This is to certify that the

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RECONSTRUCTING THE OVULIFEROUS SCALE IN PICEA PUNGENS TO EXAMINE THE MECHANISMS SURROUNDING POLLINATION DROP SECRETION.

presented by

GEOFFREY LLOYD WILLIAMS

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Reconstructing the ovuliferous scale in *Picea pungens* to examine the mechanisms surrounding pollination drop secretion.

By

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ABSTRACT

Reconstructing the ovuliferous scale in *Picea pungens* to examine the mechanisms surrounding pollination drop secretion.

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The pollination drop is the primary mechanism in *Picea pungens* and other *Picea* species by which the pollen is brought into the micropyle. Three-dimensional reconstruction using Laser Scanning Confocal Microscope was used to elucidate the proximity and involvement of ovuliferous scale vasculature in the pollination drop emergence and disappearance in *Picea pungens*. The development of the xylem trace from the main ovuliferous scale vasculature to the proximity of the base of the ovule is consistent with pollination drop emergence, in that the pollination drop does not emerge until the trace is complete. The drop disappears as the trace breaks from ovuliferous scale cellular expansion. These data support the supposition that the pollination drop emerges once the xylem vascular trace completes its differentiation from the cone axis to the base of the ovule and integument, and ceases as the scale cells expand, severing the mature xylem elements supporting the pollination drop.

This is dedicated to all those who provided support and patience through the process, with a special dedication to my wife, Erin.

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INTRODUCTION

One of the least understood aspects of the pollination mechanism in the Coniferae is the development and subsequent disappearance of the pollination drop. The pollination mechanism, as defined by Owens and Blake (1984) refers to the structure of the ovule tip and the process by which pollen is taken into the micropyle. The pollination drop is the primary mechanism in *Picea pungens* and other *Picea* species by which the pollen is brought into the micropyle. The drop consists of a small volume of fluid that exudes from inside the micropyle and fills the pollen capture chamber. The origin of the fluid in the pollination drop, and how it fills the micropylar canal, have not been fully explained for the genus *Picea*, but may be related to the vasculature in the ovuliferous scale in the female, or seed-bearing, cone.

The last time coniferous species vasculature was investigated in depth was at the turn of the last century. Now 100 years later, new investigative tools allow a more detailed examination of the development in the female reproductive system of the conifers. This study focuses specifically on *Picea pungens*, as it has been least studied of the *Picea* genus over the last 25 years.

As new imaging techniques that increasingly involve computers and modeling take the fore front, they allow us to expand knowledge in the area of structure and function. These same technologies can also be used to re-examine data in previously published studies, to aid in instruction, and to provide more developmental structure information of the general anatomy of well-known and economically important families in the Plant Kingdom.

Research into the vasculature in coniferous cones can be traced back to the last century. Van Tieghem's 1869 publication was the first to report on the development and evolution of the female cone with particular emphasis on the vasculature. In his paper, Van Tieghem did a comparative anatomical study of the female "flower" and the fruit of the "Cycadées, des Conifères et des Gnétacées," or as they are referred to now as the Cycads, the Conifera, and the Gnetophyta. Of particular interest in this study were his figures and description of the Conifères, and *Picea nigra* in particular. The focus on the fibers and the tracheids in relation to the female cone were very useful in organizing this study.

Van Tieghem was focused on trying to comprehend whether the scales on the cone were the result of modified branches or modified leaves. He described vascular bundles as

independent units. The upper bundles in the scale form an arc with inverted orientation, (xylem directed outwards and downwards) and the lower bundles with normal orientation belong to the bract. He concluded that the arrangement of the bundles in an arc showed that the ovuliferous scale is a leaf and not a branch and the orientation of the arc showed that the leaf is diametrically opposite the bract. So this modified leaf belongs to an axilary branch of which it is the first and only appendage, and it is this 'leaf' that bears the ovules on its dorsal surface. The pollination mechanisms might not have been completely understood for the species examined. Van Tieghem's work was the foundation for continued studies by both Wordsell and Aase.

W. C. Wordsell (1900) wrote that understanding the structure of the female 'flower' in Coniferae "will occupy a paramount place in the minds of the foremost botanists of the day." This did not seem to be the case. Very little published work examined the full range of the Coniferae. Many papers examined various genera but, as mentioned before, *Picea* was the least studied then as it is now, with the main focus still on trees in the *Abies* genus.

Wordsell (1899, 1900) provides an interpretation of the work of Van Tieghem after 30 years of research in the field had elapsed. Wordsell compiled an extensive review in this

paper covering the various theories of development of the "female 'flower' in Coniferae" from 1682 to 1897. Much of the information presented and analyzed by Wordsell has been forgotten or become accepted as dogma in the modern study of botany yet pollination mechanisms were not the focus of study during that time. His 1900 publication is a historical collection of data and analyses that are of great value to the modern study of conifers, providing perspective as to how far the science has progressed.

Even Wordsell (1899) himself, in his publication describing observations on the vascular system of the 'female flowers' of Coniferae, did not describe any *Picea* cones. He did, however, provide diagramatic evidence of vascular support for the ovule in *Sciadoptis verticillata*. His study was primarily focused on describing the anatomical characters in general and using these characters to throw "some light upon the phylogenetic relationship[s] of the order as a whole" (Wordsell 1899).

Similarly, Hanna C. Aase (1915) published a review and investigation into the vascular anatomy of the coniferous megasporophyll. As with Wordsell, Aase's paper did not include an examination of the vasculature of any *Picea* species. Although Aase did not solidify the understanding of *Picea*, her publication began to cement the wild variation

in interpretation of cone morphology into a more modern understanding, that emphasized the importance of the vasculature.

Over a century after Van Tieghem, we still do not have a complete examination of the vasculature of *Picea*. There are, however, publications that indirectly describe the nature of the vasculature in the ovuliferous cone or 'flower,' most of which are from the last 25 years. Most of these examine the reproductive cycle of various members of the genus *Picea*.

The events surrounding reproduction and pollination have been studied in *Picea glauca* (Owens and Molder, 1977; Owens and Molder, 1979), *P. stikensis* (Owens and Blake, 1984; Owens and Molder, 1980), *P. orientalis* (Runions et al. 1999), *P. engelmannii* (Runions et al. 1995; Runions and Owens, 1996; Owens and Simpson, 1987; Owens et al., 1987; Harrison and Owens, 1983; Singh and Owens 1981) and in a limited scope, *P. pungens* (Cram, 1984).

Picea glauca, *P. stikensis*, and *P. engelmannii*, represent the more important economic trees in the southwest of British Columbia, Canada, where the preeminent laboratories for the study of conifer sexual reproduction, that of Dr. John Owens, is located. The contribution to the understanding of spruce reproduction and cone development is

nearly complete from the papers listed above. These papers are primarily a collection of descriptive articles detailing almost all aspects of observable development. Owens and Molder (1977), in their paper with an examination of cone differentiation and early development of the bud in *Picea glauca*, concluded that one can accurately estimate or track seed cone differentiation based on lateral shoot elongation, which proved to be an invaluable aid to track bud development in *Picea pungens* for the research presented in this thesis.

Owens et al. (1987) classified six stages to describe the development of *Picea engelmannii* ovulate cones. These stages were slightly modified after further investigation by Runions et al. 1995 (Table 1). Stage one begins from the

Stage 1: •After dormancy till •Ovuliferous scales grow	**Stage 4:** •Continued axis elongation •Ov. scales reflexed •even more receptive
Stage 2: •Micropylar arms develop •Cones elongate	**Stage 5:** •Basal Ov. scales begin to close •Pollination drops emerge
Stage 3: •Ov. scales enlarged •Micropylar arms elongate •Receptive to pollen	**Stage 6:** •Cones become pendant •Bract basal tissue expands

Table 1. Ovuliferous cone developmental stage summary of key features. Table adapted from Owens et al. 1987, and Runions et al. 1995.

developmental point at which the bud breaks dormancy to the point at which the bud stalk and axis curve upwards and begin elongation. From the time the cone just partially emerges from the bud scales to when the distal ovuliferous scales expand is deemed stage two. Stage two cones are not yet receptive to pollen, but the micropylar arms are almost fully developed. The cone axis in stage three continues to elongate, enlarging the spaces between the ovuliferous scale wide enough for pollen to begin to enter and settle in the hydrophilic region in the axis below the micropylar arms. Pollen also beings to collect on the secretory droplets on the micropylar arms in this stage, but the pollination drop has not yet emerged. Stage 4 cones undergo further axis elongation, widely separating and exposing more of the ovuliferous scales. The ovuliferous scales are reflexed with distinctly curled margins. The wind born pollen easily collects on and around the micropylar arms. At the end of this stage, pollination drops begin to emerge in the basal scales of the cone and continue acropetally, immediately prior to the ovuliferous scales bending upwards and closing. The closing of the ovuliferous scale creates a closed environment for the pollination drop to fill the space out side the micropylar arms to efficiently collect any pollen that is in the space. Stage 5 is the time at which the scale closure continues and the cone starts to bend down.

After the scales close they elongate and thicken, and become tightly appressed. At this stage of development, the cone is no longer receptive. In stage six all of the ovuliferous scales are tightly appressed and begin to fill the air space previously occupied by the pollination drop. This last stage is when the cones begin to enlarge and become completely pendant.

Picea pungens is most closely related to *Picea engelmannii* (Wright, 1955), the species examined by Owens et al., (1987) which prompted the most interesting questions about the pollination drop. Specifically this statement piqued my interest: "No vascular tissue extended into the tip of the nucellus. Only a weak vascular strand terminated in nucellar tissue at the base [chalazal end] of the ovule" (Owens et al. 1987). The hypothesis introduced to explain the pollination drop withdrawal was that an increased surface area caused by the pollen in the micropyle accelerated the evaporation of the drop (attributed originally to Doyle, 1945). Later publications (Runions et al., 1995; Runions and Owens 1996) explained this process based on further observations of interior spruce, the term used for *Picea engelmannii, Picea glauca* and hybrids of the two growing in mixed stands. These papers identified the importance of ambient and secreted moisture in the pollination mechanism of these species, but without

explaining how the pollination drop fluid appeared. Runions and Owens (1996) concluded that the pollination mechanism in certain environments may have provided the selection pressure for the evolution of the pollination drop.

While the most significant accumulation of information about pollination mechanisms exists for *Picea engelmannii*, *P. pungens* has been largely unexplored. Jonathan Wright (1955) was focused on the relationship and distribution of spruce in relation to species crossability. Wright found that *Picea pungens* did not successfully cross with *P. gluaca*, *P. sitchensis*, or *P. orientalis*, yet he published morphological data that suggested that *P. pungens* was most similar to *P. engelmannii*. Daubenmire (1972), examined the relation of *Picea pungens* and *P. engelmannii* in the Rocky Mountains, and theorized that a recent single mutation in *P. engelmannii* produced a derivative (*P. pungens*) that was at once incompatible and had differing environmental requirements.

Mitton and Andalora (1981), used genetic and morphological data to explore the relationship between these two species in the Colorado Front Range, (the eastern edge of the Central Rocky Mountains where the mountains rise out of the Great Plains, also the eastern most distribution of *Picea pungens*). They found that genetically there were no

hybrids between *Picea pungens* and *P. engelmannii* in an area of suspected introgression, yet discriminant analysis of morphological data did not resolve two groups from the data. While these publications did not help with our understanding of the specifics of the pollination mechanism in *Picea pungens,* they provided a reasonable foundation to use *P. engelmannii* as a model system to begin an investigation into the pollination mechanism of *P. pungens*.

Research examining the pollination drop in other coniferous species (Tomlinson et al., 1991, Tomlinson, 1992, Takaso, 1990) has not fully elucidated the cellular processes associated with the functions and activities of the pollination drop. Takaso (1990) gives a brief summary of the pollen capture mechanisms, but concludes that there is no consensus on pollination drop exudation and withdrawal. Tomlinson et al., (1991) introduced the concept of "pollen scavenging", describing the process of the pollination drop extending over adjacent bract surface or cone axis, passively collecting pollen that landed prior to drop secretion. The drop, therefore, functionally provides a pathway for the pollen to float into the micropyle, extending the process of pollination in time and space. Tomlinson's studies provided a new aspect to examine in all species with a pollination drop, but there was no mention of mechanism for the timing of the event.

