CHARACTERIZATION OF CRANBERRY FIELD DECLINE SYNDROME IN BRITISH COLUMBIA

by

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Abstract

A condition called Cranberry Field Decline (CFD) has affected several cranberry beds in British Columbia, resulting in patches of severely reduced canopy density. To prevent the further expansion of declining patches, early diagnosis of CFD is critical. The symptoms of CFD were characterized by evaluating soil chemistry (pH and redox potential), plant growth (root health, upright density, canopy depth, and yield), and carbohydrate dynamics (Starch, glucose, fructose, and sucrose) in relation with the three levels of CFD development (declining, transitional, and normal) in four affected beds. For the carbohydrate analysis, it was hypothesized that starch content in stems (S_Sta) was different among the CFD development. Additionally, the effectiveness of sanding in beds for rehabilitating stressed vines was evaluated by measuring the growth characteristics under three levels of sand depth (0, 1.3, and 2.5 cm). The characterization of CFD showed no clear relationship between pH or redox potential and CFD development. Shoot density and growth did not change significantly, while lower canopy depth and root health constantly declined in the early phase of CFD development. However, all growth parameters sharply declined after the transitional condition. Starch content in stems declined from normal to declining areas, supporting the hypothesis. Hexose (sum of glucose and fructose) in uprights (U_Hex) to S_Sta ratio increased with the increasing severity of CFD. The results suggest that the stress-induced alteration of carbohydrate allocation under carbon deficiency may explain the changes in canopy structure in CFD-affected areas. Sanding at 2.5 cm significantly increased total upright density compared to control but slightly decreased yield. However, such impact was only seen in a bed with poor root health and deep brown canopy, suggesting the effect of sanding is influenced by bed condition.

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Lay Summary

Several cranberry beds in British Columbia have been exhibiting patches of stressed vines and reduced canopy density. This condition, called Cranberry Field Decline (CFD), may pose a significant impact on the yield. As cranberries are one of the most important fruits crops in Canada, accounting for 11% of total fruit commodity, the investigation into CFD can provide a significant contribution to ensuring the productivity of the cranberry industry. The key goals of the present study were to understand the characteristics of CFD symptoms and to investigate how such symptoms are related to the plant resource dynamics, such as sugar content within plant tissues. The present study also included an evaluation of the effectiveness of sand applications to the cranberry canopy for rehabilitating stressed vines. The outcome of the present study can contribute to a deeper understanding of CFD and how to manage its development in British Columbia.

Preface

This thesis is an original and unpublished work by the author, Takuhiro Someya. The sampling arrangements for Chapter 1 and Chapter 2 were adapted from the preliminary study in 2015 (unpublished) which was designed by my thesis supervisor Dr. Rebecca Harbut at Sustainable Agriculture at Kwantlen Polytechnic University in Richmond. The measurements of the carbohydrate content were carried out by the Analytical Chemistry Services Laboratory, Ministry of Environment and Climate Change Strategy in Victoria, British Columbia. I was responsible for all other sampling, measurements, and analyses.

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List of Symbols and Abbreviations

ADP-glucose	: Adenosine diphosphate glucose
AGPase	: Adenosine diphosphate glucose pyrophosphorylase
ANOVA	: Analysis of variance
CC	: Companion cell
CFD	: Cranberry Field Decline
Fru-2,6- <i>P</i> ₂	Fructose 2,6-bisphosphate
F6P	: Fructose 6-phosphate
FBP1	: Fructose 1,6-bisphosphate
G1P	: Glucose 1-phosphate
GAP	: Glyceraldehyde 3-phosphate
GWD	: Glucan water dikinase
K _{sat}	: Saturated hydraulic conductivity
Hex-P	: Hexose phosphate
NSC	: Nonstructural carbohydrate
PCA	: Principal component analysis
Pi	: Inorganic phosphate
PGD	: Phosphoglucan water dikinase
PGM	: Plastidic phosphoglucomutase
PP	: Phloem parenchyma cell
PSI	: Photosystem I
PSII	: Photosystem II

