental term to describe genetic variants of a species, a further distinction was made by some of the earliest researchers in this field. Donselman and Flint (1982) refer to Turesson (1922, 1925) who distinguished between clinal (continuous) and ecotypic (discontinuous) morphological and physiological variation. Heide (1985) also refers to the early studies of ecotypes by Turesson (1922). Turesson gathered individuals of the same species from throughout the species range and observed them in one location. He found many persistent differences among what he called ecological races or ecotypes. According to him, they represented a "genotypic response to the various environments where the species is found".
Florida ecotype of this species did not require the satisfaction of a chilling requirement.

2.7 Ecotypes

2.7.1 Terminology

Generally, plants of the same species have similar morphologies and metabolic systems. However, members of a species that are spatially separated must adapt to local environments, which may lead to variations in plant growth, morphology and environmental response. It is at this point that geographical groups within a species begin to be called ecotypes. That is they are genetically distinct. The individuals of each group are "especially adapted to a specific environmental niche" (Stebbins 1942 from Heide 1985).

While the term ecotype is a widely used environmental term to describe genetic variants of a species, a further distinction was made by some of the earliest researchers in this field. Donselman and Flint (1982) refer to Turesson (1922, 1925) who distinguished between clinal (continuous) and ecotypic (discontinuous) morphological and physiological variation. Heide (1985) also refers to the early studies of ecotypes by Turesson (1922). Turesson gathered individuals of the same species from throughout the species range and observed them in one location. He found many persistent differences among what he called ecological races or ecotypes. According to him, they represented a "genotypic response to the various environments where the species is found".
of ecotypes in normal forest conditions and observe differences during tree growth. He indicates, however, this can be expensive and time consuming. In these cases, valuable information can also be gained from controlled environment studies.

Deciduous species ecotype studies are fewer than coniferous. Donselman and Flint (1982) observed ecotypical variation in morphology, dormancy, acclimation and chilling requirement of eastern redbud from 13 locations. While this species does not range into areas of environmental extremes like the dogwood (*Cornus sericea* L.), results indicated some interesting trends. Similar to the basis for this thesis, Donselman and Flint (1982) felt latitudinal differences and sensitivity in photoperiod would influence the timing of growth cessation in eastern redbud. Further, they considered this would also be reflected in acclimation and hardiness. As predicted, they found the more northern ecotypes acclimated rapidly. These ecotypes also entered dormancy quickly under short days, were sensitive to long photoperiods, and had greater chilling requirements than the southern ecotypes. Heide (1985) also notes that with increasing latitude, a longer critical photoperiod for growth cessation is required.

The relationship between the first stage of acclimation and origin did not extend just latitudinally, but also longitudinally (Donselman and Flint 1982). They found ecotypes from the central USA cease growth at longer photoperiods than ecotypes from coastal states at the same latitude. Also, the ecotypes from the most southern location (Florida) had no chilling requirement at all. They equate most of the discussed variations to selection pressures of the environment in which the
Ecotypes are found. In a study with *Salix pentandra*, Juntilla and Kaurin (1985) observed a clinal relationship between inductive photoperiods and growth cessation. This increased with increasing latitude of origin. Similarly, Heide (1985) reports previous work established that Norway spruce between 64°N and 47°N have a critical photoperiod difference of 6 hours.

Ecotype studies in dogwoods have been relatively limited, and those tests that have employed ecotypes were often limited to only a few. As a result, generalizations have been made concerning dormancy induction and freezing tolerance without due attention to ecotypes from the more extreme locations of the species range. The only large scale dogwood ecotype study (21 ecotypes), showed that the acclimation onset trait varied greatly among ecotypes grown at a common site (Smithberg and Weiser 1968). Smithberg and Weiser also found that cold acclimation begins well in advance of cold weather, particularly in the northern ecotypes. While the northern ecotypes acclimated earlier than the southern ones, all eventually reached the same level of hardiness.
3.0 ATTAINMENT OF VEGETATIVE MATURITY (VM) IN DOGWOOD CLONAL ECOTYPES UNDER FIELD, SHADEHOUSE AND CONTROLLED ENVIRONMENT CONDITIONS.

3.1 INTRODUCTION

Fall growth cessation in temperate woody plants is believed to be regulated by shortening photoperiod and warm temperature (Renquist et al. 1978, Weiser 1970). According to Fuchigami et al. (1982), plants only become receptive to the shortening photoperiods following attainment of a state known as the Maturity Induction Point (MIP). This state follows spring bud flush, and occurs in late spring to early summer. After MIP, plants progress to a stage known as Vegetative Maturity (VM). On attainment of VM, plants will no longer re-leaf and resume growth if defoliated (Fuchigami et al. 1982, Kobayashi and Fuchigami 1982). Importantly, cold acclimation is considered to not commence until attainment of VM (Friesen and Stushnoff 1989, Nissila and Fuchigami 1978). Therefore, VM attainment is critical to acclimation and subsequent winter survival.

Plants do not maintain the same hardiness levels throughout the year. In dogwood, hardiness during periods of active growth is only about -4°C (Chen and
Li 1978). After cold acclimation in the fall, hardiness levels can surpass liquid nitrogen levels (-196°C) (Hurst et al. 1967, Guy et al. 1986). The timing at which acclimation occurs is central to cold acclimation and winter survival. Plants may be injured if acclimation begins too late (Fuchigami et al. 1971, Weiser 1970, Fuchigami et al. 1982). Thus, the relationship between VM and the commencement of hardening makes timing of VM attainment critical.

Following VM attainment, plants progress through deeper stages of rest, until Maximum Rest (MR) is attained (Fuchigami et al. 1982). The progression towards maximum rest and simultaneous cold hardening, is considered to be mediated by chilling temperatures (Kobayashi, 1982). Similar to VM, a plant in rest will not grow when placed under ideal growing conditions. At maximum rest a plant will take longer to resume growth than at any other stage of dormancy (Fuchigami et al. 1982).

In order for a plant to be competent for spring bud flush, it must overcome the growth inhibitory effects of rest (Lavender and Stafford 1984, Weiser 1970). Satisfaction of a chilling requirement is the usual method of overcoming rest in temperate plants (Lavender and Stafford 1985, Fuchigami et al. 1982, Weiser 1970). Conditions may differ with plants from sub-tropical areas (Donselman and Flint 1982). Aside from its function in overcoming rest, it has been suggested that a chilling requirement may act as a protective mechanism. Lavender and Stafford (1985) suggest that it serves to prevent flushing of Douglas-fir during periods of mild winter temperatures.
Both attainment of VM and satisfaction of a chilling requirement are important aspects of the dormancy cycle. Winter survival and resumption of spring growth depend on these processes. Since both processes appear to be environmentally regulated, ecotypical variation in these processes will reflect the native environment of the ecotype. However, ecotype studies of VM and chilling requirement in woody plants are few (Donselman and Flint 1982, Mergen 1963, Juntilla and Kaurin 1985).

This study will, in part, determine if there is ecotypical variation among a wide range of dogwood (Cornus sericea L.) clonal ecotypes, with respect to timing of VM attainment and the satisfaction of a chilling requirement. Dogwood is chosen as the test species since a significant portion of the deciduous woody plant dormancy induction studies have been conducted using Cornus sericea L. (Fuchigami et al. 1982, Fuchigami et al. 1971, Kobayashi et al. 1982, Kobayashi and Fuchigami 1983, Nissila and Fuchigami 1978, Renquist et al. 1978, Seibel and Fuchigami 1978). Dogwood also has the advantage of easy propagation from cuttings, rapid growth, high stress tolerance, and a wide geographical distribution (Smithberg and Weiser 1968).

This study will further compare several of the systems commonly used to test dormancy induction and cold acclimation processes in dogwoods and other woody species. Most experiments utilize only one test system when conducting dormancy studies, due to economic and time constraints. Nevertheless, before selecting a test system, it is important to evaluate and compare systems of plant response under
natural conditions. The most commonly selected systems are shadehouse/potted plants (Litzow and Pellett 1980, Lavender and Stafford 1985, Kobayashi et al. 1982, Fuchigami et al. 1977, Nissila and Fuchigami 1978), greenhouse (Proebsting 1983) and controlled environment (Chen and Li 1978, Renquist et al. 1978, Seibel and Fuchigami 1978), in contrast to the few field systems (Kaurin et al. 1984). While field studies yield the most accurate indication of environmental influence on dormancy induction, they do not offer the ease or flexibility of the other systems. Potted shadehouse plants are easily moved. Greenhouse studies allow year round testing and a limited degree of environmental control. Controlled environment systems have been attractive largely because of controlled environment capabilities. Each of these systems assumes plant response will be similar to field plants. However, no tests have been undertaken to verify the accuracy and similarity of these systems. This study will, in part, evaluate field, shadehouse, and controlled environment systems for studies of ecotypical variation in VM attainment.

3.2 MATERIALS AND METHODS

3.2.1 Field Studies

Field Design and Maintenance

Six clonal ecotypes (based on a collection by researchers at the University of Minnesota) of red-osier dogwood (Fig. 3.1) (Cornus sericea L.) were planted in the
Figure 3.1 Geographical distribution of dogwood (Cornus sericea L.) clonal ecotypes.
University of Saskatchewan Horticulture field plots (orthic dark brown chernozem) at Saskatoon, Saskatchewan, Canada (52°07'N). Ecotypes originated from Utah (42°N), Massachusetts (42°23'N), Chalk River, Ontario (46°03'N), Saskatoon, Saskatchewan (52°07'N), Northwest Territories (62°N), and Alaska (64°43'N). Massachusetts (Mass), Utah, Chalk River (CR), and Northwest Territories (NWT) ecotypes were planted in July 1991. Alaska (Ala) and Saskatoon (S'toon) ecotypes were planted in July 1992.

Plants were propagated by softwood cuttings taken from mother plants grown under greenhouse conditions (25°C ± 5°C, approximately 22 hr days at 600-800 μmol·m⁻²·s⁻¹ - extended through supplemental incandescent/cool-white fluorescent lighting). Cuttings were dipped in STIM-ROOT No.3 (0.4% IBA) (Plant Products Co. Ltd., Bramalea, Ont.) rooting powder before being placed into a mistbed. Rooted cuttings were potted up into 4 or 6 inch pots, or into root trainers (model 170-4, Spencer-Lemaire Industries, Edmonton), using Redi-Earth media, and grown under greenhouse conditions (as above). At the time of field planting, plants were one to three years old. In all cases, sampling was performed on current year growth.

Ecotypes were planted in east-west rows with 2 meter row spacing and 1 meter plant spacing (30 plants per row). Plants were watered regularly through the summer using a trickle irrigation system. Irrigation was terminated approximately mid-August each year. Weeds were removed as necessary both mechanically and by hand. Plants were mulched with barley/wheat straw and/or wood chips, at a depth
of 1-2 ft., for winter protection. Mulch was applied about mid-October when the night temperatures began to dip below -6°C.

Field Studies on the Attainment of Vegetative Maturity (VM)

Ecotypes were sampled weekly from late July until vegetative maturity was attained. Vegetative maturity was defined as the date when, under growth-inductive mist tent conditions (see below), lateral buds did not burst and grow following plant decapitation and defoliation.

At each sampling time, 4-7 random stem sections (10-20 cm in length, apical bud included) were taken from each ecotype. Apices were removed and cuttings were defoliated. Active growth conditions involved placement of the basal ends of cuttings into a sand bed in a warm plastic covered mist tent (25°C ± 5°C, approximately 22 hr days at 200-300 μmol·m⁻²·s⁻¹ - extended through supplemental incandescent/cool-white fluorescent lighting). Sand beds were misted twice daily for approximately 5 minutes. Cuttings were monitored for bud break (the first lateral bud to break and produce two fully expanded leaves). This sampling process is referred to as the defoliation test (based on Fuchigami et al. 1982, Seibel and Fuchigami 1978). Attainment of vegetative maturity was the date, determined by interpolation, at which greater than 50% of the cuttings of one ecotype did not break bud within 60 days.
Field Studies on the Satisfaction of the Chilling Requirement

Ecotypes were sampled in the same manner described in the previous section. Following attainment of vegetative maturity, sampling continued until field cuttings began to break bud under mist tent conditions, indicating chilling requirement had been fulfilled. Satisfaction of the chilling requirement was the date, determined by interpolation, by which at least 50% of the cuttings of one ecotype broke bud following the attainment of vegetative maturity.

3.2.2 Shadehouse studies

Shadehouse Design and Maintenance

Cuttings of five dogwood clonal ecotypes (Mass, Utah, NWT, Alaska, S'toon) were propagated from greenhouse softwood cuttings, using STIM-ROOT No.3 (Plant Products Co. Ltd., Bramalea, Ont.). Rooting was established in a mist tent sand bed (25°C ± 5°C, approximately 22 hr days at 200-300 μmol·m⁻²·s⁻¹ extended through supplemental incandescent/cool-white fluorescent lighting) containing a 6:3:1 sand, peat, perlite medium. Once rooted, cuttings were potted into Spencer-Lemaire root trainers using Redi-earth medium. Plants were grown under greenhouse conditions (see Field Design and Maintenance) to a height of 30-60 cm before being re-potted into 6 inch square peat fibre pots. In July 1992, pots were placed into a shadehouse at the University of Saskatchewan Horticultural field plots (light intensity approximately 170 μmol·m⁻²·s⁻¹). Plants were watered
regularly, and in late September, plants were mulched with wood chips to provide winter protection.

**Shadehouse Studies on VM**

Beginning in late July, weekly samples of 4 pots of each ecotype were taken from the shadehouse. Plants were decapitated and defoliated before being placed into a greenhouse under active growth conditions (see Field Design and Maintenance). Plants were monitored for attainment of vegetative maturity as described in the field studies.

**Shadehouse Studies on the Satisfaction of the Chilling Requirement.**

Plants were sampled and monitored for satisfaction of the chilling requirement as previously described (see Studies on the Satisfaction of the Chilling Requirement).

### 3.2.3 Controlled Environment Studies

**Design and Maintenance**

Dogwoods were propagated from greenhouse cuttings as per the field studies section. Once cuttings had been rooted in a mist tent, they were potted up into root trainers using Redi-earth, and grown under greenhouse conditions as previously described (see Field Design and Maintenance). Plants were tested at a height of 10-20 cm. Plants received daily watering and weekly fertilization in the greenhouse.
During controlled environment experiments, plants were watered once every three days, or as necessary.

Controlled environment chambers were manufactured by Conviron (models E8H and PGR15). Chamber humidity was maintained at 60-80%. Light intensity was approximately 225 $\mu$mol·m$^{-2}$·s$^{-1}$, produced by incandescent and cool-white fluorescent fixtures. Plants in the controlled environment chambers were sprayed, as required, with TRUMPET (at recommended rates) to control whitefly.

**Controlled Environment Studies on Attainment of VM**

Four ecotypes (Mass, Utah, NWT and Alaska) were placed under previously reported VM inductive conditions (SD/WT - 8/16 hr day/night, 20/15°C day/night) (based on Fuchigami et al. 1982, Chen and Li 1978). At approximately ten day intervals, one root trainer sleeve (4 plants) of each ecotype was sampled for attainment of VM using the defoliation test. Defoliated plants were placed under active growth conditions in a controlled environment chamber (LD/WT - 22/2 hr, 20/15°C day/night) and monitored for attainment of VM as previously described.

**Controlled Environment Studies on the Satisfaction of the Chilling Requirement.**

Plants were sampled similarly to the previous VM attainment section (see Controlled Environment Studies on Attainment of VM). Once an ecotype was determined to have achieved VM, the remainder of the root trainer sleeves was
transferred to chilling requirement satisfaction conditions (4°C in darkness). At approximately 10 day intervals, four plants of each ecotype were sampled in the same manner described in the previous VM attainment section. Defoliated samples were placed into LD/WT conditions and monitored for bud break as previously described.