In summary, previous work on pollination in *Picea* and other gymnosperms has resulted in no clear understanding of the mechanisms providing the relatively large amount of fluid needed for the pollination drop. *Picea pungens* is ideal for examining this mechanism as cones are generally larger than *Picea engelmannii*, the most studied species, but the ovuliferous scales are small enough to allow easy cellular and tissue investigation using a variety of microscopy techniques.

New microscope techniques such as Laser Scanning Confocal Microscopy (LSCM) can, of course, give us more information than was possible to obtain in 1869, and more than was obtainable even into the late 1980's. An associated technique, three-dimensional (3-D) reconstruction, is a powerful tool for examination of morphology and developmental events. This thesis takes advantage of 3-D reconstruction using LSCM to elucidate the proximity and involvement of ovuliferous scale vasculature in the pollination drop in *Picea pungens*. The objective was to begin to clarify the pollination mechanisms in *Picea pungens* specifically the events surrounding the development and disappearance of the pollination drop. This was tested by examining and reconstructing, digitally, in three dimensions, a time series of ovuliferous scales from developing cones.

Materials and Methods

Collection

Sample collection was done at W. K. Kellogg Forest, Augusta, Michigan located in Ross TWP T1S-R9W. It is an ideal site for collecting *Picea pungens* samples, as the trees are just becoming reproductive (30 y old), which simplified collection. The other advantage is the wide genetic diversity and known geographic origin of the trees in the plantation. The plantation is a collection of half-sib progeny tests from seed collected all through the natural range (Fig. 1) of *P. pungens*.

Eight seed sources were selected for consistent reproductive set and uniform morphology. Trees were selected for high cone yields in the late spring of 1997. One tree from each MICHCOTIP (Michigan Cooperative Tree Improvement Program) stock numbers 67318097 and 67318201, specifically locations RR-20 in MSFG-P-1-71 (Michigan State Forest Genetics Plantation Number One planted in 1971) and B-94 in MSFG-P-1-73, were selected for the primary study (Fig. 2). The source of tree RR-20 was open pollinated seed collected by Ross E. Mosier (on Sept. 6, 1969) from a green *Picea pungens* tree (height = 60' and D.B.H. = 14") located near thinning cabins on Mushroom Gulch Road in Chaffee Country,

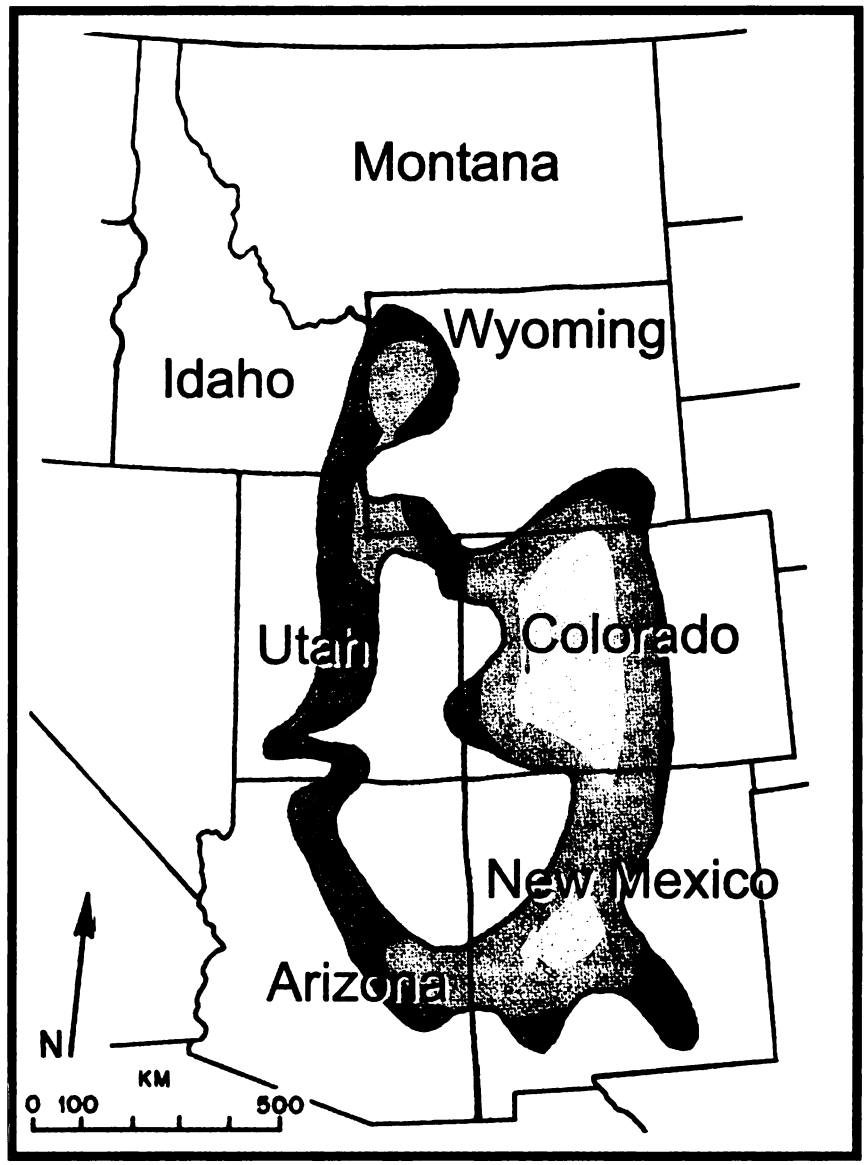


Figure 1. Natural range of *Picea pungens* (gray shaded area) in the United States. Map adapted from Daubenmire, 1972.

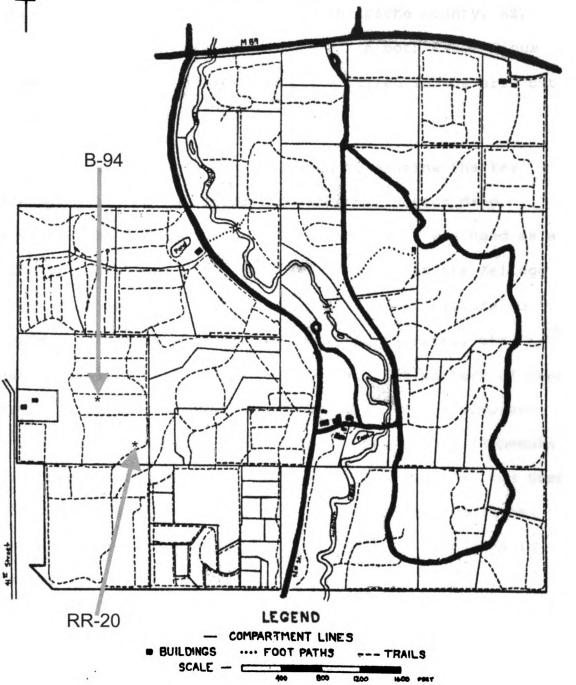
Figure 2. Compartment map of W. K. Kellogg Forest in Augusta, Michigan identifying the specific location of the trees used for cone collection in 1997, B-94 and RR-20. Courtesy of the W. K. Kellogg Forest.

W. K. KELLOGG FOREST

AUGUSTA, MICHIGAN

KALAMAZOO COUNTY

ROSS TWP. - T1S R9W



3/78

CO, Sec. NE 1/4 1, T14s, R77W, elevation 9400'. The source of tree B-94 was open pollinated seed collected by L. R. Rich, G. J. Gottfried and J. B. Ryan (on Sept. 24, 1969) from a green *Picea pungens* tree (height = 55') located near Buffalo crossing and Big Lake Road in Apache County, AZ, Sec. 14, T5N, R28E, elevation 8520'. In both cases *Pinus ponderosa* and *Pseudotsuga menzesii* occurred in the area but *Picea engelmannii* did not.

Collection times were optimized to examine the key developmental stages surrounding the pollination drop release. The first year of collection, 1996, was used as a guide to understand *P. pungens* reproduction at the Kellogg Forest site in comparison to the published literature on *P. engelmannii* and other *Picea* species. Unfortunately the weather of 1996 resulted in a very irregular pattern of cone development, and it wasn't possible to collect a complete sequence of development from a single tree source (Appendix A). However, the process resulted in material that was used to optimize fixation, embedding and examining techniques. The data collected in the first year were not included in the results.

The second year of collection, 1997, was timed to collect and sample ovuliferous cones in the necessary stages for completion of this study. Ovuliferous cone samples were

Collection Date	Sample #	Tree #	Field evaluation
5/20/97	A3	B94	early stage 1
5/20/97	A2*	B94	stage 1
5/20/97	A1	B94	stage 1-2
5/22/97	B1&2	B94	one cone, stage 2-3
5/25/97	C1&2*	B94	one cone two vials, stage 4-5
5/28/97	D*	B94	late stage 5, early stage 6
6/1/97	E	B94	stage 6 and on
6/3/97	F	B94	
6/5/97	G	B94	
6/5/97	Z	RR20	
6/8/97	Y	RR20	(could not access B94)
6/10/97	X	RR20	
6/10/97	H	B94	
6/12/97	I	B94	
6/12/97	W	RR20	becoming pendant
6/17/97	V	RR20	nearly II to ground
6/17/97	J	B94	almost pointed down
6/26/97	K	B94	Pendant and enlarging
6/26/97	U	RR20	Pendant and enlarging
* = cones used for full reconstruction			

Table 2. Collection times, sample allocations, location source and field notes for the 1997 field season at Kellogg Forest.

collected from the selected trees from the time they broke dormancy until seed maturation began. Dates and times of collection are noted here (Table 2), but the second field year was another unusual year for weather patterns at Kellogg Forest (Appendix A). The weather, while unusual was not disruptive once the cones broke dormancy. The most significant factor affecting the onset of cone development was the delay in degree day accumulation in 1997 (Appendix A).

One to two ovuliferous cones were collected per tree every two or three days. All the samples were examined, however, one tree (B-94), with the most consistent cone development and highest cone set, was used for full three-dimensional reconstruction and analysis.

Fixation

The fixation protocol was the same for every sample regardless of the microscope used for examination. Once the cones were collected, they were immediately dissected in the field into the primary fixation solution, which was based on research on developing spruce meristems (Heckman, 1985). The distal and basal ends of the cones were discarded to keep collection times as developmentally uniform as possible. The primary fixative was 1% paraformaldehyde, 3% glutaraldehyde in a 0.05 M cacodylate buffer. The fixative temperature was held between 18 and 25°C. After immersion in the solution a low vacuum (0.05 MPa) was applied for 20 min then vented and repeated five times in the field using a hand-operated piston vacuum pump, for a total fixation time of 2 h. The samples were washed twice for 2 h each, in 0.05M cacodylate buffer, at room temperature and stored in buffer overnight at 4°C. The samples were transported at ambient temperature to the Center for Electron Optics, on the campus of Michigan State University, East Lansing,

Michigan. Samples were then divided into subsets for Scanning Electron Microscopy, and Laser Scanning Confocal Microscopy.

Scanning Electron Microscopy

After fixation, whole or partially dissected ovuliferous scales were dehydrated to 100% ethanol in a graded series over the period of 5 days. They were then critical point dried, and sputter coated with gold. Alternatively images from 10 µm thick sections were obtained from material processed for the Laser Scanning Confocal Microscope (see below). Series of slides were selected and placed in a xylene bath to remove the paraffin. The slides were then air-dried and sputter coated with gold. Imaging of all samples was done at 15 kV on a JEOL 6400V. Images were collected and stored digitally and processed with Adobe Photoshop version 4.0 software.