S_Frc	: Fructose content in stems
S_Glc	: Glucose content in stems
S_Hex	: Hexose content in stems
S_Sta	: Starch content in stems
S_Suc	: Sucrose content in stems
SE	: Sieve tube element
T6P	: Trehalose 6-phosphate
TCA	: Tricarboxylic acid
TNSC	: Total nonstructural carbohydrate
TP	: Triosephosphate
Tukey's HSD	: Tukey's Honestly Significant Difference
U_Frc	: Fructose content in uprights
U_Glc	: Glucose content in uprights
U_Hex	: Hexose content in uprights
U_Sta	: Starch content in uprights
U_Suc	: Sucrose content in uprights
UDP-glucose	: Uridine diphosphate glucose
UVC	: Unrooted volume under the canopy
W_TNSC	: Total nonstructural carbohydrate in whole vines

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Chapter 1: Introduction

1.1 Background

American cranberry (*Vaccinium macrocarpon* Ait.) belongs to genus *Vaccinium* under family Ericaceae but can also be classified into subgenus *Oxycoccus* in Genus *Vaccinium* (Eck, 1990). European cranberry (*Vaccinium oxycoccus*), a close relative to *V. macrocarpon*, is also classified into the same taxonomic group (Eck, 1990). Another close relative to *V. macrocarpon* is Lingonberry (*Vaccinium vitis-idaea L.*) which is defined under genus *Vaccinium* (Eck, 1990). While European cranberry and lingonberry are found in North America, Asia, and Europe, American cranberry is found only in North America (Eck, 1990).

The first cultivation of American cranberry started in Cape Cod, Massachusetts in 1816 (Caruso, Bristow, & Oudemans, 2000). The earliest cultivar was selected from the wild population in 1845 and was named "Early Black" (Trehane as cited in Zdepski et al., 2011). In 1885, vines of cranberry plants were brought from Cape Cod to Coos County, Oregon and were propagated from vine cuttings (Bernadine et al., 2002). The cultivation of cranberry began in British Columbia (BC), Canada in the 1930s in a small acreage of a post-harvest peat bog (Bernadine et al., 2002).

Globally, the United States accounts for the largest production of American cranberry (399,734 t/y), followed by Canada (163,812 t/y), Chile (103,475 t/y), Turkey (11,020 t/y), Azerbaijan (2,800 t/y) and, on a smaller scale, Romania, Belarus, Latvia, Ukraine, the former Yugoslav Republic of Macedonia, Tunisia, Spain, Bulgaria, and France (Food and Agriculture

Organization of the United Nations, 2016). In the United States, Wisconsin produces the highest yield of cranberry (57%), followed by Massachusetts (27%), New Jersey (7%), Oregon (7%), and Washington (2%) (United States Department of Agriculture, 2016). In Canada, the largest producing province is Quebec (64%), followed by BC (30%), New Brunswick (5%), and Nova Scotia (1%) (Statistics Canada, 2016). Cranberries are one of Canada's top 5 fruits in farm gate value among other important fruits crops, such as blueberries, apples, cherries, and grapes. In 2017, the farm gate value of cranberry accounted for 11% of the total fruit commodity in Canada (Statistics Canada, 2016).

American cranberry is a low-trailing, perennial, woody vine naturally inhabiting cool, acidic, and moist environments, such as peat bogs and marshes in the temperate regions (Vander Kloet, 1988). The plant structure consists of uprights (vertical shoots), runners (horizontally trailing stolons), stems, underground stems, and a fibrous, shallow root system (Bernadine et al., 2002): these structures collectively form a low-lying, mat-like canopy (Eck, 1990). Primary shoot growth occurs at the apical meristem formed at the tip of uprights but also occurs at axillary positions on runners and vines (Bernadine et al., 2002). Upright density varies in the range of 150-700 uprights per square foot area (Bernadine et al., 2002). Uprights and runners accumulate over the existing biomass, which can lead to the formation of a deep canopy. Cranberries tend to be biennial bearing, and therefore uprights typically alternate between vegetative buds, which contain only leaf primordia, and mixed buds, which contain both flower and leaf primordia (Eaton as cited in DeVetter, Colquhoun, Zalapa, & Harbut, 2015). Each upright with a mixed bud can produce 2-7 flowers (Averill, Caruso, DeMoranville, Jeranyama, & LaFleur, 2008), which are formed singly and acropetally along the stem between the previous and current

seasons' foliage (Roper, 1997); however, typically only less than 40 to 50 percent of flowers on an upright will set fruit (Hart, Strik, DeMoranville, Davenport, & Roper, 2015). The foliage can persist on both flowering and vegetative uprights and functional in photosynthesis for up to two growing seasons (Eck, 1990).