3.2.4 Comparison of Field, Shadehouse and Controlled Environment as Systems for Evaluation of Ecotypical Variation in the Attainment of VM.

VM and chilling satisfaction date were determined under both field and shadehouse conditions. Since VM is defined as a state in which growth does not occur under ideal conditions, measurement of this phenomenon could require an indefinite period of time. For tested plants however, it was observed that 40 days appeared to be a consistent division between bud break and dormancy acquisition. Below 40 days to bud break, development to VM was not committed. Beyond 40 days to bud break, most ecotypes were irreversibly progressing towards the attainment of VM. Interpolation was used to determine the date at which plants reached the 40 days to bud break stage. This date was determined for each test replication using the closest data points above and below 40 days to bud break (based on a linear interpolation).

Values for the reps in the shadehouse and field studies were compared by 2-way ANOVA at α.05. Since controlled environment chamber-tested plants were not gradually exposed to VM inducing conditions (as under natural conditions),
comparison of timing of VM and chilling requirement satisfaction between controlled environment chamber, shadehouse and field studies was not appropriate. Instead, field, shadehouse and controlled environment systems were compared on the relative order of dormancy acquisition and satisfaction of the chilling requirement in dogwood ecotypes.

3.3 RESULTS

3.3.1 Field Studies

Under natural conditions there was a noticeable difference in date of VM attainment between the more northern ecotypes (Alaska and NWT) and the more southern ecotypes (Mass, Utah and CR - Fig. 3.2). VM was induced in the more northern ecotypes during August (Alaska) and early September (NWT). The southern ecotypes exhibited later VM attainment (Mass in September) or prolonged growth cessation rather than true dormancy (Utah and CR). Utah and CR days to bud break never exceeded much more than 50 days.

The Alaska ecotype attained VM first and by early August (daylength 15-16 hrs., approx. 25/10°C day-night temp. - Figs. 3.3 & 3.4) did not break bud under inductive conditions (Table 3.1). The Northwest Territories ecotype followed Alaska, attaining VM in late August (daylength 13-14 hrs., approx. 18/5°C day-night temperature - Table 3.1, Figs. 3.3 & 3.4). The dates of VM attainment (40
Table 3.1 Attainment of vegetative maturity (VM) under field conditions (Saskatoon, SK) for five dogwood (*Cornus sericea* L.) clonal ecotypes.

<table>
<thead>
<tr>
<th>Ecotypes***</th>
<th>VM Attainment Date***,******</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alaska</td>
<td>Aug. 10 a</td>
</tr>
<tr>
<td>NWT</td>
<td>Aug. 31 b</td>
</tr>
<tr>
<td>Mass</td>
<td>Oct. 4 c</td>
</tr>
<tr>
<td>CR</td>
<td>Oct. 12* c</td>
</tr>
<tr>
<td>Utah</td>
<td>Oct. 15* c</td>
</tr>
</tbody>
</table>

* Did not attain equivalent depth of dormancy as Mass  
** Time measurements taken from first sampling date  
*** n = 3 reps.  
**** Tested by 2-way ANOVA and LSD at 0.05 level

Table 3.2 Satisfaction of the chilling requirement under field (Saskatoon, SK) conditions for five dogwood (*Cornus sericea* L.) clonal ecotypes.

<table>
<thead>
<tr>
<th>Ecotypes***</th>
<th>Chilling Requirement Satisfaction Date***,******</th>
<th>Length of Chilling Period (days)<em><strong>,</strong></em>***</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alaska</td>
<td>Oct. 17 a</td>
<td>67.0 c</td>
</tr>
<tr>
<td>NWT</td>
<td>Oct. 25 b</td>
<td>55.0 c</td>
</tr>
<tr>
<td>CR</td>
<td>Nov. 2 c</td>
<td>20.7 a</td>
</tr>
<tr>
<td>Utah</td>
<td>Nov. 7 d</td>
<td>22.7 a</td>
</tr>
<tr>
<td>Mass</td>
<td>Nov. 10 e</td>
<td>36.7 b</td>
</tr>
</tbody>
</table>

** Time measurements taken from first sampling date  
*** n = 3 reps.  
**** Tested by 2-way ANOVA and LSD at 0.05 level
Figure 3.2 Dormancy induction and satisfaction of the chilling requirement of field planted dogwood (Cornus sericea L.) clonal ecotypes
Daylengths are calculated on mid-month values.

Figure 3.3 Daylength in Saskatoon, SK, Canada plotted on a mid-monthly basis (latitude: 52.07N, 106.38W). Supplied by Environment Canada
Figure 3.4 Saskatoon, SK, Canada max/min temperatures - 1992 (supplied by Environment Canada)
Figure 3.4 Saskatoon, SK, Canada max/min temperatures - 1992 (supplied by Environment Canada)
Figure 3.4 Saskatoon, SK, Canada max/min temperatures - 1992
(supplied by Environment Canada)
days to break bud following defoliation) between Alaska and NWT were significantly different from each other (Table 3.1).

Although Figure 3.2 indicates a rapid transition between active growth and dormancy in the northern ecotypes, plants were noticeably changing in other respects before VM was detected. By early July, the bark of northern ecotype stems was beginning to redden and by mid-August leaf abscission was marked. Early growth cessation and VM attainment resulted in a short active growth season for these ecotypes. Consequently, very little new growth was put on during the year.

Generally, the southern ecotypes (Mass, Utah and CR) responded more similarly to each other than the northern ecotypes (Fig. 3.2). However, the southern ecotype response was shifted to a later date (late September to early October - daylength 11-12 hrs., approx. 15-20/1-5°C day-night temperature). Although the initial growth cessation was similar between the southern ecotypes, CR and Utah did not attain the equivalent depth of VM as Mass. At maximum growth cessation, CR and Utah ecotypes would burst bud in under 50 days. Mass, however, did attain VM by late September, and had not broken bud after more than 100 days of observation. A comparison of Mass VM date with Utah and CR growth inhibition date showed no significant difference between ecotypes (Table 3.1). VM attainment or growth inhibition dates of all southern ecotypes were, however, significantly later than those of NWT and Alaska (Table 3.1).

Unlike northern ecotypes, southern types exhibited a lack of significant leaf abscission before killing frosts. Further, the Utah ecotype maintained active growth
until the first hard frosts (October). CR ecotype produced large numbers of viable, visually differentiated flower buds in the fall. Interestingly, despite differences in VM attainment and phenotypic traits, all ecotypes, including Utah, eventually set terminal buds. Following terminal bud set, growth cessation was maintained throughout the winter.

Over the duration of the field studies, the ecotypes satisfied their chilling requirements, and in the process progressed from a state of rest to a quiescent state. On attainment of quiescence, samples brought into the greenhouse from the field for forcing would begin to grow within a few weeks. However, plants remained in a quiescent state in the field until favourable growth conditions in the spring.

The range of chilling requirement satisfaction dates, measured from the attainment of VM, was more tightly grouped (mid-October to early November) than the range of VM attainment dates (Tables 3.1 & 3.2). Despite the narrow range of chilling requirement satisfaction dates, a high degree of synchrony within ecotype samples led to significantly different satisfaction dates (Table 3.2). The ecotype order of satisfaction of the chilling requirement was similar to the order of VM attainment. The two northern ecotypes satisfied their chilling requirement first (Alaska and NWT respectively), followed by the southern ecotypes (CR, Utah, Mass respectively). The northern ecotypes required the greatest time after VM attainment to reach chilling requirement satisfaction (Alaska and NWT, not significantly different), while the southern ecotypes required a significantly shorter time (Table
3.2). Although CR and Utah did not attain the same level of VM as other ecotypes, a chilling period was required to hasten bud break.

3.3.2 Shadehouse Studies

The results of the shadehouse studies were similar to the field studies, with the exception that Utah attained true VM under shadehouse conditions where bud break did not occur after more than 100 days of inductive conditions. Northern ecotypes attained VM earlier than the southern ecotypes (Fig. 3.5). Both the Alaska and the NWT ecotype attained VM in mid-August (daylength 14-15 hrs., approx. 25/10°C day-night temperature), and there was no significant difference in date of attainment between the northern ecotypes (Table 3.3). The other three ecotypes (S'toon, Mass, Utah) attained VM in late September (daylength 11-12 hrs., approx. 18/5°C day-night temperature). The Saskatoon ecotype attained VM significantly earlier than Utah, while Mass did not differ significantly from either Utah or Saskatoon (Table 3.3).

Similar to field studies, the range of dates for chilling requirement satisfaction were more tightly grouped than the dates of VM attainment. Most shadehouse ecotypes satisfied their chilling requirement mid to late October (Table 3.4). Alaska satisfied its chilling requirement first and significantly earlier than Saskatoon and NWT. The latter two ecotypes satisfied their chilling requirements significantly earlier than Utah and Mass. Mass was the last ecotype to satisfy its chilling requirement (Table 3.4).
Figure 3.5 Dormancy induction and satisfaction of the chilling requirement of shadehouse-grown dogwood (Cornus sericea L.) clonal ecotypes
Table 3.3 Attainment of vegetative maturity (VM) under shadehouse conditions (Saskatoon, SK) for five dogwood (*Cornus sericea* L.) clonal ecotypes.

<table>
<thead>
<tr>
<th>Ecotypes***</th>
<th>VM Attainment Date**,******</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alaska</td>
<td>Aug. 24 a</td>
</tr>
<tr>
<td>NWT</td>
<td>Aug. 26 a</td>
</tr>
<tr>
<td>S’toon</td>
<td>Sept. 26 b</td>
</tr>
<tr>
<td>Mass</td>
<td>Sept. 30 bc</td>
</tr>
<tr>
<td>Utah</td>
<td>Oct. 1 c</td>
</tr>
</tbody>
</table>

** Time measurements taken from first sampling date  
*** n = 4 reps.  
**** Tested by 2-way ANOVA and LSD at 0.05 level

Table 3.4 Satisfaction of the chilling requirement under shadehouse conditions (Saskatoon, SK) for five dogwood (*Cornus sericea* L.) clonal ecotypes.

<table>
<thead>
<tr>
<th>Ecotypes***</th>
<th>Chilling Requirement Satisfaction Date**,******</th>
<th>Length of Chilling Period (days)******</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(measured from VM date)</td>
<td></td>
</tr>
<tr>
<td>Alaska</td>
<td>Oct. 12 a</td>
<td>47.7 c</td>
</tr>
<tr>
<td>NWT</td>
<td>Oct. 21 b</td>
<td>55.0 d</td>
</tr>
<tr>
<td>S’toon</td>
<td>Oct. 24 c</td>
<td>29.7 ab</td>
</tr>
<tr>
<td>Utah</td>
<td>Oct. 27 d</td>
<td>25.3 a</td>
</tr>
<tr>
<td>Mass</td>
<td>Nov. 2 e</td>
<td>32.0 b</td>
</tr>
</tbody>
</table>

** Time measurements taken from first sampling date  
*** n = 3 reps.  
**** Tested by 2-way ANOVA and LSD at 0.05 level
Similar to field studies, the more northern ecotypes (NWT and Alaska) appeared to have the longest chilling requirements (NWT significantly longer than Alaska). The southern ecotypes satisfied their chilling requirements more quickly. Utah satisfied significantly earlier than Mass, with S'toon being intermediate between the two (no significant difference (Table 3.4).

3.3.3 Controlled Environment Studies

The order of VM attainment under controlled environment conditions was similar to the field and shadehouse systems (Fig. 3.6). Alaska entered dormancy first followed by NWT, Mass and Utah (Fig. 3.6). Unlike field and shadehouse studies, VM attainment dates were evenly distributed with no apparent northern and southern groupings. All ecotypes had significantly different VM attainment dates (Table 3.5).

While each ecotype attained VM according to our 40 days to bud break division, the level of VM varied. Alaska and NWT appeared to attain true VM according to our guidelines, but some Mass and Utah plants would still burst bud following defoliation although it required more than 100 days to do so. However, the vigour of new Mass and Utah leaves at this time was poor, and subsequent growth was slow and minimal. It appears that the depth of VM of the more southern types did not attain the same level as the northern ecotypes.

Attainment of dormancy is required before satisfaction of the chilling requirement can commence. NWT and Mass ecotypes were tested for satisfaction of
Figure 3.6  Controlled environment vegetative maturity (VM) induction under short day/warm temperature (SD/WT) conditions.
Table 3.5 Vegetative maturity (VM) attainment of four dogwood (*Cornus sericea* L.) clonal ecotypes under a controlled environment short day/warm temperature (SD/WT) regime.

<table>
<thead>
<tr>
<th>Ecotypes***</th>
<th>Days to Attain VM**.****</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alaska</td>
<td>29.8 a</td>
</tr>
<tr>
<td>NWT</td>
<td>51.8 b</td>
</tr>
<tr>
<td>Mass</td>
<td>78.0 c</td>
</tr>
<tr>
<td>Utah</td>
<td>107.8 d</td>
</tr>
</tbody>
</table>

** Time measurements taken from first sampling date

*** n = 4 reps.

**** Tested by 2-way ANOVA and LSD at 0.05 level

Table 3.6 Comparison of satisfaction of the chilling requirement for four dogwood (*Cornus sericea* L.) clonal ecotypes under field and shadehouse conditions (Saskatoon, SK).

<table>
<thead>
<tr>
<th>Ecotypes***</th>
<th>Field Satisfaction Date**.****</th>
<th>Shadehouse Satisfaction Date**.****</th>
</tr>
</thead>
<tbody>
<tr>
<td>NWT</td>
<td>Oct. 26*</td>
<td>Oct. 21*</td>
</tr>
<tr>
<td>Alaska</td>
<td>Oct. 17*</td>
<td>Oct. 12*</td>
</tr>
<tr>
<td>Mass</td>
<td>Nov. 10*</td>
<td>Nov. 2*</td>
</tr>
<tr>
<td>Utah</td>
<td>Nov. 8*</td>
<td>Oct. 27*</td>
</tr>
</tbody>
</table>

* Field and shadehouse values significantly different

** Time measurements taken from first sampling date

*** n = 3 or 4 reps.

**** Tested by 2-way ANOVA and LSD at 0.05 level
the chilling requirement. Although Mass did not attain the same depth of VM as NWT, both the dormant NWT and the Mass control exhibited the same chilling satisfaction trend (Fig. 3.7). Both ecotypes exhibited a very rapid response to the chilling temperatures, having completely overcome their dormant or dormant-like states after 30 days in the dark at 4°C. It appears that low temperature enhances bud break in all ecotypes irrespective of the depth of VM attainment.

3.3.4 Field, Shadehouse and Controlled Environment System Comparison

A comparison of the field and shadehouse systems revealed variation in dates of chilling requirement satisfaction (Table 3.6). All ecotypes satisfied chilling requirements significantly later under field conditions. Field and shadehouse system VM attainment dates were more similar, as only Alaska exhibited significantly different dates of VM attainment between the systems (Table 3.7). When comparing all three systems (field, shadehouse and controlled environment), ecotype order of VM attainment was consistent among all systems. However, unlike field and shadehouse conditions, controlled environment chamber treated ecotypes did not exhibit a distinct northern and southern grouping.
Figure 3.7 Chilling requirement of two growth chamber induced vegetatively mature dogwood (Cornus sericea L.) clonal ecotypes
Table 3.7 Comparison of vegetative maturity (VM) attainment date for four dogwood (*Cornus sericea* L.) clonal ecotypes under field and shadehouse conditions (Saskatoon, SK).