Laser Scanning Confocal Microscopy

In preparation for LSCM, the ovuliferous scales were dehydrated to 50% in a graded ethanol series and then into a 100% t-butyl alcohol at 35°C. They were then infiltrated with paraplast over 7d before embedding. The samples from each set were serially sectioned at 10 µm on a rotary microtome. The scales were sectioned tangentially in

relation to the cone axis from the micropylar arms to end of the seed wing primordia. Sections were then mounted on Fisher Superfrost Plus slides for staining and viewing with a Zeiss LSM 210. Sections were stained with 1% aqueous Safranin O for 15 min and mounted under No. 1 ½ coverslips with Fluka DPX. Confocal, fluorescent images of the serial sections (from A to B in Fig. 3), were collected and hand registered using a 5x Plan-Neofluar lens (NA 0.15) with an optical section thickness about 2 microns thicker than the serial sections. Images used in the detailed reconstruction of small groups of individual xylem cells were collected using a 40x Plan-Neofluar oil (NA 1.30) lens. Once the fluorescent images of the serial sections were collected, they were treated as a series of optically sectioned images.

Computer Reconstruction and Image Processing

Images for 3-D reconstruction were all processed using the same procedure on the Silicon Graphics Inc. (SGI) workstation. Raw images were transferred from the Zeiss LSM 210 to an intermediate computer between the microscope and the SGI for conversion to TIFF images. From there the sequence was imported to the SGI and a "volume" was created from this sequence in Vital Images Voxel_View_E software.

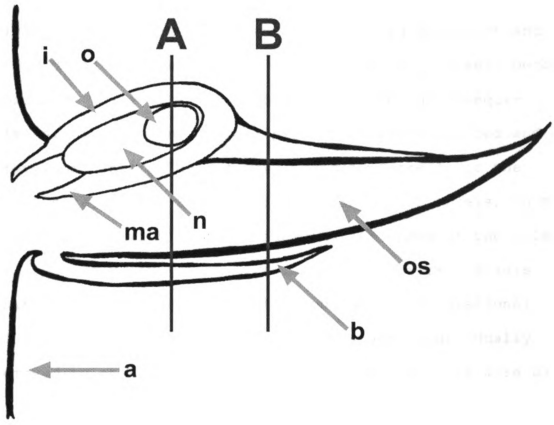


Figure 3. Schematic diagram of a *Picea* ovuliferous scale illustrating the starting (A), the axis end, and ending (B) points, chalazal end, for the serial sections examined. (o) ovule, (n) nucellus, (i) integument, (ma) micropylar arms, (a) cone axis, (b) subtending bract, (os) ovuliferous scale.

The volume is a serial collection of two-dimensional digital images that have been given a third dimension and stacked on top of each other in order, so that pixels become voxels (a voxel is a pixel that has volume and is equi-dimensional). The volume aspect ratio was corrected and fractional interpolations were added to correct for the voxel size in the 'Z' dimension. Turning off voxels, in the whole volume, with a value dissimilar to those of the xylem, created the xylem trace movies and stereo pairs. Voxels that had similar values but that obscured the rotational view of the xylem trace and the fibers were individually removed to enhance the images. No digital filters were used to create the images.

The images appear as they were collected, except for their combination into a 3-dimensional volume. Once the volume was correctly sized, movies and images were generated and were transferred to a Windows NT workstation where they could be converted from SGI formats to Microsoft Video Clip format (AVI) and Tagged Image File Format (TIFF) using Adobe Photoshop 5.0 and After Effects 4.0 software.

Results

The SEM examination of the sections provided more information than available with traditional or advanced light microscopy techniques. Specially prepared slides for SEM were used to examine the fibers and xylem in individual 10 μm sections (Fig. 4). Sections from similar stages of development showed fibers with identical patterns (Figs 4A and 4B). There was much more information in the confocal, fluorescent image (Fig. 4B) than in the standard SEM image (Fig. 4A) at this magnification. Additional SEM images (Fig. 4C and 4D) were collected from the area shown at the arrows in Figure 4A. At these higher magnifications, the cell type was apparent, confirming that the lower fluorescent bundles were xylem (X) and the upper fluorescent bundles were fibers (F). Phlouroglucinol-HCL tests verified the presence of lignin in the vessels and fiber tissues (data not shown).

The first and last serial section of each selected area of the ovuliferous scale at three key developmental times, represented the basis for the reconstruction (Fig. 5). The ovuliferous scales from cones that were chosen for specific stages of development from tree B-94 were used (Fig. 5).

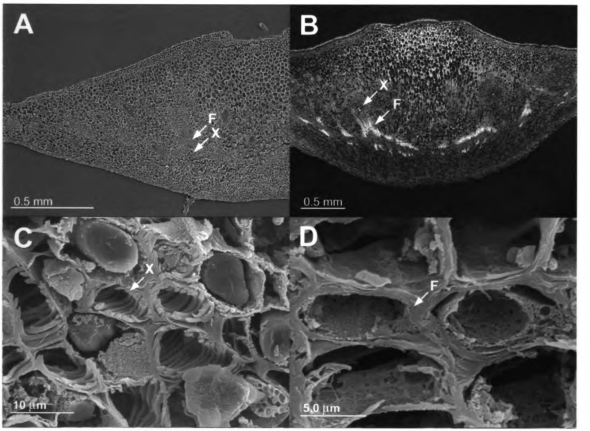
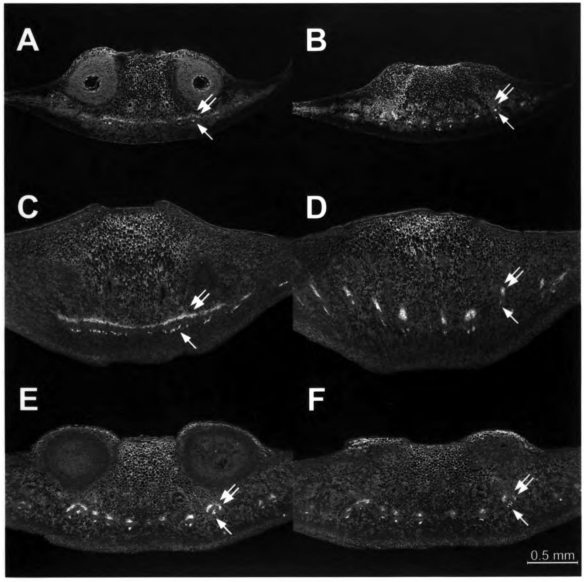


Figure 4. Ovuliferous scales of *Picea pungens* at identical stages of development sectioned at 10 µm and examined using SEM and LSCM. A. SEM digital image of a scale section. B. LSCM confocal, fluorescent digital image of a scale. C. SEM detail of the xylem at the X arrow in Fig. 4A. D. SEM detail of the fibers at the F arrow in Fig. 4A. For all images in this figure: (F) fiber, (X) xylem.

Figure 5. Single LSCM images representing the first and last images in each of the three serial-sectioned ovuliferous scales. The double arrow identifies fiber fluorescence and the single arrow identifies the xylem fluorescence. A and B are from an ovuliferous scale in developmental stage 3-4, C and D are from a late stage 5 scale, and E and F are from a stage 6 scale.


A
B
C
D
E
F
0.5 mm

The samples were from three sequential collection dates and were selected from the middle section of each cone. These single, digitally collected, confocal, fluorescent images of the ovuliferous scale, were combined to create the three dimensional structure used to examine the xylem pathways in the ovuliferous scale at the chalazal end of the ovule.

The vasculature on the right side of these images was selected for examination for simplicity and clarity. The movies (on the accompanying digital media Appendix B Fig. 5AB, Fig. 5CD, Fig. 5EF) are "slice parades", showing the series of serial sections that start at the axis end (A, Fig. 3) and progress through to the chalazal end (B, Fig. 3). This series of images (soon to be a "volume") represents the entire area between A and B in Fig. 3, which was about 250 microns thick, and consisted of 25 serial mechanically-sectioned images (these vary depending on the volume).

The highest fluorescent signal comes from the vasculature (xylem) and the fibers. The fibers on top (double arrows in Fig. 5) are elastic and provide the primary mechanical support for the mature ovuliferous scale and the mechanism for ovule opening and on the bottom is the xylem (single arrows in Fig. 5). The ovuliferous scales showed a variety of ovule shapes and orientation, even though they were

selected from a single tree. This variety, however, was not detected in the vasculature inside the scale. The patterns illustrated by these three series of images, or volumes, are representative.

When compared to the stages of development presented by Runions et al. (1995), the *Picea pungens* cones studied here represented a similar progression. The first series of images is from a late stage 3, early stage 4, cone (Fig. 5A and 5B). In stage 3-4 cones, the xylem was still developing and had not yet completed differentiation to the base of the ovule. The second set of images (Fig. 5C and 5D) is from a larger cone in late stage 5, at the approximate time of pollination drop secretion. Here the xylem had completed the pathway for the fluid in the xylem to make the pollination drop. Stage 6 is represented by the last series of images (Fig. 5E and 5F). This scale had started to elongate and the seed was beginning to develop.

The next set of figures is constructed from the data collected from the serial sections represented in Fig. 5E and 5F. There are no data missing from the reconstruction. All depictions are in the same orientation, left to right in the image (Fig. 6) is the same orientation as A to B in Fig 3. Figures 6, 7, and 8 are stereo pair representations of the vasculature at the chalazal end of the ovule on the same

side in each volume. The volumes were rendered from the same perspective and the stereo nature was produced by using projections of the volume with 15 degrees of separation. These volumes were constructed by either digitally removing the surrounding cells leaving the fibers (darker gray) and the xylem (lighter gray and white) (Figs. 6 and 7) or by digitally removing most of the fibers, allowing clearer presentation of the xylem (Fig. 8).

In the first stereo pair image (Fig. 6), the xylem shown had barely begun to differentiate 'up' to the base of the integument and ovule through the middle of a distinct group of intensely stained cells (for Fig. 6, 7, 8, and 9 full digital movies can be viewed on the accompanying digital media Attached as Appendix B). The fibers had branched just below the base of the ovule and the xylem showed a slight bend up through the fibers. The fibers would eventually form a sheath around the single xylem strand, which is shown in the next volume (Fig. 7, Appendix B Fig. 7).

In the next stereo pair image (Fig. 7, Appendix B Fig. 7), the xylem shown had developed to the base of the ovule, thereby completing the supply of water to the ovule and providing vascular support for the production of the pollination drop. These vascular traces appeared thin (i.e. Fig. 9, Appendix B Fig. 9), because they were made up of a

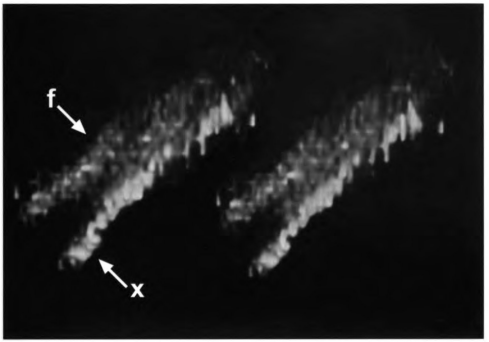


Figure 6. A volume represented as a stereo pair rendered from the digitally reconstructed serial sections from the LSCM shown in Figure 5A and B, illustrating the path of the xylem and fibers in an early pre-pollination drop ovuliferous scale. (f) fiber, (x) xylem. The length of this sample is approximately 200 µm edge to edge of one of the stereo pairs (A to B in Fig. 3)

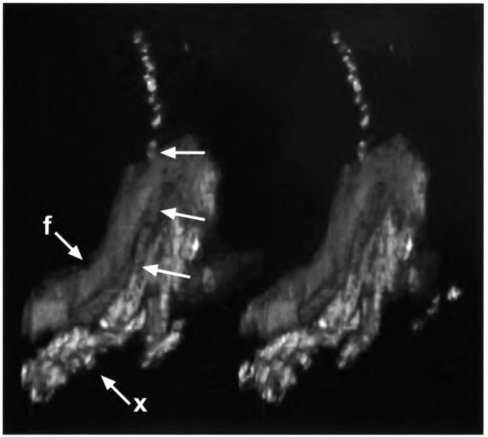


Figure 7. A volume represented as a stereo pair rendered from the digitally reconstructed serial sections from the LSCM in Figure 5C and D, illustrating the path of the xylem and fibers during pollination drop secretion. The unlabeled arrows identify the xylem trace as it passes through the fiber sheath. (f) fiber, (x) xylem. The length of this sample is approximately 200 μm edge to edge of one of the stereo pairs.

