Frost Hardiness of Cranberry Plant:

A guide to manage the crop during critical periods in spring and fall

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Introduction

The cranberry plant is a perennial evergreen woody vine native to wetland areas of northern North America. Cranberries (*Vaccinium macrocarpon* Ait.) are one of the highest value crops grown in Wisconsin.Wisconsin is the top cranberry-producing state in the US in both total weight and yield per acre.

Cranberries are produced commercially in large low-lying beds of peat and sand, surrounded by earthen dikes for water management. Due to their low elevations, **there is no month free from the threat of frost in the cranberry-growing areas of Wisconsin, thus, frost protection is a major concern for growers in Wisconsin.** Regardless of this fact, there is relatively little published work on this topic in the scientific literature.

Sprinkle irrigation is the main frost protection method used by Wisconsin growers from early spring to harvest, although flooding may be utilized in early spring and late fall. **During the coldest periods of Wisconsin winters, cranberry plants are protected from both low temperature and desiccation by a layer of ice** that is formed after a flooding event, typically performed in mid to late December. Irrigation pipes are removed for harvest, and thus the only form of frost protection after harvest until the putting on of the winter flood and in the early spring after drainage of the winter flood is to **temporarily flood the beds**.

Early spring is one of the most vulnerable times of the year. After the winter flood ice has melted, failure to initiate frost protection measures can result in crop damage ranging from slowed growth to complete crop loss. In contrast, overprotection can lead to deacclimation of the plants, as well as increased labor and fuel costs.

The objective of this publication is to help the cranberry growers in the management of frost protection of their crop at critical periods in spring and fall. Some basic information on frost hardiness is included to make the experimental data more meaningful.

Basic Concepts In Frost Hardiness

Mechanisms of freezing stress survival

Freezing stress resistance is the ability of a plant to survive subfreezing temperatures. **Freezing tolerance** and **freezing avoidance are the main mechanisms** by which plants mitigate the stress of freezing temperatures (Levitt, 1980). During frost episodes air temperature generally drops at a rate of 1-3 °F per hour (Steffen et al., 1989). At these rates **ice is generally initiated (nucleation) in the water outside of the plant cell (in the extracellular spaces)**. Ice nucleation occurs in or on plant tissues due to the presence of a nucleating agent, such as dust, bacteria, fungi, or wind/agitation that are present in the water outside the plant cell or plant tissue.

Water inside the cell does not freeze for two reasons: 1) The water inside the cell (the cell sap) contains sugars, salts, and other solutes that depress the freezing point of water. The freezing point of water for a typical plant leaf cell is about 30 °F. 2) Water inside a plant cell lacks the nucleating agents described above.

Once initiated, ice spreads via the xylem vessels. Ice can also form on the surface of plants, such as from dew. The ice is "drier" than the surrounding liquid water at the same temperature (a lower vapor pressure). As the temperature drops, this **ice pulls water out of the cell**, resulting in both the further growth of the ice in between the cells and an increase in the solute concentration inside the cell (Levitt, 1980; Palta, 1990)). In this way, **freezing stress is actually like drought** or dehydration.

The ability to tolerate and (thereby survive) these various stresses caused by the presence of ice outside the cell is referred to as **"freezing tolerance."** Woody plant tissues, such as bark, **bud scales, and leaves, cannot avoid ice nucleation, and so survive freezing stress by tolerating the presence of extracellular ice in their tissues**.

By extension then, **"freezing avoidance"** is a plant tissue's ability to resist freezing stress by not allowing ice to form. In these tissues, **water remains liquid at temperatures lower than 32 °F, or "supercools"**. Supercooling can occur, at least temporarily, in almost all tissues, yet extracellular ice nucleation typically occurs by 28-30 °F in nature (George et al., 1974). The tissues that survive by supercooling are able to prevent ice nucleation for long periods at freezing temperatures. If this metastable condition is terminated by the nucleation of very rapid ice, damage is typically lethal because of ice formation inside the cell (Levitt, 1980; Palta and Weiss, 1993). **Ice formation inside the cell results in faster and more severe injury due to the rupture of organelles and cell membranes**.

Mechanisms of freezing stress injury and recovery

Common **symptoms** of freezing stress injury in plant tissues are a **water-soaked appearance (darkening of the tissue) and the inability to regain turgidity** once the stress has been removed (Levitt, 1980; Palta, 1990; Palta and Weiss, 1993). These symptoms indicate that **cell membranes have been injured and sugars and salts start to leak from the cell and tissue**. This can result in the growth of fungus and bacteria, thus resulting in tissue rot as a secondary form of injury to freeze damage. If cell membranes can heal from the injury, plants can recover from freezing injury (Palta et al., 1977).

Patterns of ice nucleation and propagation

Infrared (IR) video thermography has recently been used to visualize ice nucleation and propagation in plants (Wisniewski et al., 1997; Workmaster et al., 1999). With this method, **freezing events are imaged as water freezes and the heat is released**, thus warming the plant tissue. **This rise in temperature in the tissue by the formation of ice from water can be seen by an infrared camera.** By observing the occurrence of freezing events as well as the extent of subsequent ice propagation, low temperature survival mechanisms (tolerance or avoidance of ice formation) of various plant parts can be determined.

Avenues to ice propagation require open areas and pores large enough for ice crystals to grow. Wounds, cracks in the cuticle and epicuticular waxes, lenticels, and open stomata have all been suggested as possible entry points for ice from outside the plant, while extracellular spaces and xylem vessels are thought to function as pathways of internal ice propagation.

Seasonal changes in cold hardiness of plant parts

Cold acclimation (**hardening**) and deacclimation (**dehardening**) of temperate zone woody plants are induced in response to changes in day length, air temperature, and soil water status (Levitt, 1980). In fall the plant hardens, which in turn results in an increase in frost hardiness either by tolerance or avoidance mechanisms. The opposite occurs in the spring. The timing of cold acclimation and deacclimation, and the extent of seasonal changes in freezing stress resistance vary by genetic makeup and geographic origin (Levitt, 1980; Sakai and Larcher, 1987).

In spring, the frost hardiness of developing buds of fruit species decreases with progression of development. Dehardening and growth capability of buds in spring corresponds with changes in hormone levels in the tissue: a decrease in abscisic acid and an increase in gibberellins, followed by later increases in auxin and cytokinin (Levitt, 1980).

Leaves are known to survive freezing stress by the mechanism of tolerance (Levitt, 1980; Palta and Weiss, 1993). This is especially important in evergreen, non-deciduous, species where leaves remain in the plant as an over-wintering structure. Desiccation injury, direct freezing injury to roots, and direct freezing injury to leaves have all been identified as factors that contribute to winter injury in these species. Desiccation and freezing of roots is limited in cranberry, due to the protection provided by the winter ice. **Overwintering dormant buds are known to survive frost by avoidance mechanisms. Intact fruits of some species are also known to have some frost avoidance ability.**

Use of Growth Degree Days (GDD) to Predict Spring Growth and Development of Woody Plants

Air temperature is widely viewed as the single most important factor driving spring growth and development. Thermal time models (also called growing degree days, GDD) have been developed to chart the progression of the growth and development of various plants (Anderson and Seeley, 1992), animals, and insects. In studies of orchard and forest trees, models have been developed to predict the timing of bud break in reference to the threat of spring frost damage and the potential impact of global warming (Cannell and Smith, 1986).

Other ecophysiological factors have been cited as contributing to these phenological changes, such as the degree of completion of rest and chilling temperatures, photoperiod, relative rates of growth in response to different temperatures, and soil temperature. Photothermal models restrict the influence of air temperatures until after the attainment of a critical photoperiod, or daylength. In cranberry, a photoperiod of 13 hours was found to be necessary for normal bud break and flower development (Lenhardt et al., 1976).

Thermal time models (GDD) require the determination of threshold temperatures for growth of the particular species or cultivar. The base temperature, the minimum temperature for plant growth and development, is the most common threshold included in models of bud break and flowering. Theoretically, the base temperature is thought to correspond to the temperature below which physiological processes resulting in crop growth and development will cease. Some attempts have been made to use thermal time to predict developmental events in cranberry (DeMoranville et al., 1996; Hawker and Stang, 1985; Wisconsin-Minnesota Cooperative Extension Agricultural Weather Page, 2001). These studies used arbitrary base temperatures, ranging from 6.5 to 9 °C (44 to 48 °F), in their thermal time calculations. We used a base temperature of 5 °C (41 °F) based on our studies that showed that temperatures below this did not contribute to growth of the plant.