Cranberry plants complete their phenological cycle in 16 months (Hart et al., 2015).

Differentiation of apical shoot meristems and inflorescence initiation in buds for the following season take place in the early summer, overlapping the current season's flowering and fruit set (Hart et al., 2015). The buds for the next season continue to develop until they became dormant in late fall (Hart et al., 2015). During dormancy, cranberry plants require more than 1000 hours of chilling between 0 - 7 °C for normal growth after bud break (Bernadine et al., 2002). In the average season in BC and South Coastal Oregon, cranberry buds start to swell in late March and break in early April (Bernadine et al., 2002). In May, new shoots emerge and develop from the buds on the apical position of uprights and grow foliage acropetally (Bernadine et al., 2002). On reproductive uprights, the early bloom starts in late May followed by the fruit set in late June (Bernadine et al., 2002). Berries develop throughout summer and reach full maturity in size in late August and undergo ripening from late summer to late September (Bernadine et al., 2002).

Cranberry production beds can be largely divided into two types of soils: organic soil (peat or muck soil) and sand (DeMoranville, 2008). Cranberry beds are established in peatlands that had been previously harvested, or in constructed sand beds which creates a well-drained, acidic environment (DeMoranville, 2008). A sand-based cranberry bed in Massachusetts contains less than 3.5% of organic matter and approximately 3% clay and silt in the rooting environment

(DeMoranville, 2008). Sand is applied (sanding) every 2-5 years on established cranberry beds in Massachusetts for both pest management and stimulation of root growth (DeMoranville, 2008). Periodic sanding can contribute to the maintenance of an appropriate canopy depth, preventing the development of a deep canopy and allows younger vines to root which is necessary to renew the root system (DeMoranville, 2008; Eck, 1990). On the other hand, cranberry beds in BC and some areas in Washington State are established directly into the existing organic soil without layering sand over the top (Bernadine et al., 2002). In BC, sanding has been periodically used to rehabilitate stressed vines in cranberry beds; however, although such practice has become more common within limited areas of a bed, it is uncommon to apply sand across an entire cranberry bed in BC. These two systems, organic or sand bed, have resulted in very different production systems and crop characteristics.

In the Lower Mainland of BC, the quality of the organic soil may vary significantly among and within beds. Botanical compositions of a peat soil may differ depending on the type of peatland (Vitt, 2014) and the depth in the profile (Verry *et al.*, 2011), which determines the degree of humification as peat soils derived from herbaceous plants, typically found in fen and marsh, decays faster compared to peat soils derived from *Sphagnum*-dominated vegetation (Verhoeven & Toth, 1995). Depth-wise, organic soils located deeper in the soil profile are generally more humified as the deepest horizon of the peat predominantly consists of easily decomposable organic residues derived from aquatic organisms overlaid by layers that are composed of easily decomposable herbaceous vegetation (Verry *et al.*, 2011). As most of the cranberry beds in the Lower Mainland of BC were established over post-harvest peatlands which had been deeply mined closer to the mineral soil profile, the existing peat at the time of cranberry bed

establishment might be highly humified. The degree of humification is the most important property of peat as it influences soil porosity and pore sizes which influence drainage (Boelter, 1968; Verry et al., 2011). Maintaining proper drainage in the soils of cranberry beds is critical as the cranberry plants require well-aerated soil for healthy root development (DeMoranville, 2008).

1.2 Cranberry Field Decline

In recent years, a condition called Cranberry Field Decline (CFD) has developed in several cranberry beds in the Lower Mainland of BC. Affected beds develop patches of stressed vines, reduced canopy density, and complete collapse of the canopy. A preliminary study of soil characteristics in CFD-affected beds in 2014 suggested a possibility of highly humified peat causing an excessively wet and poorly aerated rooting environment for cranberry plants (Lavkulich, 2014). In 2015, this suggestion was followed up by assessing the degree of humification of peat soils with von Post index, which indicated a possible relationship between the humification of peat soils and overall severity of CFD in affected beds (Someya & Harbut, 2015). In the same study, characteristics of plant growth under the influence of CFD was also investigated, and the results showed a trend indicating a faster reduction of the depth of brown canopy (lower canopy without leaves) compared to the depth of green canopy (upper canopy with leaves) in the early phase of CFD development (Someya & Harbut, 2015). Also, a visual assessment of cranberry root samples collected from CFD-affected areas showed a greater reduction of the number of feeder roots and stunted growth of the root tips (British Columbia Cranberry Marketing Commission, 2014). Moreover, in the vicinity of CFD-affected areas, a large mass of canopy was easily peeled off from the soil surface by hand with very little force. In