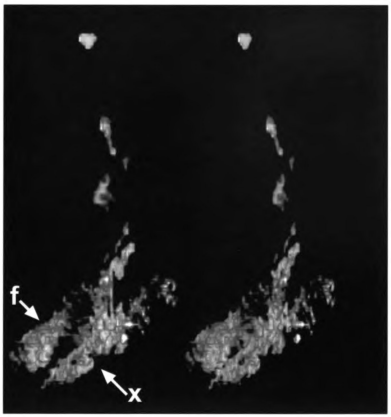


Figure 8. A volume represented as a stereo pair rendered from the digitally reconstructed serial sections from the LSCM in Figure 5E and F, illustrating the path of the xylem and fibers after pollination drop secretion. (f) fiber, (x) xylem. The length of this sample is approximately 200 µm edge to edge of one of the stereo pairs.

continuous one to two cell thick, connected line of xylem elements. In all scales that were examined there was always a xylem element paired with a fiber bundle that was associated with the base of the ovule at the point at which the fiber bundle branches.

The last stereo pair image (Fig. 8, Appendix B Fig. 8) demonstrates an ovuliferous scale at developmental stage 6. At this stage the scale had grown and expanded, disrupting the single xylem cell trace connecting the cone vasculature to the point of pollination drop exudation. The developmental break in the xylem cells resulted in the retraction of the pollination drop.

The vascular traces in each of the three volumes (Fig. 6, 7, and 8, Appendix B Fig. 6, 7, and 8) were structurally identical with small, short xylem cells. A stereo pair detail from a single section of the mature xylem cells from stage 5 is representative of the xylem in the vascular traces supporting the pollination drop. The vasculature that provides primary support for the rest of the ovuliferous scale was comprised of tracheids with more regular and even, helical thickenings and two to three times longer than those shown in Figure 9 (Appendix B Fig. 9).

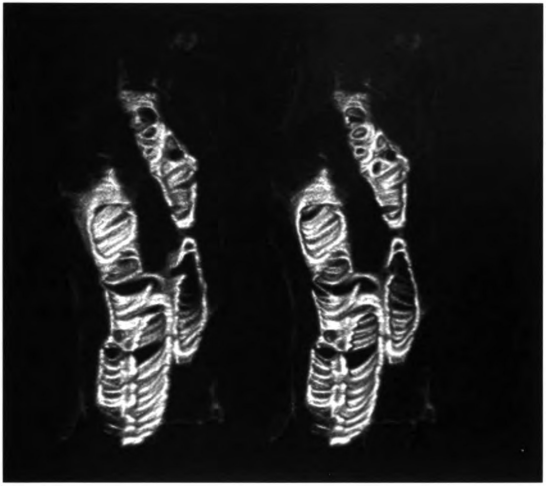


Figure 9. Stereo pair representation of an LSCM-collected series of digital images of a group of tracheids from a single 10 µm section of an ovuliferous scale in developmental stage 5.

Discussion and Conclusions

There are six stages of cone development related to receptivity of the ovules as proposed by Owens et al (1987). Runions et al. (1995) suggested minor changes in this model that affect stages 4, 5 and 6, specifically that the pollination drop was released later in cone development and that it persisted after the scales became appressed. These six stages generally occur in Michigan's Lower Peninsula any where between late April to the beginning of June, depending on the weather. The research presented here focuses on the development represented by stage 5 (Runions et al., 1995). In stage 5, the basal ovuliferous scale begins to close. It is at this point that the pollination drop begins to emerge.

Runions and Owens (1996) have described in detail the pollination drop and pollen scavenging for interior spruce (*Picea engelmannii*, *Picea glauca*, or their hybrid). They reported that the pollination drop did not emerge until just before the ovuliferous scale closes. The closed scale creates a chamber reducing evaporation allowing the drop to get larger, collecting more pollen. When the ovuliferous scale closes, the ends of the scale have drops of resin, which help to seal the chamber. My field observations provide additional support for Runions and Owens results as

Picea pungens pollen scavenging followed similar patterns as interior spruce.

Data (the reconstructed images) presented here, clarify the events relating to pollination drop release and cessation in *P. pungens*. From this research, the serially reconstructed images, in particular, provide support for the concept that the cause of the pollination drop formation and subsequent disappearance results from the various stages in development of a particular xylem trace as related to the growth and expansion of each ovuliferous scale.

In all cases, the development of the xylem trace is consistent with pollination drop emergence, in that the pollination drop does not emerge until the trace is complete and it begins to disappear as soon as the trace breaks. The actual observance of the pollination drop, or the presence of pollen in the micropylar canal combined with the degradation of the nucellar tip, was used to determine pollination drop occurrence.

Once the pollination drop liquid moves to the end of the vascular pathway, how does it move micropyle? One pathway might be via the intercellular space separating the nucellar tissue from the integument on all sides except for the chalazal end of the nucellus. This space is sufficiently large for the fluid to move through and

completely continuous and may provide the pathway for the fluid. As the pollination drop fluid fills the space, nucellar tip degradation occurs which could account for the elevated glucose and fructose content in the drop compared to the xylem sap as observed by Owens et al., (1987).

The vasculature in the ovuliferous scale is similar to most modified leaf structures in that there are vascular bundles with both phloem and xylem (tracheids). These bundles also contain a group of fibers providing support as well as the mechanism for opening the ovuliferous scales to disperse the seeds at maturity. At seed maturity the cone desiccates completely, resulting in the fibers dehydrating and mechanically opening the scales. The tracheids are dead at cellular maturity (tracheids have to be dead to be functional), and once mature there is little flexibility with the short cell length found in the ovuliferous scale. The overall cell length is much shorter than in the axis xylem or the fibers, and most importantly, the xylem matures before the ovuliferous scale completes its development.

There are three types of xylem cells in the ovuliferous cone and scale. The first type is in the cone axis. This xylem branches off to form the primary connection to the ovuliferous scale. These xylem cells are extremely long and have regular thickenings with few cell junctions. The

second type branches out of the cone axis and provides the vascular support for the ovuliferous scale. These cells retain many of the characteristics of the axis, i.e. longer cells, and somewhat orderly thickenings of the cell wall. The third type is xylem that develops and connects from the main vasculature to the base of the ovule. These xylem cells have slightly different characteristics, as these xylem traces develop not from meristematic initial cells, but rather are differentiated from parenchymous cells. These xylem trace cells resemble, in all forms, cells grown in tracheid inducing cultures in Zinnia (Williams 1994, Liskova 1985 and Fukuda 1997).

The sequence of the xylem trace development is a rapid event in the overall timing of the development of an ovuliferous scale, 2-4 days from the start of its development to drop emergence. The timing of this development correlates closely to the differentiation of isolated parenchymous cells into tracheids in an *in vitro* system (such as *Zinnia elegans*). The *in vitro* differentiation generally occurs in 24-36 hours, start to finish, with the first complete cells visible as soon as 8 hours (Williams, 1994). An assumption could be made that *in vivo* systems are much more efficient and possibly faster at differentiating than *in vitro* systems and thus it could be

surmised that the single cell trace can develop quite rapidly.

The completion of the xylem pathway corresponds to the most rapid phase of cell expansion in the ovuliferous scale and this thin 1 to 2 cell branch of xylem supporting the pollination drop is fragmented and disrupted by ovuliferous scale cell expansion. It is important to remember that the xylem cells are dead and rigid at maturity, and are unable to keep pace with the cell expansion occurring in the rest of the ovuliferous scale. It is at this developmental stage that the pollination drop begins to disappear as the xylem path is no longer intact. This ovuliferous scale cell expansion does not break the other vascular pathways because they are protected by the fibers. The primary direction of expansion is in the Z direction, parallel to the cone axis, hence the fibers reduce most of the expansion in the X-Y direction, perpendicular to the cone axis. These fibers provide more than just the mechanism for opening the scale upon maturity, they protect the primary xylem and phloem vasculature.

An comprehesion of where particular xylem originates is important to understand the different morphological types of xylem present in the cone. The vasculature in the cone axis results from a uniform meristem, giving rise to an ordered

and specific orientation. As the cone develops the axial vasculature branches out to support the primordial ovuliferous scales. This vasculature is slightly more irregular in shape than the xylem in the cone axis, but it still resembles xylem developing from a meristematic initial. The tiny vascular traces are distinct from the first two types of xylem as discussed above. From the results presented here and observations made on the tissue during examinations this difference appears to be due to the manner in which the xylem develops.

There may be many explanations for the origin of the vascular trace. Following Runions and Owens (1996) statement that "the conifer pollination drop may not be ancestral but derived from a pollination mechanism in which rain water was required for pollen delivery," it is possible to theorize that the xylem trace developed to support a pollination drop as a mechanism to supplement rainwater and then worked so well that it became a distinct advantage.

Another possible explanation is that the xylem trace differentiates to the base of the ovule along a signal gradient. In cell culture an elevated auxin level in a cell suspension triggers formation of tracheids (Williams 1994, Liskova 1985 and Fukuda 1997). It is possible that the ovule is producing elevated levels of a specific hormone or

combinations that may be carried through the distinct cell types at the chalazal end of the ovule, signaling the nearest vascular bundle to grow towards the ovule. As the xylem pathway, or trace, forms, it creates the path for the pollination drop. This signal may be involved in the selection of the pollination drop mechanism in coniferous species.

The final potential explanation is that the pollination drop existed prior to the fusing of the ovules into a cone (ancestral), and that it has been there all along in the evolution of *Picea* from an ancestral form. Those coniferous genera without a pollination drop may have lost it due to an environmental factor such as a migration or ecological change to a wet climate. The pollination drop may prove to be an additional tool in the understanding of the evolution of the Conifers.

Van Tieghem's figures (1869) of selected schematic line drawings, in a general way support the evidence presented in this thesis. His drawings of sections through the ovuliferous scales of *Picea nigra* are of particular importance despite the fact that the are primarily fully mature cones (very late stage 6). His observations of the orientation of the arc bundles, the vascular support for the

ovule was documented but not directly correlated with the pollination drop.

The research presented here supports the supposition that the pollination drop emerges once the xylem vascular trace completes its differentiation from the cone axis to the base of the ovule and integument. The pollination drop ceases as the scale continues its development and growth, thereby severing the mature xylem elements supporting the supply of fluid into the pollination drop.

Further experiments need to be conducted to further elucidate the pollination drop mechanism and to provide correlative data for the anatomical and structural data presented here. These might include using tracers that can be fixed in place inside the xylem tracheids and pollination drop to conclusively link the differentiation of the xylem with the emergence of the pollination drop. The difficulty is that unlike the wide open stem/cone xylem the tracheid trace is individual cells linked together, any tracer particle size must be small. Ideally an ultra-high resolution MRI and a detectable tracer would be perfect allow the imaging of the xylem and contents on a whole cone basis as there are no other traditional techniques available to follow the dynamics of the whole system *in vivo*.

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Appendix A

Weather Data from Kellogg Forest

The data presented in this section was collect as standard procedure by the staff at The W. K. Kellogg Forest in Augusta, Michigan over the years the forestry station has been in operation. Some of the incomplete years have been removed for simplicity, specifically 1941 through 1946 and the early data from 2000. The information was compiled and provided by Karen Bushouse. The years material was collected for this research have been shaded in following tables listed below. The degree data was only collected starting in 1992 but it provides an explanation for the difference in bud break dates between 1996 and 1997.

LIST OF TABLES

Table 1. Summary of Monthly Temperatures (part 1 of 4).