Changes in frost hardiness of cranberry plant parts during spring growth and development

Changes in the frost hardiness of the cranberry plant are most pronounced in springtime as warmer temperatures and longer days stimulate growth and the emergence from dormancy (Workmaster and Palta, 2006). With the receding of the winter ice cover, cranberry buds can tolerate temperatures below 5 °F (–15 °C). Significant frost hardiness is lost as physiological and anatomical changes begin to occur in the plant, resulting in the buds only having tolerances ranging from 23 to 32 °F (–5 to 0 °C). All of our studies were conducted using 'Stevens' cranberry uprights collected from a farm near Nekoosa, Wisconsin.

Stages of upright growth and development

We approached the challenge of documenting these dramatic changes in frost hardiness by first characterizing the stages of cranberry upright growth and development. The current terminology was determined through consultation with growers and was published in *Cranberries Magazine* in 1997. Pictures depicting the defined stages, based on this original publication, are presented in **Figure 1 (next page)**. A summary of the stages is as follows presented in **Table 1**.

Table 1. Definitions of spring cranberry bud stages of growth and development.

Bud stage	Description
1. Tight	This is a resting bud with tightly wrapped bud scales that has fulfilled dormancy and chilling requirements. Initially in early spring, buds scales are red, subsequently turning green.
2. Swollen	No longer at rest, the bud has begun growth, causing the bud scales to push outwards and have a slightly loosened appearance. Bud scales can be red to green.
3. Cabbage head	Substantial swelling pushes the bud scales farther open, but new growth is still concealed. Viewed from the side, buds appear pointy and lengthened.
4. Bud break	New growth emerges through the bud scales. Tips of the uppermost new leaves are visible.
5. Bud elongation	New leaves and some flower bracts, which envelope the flower buds, emerge. All new growth is held tightly and parallel to the stem.
6. Rough neck	The new stem elongates significantly, making all the flower bracts and buds visible. Flower stalks have not elongated.
7. Early hook	The lowest flower stalks begin to elongate, pushing away from the stem.
8. Hook	Flower stalks have elongated, drooping to form the characteristic hook shape. New leaves are becoming more perpendicular to the stem.
9. Bloom	Flowers open, starting from the lowest buds.

Influence of temperature on growth and development

Temperature is the most powerful environmental factor influencing the rate of growth and development of plants. We monitored the

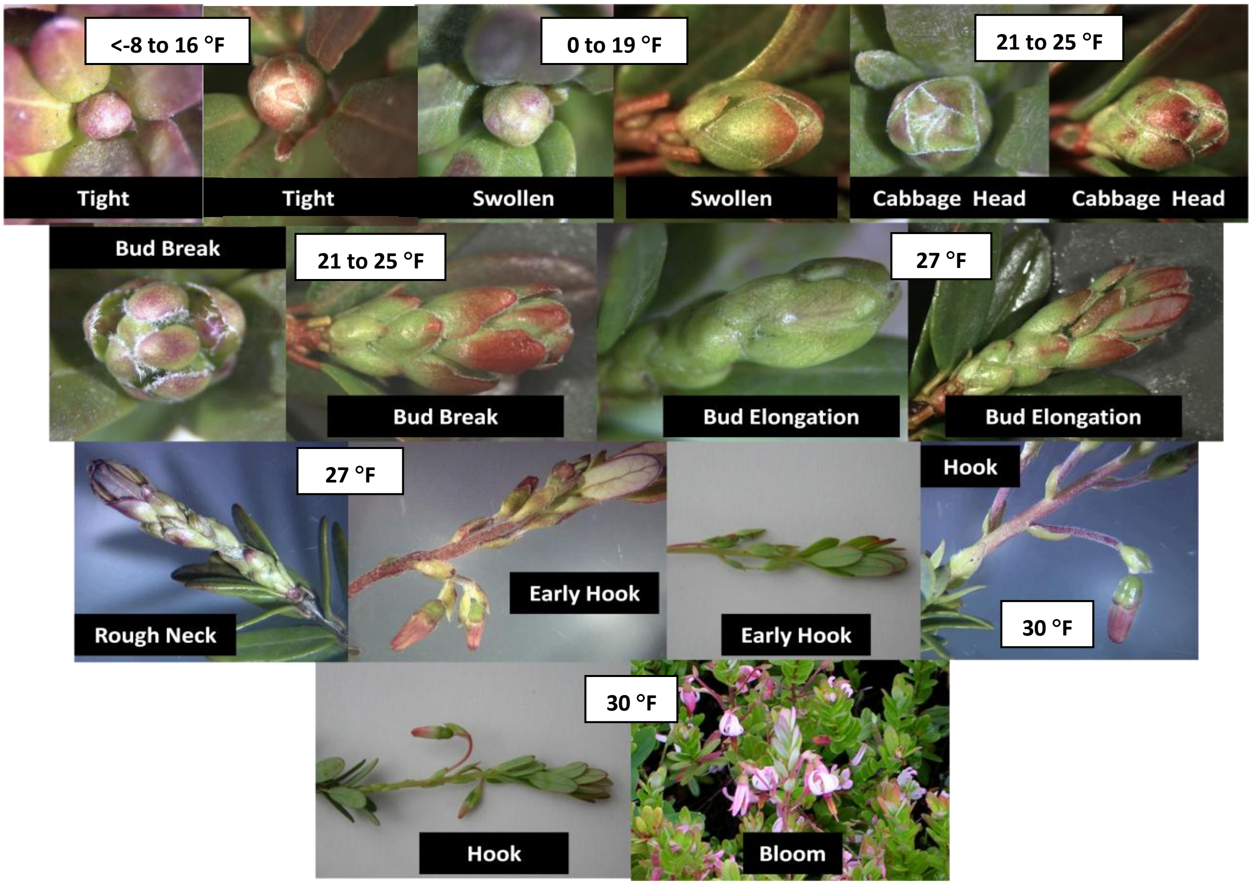


Figure 1. Developmental stages of cranberry bud during spring growth. Although at a given time multiple stages will be present, in our studies the most abundant bud stages at the time of collection were used for frost hardiness evaluation. The range of temperatures accompanying each bud stage represents the frost hardiness changes within that stage during spring growth. These numbers represent the minimum survival temperatures. All of the studies were conducted using ‘Stevens.’

temperatures of the cranberry canopy and the root zone. From these data, we calculated the temperature experience of the plants that would be contributing to growth and development and summarized this on a daily basis, commonly known as “growing degree days” (GDD), “heat units,” or “thermal time.” In order to calculate GDD for a given plant species we first need to determine the lowest temperature at which growth and development can occur. This is called the base temperature, T_b. In addition, a daylength of 13 hours has been found to be necessary for the stimulation of bud growth and development in the cranberry plant (Lenhardt et al., 1976). Based on our experimental work in the laboratory and greenhouse and from previously published work in the scientific literature, we determined that:

1) **41°F (5 °C) is a reasonable minimum canopy temperature for cranberry plant growth;**

2) **the cranberry plant may require a day length of 13 hours** (reached on April 7 in central Wisconsin) to commence spring growth, which could be an additional factor in years when the winter ice melts early (such as 1998). This is based on the early research by Lenhardt et al. (1976).

These authors concluded that a daylength of 13 hours was necessary for the stimulation of bud growth and acceleration of bud break if the cranberry plant.

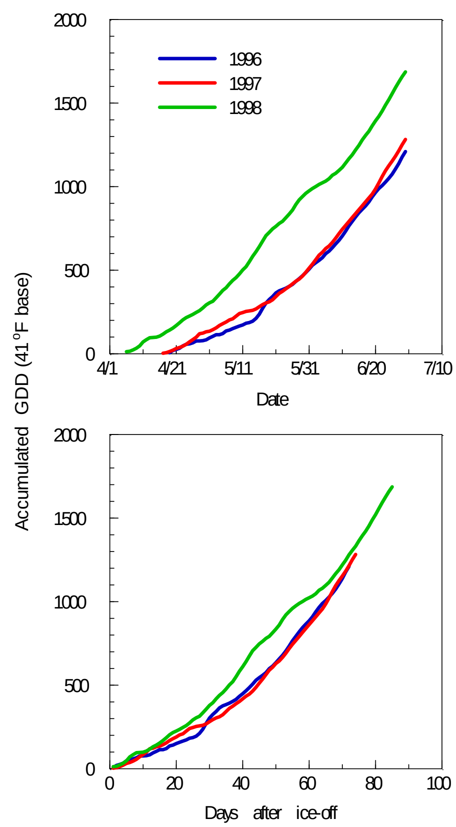
See the inset box to learn more about the calculation of GDD.