a healthy bed, the canopy was stable as it was tightly anchored to the soil with healthy roots, suggesting that the density and stability of roots were reduced in the CFD affected areas.

To prevent further expansion of declining patches, early diagnosis and effective management of CFD symptoms are critical. The overall objective of the present thesis was to characterize the symptoms of CFD and to evaluate the effectiveness of sanding in cranberry beds. In detail, soil chemistry and plant growth were characterized with respect to CFD development to understand the soil condition and physical symptoms of cranberry plants under the influence of CFD. Also, carbohydrate content in uprights and stems were compared among CFD conditions and analyzed for the dynamics with the increasing severity of CFD to investigate the biochemical characteristics under the influence of CFD. As carbohydrate depletion in stems was suspected of being the cause of the abrupt reduction of canopy density at some point of CFD development, it was hypothesized that starch content in stems was different among different levels of CFD development. Additionally, to understand the effectiveness of sanding in BC cranberry beds, the impact of sanding for rehabilitating stressed vines was evaluated by comparing the growth characteristics at different depths of sanding.

1.3 Carbohydrate Synthesis, Functions, Allocation, and Partitioning

1.3.1 Carbohydrates: An Essential Resource for the Plants' Survival

Plants synthesize photosynthates that are rich in chemical energy by assimilating inorganic carbon from the atmosphere (Taiz & Zeiger, 2010). The resulting carbohydrate compounds are essential for the plants' survival as they are the energy and material sources for the plants' growth and development (Taiz & Zeiger, 2010) and account for nearly half of plant's dry mass

(Lambers, Chapin III, & Pons, 2008). The carbohydrate in plants exists as structural carbohydrate, including cellulose, hemicelluloses, pectin, and various oligosaccharides, and nonstructural carbohydrate (NSC), commonly including glucose, fructose, sucrose, and starch (Taiz & Zeiger, 2010). Glucose, fructose, and sucrose (soluble sugars) are more reactive and readily available for uses in plant metabolism (Dietze et al., 2014) as opposed to starch which functions as purely a carbohydrate storage and is inactive in plant metabolism (Smirnova, Fernie, & Steup, 2015). However, starch is the largest carbohydrate stored in plants and is essential for the plants' survival, especially in perennial crops (Taiz & Zeiger, 2010).

1.3.2 Photosynthesis: Light Reaction and Carbon Assimilation

Photosynthesis consists of two separate processes in chloroplasts: light reaction occurring in thylakoid membranes and carbon assimilation occurring in the Calvin-Cycle (Malkin & Niyogi, 2000; Taiz & Zeiger, 2010). The light reaction involves the photosystem II (PSII), photosystem I (PSI), transmembrane protein complexes, and electron transport chain embedded in the thylakoid membrane (Malkin & Niyogi, 2000; Taiz & Zeiger, 2010). In PSII, red light is absorbed by the antenna complex consisted of carotenoid and chlorophylls, through which photon energy is transferred to reaction center complex P680 (Malkin & Niyogi, 2000; Taiz & Zeiger, 2010). The photon energy strongly oxidizes P680 which splits a water molecule into OH⁻ and H⁺ and becomes a weak reductant while harvesting two electrons (Malkin & Niyogi, 2000; Taiz & Zeiger, 2010). The reduced P680 transfers the electrons through the series of proteins embedded in and on the thylakoid membrane towards PSI in which absorption of far-red light by the antenna complex excites reaction center complex P700 which becomes a strong reductant and passes the electrons to ferredoxin (Malkin & Niyogi, 2000; Taiz & Zeiger, 2010). Ferredoxin

nicotinamide adenine dinucleotide phosphate reductase then removes electrons from the ferredoxin and reduces nicotinamide adenine dinucleotide phosphate (NADP⁺) into NADPH (Malkin & Niyogi, 2000; Taiz & Zeiger, 2010). During the process of electron transport, protons are shuttled out to the thylakoid lumen, which increases electrochemical proton gradient across the thylakoid membrane (Malkin & Niyogi, 2000; Taiz & Zeiger, 2010). The accumulated proton in the thylakoid lumen drives the adenosine triphosphate (ATP) synthase which generates ATP in stroma which, together with NADPH, are used in Calvin-Cycle (Malkin & Niyogi, 2000; Taiz & Zeiger, 2010).