	JAN. Mean Max.	JAN Mean Min.	JAN High	JAN Low	FEB Mean Max.	FEB Mean Min.	FEB High	FEB Low	MAR Mean Max.	MAR Mean Min.	MAR High	MAR Low
1947	30.1	16.1	51.0	-16.0	26.1	9.5	47.0	-7.0	36.1	17.6	54.0	2.0
1948	25.2	5.0	42.0	-31.0	32.4	10.4	50.0	-16.0	42.5	21.7	67.0	-13.0
1949	33.7	18.8	53.0	-8.0	35.3	16.8	57.0	-7.0	43.9	21.4	74.0	-11.0
1950	37.5	20.8	67.0	-4.0	32.6	15.1	43.0	-21.0	37.4	20.2	56.0	-7.0
1951	31.1	16.6	50.0	-26.0	33.4	16.1	56.0	-20.0	42.3	24.7	68.0	7.0
1952	33.2	17.2	61.0	-5.0	37.1	17.5	51.0	2.0	41.3	20.5	68.0	2.0
1953	33.7	18.9	57.0	-5.0	36.5	18.7	51.0	-5.0	46.3	26.8	72.0	1.0
1954	29.0	16.0	46.0	-7.0	40.5	21.6	61.0	-5.0	41.1	19.5	70.0	-7.0
1955	30.3	14.3	44.0	-9.0	34.7	15.8	51.0	-15.0	45.3	20.8	64.0	3.0
1956	32.0	13.6	41.0	-8.0	35.2	13.5	45.0	-9.0	40.8	19.4	52.0	-2.0
1957	27.2	10.0	52.0	-10.0	37.7	18.4	57.0	0.0	47.0	21.3	71.0	-1.0
1958	31.6	14.4	43.0	-13.0	29.9	8.2	50.0	-25.0	43.3	33.7	57.0	15.0
1959	27.8	6.4	40.0	-14.0	32.9	11.1	45.0	-22.0	44.7	22.1	70.0	6.0
1960	32.9	20.7	55.0	-2.0	32.8	18.0	42.0	-8.0	35.5	9.4	66.0	-13.0
1961	29.4	10.5	52.0	-22.0	39.7	18.1	57.0	-10.0	48.0	28.0	72.0	11.0
1962	26.9	9.8	43.0	-12.0	30.1	13.7	53.0	-11.0	42.1	22.7	75.0	-9.0
1963	22.1	5.8	41.0	-17.0	28.0	4.9	46.0	-22.0	47.1	25.6	80.0	-4.0
1964	36.1	17.2	53.0	-17.0	35.7	13.2	49.0	-9.0	45.0	23.8	64.0	1.0
1965	30.0	15.4	59.0	-10.0	34.3	15.4	52.0	-4.0	36.2	19.6	52.0	-11.0
1966	28.2	8.5	49.0	-20.0	34.9	15.7	54.0	-11.0	48.4	26.6	72.0	5.0
1967	34.6	17.6	60.0	-15.0	30.8	7.4	49.0	-22.0	44.5	23.6	75.0	-17.0
1968	30.2	12.9	46.0	-13.0	32.2	11.5	53.0	-11.0	50.5	25.5	73.0	-3.0
1969	29.6	16.1	49.0	-7.0	35.3	17.8	45.0	-2.0	43.9	19.6	69.0	5.0
1970	26.4	7.5	47.0	-16.0	33.5	12.9	49.0	-12.0	40.8	19.6	53.0	1.0
1971	27.0	8.4	43.0	-12.0	33.6	13.6	52.0	-24.0	40.7	21.0	66.0	-4.0
1972	30.1	13.2	44.0	-22.0	32.0	14.5	48.0	-15.0	41.0	22.7	61.0	-2.0
1973	34.3	19.9	54.0	2.0	33.3	16.8	46.0	-17.0	51.9	33.9	69.0	17.0
1974	32.8	18.8	49.0	-4.0	31.7	12.8	52.0	-14.0	44.4	27.8	70.0	-1.0
1975	34.4	20.6	56.0	-8.0	32.1	19.0	47.0	-9.0	40.4	22.5	59.0	5.0
1976	27.7	11.1	38.0	-16.0	42.7	22.3	65.0	-10.0	50.7	29.6	73.0	14.0
1977	19.2	5.2	29.0	-9.0	31.8	14.2	53.0	-13.0	50.7	19.5	71.0	7.0
1978	25.7	11.3	38.0	-9.0	25.2	0.5	35.0	-18.0	37.4	19.0	71.0	-9.0
1979	23.0	9.9	34.0	-19.0	28.5	5.8	44.0	-18.0	46.9	28.2	69.0	7.0
1980	30.8	17.2	51.0	-4.0	28.8	13.5	44.0	-3.0	40.5	22.1	58.0	-7.0
1981	28.1	10.2	45.0	-23.0	35.8	19.9	49.0	-7.0	45.8	25.9	78.0	14.0
1982	23.9	7.4	41.0	-11.0	30.0	11.1	47.0	-8.0	39.9	23.6	57.0	-2.0
1983	33.3	21.7	44.0	-2.0	38.7	22.2	56.0	1.0	48.1	28.0	68.0	2.0
1984	26.4	10.7	40.0	-17.0	41.6	25.0	59.0	5.0	36.7	19.3	49.0	0.0
1985	26.4	11.6	34.0	-17.0	30.0	13.7	46.0	-13.0	46.2	27.1	60.0	10.0
1986	29.0	17.2	44.0	-5.0	27.4	16.6	38.0	4.0	44.7	26.0	74.0	-4.0
1987	28.5	17.2	42.0	-9.0	35.4	19.1	46.0	6.0	46.3	28.2	68.0	16.0
1988	33.1	21.8	46.0	5.0	29.8	13.7	46.0	2.0	42.3	24.8	65.0	9.0
1989	33.2	21.2	52.0	1.0	26.0	9.3	38.0	-10.0	39.8	21.4	74.0	3.0
1990	35.9	23.5	48.0	17.0	36.4	20.3	53.0	2.0	48.6	33.6	74.0	17.0
1991	31.3	21.1	42.0	3.0	38.9	25.3	52.0	8.0	48.1	30.8	70.0	18.0
1992	31.9	23.7	40.0	0.0	35.6	25.6	47.0	8.0	43.1	27.0	62.0	6.0
1993	33.1	22.4	53.0	2.0	30.6	16.7	43.0	-11.0	40.5	28.3	60.0	5.0
1994	19.7	3.8	41.0	-21.0	20.8	6.1	48.0	-16.0	36.9	21.7	61.0	9.0
1995	37.6	29.4	57.0	14.0	32.6	21.1	49.0	3.0	50.5	34.5	74.0	12.0
1996	30.0	13.8	58.0	-6.2	33.0	15.7	58.0	-21.0	39.3	17.6	61.3	-3.7
1997	29.0	13.0	60.0	-14.0	34.5	20.5	51.1	-0.1	47.6	29.2	66.9	8.4
1998	35.8	26.1	53.0	1.2	41.4	28.2	56.2	15.0	44.4	29.3	77.7	4.3
1999	29.6	15.8	52.4	-10.2	39.4	24.0	68.1	7.4	48.2	21.0	78.4	-6.0
10yr avg	31.6	19.4	50.6	-1.2	33.6	19.3	51.2	-1.3	44.3	26.8	69.0	6.6
avg	30.0	15.0	47.7	-9.4	33.4	15.6	50.0	-8.3	43.7	24.1	66.8	2.0

Table 1. Summary of Monthly Temperatures (part 2 of 4).

	APRIL Mean Max.	APRIL Mean Min.	APRIL High	APRIL Low	MAY Mean Max.	MAY Mean Min.	MAY High	MAY Low	JUNE Mean Max.	JUNE Mean Min.	JUNE High	JUNE Low
1947	53.8	34.9	77.0	19.0	62.0	40.6	81.0	18.0	74.5	49.0	88.0	32.0
1948	61.1	37.9	84.0	17.0	65.2	39.2	82.0	28.0	76.6	48.2	88.0	35.0
1949	59.2	27.7	77.0	14.0	72.0	40.6	88.0	23.0	82.2	54.1	90.0	29.0
1950	48.0	30.4	69.0	17.0	71.6	42.5	87.0	28.0	77.0	50.4	90.0	33.0
1951	53.9	33.0	81.0	16.0	72.4	42.3	85.0	27.0	76.5	50.2	88.0	34.0
1952	58.5	31.1	82.0	13.0	66.7	40.5	86.0	28.0	81.5	55.4	94.0	38.0
1953	54.7	31.0	75.0	15.0	73.9	46.1	90.0	32.0	82.0	52.5	97.0	35.0
1954	62.3	36.6	80.0	8.0	65.4	35.9	84.0	23.0	81.3	54.2	90.0	32.0
1955	68.3	36.0	78.0	23.0	74.3	42.5	86.0	23.0	77.8	47.8	88.0	34.0
1956	57.9	29.2	78.0	16.0	69.4	43.3	85.0	25.0	81.4	52.5	93.0	29.0
1957	57.6	34.3	79.0	12.0	69.1	43.0	85.0	25.0	79.1	53.9	92.0	34.0
1958	60.7	33.3	81.0	17.0	72.7	38.1	82.0	24.0	74.3	47.4	87.0	31.0
1959	58.9	32.8	75.0	19.0	75.8	48.1	88.0	28.0	82.4	53.3	91.0	34.0
1960	61.9	37.0	85.0	14.0	68.0	44.3	82.0	30.0	76.8	51.1	85.0	40.0
1961	53.3	31.7	72.0	15.0	67.7	39.1	82.0	26.0	79.2	49.2	92.0	36.0
1962	59.3	32.0	85.0	15.0	76.0	50.7	91.0	33.0	80.9	52.5	90.0	42.0
1963	62.3	33.7	81.0	18.0	69.0	41.0	86.0	24.0	83.0	50.0	94.0	34.0
1964	60.5	36.4	79.0	10.0	76.4	46.4	89.0	31.0	82.7	52.7	96.0	31.0
1965	57.5	32.1	75.0	3.0	77.0	46.6	86.0	32.0	79.0	49.7	91.0	39.0
1966	55.8	32.8	75.0	21.0	65.6	37.1	82.0	18.0	81.1	52.5	91.0	31.0
1967	60.6	36.0	74.0	17.0	66.1	40.6	83.0	26.0	80.7	56.1	89.0	40.0
1968	62.3	36.4	78.0	18.0	67.6	41.4	83.0	23.0	79.7	53.5	91.0	40.0
1969	62.6	36.2	77.0	21.0	71.6	43.3	86.0	28.0	73.6	52.0	92.0	36.0
1970	59.5	35.4	82.0	16.0	73.5	47.6	86.0	24.0	79.2	53.6	93.0	37.0
1971	59.7	31.2	81.0	13.0	69.9	40.1	85.0	27.0	83.8	57.6	95.0	39.0
1972	55.4	32.3	75.0	7.0	72.2	45.8	84.0	29.0	74.9	51.0	85.0	33.0
1973	56.9	38.1	76.0	17.0	64.7	44.3	76.0	27.0	79.4	57.8	88.0	46.0
1974	60.5	37.6	79.0	21.0	65.7	44.5	84.0	24.0	74.7	52.8	83.0	41.0
1975	51.1	31.3	72.0	13.0	73.8	50.1	88.0	37.0	76.9	57.0	88.0	42.0
1976	61.9	35.0	82.0	20.0	67.8	42.3	77.0	27.0	80.1	54.8	87.0	41.0
1977	65.6	38.8	84.0	18.0	79.6	49.0	94.0	29.0	75.8	51.0	85.0	35.0
1978	58.9	33.8	71.0	23.0	70.7	46.2	88.0	25.0	77.3	53.1	87.0	35.0
1979	55.1	34.4	73.0	15.0	69.4	44.8	86.0	27.0	77.6	54.3	85.0	38.0
1980	52.6	32.4	86.0	23.0	71.8	45.4	85.0	30.0	73.9	51.6	84.0	34.0
1981	62.4	39.3	78.0	23.0	68.6	43.1	79.0	28.0	77.6	56.1	88.0	44.0
1982	53.5	29.8	74.0	0.0	76.1	51.8	86.0	35.0	72.4	51.6	82.0	42.0
1983	54.5	33.8	77.0	18.0	66.3	42.6	80.0	30.0	80.6	53.4	94.0	38.0
1984	57.7	37.2	84.0	23.0	66.3	42.9	83.0	27.0	83.5	57.3	98.0	43.0
1985	64.2	41.1	86.0	23.0	74.1	48.1	86.0	34.0	75.7	56.5	90.0	42.0
1986	59.1	35.3	81.0	22.0	67.0	46.7	84.0	29.0	73.9	50.9	84.0	38.0
1987	59.0	36.0	82.0	17.0	73.0	51.0	91.0	31.0	78.9	57.3	96.0	41.0
1988	55.6	32.5	68.0	22.0	72.2	46.3	89.0	33.0	81.3	51.1	97.0	37.0
1989	53.3	34.0	72.0	15.0	65.7	42.7	80.0	25.0	74.7	54.9	91.0	41.0
1990	59.1	35.6	88.0	18.0	64.4	43.0	80.0	20.0	80.1	55.9	93.0	39.0
1991	61.6	42.7	82.0	25.0	77.0	55.3	92.0	36.0	84.3	62.7	94.0	46.0
1992	50.9	36.9	75.0	25.0	67.5	41.3	84.0	30.0	73.2	50.5	91.0	38.0
1993	53.1	36.5	69.0	25.0	67.9	47.4	84.0	37.0	70.3	53.9	85.0	38.0
1994	53.2	34.8	78.0	18.0	62.7	39.2	82.0	29.0	74.3	52.6	90.0	33.0
1995	57.9	41.5	75.0	22.0	71.8	47.3	84.0	34.0	84.4	58.3	98.0	44.0
1996	54.2	32.0	77.0	16.0	68.7	46.4	93.2	26.6	80.7	57.1	94.3	49.1
1997	55.4	31.6	76.4	16.9	61.8	39.2	79.7	29.8	81.0	55.8	93.6	43.1
1998	60.1	36.6	73.3	27.5	78.4	51.5	92.2	42.5	82.5	57.3	98.0	36.0
1999	63.8	38.6	80.3	28.2	78.9	50.6	91.0	37.0	86.9	58.6	100.0	42.6
10yr avg	56.6	36.4	76.9	21.5	69.5	45.8	85.6	31.5	79.3	56.1	93.4	40.9
avg	58.0	34.7	78.0	17.5	70.2	44.3	85.1	28.4	78.7	53.5	90.6	37.6