For one calendar day, calculate growth degree days (GDD) by using the hourly average canopy-level air temperature (T_i) and the following equation:

$$GDD = \sum_{i=24}^{n} \frac{T_i - T_b}{24}$$

T_b is the base temperature for the growth and development for the cranberry plant, (41 °F, 5 °C). For example, the average temperature in the field between 8 and 9 am was 53 °F, GDD for that hour will equal (53 – 41)/24 = 0.5 GDD. If the hourly average temperature was below the base temperature, then no GDD are accumulated. Calculate GDD for every hour of the day, then sum ($\sum$) for a daily total.

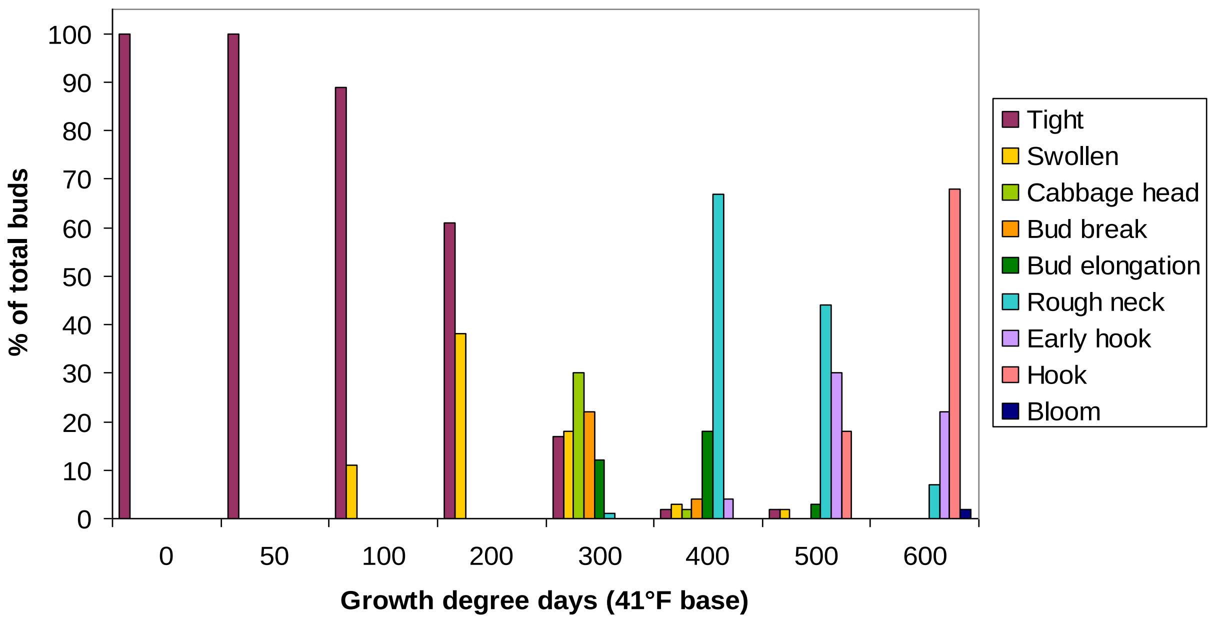
Figure 2. Plots of accumulated growth degree days (GDD) by calendar date (A) and by days after ice-off (B) for three years (1996-1998) at a cranberry farm near Nekoosa, Wisconsin. Both graphs have been adjusted for 13-hour day length (photoperiod), which is reached on April 7 in central Wisconsin. The minimum temperature required for cranberry bud growth, also called the “base” temperature, was experimentally determined to be around 41 °F (5 °C). See text for the details on the calculation of GDD. Note that when accumulated GDD are adjusted to days after ice-off, the pattern for the three years of study is similar.



Growth degree days for three seasons for a cranberry marsh near Nekoosa are given in Figure 2. The data in Figure 2A represent GDD accumulation after 13 hour daylength (April 7) in central Wisconsin. Clearly, 1996 and 1997 were similar years in terms of heat unit accumulation, whereas 1998 was an earlier and warmer spring. Since heat units, in terms of growth and development, would not be of use to a cranberry plant under the winter ice, we re-plotted accumulated GDD as a function of days after ice-off (Fig. 2B). Using these criteria, the three years show somewhat similar patterns of GDD accumulation. Temperature experience over the springtime varies from year to year, **heat units could then be used to compare cranberry growth and development, as well as frost hardiness, across years**.

Different bud stages are present in the field for varying lengths of time, resulting in demographic changes over the course of the spring

Figure 3. Phenology changes of cranberry bud stages over increments of GDD accumulation during spring growth. The data on the proportions of the various bud stages present were averaged over three years of study. At each collection time, uprights were sampled from various locations within a bed. Uprights were sorted and counted by bud stage, with the most numerous stages used for frost hardiness evaluation.



season. **Figure 3** shows the proportions of the various bud stages present at given GDD intervals for the three years of our study. We sampled periodically throughout the spring, sorted the collected uprights into the different bud stage categories present, and then tested the frost hardiness of the most numerous bud stages in the laboratory.

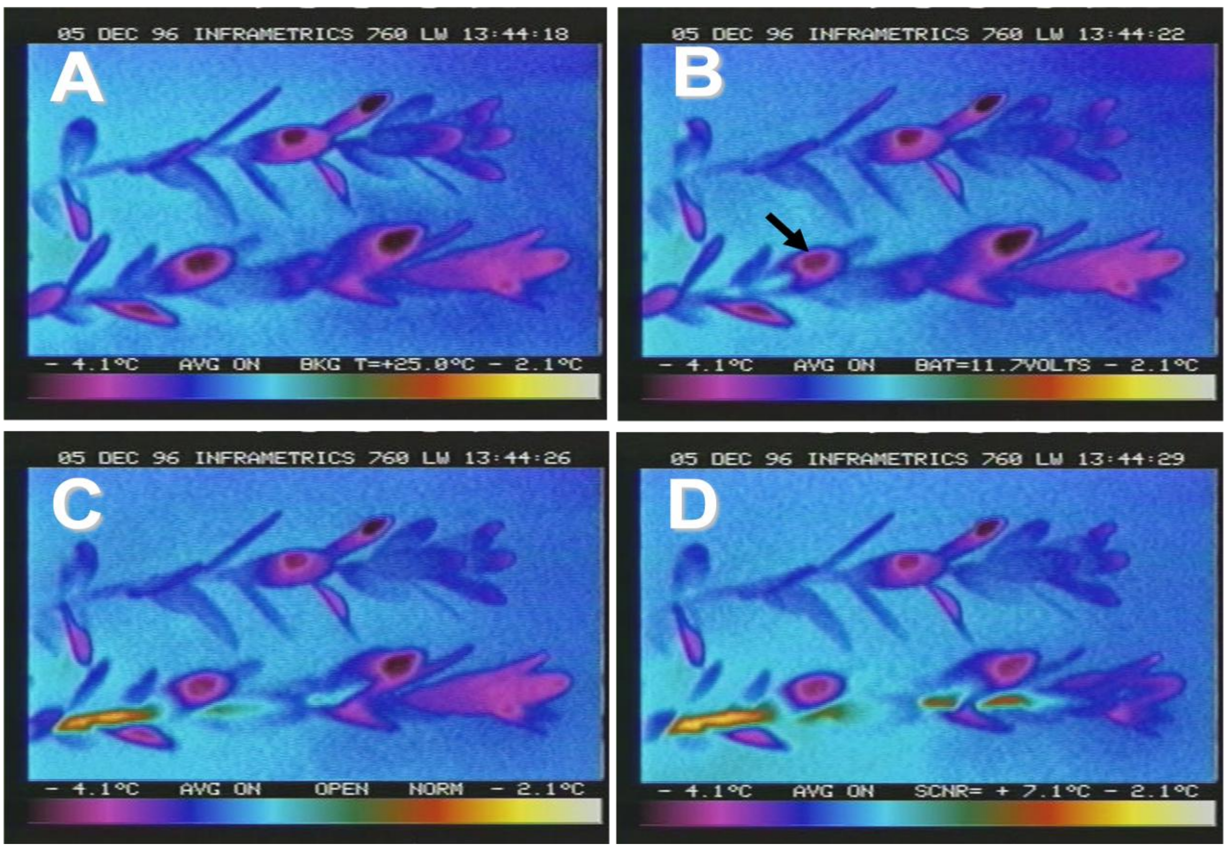
How cranberry uprights freeze

Ice forms in plant tissue in one of two ways, either it enters into the plant via an opening or ice crystals originate inside of the tissue. In both cases, ice forms, or "nucleates," because the motion of liquid water molecules has been slowed down by the dropping temperature and the presence of very small particles or "nucleators" (such as dust, proteins, and bacteria), that lock the water molecules in the crystalline structure known as ice. **Small isolated amounts of pure water can remain in a liquid state at temperatures below 32 °F (0 °C), a phenomenon known as supercooling.**