The Calvin-Cycle utilizes the products of the light reactions to assimilate atmospheric carbon (Malkin & Niyogi, 2000; Taiz & Zeiger, 2010). Carbon dioxide (CO₂) enters the spaces among spongy mesophyll cells of photosynthetic tissue through stomata and is absorbed into the mesophyll cells (Malkin & Niyogi, 2000; Taiz & Zeiger, 2010). In the mesophyll cells, CO₂ enters the Calvin-Cycle which is composed of carboxylation, reduction, and regeneration stages resulting in the synthesis of triose phosphate (TP) (Malkin & Niyogi, 2000; Taiz & Zeiger, 2010). At this point, one out of every six TP exits the Calvin-Cycle, and the remaining five TP are recycled to regenerate Ribulose 1,5-bisphosphate (Malkin & Niyogi, 2000; Taiz & Zeiger, 2010). The expelled TP are converted into starch in the chloroplasts and/or transported to the cytosol in which the TP is converted to hexose phosphate (Hex-P) (Malkin & Niyogi, 2000; Taiz & Zeiger, 2010). Hexose phosphate is allocated to sucrose synthesis and/or respiration and amino acid synthesis, depending on demand and supply balance within and among source and sink tissues across the plant structure (Malkin & Niyogi, 2000; Taiz & Zeiger, 2010).

1.3.3 Starch Synthesis

Starch is an osmotically and metabolically inactive, large polymeric storage carbohydrate composed of numerous glucose molecules (Smirnova et al., 2015) and is by far the most dominant carbohydrate store in higher plants (Taiz & Zeiger, 2010). The structure of starch can be linear or branching: the linear starch is called amylose which composed of $(1\rightarrow 4)\alpha$ -linkages, while the branching starch is called amylopectin which contains $(1\rightarrow 6)\alpha$ -linkages and $(1\rightarrow 4)\alpha$ linkages (Taiz & Zeiger, 2010). In general, amylopectin accounts for a greater portion (80-90%) of a starch granule than amylose (20-30%) (Hanashiro, 2015).

In higher plants, starch can be found in both photosynthetic plastids (chloroplast) and heterotrophic plastids (amyloplast) (Dennis & Blakeley, 2000; Taiz & Zeiger, 2010). Starch synthesis begins with the reaction between glucose 1-phosphate (G1P) and ATP to produce adenosine diphosphate glucose (ADP-glucose), which is catalyzed by ADP-glucose pyrophosphorylase (AGPase) (Dennis & Blakeley, 2000; Geigenberger, 2011; Taiz & Zeiger, 2010). This reaction releases pyrophosphate (PPi) which is split by pyrophosphatase into inorganic phosphates (Pi) in the stroma, thereby making the reaction irreversible (Yasunori Nakamura, 2015). Catalyzed by starch synthase, the non-reducing end of existing α -glucans of starch molecules is attached with ADP-glucose, elongating amylose chain which is subsequently converted into amylopectin by branching enzyme I and II (Dennis & Blakeley, 2000; Taiz & Zeiger, 2010). In both chloroplast and amyloplast, G1P is supplied by converting glucose 6phosphate (G6P) catalyzed under plastidic phosphoglucomutase (PGM) (Dennis & Blakeley, 2000; Geigenberger, 2011). Glucose 6-phosphate in chloroplasts can be supplied directly from Calvin-Cycle and indirectly from the conversion of TP, while G6P in amyloplast is imported

from Hex-P pool in cytosol supplied from the degradation of sucrose (Dennis & Blakeley, 2000; Geigenberger, 2011). Energy required for the first reaction catalyzed by AGPase is supplied by the ATP produced through photosynthesis in the chloroplasts (Geigenberger, 2011).