<table>
<thead>
<tr>
<th>Ecotypes**</th>
<th>Field Attainment Date***,****</th>
<th>Shadehouse Attainment Date***,****</th>
</tr>
</thead>
<tbody>
<tr>
<td>NWT</td>
<td>Aug. 31</td>
<td>Aug. 26</td>
</tr>
<tr>
<td>Alaska</td>
<td>Aug. 10*</td>
<td>Aug. 25*</td>
</tr>
<tr>
<td>Mass</td>
<td>Oct. 4</td>
<td>Sept. 30</td>
</tr>
<tr>
<td>Utah</td>
<td>Oct. 14</td>
<td>Oct. 1</td>
</tr>
</tbody>
</table>

* Field and shadehouse values significantly different  
** Time measurements taken from first sampling date  
*** n = 3 or 4 reps.  
**** Tested by 2-way ANOVA and LSD at 0.05 level
3.4 DISCUSSION

3.4.1 Systems Comparison

In general, ecotypes attained vegetative maturity and satisfied their chilling requirements in a consistent order regardless of the system utilized. However, variation in depth of bud dormancy and differences in ecotype grouping were observed between systems. Field and shadehouse conditions tended to segregate ecotype responses into distinct "northern" (north of 60°N) and "southern" (south of 60°N) groups, while controlled environment conditions equally partitioned all ecotypes. Further, depth of bud dormancy induced under controlled environment chamber conditions of SD/WT was not equivalent to either field or shadehouse systems. This suggests that natural VM-inductive conditions could not be replicated in the controlled environment system. Murakami et al. (1990) found they could not induce rest in Washington hawthorn under controlled environment conditions, while plants attained rest under natural conditions.

Differences in depth of dormancy existed not only between field/shadehouse and controlled environment chamber, but also between field and shadehouse systems. Utah only achieved the depth of dormancy approaching that of true VM under shadehouse conditions. The only major differences between the two outdoor systems were that shadehouse plants were in pots, and that one system received shade from the summer sun by the shadecloth and surrounding trees. Photoperiods
may have become artificially short early due to interference effects of the trees.

This may lead to early induction of growth cessation.

Pots may have had an influence on Utah VM attainment through stress and temperature alterations. In late summer and fall, it is likely that roots of pot plants were exposed to cooler conditions than field plants. Weiser (1970) notes that while roots are less frost resistant than stems, exposure of roots to low temperatures could lead to cold resistance levels equivalent to the stem. It may be that cooler root temperatures can also accelerate dormancy induction in Utah shadehouse plants. This phenomenon could also account for earlier VM attainment under shadehouse conditions compared to field conditions. Our other studies indicate that cool temperatures can enhance dormancy attainment (see chapter 4). It is also possible that pots acted to impose a stress on the plants through restriction of root growth and reduction in water availability. Plants will often enter a state of growth cessation (ecodormancy) during times of stress (Lang 1987). As plant growth cessation is pre-requisite to dormancy attainment, induction of growth cessation, due to water stress or inhibited root growth may have hastened VM attainment.

A comparison of chilling requirement satisfaction dates reveals the same trends as VM attainment. All ecotypes had satisfied their chilling requirement significantly earlier under shadehouse conditions. Again, cool root temperatures may potentially have led to early satisfaction of the chilling requirement. The influence of root temperatures on dormancy acquisition and satisfaction of the chilling requirement merits further investigation.
This study indicates that all systems produce the same order of ecotype VM attainment. Nevertheless, controlled environment chambers could not always induce the VM and the same depth of dormancy as field and shadehouse conditions. Further, shadehouse conditions where plants are grown in containers appear to stimulate slightly earlier VM attainment and satisfaction of the chilling requirement over field conditions. This latter point is of particular relevance to the nursery industry, where timing of dormancy attainment and subsequent satisfaction of the chilling requirement can be critical to plant survival and potential sales.

3.4.2 VM Attainment

Field Studies

Under field conditions, there was a segregation of ecotypes into northern and southern groups. This is likely due to the similarity of environments of certain ecotypes in these groups (see Appendix 1 for temperature and photoperiod data). The Alaska and NWT ecotypes originate from northern environments with extreme temperatures (Heide 1985), short growing seasons and considerable seasonal differences in light quality and duration (Nilsen 1985, Lindgren and Lindgren 1985). Both ecotypes expressed early VM attainment; becoming dormant in August. This coincided with the beginning of the rapid decrease in photoperiod which occurs at the onset of fall in Saskatoon, while temperatures during August reflected a relatively warm 25/10°C day-night. Detection of changing photoperiod is a classic dormancy induction response (Weiser 1970). Many temperate plant species are

Utah, Mass and CR all originate from moderate environments with long growing seasons, gradual temperature fluxes, and few radical shifts in light quality and duration (see Appendix 1 for temperature and photoperiod data). Under field conditions, these ecotypes began to attain VM in late September and early October. During this period, the photoperiod was shorter (by about 4 hours) than in August when the northern ecotypes attained VM. However, the reduction in average temperatures was more noticeably different. Day temperatures were approximately 15-20°C, and night temperatures were slipping to a 1 to 5°C range. While the northern ecotypes responded to a decreasing photoperiod, it is more difficult to identify specific environmental stimuli with the southern ecotypes. Both photoperiod and temperature are changing at the time VM is induced. Fuchigami *et al.* (1982) also found that the Mass ecotype attained VM under similar conditions in late September in Oregon. These conditions reflected a photoperiod of about 12 hours and temperatures of about 17/2°C day/night. These conditions compare favourably with our results. While warm days are likely necessary for normal metabolic and photosynthetic rate, cool nights may act to drive the plant towards dormancy. Kobayashi (1982) indicates that low temperatures (above freezing) are very effective for driving plants towards deeper rest. However, he states this effect follows the attainment of VM. A test by Renquist *et al.* (1978) found 20°C to be the optimal
temperature for VM induction in dogwoods. However, this was based on regimes of constant warm temperatures and one regime with a relatively constant cool diurnal fluctuation. No tests were undertaken with warm days and cool nights. The question of low temperature efficacy on dormancy induction and enhancement is addressed in Chapter 4.

Despite the fact that dormancy induction appeared to be initiated in the southern ecotypes in late September and early October, only the Mass ecotype truly attained VM under field conditions. The Utah and CR ecotypes did not exhibit a deep level of VM since bud break occurred in less than 60 days. Prior tests indicated that attainment of true rest was a standard component of dormancy development in *Cornus sericea* L. (Fuchigami *et al.* 1982, Kobayashi *et al.* 1982, Tanino *et al.* 1989, Fuchigami *et al.* 1977, Nissila and Fuchigami 1978). Despite lack of true VM attainment, the ecotypes set bud and remained in a state of inactivity in the field until spring conditions were adequate for growth. Further, shadehouse studies indicate that Utah is capable of attaining VM. Interestingly, other tests have suggested that effective cold acclimation only occurs after the induction of rest (attainment of VM) (Friesen and Stushnoff 1989, Nissila and Fuchigami 1978), yet spring re-growth of Utah revealed that plants had cold acclimated to levels below -30°C. This strongly suggests that attainment of true VM is not always a pre-requisite for winter survival.

While the attainment of VM was the measured parameter in this test of dormancy induction, other changes in plant growth were evident prior to observation
of the onset of VM. Bud set, leaf abscission, and colour change all occurred before the attainment of VM. Traits appeared to be ecotype-specific, and while correlation studies were not undertaken, there did not appear to be any relationship between these characteristics and the attainment of VM. Nevertheless, these phenotypic observations when coupled with a slow increase in days to bud break before the rapid increase, suggest that plants undergo a gradual transition from active growth to growth cessation to true dormancy (Carter and Brenner 1985, Kaurin et al. 1984) rather than discrete points as indicated by the "GS model (Fuchigami et al. 1982).

Shadehouse Studies

Similar to the field studies, there were northern and southern groupings of shadehouse ecotypes with respect to dormancy induction. The northern ecotypes (NWT and Alaska) attained VM before the southern ecotypes (S’toon, Mass and Utah). As with the field studies, this is likely due to a similarity of ecotype native environments in northern or southern regions. As discussed in the systems comparison section, ecotypes attained VM at similar times to field plants.

A similar discussion of photoperiod and temperature influence on VM attainment for field plants applies to shadehouse plants. In general, there were only a few notable differences between shadehouse and field studies. Unlike field conditions, Utah ecotype attained true VM under shadehouse conditions. As previously discussed, this may have been a result of an influence of light or pots. The shadecloth of the shadehouse would have reduced light intensity and perhaps
lowered air temperatures slightly. Further, shadehouse proximity to large trees and hedges also may have effectively shortened the daylength under shadehouse conditions, and potentially reduced end of day light.

The effect of pots on root temperature must also be considered as a possible explanation for Utah VM attainment under shadehouse conditions. Pots effectively brought plant root systems above ground. Under these conditions they would experience cooler temperatures than the roots of field planted dogwoods. This was visibly noticeable as soil in pots froze before soil around field dogwoods. Studies have already shown that roots can respond to temperature, as exposed roots can acclimate to the same extent as above ground stems (Weiser, 1970). Based on the close association between acclimation, dormancy development and cool temperatures, it is plausible that cooling of root systems could enhance dormancy induction.

VM attainment of other ecotypes was also affected by shadehouse conditions. Most ecotypes attained VM earlier under shadehouse conditions than in the field. Similar to Utah results, early VM attainment by other shadehouse ecotypes may have been due to a root cooling influence. The exception was Alaska ecotype, which attained VM earlier under field conditions. There were, however, concerns about Alaska juvenility in the field. Plants were very small at time of transplanting, and grew very little following transplanting. Transplant shock, potentially leading to growth cessation, may have encouraged earlier VM attainment in this ecotype.
In a previous test with potted dogwoods at the University of Saskatchewan campus, Friesen and Stushnoff (1989) found that dogwoods from a local source attained VM on Aug. 7 and Aug. 6 in successive years. Our most northern ecotype (Alaska) did not attain VM by this date. Our local ecotype attained VM on Sept. 26. The difference between the two studies may be due to sampling technique. Our technique involved bringing manually defoliated whole plants into a greenhouse with long daylengths, warm temperatures and adequate water; conditions stimulatory to active growth. A plant that does not grow under these conditions is assumed to be vegetatively mature. Friesen and Stushnoff appear to have left branch samples attached to the plant. Under natural conditions, with daylengths continuing to shorten, defoliation may have been a sufficient stress to induce ecodormancy or correlative inhibition, during which re-growth would not occur in the field. Early growth cessation may have lead to early attainment of VM. Consequently, the sampling technique would result in pre-mature determination of VM attainment date. These two studies indicate how slightly different methodologies can lead to vastly different results.

**Controlled Environment Studies**

The traditional SD/WT regime was used to induce VM attainment under controlled environment conditions (based on Fuchigami et al. 1982, Chen and Li 1978). However, this regime is markedly different from the field and shadehouse studies. Although such controlled environment testing conditions have been
successfully used to induce VM (Chen and Li 1978, Seibel and Fuchigami 1978),
they are still artificially produced and cannot be assumed to be perfect reproductions
of natural conditions. Normal (i.e. end of day light, inter- and intra-species
competition) and random variation (i.e. wind, cloud cover, freeze/thaw, fluctuating
soil water status) in environment, are difficult to reproduce under chamber
conditions and may have a significant influence on plant response.

Attainment of VM occurred in the same order as the field and shadehouse
systems. Northern ecotypes attained VM first, followed by the southern ecotypes.
However, unlike the field and shadehouse studies, there were no distinct
northern/southern ecotype groupings. This indicates chamber conditions are not
complete representations of field conditions. Further evidence of controlled
environment limitations was observed in analysis of dormancy status. By definition
of the 40 days to bud break method, all ecotypes attained VM under controlled
environment conditions. However, there were different depths of VM rather than
the presence/absence of true VM attainment. Certain Mass and Utah plants would
still burst bud after 60-80 days under active growth conditions. Conceivably,
controlled environment conditions were adequate for initiation of growth cessation or
dormancy induction processes in Mass and Utah, but were not quite sufficient to
stimulate true VM attainment.
3.4.3 Satisfaction of the Chilling Requirement

Field Studies

Date of satisfaction of the chilling requirement was more synchronized than date of VM attainment, but still produced northern and southern groupings similar to those observed with VM attainment. Ecotypes tended to satisfy their chilling requirements uniformly. All five ecotypes satisfied chilling requirements at significantly different dates, despite a satisfaction date range of only 25 days. It appears that any sample variation which exists during attainment of VM, is greatly reduced during satisfaction of the chilling requirement.

Alaska and NWT were the first ecotypes to satisfy their chilling requirements (mid to late October). This is in agreement with other studies which found northern woody species satisfied chilling requirements early (Powell 1987, Kaurin et al. 1984). The southern ecotypes, including CR and Utah, satisfied a chilling requirement by early November (CR, Utah and Mass respectively). It appears that CR and Utah, which did not attain true VM in the field, still required chilling temperatures to overcome growth cessation. In fact, shadehouse results (next section) indicate that Utah required the same length of time to overcome incomplete VM attainment in the field, as it did to overcome true VM in the shadehouse. Lesser degrees of rest and satisfaction of a chilling requirement were reported by Murakami et al. (1990). Hawthorn and maple were in a state of rest when the maximum time to bud break over the winter season was only 25 days. In our studies, this level of dormancy would not have been considered VM, let alone rest.
The definitions for VM, rest, and chilling requirement may need to be revised to take into account lesser degrees of dormancy and the absence of some dormancy stages in regular growth cycles (i.e. lack of VM in Murakami et al. (1990) studies).

Although the first to satisfy their chilling requirements, Alaska and NWT took significantly longer to do so (as measured from VM) than the southern ecotypes. This measurement of length of time to satisfy the chilling requirement however, may not be correct. Following the attainment of VM, plants progress towards maximum rest (Fuchigami et al. 1982). Plants are driven to this deeper state of rest by cool temperatures (Kobayashi et al. 1982). Hence, low temperatures received following the attainment of VM (our measurement point for commencement of chilling requirement satisfaction) would drive a plant to deep dormancy, rather than release it. More accurately, satisfaction of the chilling requirement would be tested following the attainment of maximum rest. It appears that other studies which measure satisfaction of the chilling requirement, also do so from vegetative maturity or some pre-determined (often temperature based) point preceding maximum rest (Holloway et al. 1983, Kaurin et al. 1984).

If dogwoods begin to satisfy a chilling requirement following VM attainment (or it can be relatively measured from this point), the temperatures at VM attainment of northern ecotypes must be considered. At this time in our field studies, night temperatures were cool (10°C), but day time temperatures remained high (25°C). During this period, those chilling units received over the night were probably negated by the warm days (Hanninen). Further, at the early post-VM stages, ability
to respond to chilling temperatures may be lower than at later stages. The influence of growth stage on chilling requirement and temperature effectiveness has been suggested by Kobayashi et al. (1982) and Weiser (1970).

Finally, results may simply reflect ecotype variation in chilling requirement length (Weiser 1970). Ecotypes may be driven to different depths of rest which require greater or fewer chilling units to overcome.

All the above suggestions are plausible explanations for the long chilling requirement of the northern ecotypes, but for the moment, lack of information on the commencement of chilling requirement satisfaction, and on proper measurement techniques, makes interpretation of results highly speculative.

Shadehouse Studies

Satisfaction of the chilling requirement under shadehouse conditions paralleled that of the field. Northern ecotypes satisfied first, while southern ecotypes required a shorter time to do so. As noted in the system comparison, under shadehouse conditions satisfaction of the chilling requirement occurred earlier in all ecotypes. Systems comparison suggests this may be due to cooling of the roots in potted plants. Similar to the discussion of chilling requirement measurement in the previous section, the need for improved description of the chilling requirement and standard measurement techniques, is vital if studies are to yield accurate and useful information.
Controlled Environment Studies

Unlike certain conifers (Lavender and Stafford 1985), field, shadehouse and controlled environment studies indicated that dogwood chilling requirement was satisfied early and quickly. However, lack of VM attainment by some ecotypes led to problems with controlled environment determination of the chilling requirement. Literature suggests that plants begin to satisfy the chilling requirement following the promotion of rest by similar low temperatures (Fuchigami et al. 1982). VM attainment was the indicator of rest used for these tests, however, only Alaska and NWT attained this state under controlled environment conditions, and were therefore eligible for testing. That a form of rest was possible without prior attainment of VM (Murakami et al. 1990, Chapter 3 field results) was not considered. As a result, only NWT was tested for chilling requirement satisfaction. Insufficient material was available for testing Alaska.