In our research using infrared video-thermography (described in 2000 in *Cranberries Magazine*, Volume 64, Issue 1 and in Workmaster et al., 1999), we saw **evidence of ice forming in cranberry uprights by ice crystals growing into the plant via the stomata on the underside of leaves** (**Figs. 4 and 5**). Once ice grows into the xylem path of the leaves, it spreads quickly throughout the stem and into other leaves.

Dormant buds appear to be cut off from the propagation of ice in the stem, probably due to a lack of a xylem connection between the stem and the bud at this stage. In addition, the bud scales encasing the bud protect the vegetative and floral growing points from ice growing outside the tissue. These two factors contribute to the bud's likely ability to supercool (the avoidance of ice formation in tissues at temperatures below 32 °F (0 °C)).

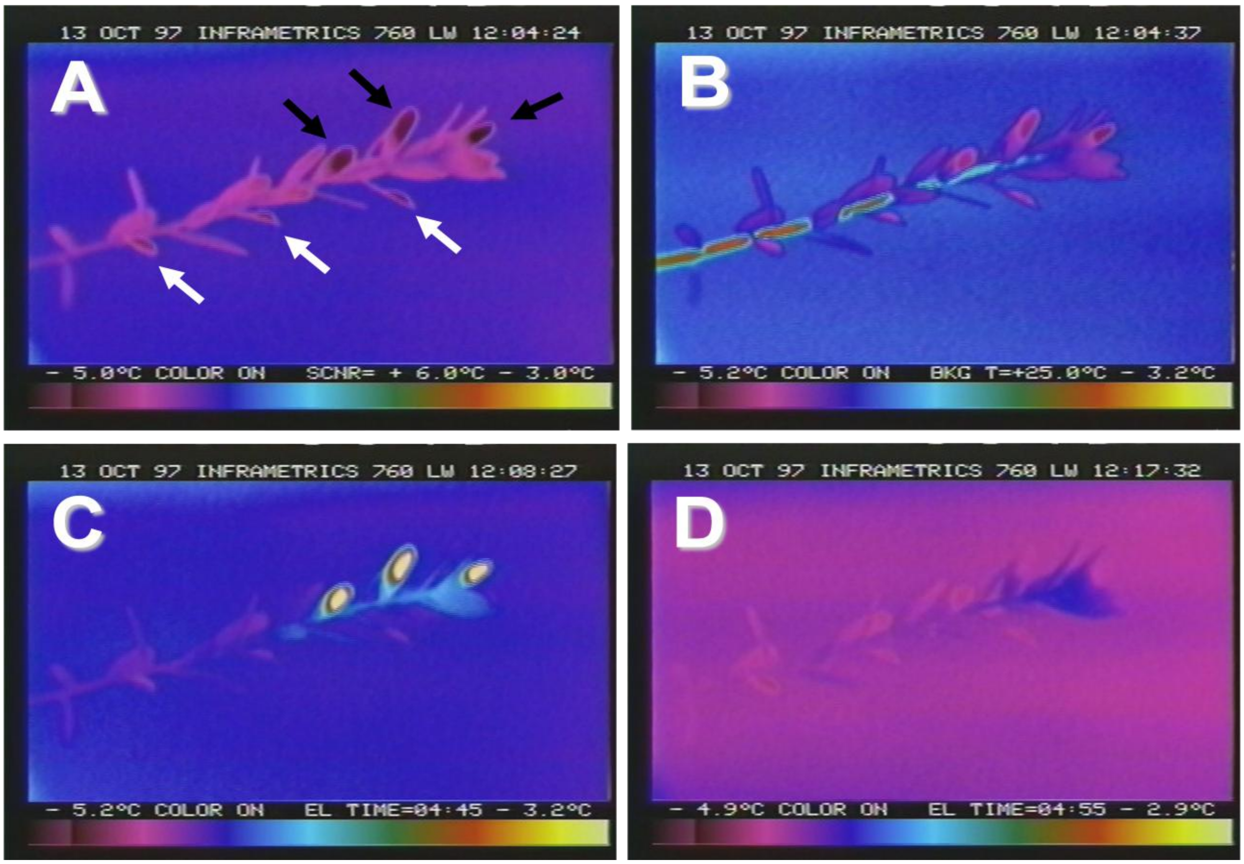
Figure 4. Propagation of ice in cranberry upright stems and leaves documented using infrared video thermography. The color scale along the bottom of each frame shows the relative temperatures of the objects in the view (pink ~-4.1 °C (24.6 °F) coldest to yellow ~-2.1 °C (28.2 °F)). Ice formation was initiated outside the plant by using droplets of water mixed with bacteria that promote the freezing of water. Ice can grow into the cranberry plant, presumably through stomata and other openings on the leaf surface. Cranberry leaves only have stomata on the lower surface. All the water droplets in this experiment were placed on the lower surface of the leaves. In the picture, the upper upright was already frozen at the time of observation. In the lower upright, the following sequence was recorded: (A) ice droplets are seen here as black areas (they are black because they are the coldest objects in the view). The water in the plant tissue remained supercooled (unfrozen at temperatures below 32 °F) at this time. (B) the ice droplet (see arrow) grew into the leaf and a portion of the stem. At the moment of ice nucleation (the changing of water into ice) in the leaf, a release of heat occurs (called an exotherm), causing the bacterial droplet to appear smaller. (C) and (D) ice grew quickly inside the stem, entering other leaves and ending at the tip of the upright. This spread of ice is depicted by the yellow and orange colors due to the exotherm produced from the freezing water.



Symptoms of freezing injury

The main site of freezing injury to dormant buds is at the base of the bud where it attaches to the stem (the bud axis) (Fig. 6). Once the xylem connection to the bud is established in spring (just before buds swell), buds become more vulnerable to freezing injury from ice that propagates within the plant. As buds swell and bud scales loosen and the upright growth begins, the growing points and

Figure 5. Propagation of ice in cranberry upright stems and leaves documented using infrared video thermography. In this series, ice formed inside the cranberry upright before the water droplets on the leaves could freeze. The ice that formed inside the plant was only able to grow into the water droplets on the lower leaf surfaces, causing these droplets to freeze. (A) white arrows point to water droplets placed on the upper leaf surfaces and black arrows point to those on the undersides of leaves. (B) the stem self-nucleated at air temperature of -7.5 °C (18.5 °F). (C) after approximately four minutes, only droplets on the lower leaf surfaces froze (exotherms indicated by yellow color). (D) up to seven minutes later, none of the droplets on upper leaf surfaces froze.



new tissues also become susceptible to ice and freezing from outside of the plant. Once the base of the bud is injured, the bud loses vascular connection with the upright and is not able to draw water, resulting in bud death.