1.3.4 Regulating AGPase Activity

Starch synthesis is predominantly controlled by AGPase activity which is regulated by environmental stimuli and metabolic signals such as redox modulation and allosteric regulation (Geigenberger, 2011). The Redox modulation of AGPase is controlled by light-dependent ferredoxin-thioredoxin reductase through the excitation of PSI upon absorption of photon energy (Tetlow, Liu, & Emes, 2015). The reducing power of ferredoxin is transferred via ferredoxinthioredoxin reductase and thioredoxin to the small subunits of AGPase through alternating breakage and formation of a disulphide bond and free thiols (Tetlow et al., 2015). The redox modulation upregulates the reactivity of AGPase to the allosteric effectors (Geigenberger, 2011). In chloroplasts, AGPase activity is allosterically activated by TP and deactivated by Pi in the stroma (Dennis & Blakeley, 2000). The TP/Pi ratio in the stroma conveys the energy status in the source tissue, and AGPase is activated or deactivated accordingly (Geigenberger, 2011). The accumulation of starch in chloroplast by activation of AGPase under high TP/Pi ratio is thought to be designed to prevent feedback inhibition on photosynthesis (Taiz & Zeiger, 2010). Trehalose 6-phosphate (T6P) was also found to be responsible for the activity of AGPase (Paul, Primavesi, Jhurreea, & Zhang, 2008). Trehalose 6-phosphate is an intermediate sugar phosphate composed of uridine diphosphate glucose (UDP-glucose) and is synthesized in the trehalose pathway during sucrose degradation (Paul et al., 2008). Although T6P exists in significantly smaller amount compared to other sugars, studies have shown that T6P positively correlates with

the sucrose concentration and acts as a signalling sugar molecule reflecting sucrose abundance (Paul et al., 2008). It has been demonstrated that T6P inhibits sucrose non-fermenting 1-related protein kinase which inhibits the expression of APL3 gene encoding AGPase; therefore, an increase of T6P upregulates starch accumulation (Griffiths, Paul, & Foyer, 2016; Y. Zhang et al., 2009). In *Arabidopsis*, upregulating the expression of T6P synthase and T6P phosphatase activities increased and decreased starch content, respectively, in the leaves compared to the wild type, indicating the importance of T6P in regulating AGPase activity (Kolthe be et al., 2005). Additionally, the irreversible reaction from G1P to ADP-glucose ensures the strict control of starch degradation irrespective of the fluctuation of sugar content during the day (Yasunori Nakamura, 2015). In amyloplast, the allosteric regulation of starch synthesis may be slightly different: TP/Pi ratio does not regulate AGPase activity; instead, AGPase is inhibited by high amyloplastic Pi which indicates the low sucrose content in the cytosol as sucrose degradation releases Pi into the cytosol (Dennis & Blakeley, 2000).

1.3.5 Starch Degradation

During the night, the transient starch stored in chloroplasts is degraded (Taiz & Zeiger, 2010). The degradation starts with the transfer of β -phosphate to carbon 6 and carbon 3 of the glucosyl moieties of starch granules catalyzed by glucan water dikinase (GWD) and by phosphoglucan water dikinase (PGD), respectively (Smith, Zeeman, & Smith, 2005). This phosphorylation of starch granule appears to be an essential step to solubilize the granule and enable hydrolases to access the glucan chain (Zeeman, Kossmann, & Smith, 2010). A mutant line of *Arabidopsis* with downregulated GWD gene expression exhibited a greater transient starch accumulation compared to the wild-type, indicating the essential roles of GWD in the starch degradation

(Baunsgaard et al., 2005). Following the phosphorylation, internal $(1\rightarrow 4)\alpha$ -glucan linkages of the starch granule are randomly hydrolyzed by α -amylase, yielding the mix of soluble, linear and branching glucans (Smith et al., 2005). Branching glucans are broken down into a linear form by debranching enzymes, and linear glucans are hydrolyzed at every other $(1\rightarrow 4)\alpha$ -glucan linkage by β -amylase and cleaved by glucan phosphorylase, which yields maltose and glucose, respectively (Smith et al., 2005). Maltose is translocated to the cytosol and is broken down to glucose which is converted into G6P under hexokinase (Smith et al., 2005).