Table 1. Summary of Monthly Temperatures (part 3 of 4).

	JULY	JULY	JULY	JULY	AUG	AUG	AUG	AUG	SEPT	SEPT	SEPT	SEPT
	Mean Max.	*Mean Min.*	*High*	*Low*	*Mean Max.*	*Mean Min.*	*High*	*Low*	*Mean Max.*	*Mean Min.*	*High*	*Low*
1947	79.8	52.2	93.0	35.0	89.2	58.8	>99	40.0	74.3	49.0	88.0	25.0
1948	82.9	55.0	89.0	41.0	82.9	49.5	96.0	37.0	76.4	45.8	90.0	31.0
1949	85.7	59.5	96.0	43.0	82.8	53.4	94.0	37.0	67.5	41.2	82.0	27.0
1950	79.8	49.1	88.0	35.0	78.8	49.9	87.0	31.0	71.0	46.9	83.0	25.0
1951	80.8	52.8	88.0	38.0	77.9	51.4	90.0	35.0	70.5	44.3	85.0	24.0
1952	84.1	55.6	94.0	40.0	81.2	51.5	92.0	33.0	75.0	43.9	93.0	31.0
1953	86.4	54.3	95.0	37.0	84.9	52.2	97.0	38.0	77.4	42.5	99.0	28.0
1954	82.3	52.5	93.0	39.0	79.0	51.5	93.0	38.0	74.2	48.2	95.0	29.0
1955	88.5	58.7	97.0	46.0	86.3	57.1	97.0	44.0	77.1	44.1	91.0	29.0
1956	80.1	54.8	91.0	41.0	81.4	53.2	94.0	35.0	75.0	42.6	90.0	25.0
1957	84.1	54.9	92.0	44.0	82.3	54.8	90.0	44.0	72.7	45.9	89.0	28.0
1958	80.6	56.5	87.0	42.0	82.2	53.9	90.0	40.0	73.2	47.1	84.0	31.0
1959	84.2	55.0	91.0	42.0	86.2	61.8	93.0	44.0	78.6	51.3	93.0	28.0
1960	82.0	53.7	89.0	43.0	81.7	55.5	89.0	46.0	78.2	52.5	95.0	31.0
1961	83.6	55.5	90.0	43.0	80.8	56.2	89.0	41.0	77.9	54.6	89.0	29.0
1962	80.0	54.8	91.0	43.0	83.2	52.9	91.0	40.0	75.5	45.2	86.0	28.0
1963	84.8	53.2	95.0	37.0	79.0	52.0	87.0	38.0	75.0	44.9	85.0	32.0
1964	84.8	58.2	93.0	40.0	79.3	51.9	99.0	35.0	73.5	48.1	89.0	29.0
1965	81.6	52.5	93.0	40.0	78.5	54.7	95.0	36.0	73.5	51.9	86.0	28.0
1966	85.8	56.4	94.0	42.0	79.5	52.9	87.0	41.0	71.5	45.9	86.0	29.0
1967	79.4	54.5	87.0	43.0	78.3	51.5	87.0	39.0	73.3	44.4	82.0	33.0
1968	82.0	55.7	91.0	42.0	81.6	57.6	93.0	40.0	73.6	50.0	83.0	34.0
1969	81.8	58.4	90.0	46.0	82.5	54.8	88.0	42.0	73.0	49.9	85.0	33.0
1970	81.9	58.5	92.0	42.0	81.2	55.2	89.0	43.0	72.8	50.8	86.0	29.0
1971	78.3	56.3	85.0	45.0	78.8	53.5	88.0	41.0	73.1	55.3	87.0	36.0
1972	79.6	57.7	90.0	41.0	77.4	58.1	86.0	42.0	70.2	52.9	81.0	36.0
1973	81.3	59.4	91.0	49.0	80.2	59.4	91.0	45.0	73.2	52.2	88.0	36.0
1974	83.0	58.1	93.0	46.0	79.5	56.6	89.0	45.0	70.2	46.3	83.0	33.0
1975	80.3	57.3	90.0	45.0	79.1	59.5	90.0	46.0	65.7	47.2	77.0	33.0
1976	81.5	58.2	92.0	44.0	79.2	52.8	87.0	38.0	71.5	46.6	86.0	29.0
1977	83.8	59.9	92.0	45.0	76.9	57.1	87.0	40.0	70.0	54.6	84.0	41.0
1978	79.2	57.5	87.0	43.0	78.6	57.2	86.0	43.0	75.3	52.9	89.0	34.0
1979	73.8	55.3	85.0	44.0	75.1	56.9	88.0	40.0	73.6	49.0	81.0	34.0
1980	80.6	60.1	91.0	43.0	78.7	61.2	85.0	51.0	72.3	52.3	80.0	35.0
1981	80.3	59.5	88.0	47.0	79.4	57.0	84.0	41.0	68.8	49.9	82.0	31.0
1982	81.9	59.9	89.0	44.0	78.2	55.3	86.0	37.0	68.0	51.1	85.0	36.0
1983	86.1	61.6	96.0	40.0	83.9	60.1	92.0	49.0	73.1	50.0	89.0	31.0
1984	82.9	56.5	93.0	43.0	81.5	55.8	90.0	43.0	70.5	50.0	85.0	29.0
1985	80.3	58.0	92.0	43.0	75.0	54.2	84.0	46.0	70.0	52.9	88.0	37.0
1986	81.1	59.6	92.0	46.0	73.9	52.9	82.0	38.0	67.0	53.0	78.0	36.0
1987	83.1	60.7	93.0	47.0	76.5	58.0	89.0	59.0	67.9	49.8	79.0	36.0
1988	85.8	58.4	98.0	42.0	80.4	57.7	96.0	42.0	67.9	45.8	78.0	38.0
1989	80.5	59.0	91.0	48.0	76.9	54.4	87.0	42.0	65.6	42.5	79.0	29.0
1990	80.8	60.7	97.0	50.0	78.7	60.2	91.0	48.0	72.4	53.1	88.0	38.0
1991	82.8	64.1	93.0	51.0	78.4	60.0	89.0	53.0	68.2	50.9	84.0	32.0
1992	72.7	56.6	86.0	48.0	71.7	53.7	87.0	44.0	66.6	49.5	78.0	35.0
1993	78.6	62.1	90.0	51.0	75.8	60.2	86.0	45.0	56.5	43.9	74.0	30.0
1994	75.1	57.7	84.0	48.0	78.1	58.9	92.0	46.0	72.3	55.1	87.0	39.0
1995	87.3	62.9	100.0	45.0	87.3	66.7	95.0	54.0	69.5	47.0	85.0	35.0
1996	81.3	55.1	92.9	42.6	83.4	58.8	95.8	50.5	70.9	51.9	84.1	36.3
1997	83.1	58.7	95.7	45.3	75.9	56.2	86.1	43.1	70.4	49.7	81.0	37.0
1998	84.9	59.5	93.0	51.1	84.6	60.6	94.9	47.0	80.6	52.0	92.9	35.7
1999	92.6	64.1	103.8	49.8	86.7	57.5	99.2	47.1	88.1	49.3	105.3	35.6
10yr avg	81.8	60.0	93.3	48.2	79.8	58.8	91.2	47.2	71.0	49.5	85.3	34.8
avg	82.1	57.3	91.7	43.6	80.2	55.9	90.2	42.3	72.3	48.8	85.9	32.1

Table 1. Summary of Monthly Temperatures (part 4 of 4).