NWT expressed early and rapid satisfaction of the chilling requirement (<20 days) following the attainment of VM. This contrasts with the 50+ days required to satisfy the chilling requirement under field and shadehouse conditions. In a preliminary test the growth-inhibited Mass ecotype exhibited the same trends during chilling requirement satisfaction as the NWT ecotype. This brings to question the true attainment of VM by NWT under controlled environment conditions, and the need of a chilling requirement by plants like Mass which ceased growth, but did not attain VM. Field studies indicated that plants, which do not become vegetatively mature over the winter, may still have to satisfy a chilling requirement to overcome
growth inhibition. Potentially, NWT only attained a prolonged state of growth cessation (similar to Mass) and not true dormancy. This would help to explain the quickness of satisfaction under the controlled environment conditions, as well as the similarity to Mass response. Quite possibly, the whole test is demonstrating ecodormancy (Lang et al. 1985). Chamber conditions may have been such that they induced a stress imposed dormancy, which was quickly overcome once conditions became suitable for growth. This would further stress the incapacity of controlled environments to induce a true dormancy similar to that attained under field conditions.

3.5 CONCLUSION

Plant response to the environment is best observed under natural or field conditions. However, it is often neither practical nor possible to test under these conditions. More commonly, tests are performed with potted material in shadehouse, greenhouse or controlled environment facilities. All of these systems provide high control of VM environmental stimuli and accurate assessment of order of VM attainment. They do not, however, provide similar dates of VM attainment, predict the time between attainment of VM by two ecotypes, nor accurately assess satisfaction of the chilling requirement. The results of this study emphasize the
growth inhibition. Potentially, NWT only attained a prolonged state of growth cessation (similar to Mass) and not true dormancy. This would help to explain the quickness of satisfaction under the controlled environment conditions, as well as the similarity to Mass response. Quite possibly, the whole test is demonstrating ecodormancy (Lang et al. 1985). Chamber conditions may have been such that they induced a stress imposed dormancy, which was quickly overcome once conditions became suitable for growth. This would further stress the incapacity of controlled environments to induce a true dormancy similar to that attained under field conditions.

3.5 CONCLUSION

Plant response to the environment is best observed under natural or field conditions. However, it is often neither practical nor possible to test under these conditions. More commonly, tests are performed with potted material in shadehouse, greenhouse or controlled environment facilities. All of these systems provide high control of VM environmental stimuli and accurate assessment of order of VM attainment. They do not, however, provide similar dates of VM attainment, predict the time between attainment of VM by two ecotypes, nor accurately assess satisfaction of the chilling requirement. The results of this study emphasize the
importance of understanding the limitation of the system, such that the goals of the test do not exceed these limitations.

Plants from different latitudes exhibit variation in date of VM attainment and satisfaction of the chilling requirement. Progression of VM attainment in dogwood (*Cornus sericea* L.) is directly related to increasing latitude. The northern ecotypes ceased growth and attained VM first. Length of the chilling requirement may vary among ecotypes, but pin-pointing maximum rest or an appropriate testing point, renders this character difficult to quantify. Satisfaction of the chilling requirement occurred by mid-December in all ecotypes, suggesting that chilling requirement does not play a significant role in preventing mid-winter bud flush during unseasonably warm periods.

It appears that environmental change initiates and maintains dormancy induction. Detection of the environmental parameter initiating VM varied among the ecotypes. Whether this indicates the need for different environmental triggers by ecotypes, or simply a variation in sensitivity to one parameter, is uncertain. Our results suggest that either is a possibility (chapter 3).

Although previous studies on dogwood have suggested that critical cold acclimation cannot occur until after a plant has become vegetatively mature, lack of VM attainment under our field conditions does not appear to have been detrimental to cold hardening and winter survival. Both Utah and CR ecotypes survived field conditions, even though VM was not attained.
4.0 INFLUENCE OF PHOTOPERIOD, TEMPERATURE AND CULTURAL PRACTICES ON VM INDUCTION.

4.1 INTRODUCTION

Detection of and response to environmental cues is essential for plant survival. Shortening days and/or low temperatures are the main environmental cues for induction of temperate woody plant dormancy (Qamaruddin et al. 1993, Weiser 1970, Fuchigami et al. 1982). Daylength has largely been associated with dormancy initiation, while temperature has been associated with acclimation and depth of dormancy. The most visually evident response to the inductive environmental cues is growth cessation.

The induction of growth cessation and VM (vegetative maturity) have been extensively studied. While the internal plant mechanisms are still unclear, the initial environmental trigger, has been demonstrated to be short photoperiod (Fuchigami et al. 1982, Seibel and Fuchigami 1978, Weiser 1970, Juntilla and Kaurin 1985). Although many studies have shown decreasing photoperiod (short days, SD) to induce vegetative maturity in woody plants, this may not be the only nor the optimal VM-inducing environmental cue. The environmental cue can vary according to
species or ecotype (see Nilsen 1985), or the inductive cue may be endogenous (Kobayashi and Fuchigami 1983, Howell and Weiser 1970), such as a cyclical rhythm.

Generally, temperate woody plants follow an annual growth cycle of:

**spring flush → active growth → gradual growth inhibition → dormancy → spring bud flush**

Fuchigami *et al.* (1982), outlined the annual major growth stages in a °GS model (degree growth stage model). In this model after spring bud flush, plants become sensitive to decreasing photoperiod (MIP stage), which leads to the attainment of vegetative maturity (VM). At the VM dormancy development stage (analogous to the endodormant stage of Lang *et al.* (1985)), plants will not begin to re-grow when placed under ideal growth conditions. This contrasts with the MIP stage, where correlatively inhibited plants would begin to re-grow when placed under such conditions. Internal mechanisms appear to be preventing growth of vegetatively mature plants.

The VM developmental stage is particularly significant, since it marks the end of the first stage of acclimation, and the beginning of the second stage. It is at this point that plants acquire the ability to attain critical cold hardening (Fuchigami *et al.* 1982). Following the attainment of VM, plants proceed to maximum rest (MR). At this stage, plants require the greatest amount of time or concentration of
GA to stimulate bud burst under ideal conditions. To attain and overcome this stage, most woody plants must be exposed to chilling temperatures (Kobayashi et al. 1982, Weiser 1970, Fuchigami et al. 1982). As a plant overcomes rest, it enters a state known as end of rest (ER - Fuchigami et al. 1982). Plants attaining this stage are fully competent for rapid growth on exposure to active growth conditions (Weiser 1970, Lavender and Stafford 1984).

Although the induction of VM is believed to be regulated by shortening photoperiods, latitudinal variation in environmental conditions may dictate that specific VM-inductive photoperiod/temperature regimes between ecotypes. Unfortunately, comparative deciduous woody plant ecotype studies in dormancy induction are few (Smithberg and Weiser 1968, Donselman and Flint 1982, Juntilla and Kaurin 1985). Further, those studies which have been conducted often test under one condition without consideration for ecotype natural environment. In addition, with the exception of Smithberg and Weiser (1968), those studies which have examined ecotypical variation usually test a species with a relatively small and non-extreme geographical range. Finally, the interaction of temperature, photoperiod, and diurnal fluctuation has never been tested. Therefore, a comparison of VM-inductive photoperiod and temperature conditions of many ecotypes, spanning a large geographical range, will be performed to better observe the environmental parameters that are critical and optimal for VM attainment and dormancy induction. Dogwood ecotypes from latitudes spanning Utah to Alaska
(42N to 64N) were used to assess ecotype variation in inductive parameters, and better observe the critical parameters of VM induction.

Although photoperiod and temperature have been implicated as the key VM induction parameters, they may not be the only factors capable of inducing VM attainment. Competition, perhaps inducing moisture stress could also induce growth cessation (Lang et al. 1985). Rick Sawatzky (personal communication) observed that orchard fruit trees better survived winters when surrounded by turf. This portion of the study will investigate the effects of turfgrass on dormancy induction in dogwood. It is proposed that turfgrass will influence the dormancy induction process, leading to earlier dormancy induction of dogwoods planted into turf as compared to those planted into bare ground.

4.2 MATERIALS AND METHODS

4.2.1 Photoperiod and Temperature Studies

Controlled Environment Design and Plant Maintenance

Design, propagation and plant maintenance followed the controlled environment studies procedures of Chapter 3.
Influence of Photoperiod and Temperature on VM Attainment Under Controlled Environment Conditions

Four dogwood clonal ecotypes (Mass, Utah, NWT and Alaska) were placed under 5 photoperiod/temperature regimes and 1 greenhouse regime. Regimes represented the following conditions:

1. Short days and warm temperatures (SD/WT) - 8/16 hr, 20/15°C day-night. Standard VM induction conditions.
2. Short days and low temperatures (SD/LT) - 8/16 hr, 15/5°C day-night.
3. Long days and warm temperatures (LD/WT) - 22/2 hr, 20/15°C day-night.
4. Long days and low temperatures (LD/LT) - 22/2 hr, 15/5°C day-night.
5. Modified long days and low temperatures (LD/LT-mod) - 22/2 hr day-night, 15/5°C over an 8/16 hr period with 5°C beginning with the night period.
6. Greenhouse - 25°C ± 5°C, approximately 22 hr days at 600-800 μmol·m⁻²·s⁻¹ - extended through supplemental incandescent/cool-white fluorescent lighting.

Light intensity in chambers was approximately 225 μmol·m⁻²·s⁻¹ (produced by incandescent and cool white fluorescent bulbs). Plants in controlled environment chambers were treated with TRUMPET for whitefly control as required.
At 10 day intervals (over 121 days for Alaska and 173 days for all other ecotypes), 4 plants of each ecotype from each regime were sampled. Plants were defoliated, placed into LD/WT chamber conditions and observed for bud break. Attainment of VM was determined as in Chapter 3.

Influence of Diurnal Temperature Fluctuation on VM Attainment

Two dogwood ecotypes, Mass and Utah, were tested in controlled environment chambers under 6 photoperiod/temperature regimes, and monitored for the date of VM attainment. Regimes represented variations in diurnal temperature and either dormancy inductive or non-inductive photoperiods. The regimes were:

1. 8/16 hr, 20/20°C day/night; 2. 8/16 hr, 20/15°C day/night; 3. 8/16 hr, 20/10°C day/night; 4. 8/16 hr, 20/5°C day/night; 5. 8/16 hr, 5/5°C day/night; 6. 16/8 hr, 20/5°C day/night. Four plants of each ecotype were sampled at time 0, 30 days and approximately every 10 days thereafter to a total of 74 days. Plants were sampled and monitored for VM as per controlled environment studies in Chapter 3.

4.2.2 Turfgrass Studies

Field Design and Maintenance

Greenhouse-propagated dogwoods (Cornus sericea L.), Mass ecotype, were planted into exposed soil or well established turf (8 years old) at the University of Saskatchewan field plots. Planting was in a north-south orientation at 1 meter
intervals. At the time of planting, plants were 1 to 2 years old. Plants were watered regularly through the summer using trickle irrigation. Irrigation was terminated approximately mid-August each year. Weeding was performed when necessary, as in Chapter 3. In the fall, plants were mulched with straw to assist overwintering.

**Dormancy Enhancement Through Turfgrass Competition**

Beginning in late July, plants were sampled every ten days until vegetative maturity was attained. At each sampling time, 5 random stem sections (approx. 10 cm in length) were cut from plants in each of the turf and bare-soil areas. Stem sections were prepared according to the defoliation test and monitored for bud break as in Chapter 3. Attainment of vegetative maturity was designated as the date at which less than 50% of the sample cuttings broke bud.

### 4.3 RESULTS

#### 4.3.1 Photoperiod and Temperature Studies

A preliminary study with 4 ecotypes (Mass, Chalk River, Utah and NWT) and 4 regimes (SD/WT, SD/LT, LD/WT, LD/LT) indicated that both SD/LT and SD/WT induced VM (by our 40 day definition) in all but the Utah ecotype. None of the treatments induced VM in Utah. The preliminary study also indicated a need
for a longer test period, as well as additional regimes to act as controls. Results of the preliminary test very closely paralleled those of the follow-up study.

The follow-up study is presented. For this test, the ecotype CR was not included, and an Alaska ecotype (now our most northern ecotype) was added. Two new regimes were also added: LD/LT-mod and greenhouse. The greenhouse regime would act as a control of the controlled environment active growth control (LD/WT). LD/LT-mod, as the name implies, was a modification of the LD/LT regime used in the preliminary test. The basis for this new regime was that LD/LT only differed slightly from LD/WT. The night temperature was $10^\circ$C lower than LD/WT, but nights only lasted 2 hours, minimally influencing growth. The new LD/LT-mod regime maintained the LD/WT photoperiod, but adopted the temperature regime (both in temperature and duration) of SD/LT. Unfortunately, material limitations meant Alaska was not tested under either the LD/LT or greenhouse (g.h.) regime.

The purpose of the test was two-fold: 1. To determine the most effective VM-inductive regime for each ecotype. 2. To compare ecotype VM attainment under each regime.

Effective VM-Inducing Regimes

The two northern ecotypes (Alaska and NWT) ceased growth under most regimes. Only under greenhouse conditions did NWT maintain active growth (Fig. 4.1). The SD/WT, SD/LT and LD/LT-mod regimes all induced VM in NWT
Figure 4.1  Photoperiod and temperature studies on vegetative maturity (VM) induction in dogwood clonal ecotypes: greenhouse regime (25 C, 22h day)
(Table 4.11), while the LD/WT and LD/LT regimes induced growth cessation rather than VM (Table 4.1, Fig. 4.2). Under the LD/WT and LD/LT regimes, apical buds were always active, and plants did not exhibit typical colour change or leaf abscission observed under the other VM inductive regimes. It appeared that the plants were under stress, such that all but the most active growing regions (apical buds) ceased growth. Despite being active, apical bud growth was slow and minimal. On removal of the apical bud during the defoliation test, all the laterals remained inactive. Thus, although it appeared that VM was attained, it was obvious that apical buds were still active prior to defoliation.

The Alaska ecotype also responded to potential VM-inducing regimes: SD/LT, SD/WT and LD/LT-mod (Table 4.2, Table 4.11, Fig. 4.3). SD/WT induced VM significantly earlier than LD/LT-mod. SD/LT and LD/LT-mod are superimposed on each other in the VM attainment stages of Fig. 4.3. Like NWT, Alaska responded later to the LD/WT regime (Fig. 4.3), but the response seemed to be more growth cessation than true attainment of VM (see explanation for NWT).

The southern ecotypes (Utah and Mass) were less similar in their responses than were the northern ecotypes. The Mass ecotype attained VM under both the SD/LT and SD/WT regimes (Table 4.11, Fig. 4.4). VM occurred slightly earlier under SD/LT, although the difference was not significant (Table 4.3). Mass ecotype also responded to three other regimes (LD/LT-mod, LD/LT, LD/WT), however the response occurred 150+ days into the trial and plants exhibited a similar appearance to the stressed NWT and Alaska plants. Further, plants did not appear truly
Table 4.11  Effective vegetative maturity (VM) inductive regimes for four dogwood (*Cornus sericea* L.) clonal ecotypes from the photoperiod/temperature study and the diurnal temperature fluctuation study.