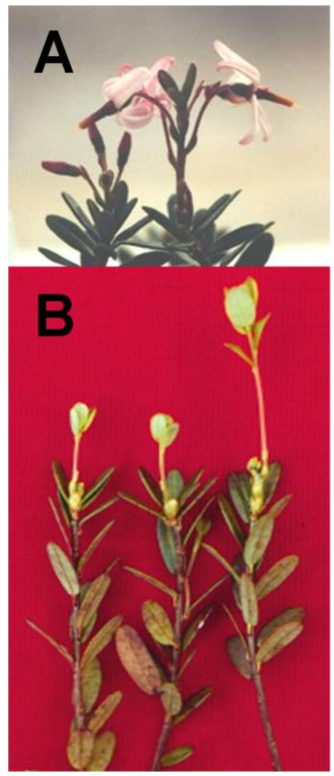
Other injury symptoms have been noted during spring growth and development of the cranberry upright (**Fig. 7**). **"Umbrella bloom"** occurs when the vegetative growing point dies, but the flowers go on to bloom, resulting in the flowers at hook stage forming an umbrella shape (**Fig. 7A**). Furthermore, stunted and weak growth also can occur when the freezing injury is sub-lethal. Bud stage development can also be delayed as a result of sub-lethal freezing injury **(Fig. 8)**. Injury to the terminal bud growing point can result in growth from the buds at the leaf axil as shown in **Fig. 7B**.

Spring frost hardiness changes

Spring frost hardiness changes were precisely determined using a controlled freezing test under laboratory conditions (Workmaster and Palta,

Figure 6. The base of the cranberry terminal bud, or axis, is a common site of freezing injury. Symptoms include a water-soaked and darkened appearance (B), while the axis of a healthy bud will be green (A). Injury to the bud axis restricts or cuts off the transport of water and nutrients to the bud. Initially after the frost injury, the internal bud tissues will appear green, but eventually turns brown, leading to death or weak and stunted growth.

Figure 7. Freeze injury symptoms visible during subsequent upright growth include umbrella bloom (A) and stunted and weak growth (B). In umbrella bloom, the vegetative meristem is damaged and very little or no new leaf growth occurs, such that the group of flower buds looks like an umbrella. When the terminal bud is fatally damaged, vegetative growth can break from the tiny axillary buds that exist at the base of the leaves.



2006). For this purpose, uprights were collected from the field at various stages of development for a period of three years. Each year the sampling began when the ice cover was fully melted and plants could be accessed. This date was called the "ice-off" day". The sampling period continued from ice-off day until the beginning of bloom. On each sampling date, uprights were taken from nine separate locations in a given bed and sorted into the different bud stages. These samples were transferred to large glass test tubes and subjected to a freeze stress using a large glycol bath in which the temperature could be precisely controlled. Following thawing of the samples, an initial evaluation of upright health was performed after two days. Uprights were then given supplemental water and light, to allow for regrowth. Two weeks after the imposition of the freeze-thaw stress, leaves were evaluated for survival and buds were rated for viability. The viability of the terminal buds was evaluated by rating each upright for the bud stage it had attained over the regrowth period (**Fig. 8**). The frost hardiness values reported in **Figure 9 and Figure 10 (following page)** are LT_{10} values (the temperature at which recovery and growth of samples is impaired by 10 %) as compared to unfrozen control samples.

Loss of hardiness occurs both within and between bud stages (Figs. 9 and 10). The largest hardiness changes occur in tight and swollen buds. For example, the tight buds were hardy to about -8 °F in early spring, however, the tight buds present in the late spring (May 25) were only hardy to about 23 °F (Fig. 9). Similarly, the hardiness of swollen buds was about 10 °F in early May, whereas the hardiness of these buds was about 28 °F in late May. Comparing different bud stages, the largest loss in frost hardiness occurred when the tight buds become swollen. In other words, tight and swollen buds sampled on a given day had very different levels of frost hardiness. Once cabbage head stage appears, cranberry uprights are sensitive to temperatures colder than 23 °F (-5 °C). **Flower petals and ovaries can be damaged at temperatures as warm as 30 °F (-1 °C).**

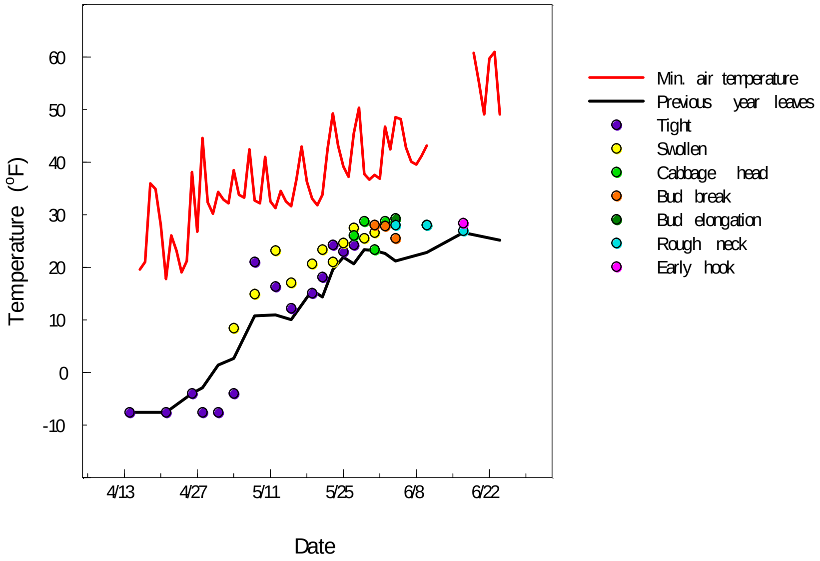
Figure 8. In our experiments, terminal buds were evaluated for frost hardiness by forcing bud regrowth following exposure to a controlled pattern of freezing and thawing. The buds on the uprights in this example were at the swollen stage when they were sampled from the field. The uprights exposed to 0 °C (32 °F) were the unfrozen control. Uprights exposed to -5 °C (23 °F) grew similarly to the controls, while those exposed to progressively colder temperatures (-9, -10, and -12 °C (15.8, 14, and 10.4 °F)) showed signs of increasing freezing damage.

Previous year leaves also experience a large loss in hardiness, but the change appears to be **more gradual over the course of the spring (Fig. 9).** In addition, previous year leaves are generally more resistant to damage by freezing temperatures than are buds.

Changes in cranberry plant frost hardiness can be due to anatomical changes in the bud, but also due to physiological changes. Buds harden when exposed to colder temperatures and they can de-harden when they experience warmer temperatures. **It is difficult to tease apart the anatomical and physiological factors in cranberry buds since both are affected by temperature.** In the course of spring warming, the minimum air temperature recorded in the cranberry canopy rises, increasing the likelihood of de-hardening, but also stimulating

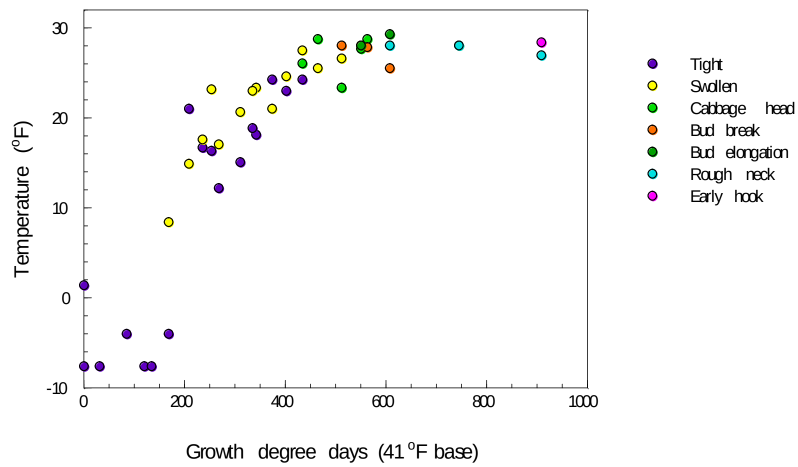
Figure 9. Changes in frost hardiness of cranberry buds (colored circles) and previous year leaves (solid black line) during spring growth in 1997. The hardiness of the bud was evaluated by recovery and regrowth following controlled freezing tests (see detail in text and Fig. 8).

The LT_{10} freezing hardiness value presented here is a statistically derived value where the temperature at which the recovery and growth of samples is impaired by 10%, as compared to the unfrozen control samples. Leaf hardiness was measured by visual evaluation of damage two weeks after controlled freezing. These plots show that the largest shifts in hardiness occurred in conjunction with a shift in the minimum air temperature (red line) to around or above 32 °F.



F igure 10. Changes in frost hardiness of cranberry buds during spring growth in relation to GDD. The frost hardiness values (LT_{10}, see details in Fig. 8) include values from 1997 and 1998.