	OCT	OCT	OCT	OCT	NOV	NOV	NOV	NOV	DEC	DEC	DEC	DEC
	Mean Max.	*Mean Min.*	*High*	*Low*	*Mean Max.*	*Mean Min.*	*High*	*Low*	*Mean Max.*	*Mean Min.*	*High*	*Low*
1947	71.4	41.9	85.0	21.0	41.5	27.0	59.0	1.0	33.1	20.1	53.0	4.0
1948	59.3	31.2	77.0	20.0	50.8	33.2	65.0	20.0	37.0	19.3	58.0	-5.0
1949	66.4	39.6	84.0	20.0	44.6	27.0	68.0	-13.0	38.1	23.1	62.0	8.0
1950	65.1	39.0	83.0	22.0	40.0	24.8	81.0	-9.0	30.2	11.1	50.0	-15.0
1951	63.1	38.0	87.0	20.0	38.7	20.2	59.0	-1.0	33.5	14.7	61.0	-11.0
1952	57.8	27.8	82.0	10.0	48.6	27.4	70.0	5.0	36.5	24.0	55.0	5.0
1953	70.2	33.4	89.0	22.0	52.3	28.9	71.0	11.0	37.3	21.8	58.0	2.0
1954	60.7	40.4	80.0	24.0	47.3	28.8	67.0	18.0	34.1	20.7	47.0	-5.0
1955	65.2	37.0	78.0	23.0	43.8	25.7	65.0	4.0	31.8	15.7	48.0	-2.0
1956	70.6	37.7	83.0	18.0	47.8	28.2	68.0	-8.0	38.3	25.0	58.0	-2.0
1957	60.2	33.8	75.0	20.0	47.6	29.2	61.0	12.0	40.6	23.0	57.0	2.0
1958	65.6	37.2	79.0	22.0	50.3	29.5	68.0	-2.0	29.0	10.4	48.0	-13.0
1959	59.6	41.0	79.0	23.0	41.7	26.5	62.0	6.0	39.2	24.5	54.0	5.0
1960	62.7	37.1	79.0	16.0	49.9	30.7	64.0	16.0	31.4	13.8	51.0	-10.0
1961	63.4	40.2	81.0	27.0	48.3	30.1	65.0	17.0	33.8	19.5	58.0	-5.0
1962	63.6	41.8	83.0	21.0	47.4	28.1	60.0	17.0	32.3	13.0	59.0	-21.0
1963	72.9	39.6	88.0	20.0	52.0	33.5	64.0	18.0	28.6	9.3	54.0	-18.0
1964	60.5	32.9	77.0	20.0	52.5	31.1	72.0	5.0	33.8	18.7	50.0	-13.0
1965	60.8	38.4	80.0	17.0	49.6	30.2	72.0	14.0	40.7	27.0	60.0	0.0
1966	60.6	35.7	75.0	16.0	47.9	32.2	61.0	17.0	34.6	19.1	62.0	-4.0
1967	60.2	39.3	83.0	15.0	41.3	28.6	57.0	10.0	37.2	23.0	59.0	1.0
1968	62.6	40.8	82.0	25.0	46.7	30.6	74.0	19.0	33.5	18.1	53.0	2.0
1969	59.9	38.8	80.0	19.0	44.6	28.6	55.0	6.0	32.8	17.9	45.0	-10.0
1970	63.3	42.2	76.0	27.0	44.6	31.1	62.0	9.0	36.1	20.4	65.0	-9.0
1971	67.4	47.5	83.0	33.0	46.9	30.6	66.0	10.0	40.3	25.5	62.0	8.0
1972	55.3	37.3	71.0	19.0	40.9	32.1	62.0	10.0	32.0	21.6	48.0	-6.0
1973	64.3	45.1	77.0	30.0	48.4	33.7	62.0	21.0	33.0	20.1	57.0	-5.0
1974	60.3	37.6	73.0	18.0	46.6	32.8	71.0	12.0	34.5	24.8	42.0	9.0
1975	64.5	40.5	83.0	24.0	52.8	35.8	73.0	12.0	35.3	21.5	61.0	-2.0
1976	55.1	35.6	76.0	17.0	39.6	23.9	54.0	9.0	28.5	8.7	47.0	-19.0
1977	58.9	38.7	69.0	24.0	47.1	34.0	70.0	9.0	31.4	19.3	50.0	-5.0
1978	58.6	39.0	74.0	14.0	48.8	30.7	72.0	15.0	33.5	21.0	40.0	-3.0
1979	58.1	42.2	78.0	29.0	46.3	31.5	70.0	20.0	38.9	24.5	56.0	5.0
1980	55.9	36.7	75.0	22.0	46.4	28.8	68.0	20.0	33.5	18.2	56.0	-5.0
1981	56.5	37.2	67.0	26.0	48.9	30.1	68.0	18.0	33.3	21.5	50.0	1.0
1982	63.1	40.5	83.0	22.0	48.8	34.3	63.0	21.0	42.9	30.6	64.0	8.0
1983	60.4	42.0	76.0	25.0	48.9	32.9	61.0	20.0	25.2	13.4	41.0	-11.0
1984	59.2	43.2	72.0	29.0	48.0	30.1	62.0	14.0	40.5	23.6	61.0	9.0
1985	57.0	42.0	69.0	31.0	41.9	33.1	62.0	24.0	26.5	16.0	35.0	0.0
1986	56.0	40.0	66.0	30.0	38.2	25.5	61.0	10.0	31.9	23.6	38.0	4.0
1987	50.8	32.6	65.0	26.0	46.0	32.0	67.0	16.0	33.9	24.7	50.0	2.0
1988	47.3	30.6	68.0	15.0	44.0	31.9	59.0	26.0	32.7	19.5	51.0	0.0
1989	56.6	35.3	76.0	24.0	40.1	26.3	64.0	14.0	24.1	9.5	37.0	-18.0
1990	58.0	39.8	79.0	26.0	50.5	34.3	68.0	24.0	35.5	23.4	53.0	5.0
1991	59.8	45.6	72.0	30.0	43.0	29.7	63.0	14.0	35.3	24.1	56.0	7.0
1992	55.1	39.6	71.0	31.0	42.5	35.2	56.0	26.0	35.9	28.0	53.0	16.0
1993	51.4	35.1	68.0	24.0	43.4	29.2	61.0	17.0	30.5	20.4	50.0	0.0
1994	64.1	48.2	79.0	38.0	54.0	40.8	67.0	28.0	44.2	35.1	57.0	19.0
1995	62.5	42.1	84.0	29.0	38.5	26.0	62.0	15.0	31.0	17.9	52.0	-1.0
1996	58.8	40.3	73.3	26.8	42.1	28.2	67.0	15.0	33.8	24.3	47.0	4.3
1997	62.2	41.2	88.0	27.0	42.0	30.0	59.0	17.7	35.2	25.6	43.2	12.3
1998	61.8	42.8	81.0	30.5	47.7	33.2	63.7	25.1	41.5	25.4	64.4	4.4
1999	63.0	38.7	79.6	28.2	52.2	32.8	72.0	22.0	37.2	23.0	56.9	-3.8
10yr avg	59.4	40.8	77.4	28.6	45.1	31.4	63.9	19.8	34.9	23.3	51.8	4.1
avg	60.9	38.9	77.8	23.3	46.1	30.2	65.0	13.1	34.4	20.5	52.9	-1.5

Table 2. Degree Day Data for the years 1992-1999.

	Jan	Feb	March	April	May	June	July	August	Sept	Oct	Nov	Dec	Yearly Totals
1992	0.00	0.00	4.00	50.10	214.50	370.00	450.50	395.00	266.00	50.00	4.00	0.00	1804.10
1993	0.00	0.00	0.00	37.50	244.00	366.00	632.00	559.50	106.00	20.50	3.00	0.00	1968.50
1994	0.00	0.00	0.00	55.00	121.00	407.00	510.50	575.00	413.00	204.50	64.50	7.00	2357.50
1995	0.00	0.00	40.00	78.50	298.00	641.50	778.50	837.50	268.50	137.50	2.00	0.00	3082.00
1996	0.00	0.00	0.00	52.65	263.10	566.85	564.40	653.55	342.80	92.85	7.00	0.00	2543.20
1997	0.00	0.00	0.65	30.10	84.70	551.65	647.95	496.40	301.40	175.30	8.50	0.00	2296.65
1998	0.45	0.00	74.95	51.45	462.50	597.50	689.05	699.55	488.90	111.25	10.05	25.70	3211.35
1999	0.00	2.55	10.75	97.10	456.75	682.90	879.05	685.08	561.10	100.25	23.05	1.80	3500.38

Table 3. Rain precipitation by month for the years 1947-1999.

	JAN.	FEB.	MAR.	APRIL	MAY	JUNE	JULY	AUG.	SEPT.	OCT.	NOV.	DEC.	TOTAL	Avg/ Mth/Y
1947	2.68	0.84	2.04	7.44	5.18	5.62	1.81	3.27	4.73	1.13	2.52	1.68	38.94	3.25
1948	1.20	2.40	4.66	3.51	5.59	3.37	1.94	1.69	2.99	1.05	2.83	3.20	34.43	2.87
1949	3.51	2.73	3.41	2.24	2.43	3.48	2.72	3.59	3.70	3.21	1.68	4.57	37.27	3.11
1950	4.08	3.49	2.47	7.41	1.32	5.00	4.80	2.71	7.92	0.56	3.01	2.25	45.02	3.75
1951	2.67	1.76	2.34	3.38	3.28	4.17	3.71	3.61	3.72	4.63	2.71	3.50	39.48	3.29
1952	2.18	1.10	2.40	3.09	4.99	2.58	4.21	3.54	2.06	0.78	3.18	2.11	32.22	2.69
1953	1.93	1.53	2.49	3.23	3.58	2.56	2.78	2.42	1.36	1.56	1.49	1.42	26.35	2.20
1954	1.95	4.10	3.51	2.81	1.37	7.27	2.52	3.72	2.63	8.06	2.70	2.18	42.82	3.57
1955	1.54	2.02	2.17	2.59	1.75	4.49	4.57	3.15	1.45	5.52	3.65	0.50	33.40	2.78
1956	0.59	2.68	2.45	5.84	3.62	2.35	2.79	1.81	0.56	0.35	1.52	1.14	25.70	2.14
1957	2.25	1.42	2.09	5.52	3.79	2.49	3.82	3.44	1.39	4.47	3.64	2.65	36.97	3.08
1958	1.37	0.94	0.84	1.83	1.55	5.71	3.92	3.52	2.42	1.80	2.37	0.74	27.01	2.25
1959	2.75	2.13	2.22	3.78	2.67	1.53	5.92	3.13	3.63	5.36	3.20	2.40	38.72	3.23
1960	4.26	3.35	1.27	2.68	5.14	4.54	3.46	1.73	2.56	1.65	2.03	0.60	33.27	2.77
1961	0.52	1.50	2.97	4.41	1.62	2.60	1.96	4.32	6.68	2.54	1.95	1.81	32.88	2.74
1962	2.94	1.73	1.58	1.75	3.47	4.22	3.51	1.48	3.98	2.53	0.88	2.36	30.43	2.54
1963	1.03	0.51	2.96	2.32	3.97	1.47	3.90	1.59	1.07	0.94	1.52	1.19	22.47	1.87
1964	1.05	0.79	2.87	4.34	2.34	2.49	4.13	5.39	4.36	1.02	2.75	1.94	33.47	2.79
1965	3.58	2.56	3.47	2.11	2.73	3.23	1.45	4.61	4.83	2.12	2.71	4.58	37.98	3.17
1966	0.87	1.28	3.32	4.07	3.52	2.42	2.08	4.50	1.52	1.01	5.61	3.70	33.90	2.83
1967	3.02	1.83	1.35	5.12	1.98	5.89	2.33	1.78	2.49	4.42	2.91	4.39	37.51	3.13
1968	1.58	2.12	1.31	4.31	2.82	6.66	3.89	2.76	3.08	3.25	3.91	3.68	39.37	3.28
1969	2.70	0.26	1.86	4.29	3.66	5.87	4.82	1.04	1.97	4.63	3.23	0.71	35.04	2.92
1970	1.03	0.77	3.06	4.14	3.96	2.42	8.91	1.88	3.47	4.88	3.63	2.09	40.24	3.35
1971	1.11	2.89	2.26	0.91	1.96	2.12	6.46	1.33	5.86	3.51	2.00	4.03	34.44	2.87
1972	1.73	0.90	3.50	3.07	2.95	2.90	3.77	4.21	4.92	3.01	3.15	4.59	38.70	3.23
1973	1.52	1.43	2.93	3.79	6.68	3.43	4.06	1.28	4.94	2.41	3.29	3.58	39.34	3.28
1974	3.27	2.49	4.07	4.12	5.11	3.90	1.19	1.75	3.59	1.52	3.08	2.29	36.38	3.03
1975	3.49	2.27	2.17	6.63	5.59	4.08	1.54	11.33	1.74	1.05	3.11	4.16	47.16	3.93
1976	1.54	2.33	3.55	3.88	3.45	3.22	3.62	0.55	2.19	2.63	1.85	1.26	30.07	2.51
1977	1.25	0.99	3.14	3.28	1.41	4.08	2.26	5.61	4.95	1.72	2.01	2.78	33.48	2.79
1978	2.88	0.39	1.43	2.31	2.36	11.03	2.35	2.15	5.85	2.99	2.07	3.34	39.15	3.26
1979	2.87	0.78	2.75	5.11	3.25	7.19	2.52	4.98	0.00	2.84	4.62	2.76	39.67	3.31
1980	1.04	1.34	2.49	3.70	2.56	5.25	4.96	5.54	4.92	2.11	1.32	4.09	39.32	3.28
1981	0.53	2.14	0.85	5.45	3.62	3.65	1.72	3.85	5.29	2.80	1.54	1.62	33.06	2.76
1982	3.08	1.04	3.45	1.66	5.05	3.39	5.47	2.12	1.49	1.08	4.09	4.56	36.48	3.04
1983	0.90	1.04	3.40	4.59	6.19	1.90	3.41	5.63	5.31	2.22	3.80	3.42	41.81	3.48
1984	0.94	1.19	2.91	2.44	4.16	0.78	4.08	1.75	7.06	3.66	3.39	4.15	36.51	3.04
1985	3.09	4.06	3.13	3.07	3.18	1.57	6.40	4.49	2.54	5.14	6.13	1.89	44.69	3.72
1986	2.04	3.25	1.65	5.20	3.96	6.43	7.40	3.82	9.92	3.67	1.59	1.40	50.33	4.19
1987	1.62	0.07	1.32	2.13	2.00	2.75	4.02	7.66	4.21	2.41	2.30	4.44	34.93	2.91
1988	2.00	2.28	1.51	3.82	0.98	1.60	2.89	4.61	7.63	4.23	4.18	2.32	38.05	3.17
1989	1.41	3.29	2.16	2.00	5.91	4.76	2.05	3.31	3.51	0.86	3.21	1.13	33.60	2.80
1990	2.35	3.56	1.96	2.36	6.21	5.24	2.63	2.60	3.70	6.53	6.56	2.88	46.58	3.88
1991	1.71	3.28	4.99	5.95	3.41	1.93	3.94	3.31	2.30	8.92	4.32	3.24	47.30	3.94
1992	1.67	1.24	2.05	3.09	1.42	1.26	5.37	3.47	5.00	2.88	4.82	2.21	34.48	2.87
1993	3.40	1.81	2.64	4.70	1.82	5.91	3.17	3.08	6.01	3.55	1.53	1.94	39.56	3.30
1994	2.10	1.75	1.78	3.95	1.25	5.88	4.36	6.19	1.20	1.82	4.52	1.40	36.20	3.02
1995	2.22	1.00	1.34	3.75	4.08	3.31	2.85	5.03	2.13	3.75	4.73	1.11	35.30	2.94
1996	1.12	0.98	0.62	2.35	2.99	5.68	1.49	1.33	2.77	3.58	2.13	3.31	28.35	2.36
1997	3.32	2.68	2.52	1.34	3.88	3.50	0.85	3.41	4.82	1.23	0.98	1.58	30.11	2.51
1998	3.71	1.39	2.98	4.29	1.83	3.12	3.95	1.56	1.36	2.34	1.37	1.16	29.06	2.42
1999	4.62	0.54	1.60	6.06	1.38	4.43	2.89	1.67	1.91	0.96	1.30	3.22	30.58	2.55
10 yr avg	2.51	1.96	2.24	3.62	3.11	4.09	3.05	3.18	3.16	3.31	3.22	2.11	35.56	
avg	2.07	1.75	2.37	3.59	3.12	3.63	3.29	3.13	3.42	2.73	2.81	2.46	33.68	