<table>
<thead>
<tr>
<th></th>
<th>Alaska</th>
<th>NWT</th>
<th>Mass</th>
<th>Utah</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>SD/WT</strong></td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td><strong>SD/LT</strong></td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
<td>?</td>
</tr>
<tr>
<td><strong>LD/WT</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>LD/LT</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>LD/LT-mod</strong></td>
<td>✓</td>
<td>✓</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Greenhouse</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(22h day, 25 ± 5°C)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8/16 hr, 20/20°C</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8/16 hr, 20/15°C</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8/16 hr, 20/10°C</td>
<td>*</td>
<td>*</td>
<td>✓</td>
<td></td>
</tr>
<tr>
<td>8/16 hr, 20/5°C</td>
<td>*</td>
<td>*</td>
<td>✓</td>
<td></td>
</tr>
<tr>
<td>8/16 hr, 5/5°C</td>
<td>*</td>
<td>*</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

✓ Effectively induced VM
? VM attainment uncertain
* Not tested under this regime
Table 4.1  NWT ecotype vegetative maturity (VM) attainment under different controlled environment photoperiod/temperature regimes.

<table>
<thead>
<tr>
<th>Regimes Tested***</th>
<th>Days to VM Attainment****</th>
</tr>
</thead>
<tbody>
<tr>
<td>SD/WT</td>
<td>51.8 a</td>
</tr>
<tr>
<td>LD/LT-mod</td>
<td>55.0 a</td>
</tr>
<tr>
<td>SD/LT</td>
<td>57.8 a</td>
</tr>
<tr>
<td>LD/WT</td>
<td>**</td>
</tr>
<tr>
<td>LD/LT</td>
<td>**</td>
</tr>
<tr>
<td>g.h.</td>
<td>*</td>
</tr>
</tbody>
</table>

* Did not attain VM  
** Not considered to have attained VM  
*** n = 4 reps.  
**** Tested by 2-way ANOVA and LSD at 0.05 level

Table 4.2  Alaska ecotype vegetative maturity (VM) attainment under different controlled environment photoperiod/temperature regimes.

<table>
<thead>
<tr>
<th>Regimes Tested***</th>
<th>Days to VM Attainment****</th>
</tr>
</thead>
<tbody>
<tr>
<td>SD/WT</td>
<td>29.8 a</td>
</tr>
<tr>
<td>SD/LT</td>
<td>35.0 ab</td>
</tr>
<tr>
<td>LD/LT-mod</td>
<td>37.5 b</td>
</tr>
<tr>
<td>LD/WT</td>
<td>**</td>
</tr>
</tbody>
</table>

** Not considered to have attained VM  
*** n = 4 reps.  
**** Tested by 2-way ANOVA and LSD at 0.05 level
Figure 4.2  Controlled environment photoperiod and temperature studies on vegetative maturity (VM) induction in dogwood clonal ecotypes: NWT ecotype
Figure 4.3  Controlled environment photoperiod and temperature studies on vegetative maturity (VM) induction in dogwood clonal ecotypes: Alaska ecotype
dormant, since the apical buds were always active. Only on the removal of the apical buds did the plant appear to have attained VM.

The Utah ecotype appeared to attain VM under SD/WT and SD/LT (Table 4.11), but the growth cessation period under SD/LT was very short. Whether this was actual VM attainment or temporary growth cessation is uncertain (Fig. 4.5). In light of this uncertainty, no statistical tests of Utah under SD/LT were performed (Table 4.4). Similar to Mass ecotype, Utah eventually responded to LD/WT, but the response was late into the test and plants appeared similar to the Mass, NWT and Alaska plants under this regime.

Ecotype/Regime Comparison for VM Attainment.

All ecotypes were tested under 6 regimes with the exception of Alaska which, due to limited material, was not tested under LD/LT or a greenhouse regime.

SD/WT

All ecotypes ceased growth under SD/WT at significantly different times (Fig. 4.6, Table 4.5, Table 4.11). Distribution of ecotype VM attainment was even, with the northern ecotypes attaining VM first. Distribution followed a latitudinal gradient.
Figure 4.5 Controlled environment photoperiod and temperature studies on vegetative maturity (VM) induction in dogwood clonal ecotypes: Utah ecotype
Figure 4.6  Photoperiod and temperature studies on vegetative maturity (VM) induction in dogwood clonal ecotypes: SD/WT (short day/warm temperature) controlled environment regime
Table 4.5 Dogwood (*Cornus sericea* L.) ecotype vegetative maturity (VM) attainment under a short day/warm temperature (SD/WT) controlled environment regime.

<table>
<thead>
<tr>
<th>Ecotypes**</th>
<th>Days to VM Attainment****</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alaska</td>
<td>29.8 a</td>
</tr>
<tr>
<td>NWT</td>
<td>51.8 b</td>
</tr>
<tr>
<td>Mass</td>
<td>78.0 c</td>
</tr>
<tr>
<td>Utah</td>
<td>107.8 d</td>
</tr>
</tbody>
</table>

*** n = 4 reps.  
**** Tested by 2-way ANOVA and LSD at 0.05 level

Table 4.6 Dogwood (*Cornus sericea* L.) ecotype vegetative maturity (VM) attainment under a short day/low temperature (SD/LT) controlled environment regime.

<table>
<thead>
<tr>
<th>Ecotypes**</th>
<th>Days to VM Attainment****</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alaska</td>
<td>35.0 a</td>
</tr>
<tr>
<td>NWT</td>
<td>57.5 b</td>
</tr>
<tr>
<td>Mass</td>
<td>66.5 c</td>
</tr>
<tr>
<td>Utah******</td>
<td>77.0**</td>
</tr>
</tbody>
</table>

** VM attainment uncertain  
*** n = 4 reps.  
**** Tested by 2-way ANOVA and LSD at 0.05 level  
***** n = 2 reps.
**SD/LT**

Response to this regime was in the same order as SD/WT (Alaska, NWT, Mass), however the distribution of ecotypes was much tighter. All ecotypes appeared to attain VM under this regime (Fig. 4.7), although Utah may not have attained true VM (see previous results) (Table 4.11). Most ecotypes attained VM at significantly different times (Table 4.6.).

**LD/LT-mod**

Under this regime, with its traditionally non-inductive photoperiod, VM was induced, but only in the northern ecotypes (NWT and Alaska) (Fig. 4.8, Table 4.11). Alaska was found to respond significantly earlier than the NWT ecotype (Table 4.7). Mass did respond to this regime, but it appeared to be a stress induced response similar to LD/WT, and not related to VM attainment. Mass attained this state late, did not exhibit typical colour change, had reduced leaf abscission, and remained marginally active in the apical bud region.

**LD/LT and LD/WT**

The only other regimes to elicit a response were LD/LT (NWT, Mass), and LD/WT (Alaska, NWT, Mass and Utah) (Figs. 4.9 & 4.10, Table 4.8). Both these regimes were intended to be controls, and VM attainment was not anticipated. Responses appeared to be stress induced, but this is uncertain. As stated before, plants did not exhibit the typical colour changes observed in inductive regimes, nor
Table 4.7 Dogwood (*Cornus sericea* L.) ecotype vegetative maturity (VM) attainment under a long day/low temperature - modified (LD/LT-mod) controlled environment regime.

<table>
<thead>
<tr>
<th>Ecotypes***</th>
<th>Days to VM Attainment****</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alaska</td>
<td>37.5 a</td>
</tr>
<tr>
<td>NWT</td>
<td>59.8 b</td>
</tr>
<tr>
<td>Mass</td>
<td>**</td>
</tr>
<tr>
<td>Utah</td>
<td>*</td>
</tr>
</tbody>
</table>

* Did not attain VM  
** Not considered to have attained VM  
*** n = 4 reps.  
**** Tested by 2-way ANOVA and LSD at 0.05 level

Table 4.8 Dogwood (*Cornus sericea* L.) ecotype vegetative maturity (VM) attainment under long day/low temperature (LD/LT) & long day/warm temperature (LD/WT) controlled environment regimes.

<table>
<thead>
<tr>
<th>Ecotypes***</th>
<th>Days to Attain VM Under LD/WT Regime****</th>
<th>Days to Attain VM Under LD/LT Regime****</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alaska</td>
<td>**</td>
<td>-</td>
</tr>
<tr>
<td>NWT</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td>Mass</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td>Utah</td>
<td>**</td>
<td>*</td>
</tr>
</tbody>
</table>

* Did not attain VM  
** Not considered to have attained VM  
*** n = 4 reps.  
**** Tested by 2-way ANOVA and LSD at 0.05 level  
- not included in study
Figure 4.7 Photoperiod and temperature studies on vegetative maturity (VM) induction in dogwood clonal ecotypes: SD/LT (short day/low temperature) controlled environment regime.
Figure 4.8 Photoperiod and temperature studies on vegetative maturity (VM) induction in dogwood clonal ecotypes: LD/LT-mod (long day/low temperature-modified) controlled environment regime
Table 4.7 Dogwood (*Cornus sericea* L.) ecotype vegetative maturity (VM) attainment under a long day/low temperature - modified (LD/LT-mod) controlled environment regime.

<table>
<thead>
<tr>
<th>Ecotypes***</th>
<th>Days to VM Attainment****</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alaska</td>
<td>37.5 a</td>
</tr>
<tr>
<td>NWT</td>
<td>59.8 b</td>
</tr>
<tr>
<td>Mass</td>
<td>**</td>
</tr>
<tr>
<td>Utah</td>
<td>*</td>
</tr>
</tbody>
</table>

* Did not attain VM
** Not considered to have attained VM
*** n = 4 reps.
**** Tested by 2-way ANOVA and LSD at 0.05 level

Table 4.8 Dogwood (*Cornus sericea* L.) ecotype vegetative maturity (VM) attainment under long day/low temperature (LD/LT) & long day/warm temperature (LD/WT) controlled environment regimes.

<table>
<thead>
<tr>
<th>Ecotypes***</th>
<th>Days to Attain VM Under LD/WT Regime****</th>
<th>Days to Attain VM Under LD/LT Regime****</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alaska</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td>NWT</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td>Mass</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td>Utah</td>
<td>**</td>
<td>*</td>
</tr>
</tbody>
</table>

* Did not attain VM
** Not considered to have attained VM
*** n = 4 reps.
**** Tested by 2-way ANOVA and LSD at 0.05 level
- not included in study
Figure 4.9 Photoperiod and temperature studies on vegetative maturity (VM) induction in dogwood clonal ecotypes: LD/LT (long day/low temperature) controlled environment regime.
Figure 4.10  Photoperiod and temperature studies on vegetative maturity (VM) induction in dogwood clonal ecotypes: LD/WT (long day/low temperature) controlled environment regime.
did they senesce many leaves. Further, all plants remained at least somewhat active in the apical bud region, however, this activity was minimal and slow.

**Satisfaction of the Chilling Requirement Under Various Photoperiod/Temperature Regimes.**

Although it was not the intent of this study to observe satisfaction of a chilling requirement, some ecotypes did satisfy a chilling requirement over the course of the study. Only the VM-inductive regimes with cool night temperatures (SD/LT and LD/LT-mod) were effective at satisfying the chilling requirement. All ecotypes that attained VM under these regimes also satisfied a chilling requirement under the same regime.

Similar to the attainment of VM, ecotypes came out of dormancy rapidly with respect to days to bud break. The order of satisfaction of the chilling requirement was the same as attainment of VM (excluding Utah, which was not considered to have attained VM) (Table 4.9).

NWT and Alaska were the only ecotypes to attain VM under LD/LT-mod conditions, and both also satisfied their chilling requirements (Fig 4.8). While chilling requirement satisfaction occurred at about the same date for both ecotypes (Fig. 4.8), Alaska took considerably longer to satisfy as measured from VM (Table 4.10). This was similar to results under the SD/LT regime, where NWT also satisfied its chilling requirement in a significantly shorter time (Table 4.9).
Table 4.9 Dogwood (*Cornus sericea* L.) ecotype satisfaction of a chilling requirement under the short day/low temperature (SD/LT) controlled environment regime.

<table>
<thead>
<tr>
<th>Ecotypes Tested***</th>
<th>Date of Chilling Requirement Satisfaction****,1</th>
<th>Length of Chilling Requirement****,2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alaska</td>
<td>74.8 a</td>
<td>39.8 b</td>
</tr>
<tr>
<td>NWT</td>
<td>86.0 b</td>
<td>28.5 a</td>
</tr>
<tr>
<td>Mass</td>
<td>108.0 c</td>
<td>41.5 b</td>
</tr>
<tr>
<td>Utah****</td>
<td>85.0**</td>
<td>7.5**</td>
</tr>
</tbody>
</table>

** VM attainment uncertain  
*** n = 4 reps.  
**** Tested by 2-way ANOVA and LSD at 0.05 level  
***** n = 2 reps.  
1 - measured from test commencement  
2 - measured from VM attainment

Table 4.10 Dogwood (*Cornus sericea* L.) ecotype satisfaction of a chilling requirement under the long day/low temperature - modified (LD/LT-mod) controlled environment regime.

<table>
<thead>
<tr>
<th>Ecotypes Tested***</th>
<th>Date of Chilling Requirement Satisfaction****,1</th>
<th>Length of Chilling Requirement****,2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alaska</td>
<td>95.8 a</td>
<td>58.3 a</td>
</tr>
<tr>
<td>NWT</td>
<td>88.5 a</td>
<td>28.8 b</td>
</tr>
<tr>
<td>Mass</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>Utah</td>
<td>*</td>
<td>*</td>
</tr>
</tbody>
</table>

* Did not attain VM  
*** n = 4 reps.  
**** Tested by 2-way ANOVA and LSD at 0.05 level  
1 - Measured from time 0  
2 - Measured from VM attainment
Influence of Diurnal Temperature Fluctuation on Dormancy Induction

The influence of various diurnal temperature fluctuations on the efficacy of short day (SD) induced VM attainment was studied using Utah and Mass ecotypes. Over the duration of the test, only Mass attained VM under any of the regimes (Table 4.11). Both the 8h 20/10 and 8h 20/5 regimes (superimposed on Fig. 4.11) were equally effective for VM induction. Warmer temperature (8h 20/20, 8h 20/15) regimes were not effective over the test period. Interestingly, 8h 20/10 and 8h 20/5 were also more effective than both the SD/WT (8h 20/15) and SD/LT (15/5) regimes used as VM inductive standards in the sections, Effective VM Inducing Regimes and Ecotype/Regime Comparison.

While the Utah ecotype did not attain VM under any regimes over the duration of the test, mean time to bud break increased noticeably under both the 8h 20/10 and 8h 20/5 regimes (Fig. 4.12). The 8h 20/15 and 8h 20/20 regimes were also tending to delayed bud break, but were less effective than the 20/10 and 20/5 treatments. For both ecotypes, the 8h 5/5 and the 16h 20/5 regimes were not effective (Fig. 4.12).

4.3.2 Cultural Practices: Enhanced Dormancy Induction by Turfgrass

Although this study was in its first year, initial data from the second year is similar, and the trends merit comment. Fig. 4.13 indicates that dogwoods planted into turf progressed towards vegetative maturity earlier than those planted into bare
Figure 4.11 Influence of diurnal temperature fluctuation on efficacy of controlled environment vegetative maturity (VM) induction: Mass ecotype

Note:
8h 20/10 and 8h 20/5 are superimposed on figure
Figure 4.12 Influence of diurnal temperature fluctuation on efficacy of controlled environment vegetative maturity (VM) induction: Utah ecotype
Fig. 4.13  Effect of turfgrass on vegetative maturity (VM) attainment of Mass ecotype dogwood (Cornus serica L.) under Saskatoon, SK field conditions
ground. Nevertheless, it was observed that at any given sampling, not all turf samples had attained VM. Some cuttings from turf plants would break bud, but resulting growth was slow to negligible. The new leaves were small, thick, and had a stressed appearance. It may be that the turf treatment stressed plants and led to early growth cessation, rather than VM attainment. Bare-ground plants progressed towards VM in a manner that appeared similar to chapter 3 studies of field planted Mass dogwoods.