1.3.6 Diurnal Starch Turnover

The diurnal control of the accumulation and degradation of the starch in chloroplast are the critical strategy to prevent carbohydrate starvation during the night and ensure continuous growth throughout day and night (Smirnova et al., 2015). The starch stored in chloroplasts is often called transient starch as it is an accumulation of overflow photosynthates beyond the capacity of the sucrose export during the day (Taiz & Zeiger, 2010). However, the amount of carbohydrate stored in the transient starch is significant: in *Arabidopsis*, approximately half of the total photosynthates produced during a day is diverted to the accumulation of transient starch in leaves (Zeeman & Rees, 1999). During the night, the transient starch is degraded to allocate the carbohydrate to carbon sinks while no photosynthesis is occurring (Taiz & Zeiger, 2010). The lack of carbohydrate supply from the source tissues during the night in the starch excess mutant line (impaired starch degradation) of *Arabidopsis* showed a growth impairment, suggesting that the transient starch is the dominant carbohydrate source for plant growth during the dark period (Zeeman, Northrop, Smith, & Ap Rees, 1998). In order to prevent carbohydrate starvation during the dark period, the diurnal starch turnover in the chloroplasts is tightly

regulated by the day and night length and the circadian rhythm (Graf & Smith, 2011; Smirnova et al., 2015). Transient starch of plants growing under short day treatment was accumulated at a lower rate during the day, which degraded at a slower rate during the night, while the plants growing under long day treatment showed an opposite response (Lu, Gehan, & Sharkey, 2005). The degradation rate of transient starch was regulated by the timing of the dusk which determines the day/night ratio (Lu et al., 2005). Regardless of day length, the rate of transient starch degradation was adjusted according to the expected length of the dark period to avoid carbohydrate starvation while maximizing the use of the starch (Graf & Smith, 2011; Lu et al., 2005). At the end of the dark period, the transient starch is almost entirely degraded regardless of the length of day and night, which is repeated every 24 hours starting from dawn (Gibon et al., 2004). Plants which exhausted transient starch supply before dawn underwent carbohydrate starvation and showed a growth inhibition early in the following photoperiod (Gibon et al., 2004). The growth inhibition ceases carbohydrate utilization, consequently elevated TP level, and thus activated AGPase activity which leads to the accumulation of transient starch (Gibon et al., 2004). The exhaustion of transient starch at the end of the dark period is suggested as a strategy to reset the circadian control of starch turnover by the following night (Gibon et al., 2004).

1.3.7 Sucrose Synthesis, Transport, and Degradation

Plants translocate the photosynthates from source to sink tissues (Taiz & Zeiger, 2010). Sucrose is one of the major NSCs and is a common form of transport sugar via phloem in the majority of plant species (Lemoine et al., 2013). Sucrose is synthesized from fructose 6-phosphate (F6P) and G1P from the Hex-P pool (Dennis & Blakeley, 2000). Glucose 1-phosphate is combined with

UDP to produce UDP-glucose in the reversible reaction catalyzed by UDP-glucose

pyrophosphorylase (Dennis & Blakeley, 2000). Uridine diphosphate glucose is combined with F6P under sucrose 6^F-phosphate synthase and produces sucrose 6-phosphate which is converted under sucrose 6^F-phosphate phosphatase to produce sucrose (Dennis & Blakeley, 2000). Sucrose synthesized in mesophyll cells is exported to bundle sheath cells, phloem parenchyma cells (PP), and companion cells (CC) and enters sieve tube element (SE) via symplast and apoplast transport (Fisher, 2000; Taiz & Zeiger, 2010). Via symplast, sucrose moves through plasmodesmata by the concentration gradient, while via apoplast, sucrose is actively transported by sucrose-H⁺ symporter which requires an electrochemical proton gradient generated by adenosine triphosphatase-H⁺ (ATPase-H⁺) pump (Fisher, 2000; Taiz & Zeiger, 2010). Sucrose in SE is moved along its concentration gradient to sink tissues where sucrose is unloaded from SE into the CC (Fisher, 2000; Taiz & Zeiger, 2010). Sucrose is imported from CC into the sink cells either via symplastic or apoplastic transport (Fisher, 2000; Taiz & Zeiger, 2010). Similar to the sucrose loading mechanism, the symplastic route involves the movement of sucrose along its concentration gradient through plasmodesmata, while apoplastic transport involves sucrose-H⁺ symporter (Fisher, 2000; Taiz & Zeiger, 2010). In addition to the symplastic and apoplastic routes, the degradation of sucrose by cell-wall invertase followed by the transport of the derived hexose molecules into sink cells may contribute to the increasing rate of sucrose transport in young leaves (Kim, Mahé, Brangeon, & Prioul, 2000). In apple fruits, the lack of plasmodesmata between SE/CC complex and PP cell and the highly localized cell wall invertase throughout the fruit development suggested that the sugar transport to the sink cells was apoplastic with hexose derived from the hydrolysis of sucrose (D. P. Zhang, Lu, Wang, Duan, & Yan, 2001).