This plot shows that the largest shift in frost hardiness corresponds with the attainment of about 200 GDD and the appearance of swollen buds.



bud growth and development. **Figure 9** shows how the pattern of hardiness changes in buds is related to the rise in minimum temperatures (red line). Once the minimum canopy temperature remains around 32 °F (0 °C) or above, leading bud stages reach a greater sensitivity to freezing temperatures.

A pattern in the loss of frost hardiness of cranberry uprights can be also be seen by tracking upright growth and development by growing degree days (Fig. 10). Before 180 GDD°F (base 41 °F) or 100 GDD°C (base 5 °C) units accumulate, buds remain primarily tight and hardy to lower than 5 °F (–15 °C). Between 180 to 360 GDD°F (100 to 200 GDD°C) units, buds begin to swell and a large loss in hardiness occurs (hardy to 23 °F or –5 °C). After 360 GDD°F (200 GDD°C) units have accumulated, subsequent stages of bud growth and development have occurred and the buds have completely lost their hardiness (hardy to 32 °F or 0 °C).

Our Recommendations For The Target Thresholds For Spring Crop Protection Are:

1) Monitor marsh temperatures with a digital logging system or weather station. Establish thermometers at canopy level in the coldest portions of a range of beds (including those that historically have always been the coldest). Record hourly canopy temperatures
2) Calculate growing degree days (GDD) either on an hourly or daily average basis. Add up the cumulative GDD from when ice has receded from beds and they are accessible, or from April 7 (attainment of 13 hour day in central Wisconsin), whichever occurs later.
3) Keep a running plot of minimum canopy temperatures.
4) Monitor changes in the physical appearance of the buds. Be aware that the largest shift in bud hardiness occurs while many buds are still tight and some are just beginning to swell. This can be a change that is very difficult to see by eye. This shift appears to correlate with the attainment of approximately 180 GDD°F (100 GDD°C). In addition, the shift is preceded by a rise in minimum canopy temperatures to around 32 °F (0 °C) and above.
5) Protect tight buds with less than 90 GDD°F (50 GDD°C) to 10 °F (–12 °C).

From 90 to 180 GDD°F (50 to 100 GDD°C), protect tight and swollen buds to 23 °F (–5 °C). After 180 GDD°F (100 GDD°C) have accumulated, protect to 32 °F (0 °C). Buds will reach the cabbage head stage after 360 GDD°F (200 GDD°C) and maximum sensitivity will be reached from that point forward.

6) Use the bud hardiness ranges shown in Figure 1 as a general guide for bud hardiness in spring.

Fall Frost hardiness changes

Fruit frost hardiness

Ripeness is an important factor in the fruit's resistance to damage by freezing temperatures. In our research (Workmaster et al., 1999), we concluded that ice forms in ripening cranberry fruit when ice crystals are able to grow into the flower (calyx) end of the fruit, via stomata in the remnant of the nectary ring (**Fig. 11**).

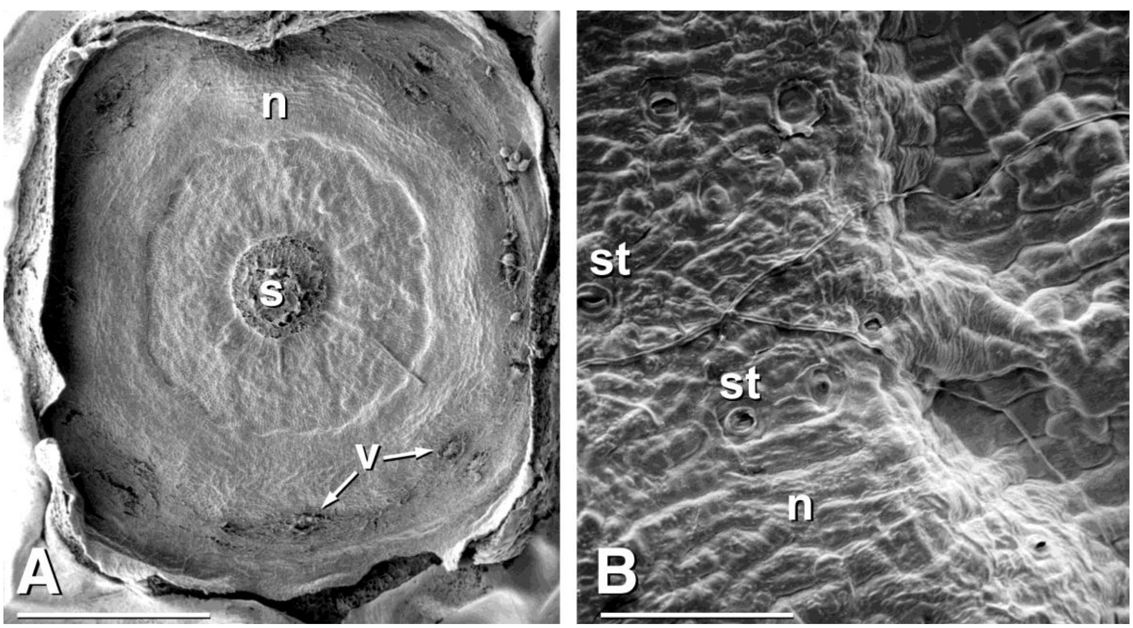
Evidence for this was obtained by tracking ice propagation in freezing fruits using infra-red video thermography (**Figs. 12 and 13**). It does not appear that ice is capable of traveling down the pedicel of the fruit from the stem during the fruit ripening period in the fall (**Fig. 12**).

During fruit filling, after pollination and fertilization, fruit are more sensitive. Presumably, at the early stage of fruit development fruit are still vascularly connected to the rest of the plant and therefore vulnerable to ice from this source. Our research shows that ice is able to enter the fruit only from the calyx end in both blush and red fruits. However, it takes longer and colder temperatures for ice to penetrate red (ripe) fruit as compared to blush fruit (**Fig. 13**).

(Figures appear on the following pages.)

In general, the more ripe a fruit is, the colder the

Figure 11. Scanning electron micrographs of the flower end of the cranberry fruit show that there are stomata in the remnant nectary from the flower. (A) overview of the area (calyx (the fused sepals of the flower) tissue has been removed to permit view of fruit end): area of stigma attachment (s), remnant of nectary ring (n), vascular bundles to anthers and petals (v). Bar represents 0.75 mm. (B) the remnant area of the nectary (n) contains stomata (st), while the area between the nectary and the stigma attachment (upper right portion of picture) does not. Bar represents 60 microns (1mm = 1000 microns).

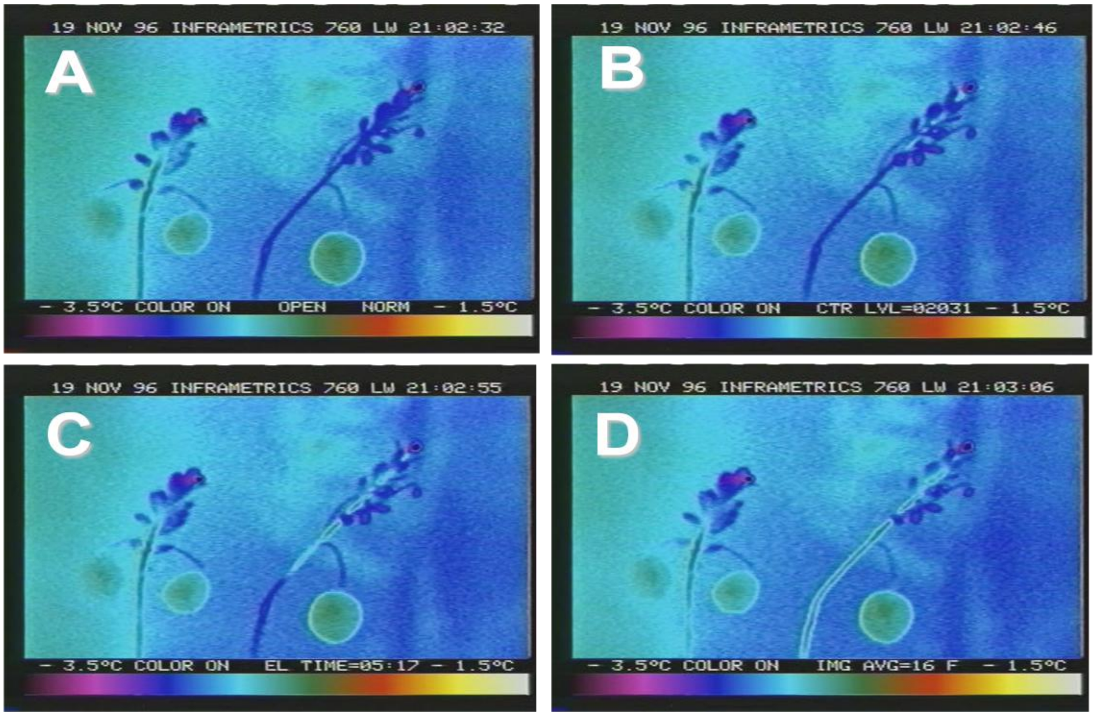


temperature it can tolerate for longer lengths of time (**Fig. 14**). This was experimentally tested on harvested fruit at different stages of color. Fruit that are relatively more ripe (about 28 mg total anthocyanin (TACY) per 100 g fresh weight) can endure 27 °F (-3 °C) for up to three hours with no damage, while some less ripe fruit (about 7mg TACY per 100g fresh weight) begin to show damage within one hour at the same temperature.