Table 4. Snowfall Amounts for the winter months October through May 1946-47 to 1998-99.

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	April	May	Total/Snow
1946-47	0.00	0.00	9.75	11.50	20.00	12.25	1.50	0.00	55.00
1947-48	0.00	9.50	8.25	13.75	5.25	7.75	0.00	0.00	44.50
1948-49	0.00	0.00	5.00	3.25	5.25	4.00	0.50	0.00	18.00
1949-50	0.00	12.50	5.00	4.00	17.00	10.00	5.00	0.00	53.50
1950-51	0.00	17.00	12.00	14.00	7.00	7.00	2.00	0.00	59.00
1951-52	0.00	17.50	38.00	8.00	4.00	5.00	5.00	0.00	77.50
1952-53	0.00	2.00	5.00	7.00	5.50	1.25	0.00	0.00	20.75
1953-54	0.00	8.75	7.50	17.25	15.50	20.00	0.50	1.00	70.50
1954-55	3.00	11.00	10.00	10.50	11.50	19.00	0.00	0.00	65.00
1955-56	0.00	20.25	7.75	7.00	16.00	21.50	5.00	0.00	77.50
1956-57	0.00	12.00	5.00	30.75	7.00	6.00	5.00	0.00	65.75
1957-58	0.50	12.25	13.25	23.50	18.00	12.50	0.00	0.00	80.00
1958-59	0.00	11.00	13.25	25.00	7.00	13.25	0.00	0.00	69.50
1959-60	0.00	13.50	10.63	17.25	28.25	17.00	1.75	0.25	88.63
1960-61	0.00	8.00	11.00	15.50	14.25	2.25	13.75	0.00	64.75
1961-62	0.00	2.50	18.25	18.75	19.75	7.50	5.00	0.00	71.75
1962-63	3.00	0.00	41.50	23.00	16.50	15.00	1.00	0.00	100.00
1963-64	0.00	0.00	16.00	7.50	11.50	12.00	1.00	0.00	48.00
1964-65	0.00	10.50	26.00	14.75	33.25	27.25	7.00	0.00	118.75
1965-66	0.00	7.50	8.75	14.75	7.25	11.50	0.00	0.00	49.75
1966-67	0.00	17.25	21.50	35.25	29.50	9.50	5.00	0.00	118.00
1967-68	4.00	10.00	10.00	15.00	7.75	15.50	0.00	0.00	62.25
1968-69	0.00	9.50	32.50	27.00	4.75	7.75	0.50	0.00	82.00
1969-70	0.00	14.00	9.75	15.50	11.50	20.50	9.25	0.00	80.50
1970-71	0.00	14.50	19.50	16.25	8.25	19.50	1.50	0.00	79.50
1971-72	0.00	14.00	3.50	15.00	12.50	9.25	0.00	0.00	54.25
1972-73	0.25	13.75	20.50	6.75	14.75	10.50	4.25	0.00	70.75
1973-74	0.00	2.00	19.75	14.50	12.25	6.25	0.00	0.25	55.00
1974-75	0.00	6.50	17.50	9.75	18.50	7.75	9.00	0.00	69.00
1975-76	0.00	7.50	15.25	26.75	4.00	2.75	2.50	0.00	58.75
1976-77	1.75	8.00	23.50	23.00	4.00	7.50	3.25	0.00	71.00
1977-78	0.00	10.00	22.50	47.50	5.75	2.50	0.00	0.00	88.25
1978-79	0.00	8.00	20.25	34.50	4.75	3.25	6.50	0.00	77.25
1979-80	0.00	8.25	5.50	12.75	9.50	10.00	4.50	0.00	50.50
1980-81	0.50	8.00	10.50	12.50	19.75	0.75	0.00	0.00	52.00
1981-82	0.75	2.00	8.75	29.00	15.50	11.00	0.00	0.00	67.00
1982-83	0.00	1.50	3.25	2.25	5.25	8.75	2.00	0.00	23.00
1983-84	0.00	4.00	32.25	12.75	0.75	9.25	0.00	0.00	59.00
1984-85	0.00	0.50	12.00	30.50	24.25	0.50	2.00	0.00	69.75
1985-86	0.00	2.00	27.25	10.50	16.75	0.00	0.00	0.00	56.50
1986-87	0.00	5.00	5.25	14.00	0.00	4.00	0.00	0.00	28.25
1987-88	0.00	0.00	10.20	6.50	16.50	2.00	0.00	0.00	35.20
1988-89	0.00	2.00	6.25	7.25	20.26	1.00	1.00	0.00	37.76
1989-90	3.25	6.25	10.50	2.00	21.00	1.00	0.00	0.00	44.00
1990-91	0.00	0.00	10.25	16.00	6.00	0.00	0.00	0.00	32.25
1991-92	0.00	6.00	14.75	18.00	1.00	14.25	0.00	0.00	54.00
1992-93	0.00	12.00	11.00	18.00	13.00	8.00	0.00	0.00	62.00
1993-94	0.00	1.00	8.50	12.25	19.00	0.50	0.00	0.00	41.25
1994-95	0.00	0.00	12.50	15.75	3.50	0.00	0.00	0.00	31.75
1995-96	0.00	11.50	6.25	6.00	3.50	10.00	0.00	0.00	37.25
1996-97	0.00	4.00	13.25	38.75	5.75	1.00	0.00	0.00	62.75
1997-98	2.00	0.00	8.75	11.25	0.00	10.00	0.00	0.00	32.00
1998-99	0.00	0.00	1.50	31.85	3.00	10.50	0.00	0.00	46.85
10 yr avg	0.48	3.89	9.41	16.10	8.73	5.11	0.09	0.00	43.81
Average	0.36	7.26	13.70	16.63	11.55	8.62	1.99	0.03	59.03

Table 5. Yearly Means and Totals for the years 1946-1999.

	Mean Max.Temp	Mean Min.Temp.	Mean Temp.	Total Precip.	Total Snow
1946	66.90	41.42	54.16	16.33	0.00
1947	55.99	34.72	45.36	38.94	55.00
1948	57.68	33.03	45.35	34.43	44.50
1949	59.29	35.27	47.28	37.27	18.00
1950	55.74	33.33	44.54	45.02	53.50
1951	56.16	33.69	44.93	39.48	59.00
1952	58.45	34.37	46.41	32.22	77.50
1953	61.30	35.59	48.44	26.35	20.75
1954	58.09	35.49	46.79	42.82	70.50
1955	60.28	34.62	47.45	33.40	65.00
1956	59.16	34.41	46.79	25.70	77.50
1957	58.76	35.21	46.99	36.97	65.75
1958	57.78	34.13	45.95	27.01	80.00
1959	59.34	36.14	47.74	38.72	69.50
1960	57.82	35.32	46.57	33.27	88.63
1961	58.75	36.06	47.41	32.88	64.75
1962	58.12	34.77	46.44	30.43	71.75
1963	58.65	32.79	45.72	22.47	100.00
1964	60.08	35.88	47.98	33.47	48.00
1965	58.22	36.13	47.18	37.98	118.75
1966	57.83	34.61	46.22	33.90	49.75
1967	57.25	35.21	46.23	37.51	118.00
1968	58.54	36.16	47.35	39.37	62.25
1969	57.60	36.12	46.86	35.04	82.00
1970	57.73	36.23	46.98	40.24	80.50
1971	58.29	36.72	47.51	34.44	79.50
1972	55.09	36.60	45.84	38.70	54.25
1973	58.41	40.05	49.23	39.34	70.75
1974	56.98	37.54	47.26	36.38	55.00
1975	57.18	38.52	47.85	47.16	69.00
1976	57.18	35.08	46.13	30.07	58.75
1977	57.55	36.77	47.16	33.48	71.00
1978	55.78	35.18	45.48	39.15	88.25
1979	55.53	36.40	45.96	39.67	77.25
1980	55.47	36.62	46.05	39.32	50.50
1981	57.12	37.47	47.30	33.06	52.00
1982	56.57	37.24	46.90	36.48	67.00
1983	58.25	38.47	48.36	41.81	23.00
1984	57.89	37.63	47.76	36.51	59.00
1985	55.61	37.85	46.73	44.69	69.75
1986	54.09	37.28	45.69	50.33	56.50
1987	56.61	38.89	47.75	34.93	28.25
1988	56.03	36.17	46.10	38.05	35.20
1989	53.06	34.20	43.63	33.60	37.76
1990	58.35	40.27	49.31	46.58	44.00
1991	59.06	42.68	50.87	47.30	32.25
1992	53.89	38.97	46.43	34.48	54.00
1993	52.64	38.01	45.33	39.56	62.00
1994	54.62	37.84	46.23	36.20	41.25
1995	59.24	41.23	50.23	35.30	31.75
1996	56.35	36.76	46.56	28.35	37.25
1997	56.49	37.56	47.02	30.11	62.75
1998	61.96	41.88	51.92	29.06	32.00
1999	63.88	39.49	51.68	30.58	46.85
10yr Avg	57.23	38.99	48.11	35.56	43.81
Average	57.68	36.67	47.17	35.85	59.03

Appendix B

Attached CD-R Digital Media

There is an attached CD-R containing the digital movie complements to Figures 5, 6, 7, 8, and 9 in some copies of this thesis. Those who do not have a copy of the digital media and wish to view the digital movies may contact the author to obtain versions of the data.

Specifications:
Recorded with a Smart and Friendly™ CD-R 4012 using the program "Easy CD Creator" on a Windows NT 4.0 workstation administered by Dr. Stanley L. Flegler at the Center for Advanced Microscopy, Michigan State University.

Movies recorded on the CD as .AVI using the current Video for Windows format in Adobe After Effects version 4.0.

Additional copies of the digital movies are included in various formats.