Aside from the VM observations, turf planted dogwoods set buds earlier and senesced most leaves at least a month earlier than bare ground planted dogwoods. Growth was also very much stunted in turf planted dogwoods compared to bare ground dogwoods. Competition with turf for resources was likely high. Growth during the following summer was similarly retarded in the turf planted dogwoods. Visual observations the following spring showed more freezing damage on the turf-grown dogwoods (dieback and splitting) than on bare-ground planted dogwoods. Turf planting did not appear to impart any advantage over bare-ground planted dogwoods.
4.4 DISCUSSION

4.4.1 Effective VM-Inducing Regimes

Vegetative maturity in both NWT and Alaska ecotypes was induced by either SD or extended LT, or a combination of both. Conversely, the southern ecotypes required short days. Low temperature alone was not sufficient for VM induction.

Northern Ecotypes

NWT and Alaska ecotypes attained some form of growth cessation under most tested regimes. SD/WT, SD/LT and LD/LT-mod all induced VM in NWT and Alaska ecotypes (Table 4.1, Table 4.2, Table 4.11). This would seem to suggest that VM or growth cessation in northern ecotypes can be induced by either short photoperiods or low temperatures (Weiser 1970). Qamaruddin et al. (1993) found that northern ecotypes of Picea abies responded to long nights. Similarly, Juntilla and Kaurin (1985) found decreasing photoperiod to induce growth cessation in the northern species, Salix pentandra. Temperature has also been shown to be an effective growth cessation parameter by Christersson (1978). Using a long day/low temperature regime, he was able to induce growth cessation in Swedish ecotypes of Scots pine and Norway spruce.

Ability to quickly respond to any of several cues would appear to be an advantageous ecological trait, particularly in a northern habitat of harsh and rapid temperature changes. Based on their studies of acclimation regimes effective for
*Picea abies*, Qamaruddin *et al.* (1993) also concluded that a fast response to inductive stimuli is likely to be an advantage to northern plant populations.

Growth cessation was also induced under LD/WT conditions. However, plants did not exhibit the characteristic colour changes or complete inhibition of growth that the previous regimes induced. Only the apical bud and the closest set of lateral buds, expressed any active growth. The defoliation test led to the removal of these areas, giving the appearance that VM had been attained. By contrast, growth cessation was not observed under the LD/WT conditions of greenhouse treated plants. Most noticeably different between the two regimes is the lighting. Light intensity in greenhouses was 3-4 times greater than in controlled environment chambers. The effects of light intensity and light quality on plant growth were discussed in chapter 2, and several studies indicate that these factors have a significant influence on plant growth (Bjornseth 1985, Nilsen 1985, Juntilla and Kaurin 1985).

Further, due to an instantaneous transition between day and night, plants under controlled environment conditions were not exposed to end of day light or early morning light. At these times under natural conditions, there is a marked difference in richness of red and far red light (red:far red ratio) compared to midday sun (Nilsen 1985). Juntilla and Kaurin (1985), among others have shown that end of day treatment with red light can influence plant growth state. However, light quality was not measured in our tests, nor was the influence of light quality on dormancy induction.
Southern Ecotypes

Utah and Mass responded to SD/WT and SD/LT (Table 4.3, Table 4.4, Table 4.11). Short daylength appears to be critical for dormancy induction and VM attainment in southern ecotypes. Low temperature alone is not sufficient to induce VM in southern ecotypes.

Many studies with dogwood have been conducted on the more southern Mass, Minnesota or North Dakota ecotypes. In almost all cases, it was concluded that short days induce growth cessation in the fall (Fuchigami et al. 1982, Proebsting 1983, Kobayashi et al. 1982, Renquist et al. 1978)

Both SD/LT and SD/WT were equally effective at inducing VM in Mass, although diurnal fluctuation studies (see later sections) suggest that lower temperatures can enhance induction of VM (Fuchigami et al. 1982). While Utah also responded to SD/LT and SD/WT, the response to SD/LT was atypical of normal inductive regime response. The depth of "dormancy" was low (less than 50 days to bud break at maximum inactivity) and the maintenance of this state was short (Fig 4.5). Plants under field conditions also did not attain a deep depth of dormancy. However, shadehouse studies indicate a more extended dormant period. Conditions in controlled environment chambers may simply be inadequate for the induction of true dormancy, instead eliciting a state of growth cessation. Further testing is needed to conclusively establish Utah response to SD/LT.

Responses to the LD/LT, LD/WT and LD/LT-mod regimes occurred late in the study, and the plants appeared stressed under these conditions (see descriptions
in Effective VM-Inducing Regimes section). Plants will cease growth under stressful conditions, and this condition has been called ecdormancy. Lang et al. (1985) and Lang (1987) describe this state as one which is regulated by external environmental conditions. Lang (1987) reports that ecdormancy is a result of limitations on growth imposed by inadequate environmental factors (i.e. water, nutrients or temperature extremes), as opposed to biochemical regulation. Plants in this state will resume growth once conditions return to normal, unlike vegetatively mature plants which will not grow under ideal conditions (Fuchigami et al. 1982). Lang et al. (1985) refer to this latter state as endodormancy.

4.4.2 Ecotype Comparison

VM Attainment

Under the SD/WT regime, the northern ecotypes attained VM first. The order of dormancy attainment corresponded with increasing latitude, and all ecotypes attained VM at significantly different times. Sensitivity to the short photoperiod became greater with increasing latitude of origin. Juntilla and Kaurin (1985) observed this response in ecotypes of Salix pentandra. Donselman and Flint (1982) found the same effect with ecotypes of Eastern redbud. The more northern ecotypes entered dormancy more quickly under short days. Further, the northern ecotypes also responded to longer photoperiods than the southern ecotypes. Hummel (1981) found it necessary to keep northern ecotypes of Cornus sericea under 22 hour photoperiod in order to prevent dormancy induction.
Photoperiod is unquestionably an important stimulus of dormancy induction. It is a constant environmental parameter from year to year, and often a reasonable predictor of average temperature. If plants do use photoperiod as a cue to initiate the dormancy process, photoperiod data (see Appendix 1) suggests that northern ecotypes would need to be very sensitive to photoperiod change, and respond more quickly to shortening photoperiod than southern ecotypes. In the north, summer lows of around 10°C will drop to -15°C in 5-6 weeks (see Appendix 1). Further, the average nightly temperature will continue to drop at a rapid rate. Rapid growth cessation and subsequent acclimation are vital if a plant is going to survive this temperature change. By contrast, further south, temperature and photoperiod change is much more gradual, and response to photoperiodic change need not be quite as rapid. In the very far north of Scandinavia, there is no change in photoperiod with the onset of fall and winter. Daylight is constant at this time of year. Here it appears that plants detect changes in the red:far red ratio, rather than photoperiod change, as the sun approaches the horizon (Nilsen 1985).

SD/LT (15/5°C) treatment produced the same ecotype order of VM attainment, however, attainment dates were more tightly grouped than under SD/WT conditions. Both NWT and Alaska attained VM slightly later than under SD/WT (although not significantly), while both Mass and Utah responded earlier under SD/LT. These results reinforce the importance of photoperiod in dormancy induction, although LD/LT-mod results also indicate temperature to be an effective inductive condition for northern ecotypes. Nevertheless, short photoperiods are still
a necessity for dormancy induction in southern ecotypes, as demonstrated by the LD/LT-mod regime.

The LD/LT-mod regime only differs from SD/LT by the length of the photoperiod, but VM was only induced in the northern ecotypes under these conditions. As this regime lacks an inductive photoperiod, it appears that the northern ecotypes are capable of responding to low temperature alone. Christersson (1978) found that LD/LT could induce growth cessation in conifers, but it did not induce dormancy. Weiser (1970) also acknowledges that low temperatures can stop growth. Contrastingly, Van Huystee et al. (1967) found that LD and a gradually decreasing temperature could not induce rest in dogwood from Minnesota. This last test complements the findings with the Mass and Utah dogwoods that southern ecotypes need a short photoperiod. However, few if any, authors suggest that low temperature alone can induce a dormant state. This is likely due to the limited consideration given to the unique conditions of sub-arctic regions. Temperature conditions can be severe in these regions, and the change of seasons rapid (Heide 1985, Lindgren and Lindgren 1985, Nilsen 1985). Plants must be highly adapted to these conditions (Heide 1985) which may include the ability to respond to any of a variety of inductive cues (photoperiod, temperature, light quality) to ensure survival.

In general, northern ecotypes can respond to either short photoperiod or low temperature (Table 4.1, Table 4.2). In our study, the combination of these two parameters did not lead to early dormancy induction. Low temperature alone was not sufficient to induce VM in southern ecotypes (Table 4.3, Table 4.4). Short
photoperiod is a necessity for VM attainment in these ecotypes. Low temperature appeared to enhance VM attainment in Mass slightly, and diurnal tests (section 4.4.3) confirm these observations.

Satisfaction of the Chilling Requirement

The VM-inductive regimes that had a low temperature component (5°C) also permitted plants to satisfy a chilling requirement. Under both SD/LT and LD/LT-mod conditions, all ecotypes that attained VM also satisfied a chilling requirement. Of the northern ecotypes, NWT satisfied its chilling requirement in a short time under both conditions. Whether this is due to ideal conditions for NWT chilling requirement satisfaction, or deep dormancy attainment by Alaska leading to requirement of a greater chilling period, is uncertain.

Southern ecotypes only satisfied chilling requirement under SD/LT. Mass required approximately the same length of time as Alaska. Utah apparently satisfied its chilling requirement in less than 10 days. While observations indicate that Utah probably never attained VM, it did cease growth and form buds. Field results in Chapter 2 indicate that plants ceasing growth without VM attainment still need to satisfy a chilling requirement before normal growth can resume. If plants were only in a state of stress-induced dormancy (ecodormancy), resumption of growth under ideal conditions would likely occur in a standard number of days. An increase in dormancy over time, followed by a decrease does not constitute an ecodormant response, particularly in light of the fact that the environment has not become more
ideal for growth over this period. Collectively, these observations suggest that plants at varying levels of VM attainment all need a chilling requirement.

It is because of results observed with Utah and with field plants, that I question the nature and description of the chilling requirement. It is often reported that the chilling requirement of a certain species is a specific number of days. This value may vary between different studies. Nevertheless, the perception is that a species has a genetically pre-determined chilling requirement. Although each cultivar does attain a maximum chilling requirement, this requirement is dependent on depth of dormancy. The results from our tests indicate that maximum depth of dormancy is not always attained. Thus, chilling requirement is likely to differ from year to year depending on efficacy of dormancy induction conditions. For this reason, maximum depth of dormancy (and hence chilling requirement), should be measured. Otherwise, it becomes simply chilling requirement based on local or test conditions with the depth of dormancy induced by these conditions.

Of further interest is the rate at which the chilling requirement was satisfied. Under the SD/LT and LD/LT-mod, as well as field conditions in chapter 3, chilling requirement was satisfied in less than 2 months. This is long before the end of extreme winter temperatures. Powell (1987) also makes the observation that chilling requirement of northern plants is often satisfied early to mid-winter, while air temperatures are too low for growth. However, there have been suggestions that chilling requirements may play a protective role in plant winter survival. Lavender and Stafford (1984) indicate that chilling requirement may serve to prevent a flush
of growth during unseasonably warm winter weather. Given the results of our study, the role of the chilling requirement as a protective mechanism against bud break during unseasonably warm periods in mid-winter does not appear to be feasible.

Perhaps the most interesting information obtained from these controlled environment studies was that ecotypes do not need to pass through the traditional SD/WT regime to attain VM. Traditionally, it has been assumed that these conditions were essential in the development of plant dormancy and acclimation (Fuchigami et al. 1982). Further, our results indicate that ecotypes were able to continue through the dormancy cycle and satisfy a chilling requirement without the attainment of VM or deep dormancy. This puts to question the necessity of SD/WT and VM in the dormancy induction process. It is the author's opinion that a period SD/WT is simply an environmental constant (occurring each year at approximately the same time) which plants must pass through. Over time, plants have adapted to using this condition as the trigger for VM induction, however, it is not the only condition that is stimulatory. SD/LT and low temperature alone are also effective for certain ecotypes. Results from the following section indicate that a short photoperiod and large diurnal fluctuation in temperature is more effective than SD/WT (20/15°C day-night) for dormancy induction.
4.4.3 Diurnal Temperature Fluctuation

The second component of this chapter was to investigate the influence of diurnal temperature fluctuation on VM induction. The study was initiated from observations that vegetative maturity may be effectively induced by short days and warm/cool diurnal temperatures. Such regimes would be more indicative of natural conditions than constant daytime and nighttime temperatures.

The test indicates that a large diurnal temperature fluctuation with cool nights and warm days is a more effective regime to induce VM in Mass than the usual SD/WT (20/15°C) regime. Utah appeared to be exhibiting similar trends to Mass, but the test was completed before Utah could fully express its response to the regimes. The Mass ecotype lies at a more northern latitude than Utah, and it has been shown that latitude influences the earliness of response (Donselman and Flint 1982). Warm days were an essential component of a VM inductive regime, since the cool days 5/5°C regime was ineffective. Based on Kobayashi (1982), cool nights may act to drive plants deep into dormancy, while warm days permit the photosynthetic and metabolic processes necessary to produce and convert energy and substrates required for dormancy induction. The results also lend credibility to the SD/LT and LD/LT-mod conditions of previous sections which induced a VM state.

4.4.4 Cultural Practices: Enhanced Dormancy Induction by Turfgrass

Dogwoods planted into turf ceased growth and progressed towards dormancy earlier than those planted into bare ground. However, late bud break data indicate
that early true VM attainment may not have been attained. Rather, turf dogwoods may have ceased growth early due to stress effects. The effectiveness of the early growth cessation in the turf planted dogwoods was negative, as plants exhibited some degree of winter injury the following spring and summer. The dogwoods without turfgrass exhibited virtually no winter injury. It may be that the injury of turf dogwoods is linked to late or incomplete attainment of true VM. Dogwoods were likely stressed from competition for water, and this influenced ability to gain full acclimation.

Observations (Sawatsky, pers. comm.) and studies by Calkins and Swanson (1993) suggest that cover crops can enhance winter survival. Calkins and Swanson (1993) observed better cold hardiness in trees planted with companion crops, as compared to bare soil treatments. In our studies, the denseness of the turf bed likely inhibited dogwood root growth and establishment into the new growing site. All these factors could lead to severe transplant shock resulting in growth retardation and inhibition of normal fall dormancy induction and cold acclimation.

Aside from the differences in dormancy attainment, there were also noticeable differences in growth. The turf-planted dogwoods had stunted growth, early growth cessation, and early senescence of leaves. Walker and Williams (1988) observed similar growth effects in studies of the influence of grass competition on container grown dogwoods.

Generally, it appeared that turf conditions were stressful and led to problems in dormancy attainment and acclimation. Further studies may find that surrounding
plants by turf, but not right to the base, would provide greater area for growth of
the dogwood root system; ultimately leading to enhanced growth and better
dormancy induction and acclimation.

4.5 CONCLUSION

Differential inductive conditions are required between ecotypes for VM
attainment. Northern ecotypes can be stimulated to attain VM through either short
photoperiods, low temperatures or both. Southern ecotypes require the presence of
short photoperiods for VM induction, but earliness of response can be enhanced by
the presence of warm day/cool night diurnal temperature fluctuation. The traditional
SD/WT regime is effective for VM induction, but other regimes with low night
temperatures proved equally or more effective.

Planting of dogwoods into turf did not induce early dormancy attainment or
enhanced winter survival. Growth cessation occurred early under these conditions,
however, plants incurred winter damage with turfgrass compared to no damage on
control plants. The turf-testing conditions appeared to be too stressful, resulting in
stunted growth.
5.0 DORMANCY DEVELOPMENTAL STAGE AND COLD ACCLIMINATION.

5.1 INTRODUCTION

Low temperature stress is perhaps the most limiting factor to plant
distribution (Hummel 1981). Ability to withstand periods of extreme cold is
essential for most temperate woody plants. However, plant ability to survive
freezing temperatures is not constant throughout the year (Weiser 1970).