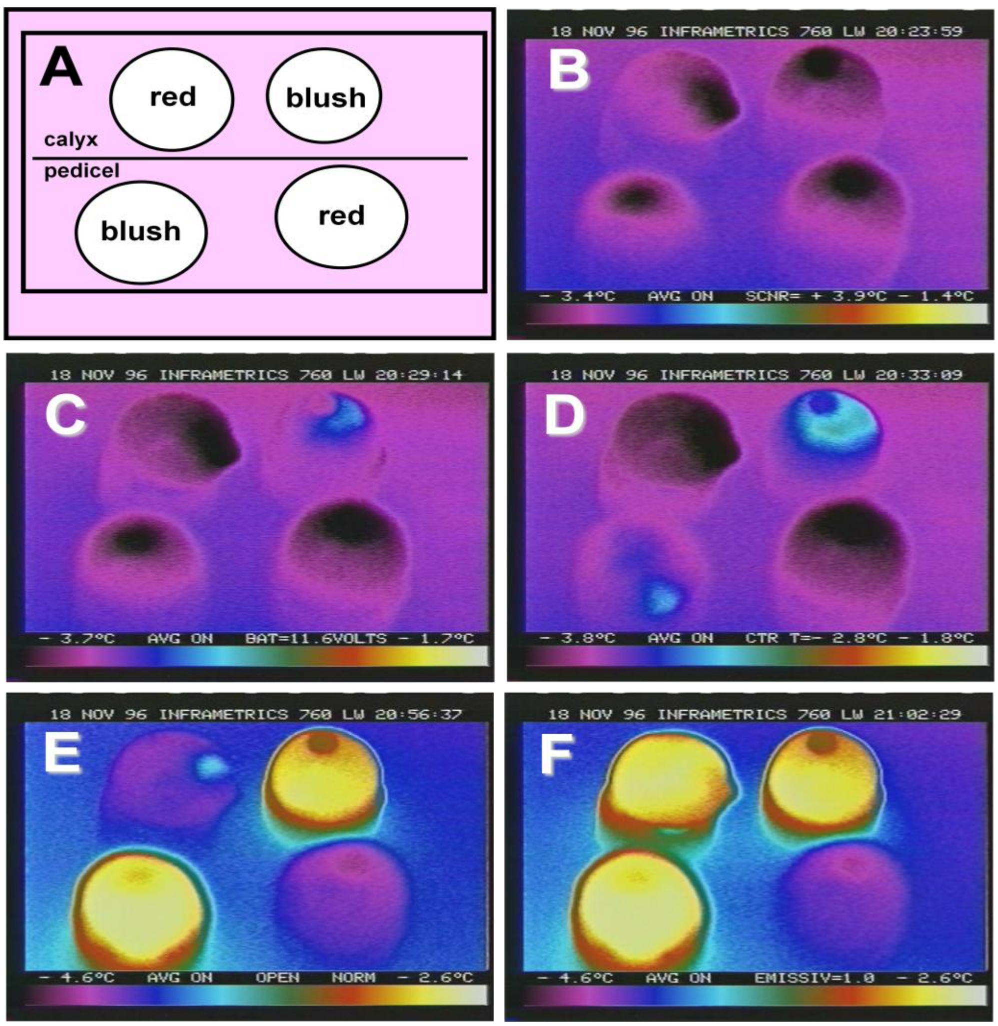
One important observation we made while testing the freezing hardiness of fruit is that the pattern of damage is very distinct. After a freezing experiment, fruit were stored for two days in a cold room to allow recovery of injured tissue and the full formation of symptoms in damaged tissue. **Typically, damaged fruit showed water soaking at the calyx end of the fruit (Fig. 15)**. This is consistent with the freezing pattern that we observed using infrared video thermography, that is, ice entering at the calyx end of the fruit (**Fig. 13**).

In addition, at every temperature and duration

F igure 12. Infrared video thermography shows that ice is not able to propagate from the upright stem to ripe fruit through the pedicel (fruit stem). The color scale along the bottom of each frame shows the relative temperatures of the objects in the view (pink ~-3.5 °C (25.7 °F) coldest to yellow ~-1.5 °C (29.3 °F) warmest). In this example, the tips of two uprights were cut and inoculated at the wound with droplets of water mixed with ice-nucleating bacteria. At the time of these frames, ice nucleation had already occurred in the stem and leaves of the left upright. In the right upright: (A) at air temperature of -2.4 °C (27.7 °F), the water in the leaves, stem, and fruit remained supercooled (liquid at temperatures below 32 °F). (B) ice propagated into the stem from the frozen water droplet (note lighter color along upper portion of the stem). (C) ice continued propagating along the stem, but did not penetrate down the pedicel. (D) the entire stem froze, with no change in either the pedicel or the fruit. This fruit continued to supercool for another 55 min, eventually freezing at around -6 °C (21 °F) from the flower end of the fruit, after being misted with water.



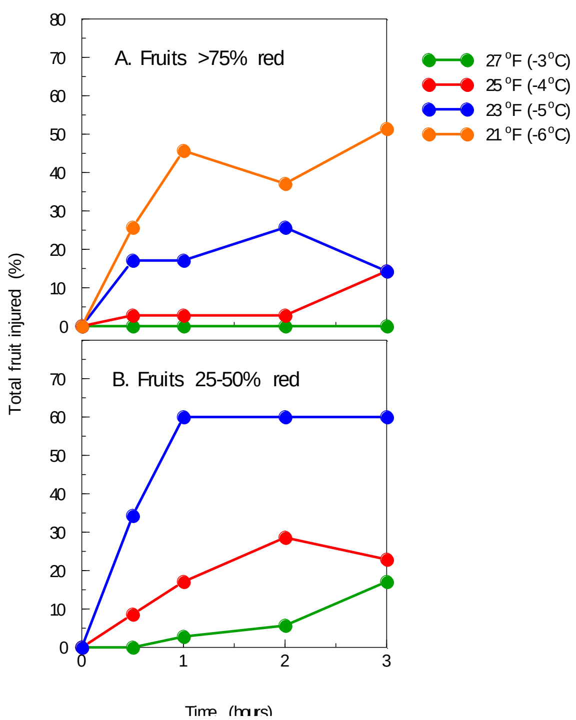
F igure 13. Infrared video thermography shows that detached cranberry fruit only freeze from the flower, end of the fruit. Red (ripe) berries supercooled (remained unfrozen at temperatures below 32 °F) to colder temperatures and for longer durations than blush (unripe) berries. In this example: (A) four berries (two red, two blush) were positioned with either the calyx (flower) or pedicel (fruit stem) end up. Droplets of water mixed with bacteria that promote the freezing of water were placed at these ends. (B) view of the fruit after all water droplets froze and cooled (they appear black since they are the coldest objects in the frame); no freezing events have occurred in the fruits yet. (C) the first fruit to begin freezing was the blush fruit inoculated at the calyx end (upper right fruit) (air temperature ~ -4.5 °C (24 °F). (D) four minutes later, the blush fruit inoculated at the pedicel end (lower left fruit) began freezing; however, the first ice formation actually occurred at the calyx end of this fruit (note difference in locations of water droplet in C and initial exotherm (light blue area) in D (air temperature ~ -5 °C (23 °F)). (E) the red fruit inoculated at the calyx end (upper left fruit) began freezing 23.5 minutes after the previous fruit (air temperature ~ -5.2 °C (22.6 °F)). (F) the red fruit inoculated at the pedicel end (lower right fruit) never froze, supercooling to a minimum air temperature of ~ -6 °C (21.2 °F) for an additional 30 minutes.