During the active growth period (spring and early summer), woody plant
hardiness rarely exceeds a few degrees below 0°C (Chen and Li 1978, Nissila and
Fuchigami 1978). Acclimation potential of these plants is minimal (Fuchigami et al.
1982). During mid to late summer, hardiness and acclimation potential slowly begin
to increase (Fuchigami et al. 1982, Smithberg and Weiser 1967). By fall and early
winter, acclimation potential is high, and by mid-winter, hardiness can exceed -
130°C (Hurst et al. 1967, Guy et al. 1986, Smithberg and Weiser 1967, Weiser
1970). With the return of spring and the flush of active growth, hardiness and
acclimation potential are lost (Fuchigami et al. 1982).

Three definable stages of woody plant cold acclimation have been identified.
These stages are referred to as the first, second and third stages of acclimation
(Weiser 1970). The first stage occurs in the summer to early fall period, and is induced by decreasing photoperiod (Weiser 1970, Howell and Weiser 1970, Fuchigami et al. 1982). Hardiness increases slightly during this period, and acclimation potential begins to rise. However, it is not until the completion of the first stage of acclimation, and the onset of the second stage, that plants can effectively respond to inductive acclimation stimuli (Fuchigami et al. 1982).

The second stage of cold acclimation is temperature mediated. Low temperatures enhance acclimation and increase hardiness (Weiser 1970). It is during this stage that plants normally attain hardiness levels needed to survive the winter. The third stage of cold acclimation is not always attained in plants (Weiser 1970). It is only achieved through prolonged exposure to extremely cold temperatures (-30 to -50°C), and rapidly disappears once temperatures rise to normal freezing levels (Weiser 1970). It is during this third stage that plant hardiness levels can be driven to -196°C and lower. The first two stages of cold acclimation have been linked to dormancy developmental stages, while the third stage appears to be strictly environment mediated; occurring only if conditions are appropriate.

The dormancy state in which plants will not grow under ideal conditions (VM), and the completion of the first stage of cold acclimation have been linked together in several studies (Fuchigami et al. 1982, Nissila and Fuchigami 1978, Friesen and Stushnoff 1989). Prior to VM attainment, plants are considered to have only a limited capacity to harden upon exposure to low temperatures. Following VM attainment, sensitivity to low temperature increases, and exposure to low
temperatures drives plants to deep rest and greater hardiness. By contrast, others have suggested that growth cessation, but not necessarily dormancy attainment (VM) is required before acclimation potential increases (Howell and Weiser 1970, Weiser 1970, Juntilla and Kaurin 1985).

The interaction between the dormancy and acclimation processes is still unclear. Most studies deal with either dormancy or acclimation. Those studies that do investigate both aspects tend to be limited to either one or two species or ecotypes (Toivonen et al. 1991, hardiness in 2 Pinus populations, Mergen 1963, ecotypic variation in Pinus chilling requirements and bud break conditions). Donselman and Flint (1982) investigated ecotypic variation in Cercis canadensis dormancy, chilling requirement and acclimation. While they did observe ecotypic variation in these traits, they did not test the relationship between specific stages.

One of the few extensive tests involving a deciduous woody species (dogwoods) and ecotypical variation was undertaken by Smithberg and Weiser (1968). They examined ecotypical variation in 21 ecotypes primarily with respect to winter hardiness. They also observed variation in onset of hardiness and rest as determined by budset among the ecotypes. There was a general relationship between these characteristics with increasing latitude of origin of ecotype. While attempts were made to correlate hardiness attainment with phenological changes, the relationship between hardiness and dormancy was not investigated. Since this study, and following the development of the Fuchigami et al. (1982) °GS model, the relationship between dormancy and cold acclimation based on tests of a wide range
of ecotypes has not been investigated. Ecotypes represent a simple yet effective system to examine dormancy hardiness interactions since ecotypes vary in rate of dormancy attainment (Smithberg and Weiser 1968).

These studies will examine the interaction between dormancy developmental stage on subsequent cold acclimation/hardiness in dogwood clonal ecotypes from NWT, Massachusetts and Utah.

5.2 MATERIALS AND METHODS

5.2.1 Plant Propagation and Preparation

Plants were propagated and maintained as outlined in chapter 4.

5.2.2 Acclimation and Freezing Tests

Ecotypes were placed in a SD/WT controlled environment chamber (see chapter 4) to trigger the attainment of VM. The ecotypes used were Mass, Utah and NWT. Plants were sampled at 4 of 5 periods during the VM induction period, and subsequently tested for freezing tolerance. In order of attainment, the developmental stages were: 1. 0 days SD/WT; 2. 20 days SD/WT; 3. budset (BS); 4. NVM (for ecotypes that did not attain VM); 5. 25 days post budset (PBS); or 6. VM. Budset was designated the date at which all plants of an ecotype had visibly set all lateral and terminal buds. VM (measured as 40 days to bud break) was determined by observing defoliated plants under LD/WT conditions for at least 60 days to
ensure greater than 50% of the plants did not break bud. NVM was a comparative testing stage for Mass and Utah at VM attainment by NWT. PBS, 25 days post budset, was the final testing stage for ecotypes which did not attain VM.

Throughout the test, plants were sampled for the attainment of VM using the defoliation test (see chapter 3). Four plants per ecotype were sampled at each of 0 days SD/WT, 20 days SD/WT, budset and every ten days thereafter. Following defoliation, plants were placed into a LD/WT controlled environment chamber and observed for bud break to determine dormancy status.

At each of the 6 previously described stages, 60 plants of each ecotype were transferred from the SD/WT conditions to an acclimation regime (8/16 hr, 5/5°C). Hardiness was tested after 0, 2, and 4 weeks of acclimation. Following each of the three acclimation periods, 20 plants per ecotype were removed from acclimation conditions and tested for hardiness. The 20 plants were divided equally to form a control and 4 freezing temperature blocks. Freezing temperatures spanned an 8 to 16°C range depending on ecotype and developmental stage tested.

Freezing was conducted in an open, thick walled (4.5 cm) Styrofoam box placed in a Revco programmable ultra low freezer. Root trainer sleeves were placed in the box and covered with moist peat moss (3-5 cm) to protect the roots from freezing temperatures. The box was placed on supports in the freezer and a fan provided air circulation. Air and soil temperatures were recorded throughout the test. Plants were held initially at -2°C overnight and the following day temperatures were lowered 2 to 3°C per hour. Following exposure to test temperatures, plants
were removed from the freezer and immediately placed into a dark 4°C cooler to thaw for at least 2 days. Plants were then moved to greenhouse conditions (see chapter 3 for regime) and monitored for re-growth. After 1-2 months under greenhouse conditions, plants were assessed for visual damage and re-growth.

Damage was assessed using a 0 - 4 visual scale (see Figs. 5.2.1, 5.2.2, 5.2.3, 5.2.4), where 0 indicated no damage; 1 indicated damage to the leaves and slight or isolated damage to the stem, as indicated by discolouring; 2 indicated substantial damage to the stem, but insufficient to cause plant death; 3 indicated death to all above ground areas of the plant, but regeneration of new shoots from near-surface and sub-surface meristems; 4 indicated complete death of the plant, with no re-growth. Half ratings (i.e. 1.5, 2.5, etc.) were given in cases where damage was borderline between whole number ratings. An average rating of 2.5 was determined to be the LT50, above which the majority of the plants were non-hardy, below which the majority of the plants were considered at least marginally hardy at that temperature.

5.3 RESULTS

At the commencement of the test (0/0), hardiness was not greater than -5°C (Fig. 5.1, Table 5.1). A 4 week acclimation period increased hardiness of 0 days SD/WT stage plants by a maximum of 3.75°C (Table 5.1). After 20 days under
Figure 5.2.1 Damage rating 1 of controlled freeze tests

1 Rating: Slight or isolated damage to the stem and/or leaves (if present) (indicated by discolouring)
2 Rating: Substantial visual damage to the stem (discolouring), but insufficient to cause plant death

Figure 5.2.2 Damage rating 2 of controlled freeze tests
3 Rating: Death to all above ground areas of the plant, but regeneration of new shoots from near-surface and sub-surface meristems.

Figure 5.2.3 Damage rating 3 of controlled freeze tests
**4 Rating:** Complete death of the plant
(brown dry stems and no re-growth)

Figure 5.2.4 Damage rating 4 of controlled freeze tests
Figure 5.1 Controlled environment studies on the influence of developmental stage (0 - 0 days vegetative maturity (VM) inductive conditions, 20 - 20 days of VM inductive conditions, NVM - intermediate of 20 days and budset (BS) stage, BS - budset, VM - vegetative maturity, PBS - post budset) on hardiness and acclimation ability in 3 dogwood (*Cornus sericea* L.) clonal ecotypes following 0, 2 and 4 weeks of acclimation at 5°C.
Table 5.1 0 days short day/warm temperature (SD/WT) stage hardiness of three dogwood clonal ecotypes following 0 and 4 weeks of acclimation at 5°C.

<table>
<thead>
<tr>
<th>Ecotypes****</th>
<th>0 Weeks Acclimation (°C)***</th>
<th>4 Weeks Acclimation (°C)***</th>
</tr>
</thead>
<tbody>
<tr>
<td>NWT</td>
<td>-5.00 a</td>
<td>-8.75 a*</td>
</tr>
<tr>
<td>Mass</td>
<td>-4.50 a</td>
<td>-8.25 a*</td>
</tr>
<tr>
<td>Utah</td>
<td>-4.25 a</td>
<td>-7.00 b*</td>
</tr>
</tbody>
</table>

* Significantly more hardy than 0 weeks acclimation
*** Tested by 2-way ANOVA and LSD at 0.05 level
**** n = 4 reps.

Table 5.2 20 days short day/warm temperature (SD/WT) stage hardiness of three dogwood clonal ecotypes following 0, 2 and 4 weeks of acclimation at 5°C.

<table>
<thead>
<tr>
<th>Ecotypes****</th>
<th>0 Weeks Acclimation (°C)***</th>
<th>2 Weeks Acclimation (°C)***</th>
<th>4 Weeks Acclimation (°C)***</th>
</tr>
</thead>
<tbody>
<tr>
<td>NWT</td>
<td>-7.00 a</td>
<td>-15.00 a*</td>
<td>-18.00 a**</td>
</tr>
<tr>
<td>Mass</td>
<td>-5.50 a</td>
<td>-12.00 b*</td>
<td>-14.75 b*</td>
</tr>
<tr>
<td>Utah</td>
<td>-4.00 a</td>
<td>-11.50 b*</td>
<td>-13.75 b*</td>
</tr>
</tbody>
</table>

* Significantly more hardy than 0 weeks acclimation
** Significantly more hardy than 0 & 2 weeks acclimation
*** Tested by 2-way ANOVA and LSD at 0.05 level
**** n = 2 reps.
SD/WT (VM-inducing conditions) inherent hardiness had increased minimally, however, after 4 weeks of acclimation hardiness now ranged between -13 and -18°C (Table 5.2). The most rapid hardening occurred in the first two weeks of acclimating temperatures, thereafter the increase in hardiness was reduced.

At the budset (BS) developmental stage, inherent plant hardiness nearly doubled from 0 days SD/WT levels (Table 5.3). Two weeks of acclimation at the budset stage increased hardiness to -20°C or greater for all ecotypes. A further 2 weeks of acclimation produced hardiness levels below -34°C for NWT and -27°C for Utah (Table 5.3). Mass hardiness did not increase over this second 2 week period of acclimation. The increase in hardiness between the 0 and 4 weeks of acclimation was significant in all ecotypes (Table 5.3). Hardiness levels of NWT were likely slightly greater than recorded, since plants just survived the lowest test temperatures at all acclimation levels. Ecotype hardiness levels were well separated at the budset stage following 4 weeks of acclimation. NWT was the hardiest with a minimum survival temperature of -34°C. Interestingly, the southern most ecotype, Utah, was hardier (-27°C) than the intermediate ecotype Mass (-22°C).

Only the NWT ecotype attained true VM over the duration of the test. Mass and Utah could not attain this state under the controlled environment conditions. As a comparison of acclimation ability of all ecotypes at a common time, rather than by stage of dormancy development, Mass and Utah were tested for acclimation potential when NWT attained VM. At this time, Mass was nearly at budset, while Utah was between the 20 days SD/WT and budset stage. This stage was given the name
Table 5.3 Budset (BS) stage hardiness of three dogwood clonal ecotypes following 0, 2 and 4 weeks of acclimation at 5°C.

<table>
<thead>
<tr>
<th>Ecotypes</th>
<th>0 Weeks Acclimation (°C)*</th>
<th>2 Weeks Acclimation (°C)*</th>
<th>4 Weeks Acclimation (°C)*</th>
</tr>
</thead>
<tbody>
<tr>
<td>NWT</td>
<td>-9.50³</td>
<td>-21.25³</td>
<td>-34.00 a³</td>
</tr>
<tr>
<td>Mass</td>
<td>-12.00³</td>
<td>-20.50 ³</td>
<td>-22.00 c³</td>
</tr>
<tr>
<td>Utah</td>
<td>-10.50³</td>
<td>-20.00³</td>
<td>-27.00 b³</td>
</tr>
</tbody>
</table>

* Significantly more hardy than 0 weeks acclimation
** Significantly more hardy than 0 & 2 weeks acclimation
*** Tested by 2-way ANOVA and LSD at 0.05 level
y - Minimum hardness level
w - n = 4 reps.
z - n = 2 reps.

Table 5.4 Vegetative maturity (VM) and NVM (intermediate 20 days short day/warm temperature and budset) stages hardiness of three dogwood clonal ecotypes following 0, 2 and 4 weeks of acclimation at 5°C.

<table>
<thead>
<tr>
<th>Ecotypes****</th>
<th>0 Weeks Acclimation (°C)**</th>
<th>2 Weeks Acclimation (°C)**</th>
<th>4 Weeks Acclimation (°C)**</th>
</tr>
</thead>
<tbody>
<tr>
<td>NWT</td>
<td>-15.00 a³</td>
<td>-26.50³</td>
<td>-33.00³</td>
</tr>
<tr>
<td>Mass</td>
<td>-12.50 b</td>
<td>-18.25³</td>
<td>-24.50³</td>
</tr>
<tr>
<td>Utah</td>
<td>-9.25 c</td>
<td>-15.50³</td>
<td>-22.00**³</td>
</tr>
</tbody>
</table>

* Significantly more hardy than 0 weeks acclimation
** Significantly more hardy than 0 & 2 weeks acclimation
*** Tested by 2-way ANOVA and LSD at 0.05 level
**** n = 4 reps.
y - Minimum hardness level
NVM for both ecotypes. Acclimation potential was high at all levels for NWT, where the majority of tested plants survived the lowest freezing temperatures (-33°C) (Table 5.4). Mass and Utah exhibited high levels of acclimation potential - just surviving the lowest test temperatures following 4 weeks of acclimation (-24.5 and -22°C respectively. Results indicate high acclimation potential in NWT at the Vm stage, while there was a significant increase in Mass and Utah pre-VM acclimation potential from the 20 days SD/WT developmental stage (Tables 5.2, 5.4, 5.8).

The final stage tested was the postbudset stage (PBS - 25 days post budset). This is not a definable point in development, but rather a means of measuring acclimation potential in ecotypes that did not attain true VM under the controlled environment conditions. Hardiness increased considerably following 2 weeks of acclimation, but underestimation of the killing temperature of Mass at 0 weeks acclimation, only permitted statistical analysis on Utah (Table 5.5). A further 2 weeks of acclimation only increased hardiness levels marginally in both ecotypes.

Alterations in ecotype hardiness with developmental stage at each acclimation period were compared (Tables 5.6, 5.7, 5.8). A gradual increase in hardiness was observed with developmental stage attainment (Fig 5.1). As indicated earlier, there were several instances where plants were not killed by the lowest tested temperatures. Trends, however, are still evident. When underestimating lethal temperatures, the lowest test temperatures were considered minimum hardiness levels. It should also be noted that temperature values may differ slightly from
Table 5.5 Post budset (PBS) stage hardiness of three dogwood clonal ecotypes following 0, 2, and 4 weeks of acclimation at 5°C.

<table>
<thead>
<tr>
<th>Ecotypes***</th>
<th>0 Weeks Acclimation (°C)***</th>
<th>2 Weeks Acclimation (°C)***</th>
<th>4 Weeks Acclimation (°C)***</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mass</td>
<td>-14.50 a</td>
<td>-25.50 a</td>
<td>-27.00 a</td>
</tr>
<tr>
<td>Utah</td>
<td>-15.50</td>
<td>-26.75 a*</td>
<td>-30.00 a*</td>
</tr>
</tbody>
</table>

* Significantly more hardy than 0 weeks acclimation
*** Tested by 2-way ANOVA and LSD at 0.05 level
**** n = 4 reps.
y - Minimum hardiness level

Table 5.6 Hardiness changes of three dogwood clonal ecotypes at 0 weeks acclimation (5°C) over all developmental stages.

<table>
<thead>
<tr>
<th>Developmental Stage***</th>
<th>NWT***</th>
<th>Mass***</th>
<th>Utah***</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 Days SD/WT</td>
<td>-5.00 a</td>
<td>-4.50 a</td>
<td>-4.25 a</td>
</tr>
<tr>
<td>20 Days SD/WT</td>
<td>-7.00 ab</td>
<td>-5.50 a</td>
<td>-4.00 a</td>
</tr>
<tr>
<td>NVM</td>
<td>-</td>
<td>-12.50 b</td>
<td>-9.25 b</td>
</tr>
<tr>
<td>BS</td>
<td>-9.50 b</td>
<td>-12.00 b</td>
<td>-10.50 b</td>
</tr>
<tr>
<td>VM</td>
<td>-15.00 c</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>PBS</td>
<td>-</td>
<td>-14.50 b</td>
<td>-15.50 c</td>
</tr>
</tbody>
</table>

*** Tested by 2-way ANOVA and LSD at 0.05 level
**** n = 4 reps.
y - Minimum hardiness level
- Not tested at this stage
Table 5.7 Hardiness changes of three dogwood clonal ecotypes at 2 weeks acclimation over all developmental stages.

<table>
<thead>
<tr>
<th>Developmental Stage</th>
<th>NWT***</th>
<th>Mass***</th>
<th>Utah***</th>
</tr>
</thead>
<tbody>
<tr>
<td>20 Days SD/WT</td>
<td>-15.00 a</td>
<td>-12.00 a</td>
<td>-11.50 a</td>
</tr>
<tr>
<td>NVM</td>
<td>-</td>
<td>-15.50 a⁺</td>
<td>-15.00 b</td>
</tr>
<tr>
<td>BS</td>
<td>-19.50 b⁺</td>
<td>-15.50 a</td>
<td>-20.00 c</td>
</tr>
<tr>
<td>VM</td>
<td>-27.00 c⁺</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>PBS</td>
<td>-</td>
<td>-24.50 b</td>
<td>-25.00 d</td>
</tr>
</tbody>
</table>

*** Tested by 2-way ANOVA and LSD at 0.05 level
**** n = 2 reps.
y - Minimum hardiness level
- Not tested at this stage

Table 5.8 Hardiness changes of three dogwood clonal ecotypes at 4 weeks acclimation over all developmental stages.

<table>
<thead>
<tr>
<th>Developmental Stage</th>
<th>NWTw.***</th>
<th>Massw.***</th>
<th>Utahz.***</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 Days SD/WT</td>
<td>-8.75 a</td>
<td>-8.25 a</td>
<td>-6.50 a</td>
</tr>
<tr>
<td>20 Days SD/WT</td>
<td>-18.00 b</td>
<td>-14.75 b</td>
<td>-15.00 b</td>
</tr>
<tr>
<td>NVM</td>
<td>-</td>
<td>-24.50 d⁺</td>
<td>-22.00 c⁺</td>
</tr>
<tr>
<td>BS</td>
<td>-30.50 c⁺</td>
<td>-23.00 c</td>
<td>-27.00 d</td>
</tr>
<tr>
<td>VM</td>
<td>-33.00 c⁺</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>PBS</td>
<td>-</td>
<td>-27.00 e</td>
<td>-32.00 e</td>
</tr>
</tbody>
</table>

*** Tested by 2-way ANOVA and LSD at 0.05 level
w - n = 4 reps.
z - n = 2 reps.
y - Minimum hardiness level
- Not tested at this stage
previous tables, due to changes in sample size necessary for analysis.

At 0 weeks acclimation for each developmental stage, hardiness levels increased steadily as plants progressed towards VM. These inherent hardiness levels would not be adequate for winter survival (Table 5.6, see Appendix 1). When given two weeks of acclimating temperatures at any developmental stage, all ecotypes expressed increased hardiness over inherent hardiness levels (Table 5.7). Although hardiness levels are high after 2 weeks of acclimation, most are still marginal for survival of lowest temperatures in native areas. Four weeks of acclimation (Table 5.8) further increased hardiness, although not at the same rate as from zero to 2 weeks acclimation.

Of particular importance is the ability to significantly acclimate at any dormancy development stage. Table 5.8 shows that even a few weeks of VM inductive conditions (20 days SD/WT) increases acclimation potential significantly. All ecotypes also exhibited ability to acclimate to -27°C, or greater, prior to the attainment of VM. In general, it appears that inherent hardiness and acclimation potential increased gradually over each developmental stage rather than by discrete jumps of hardiness at each stage.
5.4 DISCUSSION

Inherent or initial hardiness describes plant hardiness prior to any acclimation treatment. In general, inherent hardiness increased with each stage of dormancy. However, these hardness levels (<-20°C) at final dormancy developmental stage may not be considered sufficient to survive measured winter temperatures (see Appendix 1 for temperatures). Acclimation potential describes the ability of a plant to harden upon exposure to acclimating temperatures. While inherent cold hardiness of ecotypes was inadequate for winter survival, acclimation potentials increased quickly, but steadily under the SD/WT regime to levels adequate for attainment of survival hardiness.

At the 0 days SD/WT stage inherent hardiness was low (< -5°C). This is not unexpected, as plants had just been transferred from active growth conditions in a greenhouse. It is generally accepted that actively growing dogwoods have low inherent hardiness (Chen and Li 1978). Further, the acclimation potential of these actively growing plants was low, which is expected of actively growing plants (Fuchigami et al. 1982). Hardiness increased by roughly 3°C over a 4 week acclimation period. These levels are insufficient for winter survival in the areas from which the ecotypes originate (see Appendix 1 for local temperatures). An environmental signal is required to trigger the internal acclimation machinery in plants. Previous studies suggest that short days, which result in growth cessation, are the most common environmental signal (Bray and Brenner 1981, Chen and Li
Chapters 2 and 3 suggest that this signal is either short days, low temperatures or a combination of both depending on the ecotype. For this study, short days were used as the signal.

Twenty days into the SD/WT conditions, hardiness and acclimation potential were tested again. After 20 days of SD/WT treatment, hardiness had increased only minimally (hardiness < -7°C). However, plant acclimation potential increased significantly. Following 4 weeks of acclimation, ecotype hardiness ranged between -13 and -18°C (Table 5.2). The NWT ecotype was the hardiest followed by the Mass and Utah ecotypes. While these levels of hardiness are insufficient to ensure winter survival, they indicate a shift in plant ability to respond quickly to environmental cues and alter pathways to permit greater acclimation. Similar to VM tests in other chapters, the results indicate that the northern ecotypes are able to respond more quickly to environmental cues. Qamaruddin et al. (1993) believe that a fast response, following triggering of acclimation processes, is an advantage to northern populations. In the north summers are short, the change of season is rapid, and temperatures are extreme (Heide 1985). Under these conditions, a slow response could significantly reduce survival.

Most importantly, the results provide evidence that plants can attain significant acclimation potential before VM attainment or growth cessation. This is further evidence that attainment of acclimation potential is more a gradual process, rather than a dormancy-stage-specific process. It is possible that sensitivity to
inductive acclimation conditions varies with plant growth and acclimation developmental stage. Plant sensitivity to acclimating conditions is initially low in the fall, but increases with time. Concurrently, temperatures are decreasing and plants are becoming more dormant. There appears to be a synergistic process between increasing acclimation potential, decreasing temperatures and perhaps dormancy development. This leads to a steady increase in acclimation potential with subsequent hardiness.

Following the 20 days SD/WT stage, plants were not tested until budset was attained. NWT attained budset first, while Mass and Utah attained this developmental stage later (3 and 7 weeks respectively). Although plants had ceased growth at this stage, true VM had not been attained.

Inherent hardiness was still not high at the budset stage (-9.5 to -12°C), however, acclimation potential had increased significantly. All ecotype minimum hardiness values ranged in the -20’s and -30’s following 4 weeks of acclimation.

The results of acclimation studies at the budset level, help support observations that plants only attaining budset were capable of significant levels of acclimation. Growth cessation, rather than rest induction, is the key to acclimation (Weiser 1970). Christersson (1978) found that Scots pine and Norway spruce acclimation was promoted without the attainment of dormancy. Using a LD/LT regime, plants would cease growth and acclimate. In our study, Utah, which did not become vegetatively mature under field conditions in Saskatoon (Chapter 3), acclimated to -27°C (Table 5.3) after only 4 weeks of acclimating temperatures.
Under Utah conditions (minimum mid-winter temperatures around -20°C), this level of acclimation would be more than adequate for winter survival. Perhaps under native conditions, Utah dogwoods do not normally attain VM.

VM was the next testing stage following budset. Only NWT attained this stage. To compare acclimation potential in time, rather than at development stage, Mass and Utah were also tested when NWT attained VM; this stage was referred to as NVM (Figure 5.1).

It is difficult to determine if there was a significant increase in NWT acclimation potential between the BS and VM stages in light of underestimated killing temperatures. Interestingly, the low temperatures of the test were sufficient to break dormancy. The results of the comparison test with Mass and Utah indicate that Utah achieved hardiness and acclimation potential levels intermediate between 20 days SD/WT and budset, while Mass levels paralleled those of the budset stage; further strengthening the concept of a gradual, rather than step-wise attainment of acclimation potential.

The final stage, PBS (post budset), was implemented since both Utah and Mass ecotypes could not attain true VM under the SD/WT controlled environment chamber conditions. In lieu of a VM stage, both ecotypes were tested 25 days after the testing of budset. Inherent hardiness of both the Utah and Mass ecotypes increased from the budset stage. These levels, however, would still not be sufficient for winter survival under native conditions. Acclimation potential of both ecotypes also increased significantly from the budset stage. These results confirm that
inherent hardiness and acclimation potential continue to increase gradually, over all developmental stages of dormancy and are not limited to specific stages.

5.5 CONCLUSION

Attainment of acclimation potential and hardiness was more a continual, than step-wise process, beginning with the first exposure to inductive conditions (SD/WT). This contradicts earlier dogwood studies which attempted to categorize acclimation into stages (Fuchigami et al. 1982, Weiser 1970). Although plants could never attain non-acclimated (inherent) hardiness levels sufficient for winter survival, adequate acclimation potential for winter survival was acquired at advanced developmental stages.

While NWT attained the dormancy development stages before the southern ecotypes (Mass and Utah) and acclimated more rapidly at each stage, any relationships between dormancy development stage and acclimation were overshadowed by the continual attainment of acclimation potential over the duration of the test. Hardiness sufficient to survive normal local winters could be attained in pre-VM stages following 2-4 weeks of acclimating temperatures, suggesting attainment of VM is not necessary for critical cold acclimation.
6.0 SUMMARY AND CONCLUSIONS

Under three different systems, field, shadehouse and controlled environment, northern ecotypes attained VM or growth cessation before the southern ecotypes, and the order of attainment was consistent between systems. Observations of chilling requirement established northern ecotypes satisfied this condition the earlier than other ecotypes.

Controlled environment studies indicate northern ecotypes were induced towards VM by short days, low temperatures or a combination of both. For southern ecotypes, the presence of short days was imperative, however, low temperatures enhanced earliness of progression towards VM under this photoperiod.

Freezing studies indicate that the attainment of VM is not essential for substantial cold acclimation. All ecotypes were able to attain significant levels of hardiness at or before budset. Increased acclimation potential was evident after only 20 days of exposure to SDWT conditions. These results indicate that attainment of acclimation potential is a more gradual, continuous process, than the step-wise process previously suggested.

Future tests are needed to correlate field dormancy status with hardiness and acclimation potential under natural conditions. Ideally, these tests would involve several locations which represent the various habitats of the dogwoods (i.e.
simultaneous tests in Alaska, Saskatoon, Mass and Utah). Further controlled environment studies should incorporate northern ecotypes into the diurnal studies tests and add short photoperiod regimes with cooler day temperatures to determine the minimum inductive daytime temperature.

Re-evaluation of the description of VM and its position as the first stage in the attainment of true dormancy is needed. Similar clarification of chilling requirement terminology and proper testing is important. Current methods of measuring chilling requirement may be inaccurate. Quantification is based on the incorrect assumption that satisfaction begins at the attainment of VM, and the progression from VM to deepest rest is relative to the satisfaction of the chilling requirement as plants progress from deepest rest to quiescence.

Finally, future cold tolerance tests should allow longer acclimation periods at each test time to determine maximum acclimation abilities, as well as testing at set times (i.e. 10, 20, 30, 40, etc. days) rather than at dormancy developmental stages. This would permit confirmation of the suggestion that attainment of acclimation potential is a gradual process.

In summary, there is variation in the timing of growth cessation and attainment of vegetative maturity (VM) among dogwood clonal ecotypes. Further, northern and southern ecotypes respond to different VM-inductive conditions. Freezing studies indicate significant acclimation potential is acquired before the attainment of VM, and that the attainment of acclimation potential is continuous. Field, shadehouse and controlled environment chamber systems all recorded the
same order of VM or induced growth cessation. Controlled environments, however, were not able to induce the same level of VM as conditions occurring in the field or shadehouse.
7.0 LITERATURE CITED


APPENDIX 1

Photoperiod and Temperature Data

Both photoperiod and temperature vary considerably among the native environments of the dogwood clonal ecotypes. Following are 30 year data (from 1931-1960 for Massachusetts, Utah and Alaska; from 1951-1980 for Saskatoon, Chalk River and Northwest Territories) supplied by the U.S. and Canadian governments.
Appendix 1a. Fairbanks, Alaska
monthly daylength, maximum, minimum and extreme minimum temperatures (30 year average)

<table>
<thead>
<tr>
<th>Month</th>
<th>Maximum</th>
<th>Minimum</th>
<th>Extreme Minimum</th>
<th>Daylength</th>
</tr>
</thead>
<tbody>
<tr>
<td>J</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>J</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>J</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>O</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>N</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>D</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Appendix 1b. Chalk River, Ontario
monthly daylength, maximum, minimum and extreme minimum temperatures (30 year average)
Appendix 1b. Chalk River, Ontario
monthly daylength, maximum, minimum and extreme minimum temperatures (30 year average)
Appendix 1c. Yellowknife, Northwest Territories monthly daylength, maximum, minimum and extreme minimum temperatures (30 year average)
Appendix 1d. Boston, Massachusetts
monthly daylength, maximum, minimum and extreme minimum temperatures (30 year average)
Appendix 1e. Saskatoon, Saskatchewan monthly daylength, maximum, minimum and extreme minimum temperatures (30 year average)
Appendix 1f. Salt Lake City, Utah
monthly daylength, maximum, minimum and extreme minimum temperatures (30 year average)