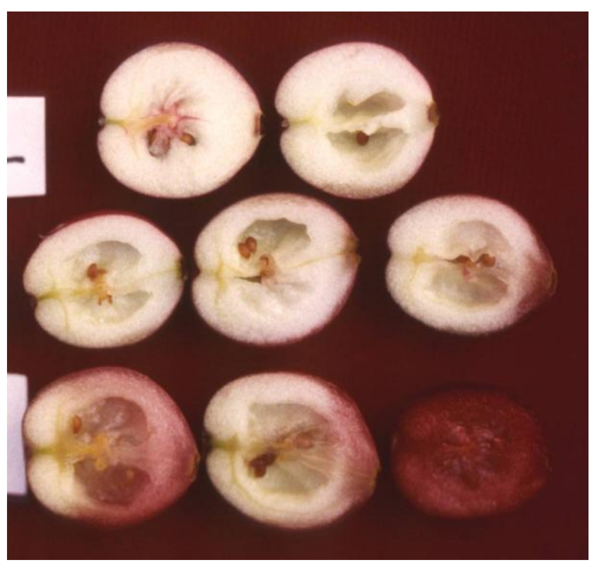
tested, a significant percentage of the fruit tested exhibited no damage. In other words, many individual **fruits can avoid the formation of ice in their tissues at temperatures down to 21 °F (-6 °C).** This means that the water in those fruit remains liquid at temperatures below freezing, a phenomenon called supercooling.

Another factor that will influence the survival of fruit in the field to freezing temperatures is the structure of the cranberry canopy. The relative thickness of the canopy will create a microclimate where temperature differences will occur. On a frost night with little to no wind, these temperature gradients will be the greatest. Less ripe fruit reside lower in the canopy where temperatures are relatively warmer, while the ripest fruit will be exposed at the top of the canopy to the coldest temperatures.

Figure 14. Frost hardiness of cranberry fruit in relation to degree of ripeness and duration of freezing temperatures. Fruit that are more ripe can survive lower freezing temperatures for longer periods of time than can less ripe fruit. In this set of experiments, individual fruit (n=35 for each type) that were more than 75% red (TACY values ~28mg/100g fresh weight) were tested with fruit that were 25 to 50% red (TACY values ~7mg/100g fresh weight) at a range of temperatures (21, 23, 25, and 27 °F) for varying durations (0.5, 1, 2, and 3 hours). Two days after thawing fruit were cut in half and evaluated for symptoms of water-soaking (see Fig. 15). The results are presented as the percent of total fruit that exhibited injury symptoms. Undamaged fruit were able to supercool (remain unfrozen at temperatures below 32 °F) for the duration of a given freezing treatment.



F igure 15. Visual symptoms of cranberry fruit frost injury. These fruit are cut longitudinally with the stem end to the left and the flower end to the right. The fruit in the top row are the unfrozen control, while the other fruit were all exposed to 17.5 °F (-8 °C) for the same length of time. Injury symptoms begin at the calyx, or flower, end of the fruit (middle fruit in middle row) and spread to the stem end. Water soaking damage ran from zero percent (left fruit in middle row) to 100 percent (right fruit in bottom row) with varying amounts of damage in between.



Influence of harvest flooding

Leading up to harvest, conditions in the field can vary greatly from year to year. Cranberry vines have stopped active growth by the end of August, and plants are entering into both physiological dormancy and acclimating to increasingly cooler temperatures throughout September and October. **The harvest flood could potentially affect the frost hardiness of buds and leaves by introducing the plants into a relatively warmer environment and, depending on the length of the flood, limiting oxygen levels**. At our study location in 1996, there was a noticeable decrease in both bud and leaf hardiness in the week following harvest (**Fig. 16A**), however, this was not found in 1997 (**Fig. 16B**). Cranberry plants harden (acquire frost hardiness) in response to low air temperatures in fall. These results suggest that an extended late season flood could cause the vines to lose hardiness (deharden) because of the exposure to the relatively warmer temperatures of the water. It is unclear how common this phenomenon is, and the factors contributing to it require further study.

Recommendations For The Target Thresholds For Fall Crop Protection Are:

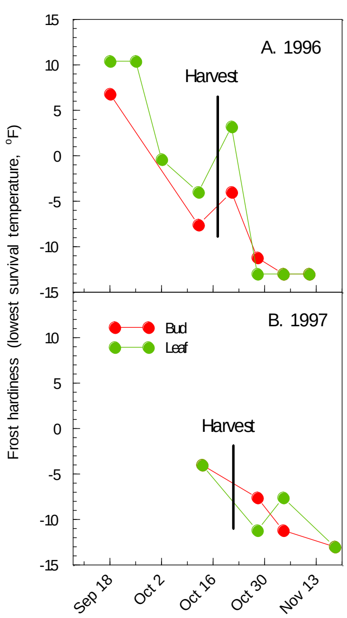
1. Monitor marsh temperatures with a digital logging system or weather station. Establish thermometers at canopy level in the coldest portions of a range of beds (including those that historically have always been the coldest).

2. Keep a running plot of minimum canopy temperatures.

3. Closely monitor the developing color of the fruit, especially those exposed at the top of the canopy.

4. In general, the more ripe a fruit is, the colder the temperature it can tolerate for longer lengths of time. Our data show that fruit that have over 75% red surface can survive exposure to temperatures of 25 °F for up to two hours. These fruit can survive over three hours of exposure to 27 °F. However, fruit with 25-50% red surface can only survive temperatures of 27 °F for 30 minutes. These fruit can not survive temperatures below 27 °F.

F igure 16. Potential influence of harvest flood conditions on bud and leaf frost hardiness. Dormant uprights were tested for hardiness in fall of both 1996 (A) and 1997 (B). Harvest dates were October 17, 1996 and October 22, 1997. In 1996 the first post-harvest testing indicated that both buds and leaves had lost a degree of hardiness as compared to immediately prior to harvest. In 1997, no effect was observed. In this set of experiments, hardiness is expressed as the lowest survival (no injury symptoms) temperature, which was determined by visual observation (cutting of buds, as well as forcing of regrowth after fulfillment of chilling requirement) only.



5. In general, fruit color is known to develop in response to low temperature and light. Frost protection will tend to keep the beds warmer, thus influencing both hardening and color development. Furthermore, as stated above, higher colored fruit can survive lower temperatures for longer durations. So, a grower's frost protection strategy should take this aspect into consideration.

6. There is a possibility that cranberry uprights can lose hardiness following an extended flood during harvest. Growers are cautioned to limit the durations of harvest floods.

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For more information, visit http://www.horticulture.wisc.edu/faculty/faculty_pages/Palta/palta.php and click on "Cranberry publications."

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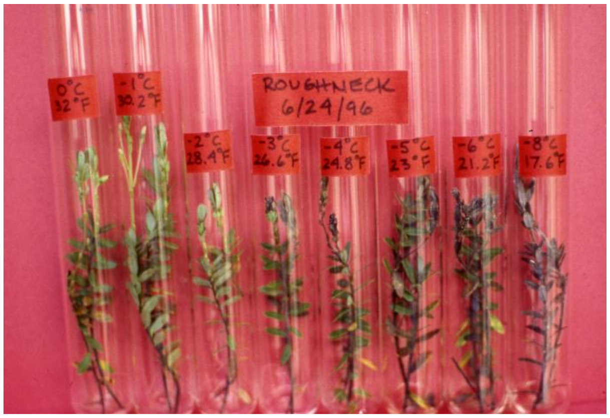
Examples of Cranberry Frost hardiness Evaluation (Field and Laboratory)

Ice encased cranberry plant during fall frost protection



Evaluation of leaf damage following a controlled freeze

Dormant Bud Swell

Changes in the buds and leaves during spring growth

Evaluation of re-growth potential of buds following a controlled freeze

Simulation of frost in controlled conditions

Evaluation of re-growth potential of buds following a controlled freeze to designated temperatures

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