1.3.8 Carbohydrate Usage

1.3.8.1 Growth and Maintenance Respiration

Respiration provides energy for growth and maintenance of tree plant and is the primary use of carbohydrate, utilizing more than 30-60% of the total daily production of photosynthates (Kozlowski, 1992). The growth respiration occurs at the point and time of new tissue generation, whereas maintenance respiration occurs when plants maintain the functionality of the existing living biomass by renewing cellular components and proteins, maintaining ionic gradients, and synthesizing secondary metabolites to cope with stresses (Kozlowski, 1992; Vries, 1975). The ratio of growth to maintenance respiration may differ across plant structures: growth respiration is generally high in developing buds and shoots, while vines and stems show a high rate of maintenance respiration (Kozlowski, 1992). In a stand of trees, the ratio of growth to maintenance respiration is also affected by the age of the stand as an accumulation of nonphotosynthetic tissue in older trees increases maintenance respiration, which in turn reduces the relative size of growth respiration as photosynthetic capacity reaches constant with the increasing size of the stand (Cannel as cited in Kozlowski, 1992). Temperature and humidity can also affect the respiration rate of tree plants as the maintenance respiration is strongly dependent on the temperature change, to which, however, the growth respiration is independent (Adu-Bredu, Yokota, & Hagihara, 1997; Kozlowski, 1992).

1.3.8.2 Aerobic and Anaerobic Respiration

Aerobic respiration is composed of a series of processes, such as glycolysis, tricarboxylic acid (TCA) cycle, and oxidative phosphorylation (Taiz & Zeiger, 2010). In anaerobic respiration, following glycolysis, fermentation occurs instead of the TCA cycle and oxidative

phosphorylation (Taiz & Zeiger, 2010). In both respiration modes, glycolysis starts with the Hex-P or TP: Hex-P is supplied from the degradation of sucrose or starch, and TP is supplied directly from the Calvin-Cycle or the Hex-P pool via phosphorylation of F6P (Taiz & Zeiger, 2010). Glyceraldehyde 3-phosphate (GAP) from TP pool is further converted into pyruvate which, in aerobic respiration, enters the TCA cycle and is completely oxidized into CO₂, during which nicotinamide adenosine dinucleotide (NADH), flavin adenine dinucleotide, and ATP are generated (Taiz & Zeiger, 2010). The NADH synthesized thus far is used to generate an electrochemical gradient across the mitochondrial inner membrane by accumulating H^+ in the intermembrane space, and this electrochemical gradient is used by ATP synthase which generates ATPs through oxidative phosphorylation (Taiz & Zeiger, 2010). In anaerobic respiration, on the other hand, pyruvate from glycolysis enters fermentation reactions in which pyruvate is converted into lactic acid catalyzed under lactate dehydrogenase and into ethanol catalyzed under alcohol dehydrogenase via acetaldehyde (Taiz & Zeiger, 2010). Both lactate dehydrogenase and alcohol dehydrogenase oxidize NADH to NAD⁺ which is recycled as the substrate for the H⁺ during the conversion between GAP and 1,3-bisphosphoglycerate, enabling the glycolysis to be functional under anaerobic condition (Taiz & Zeiger, 2010). Due to the differences in the pathways following the glycolysis, anaerobic respiration produces a substantially lower number of ATPs per single sucrose molecule (9 ATPs) compared to aerobic respiration (60 ATPs) (Taiz & Zeiger, 2010).

1.3.8.3 Synthesis of Cell Wall Materials and Carbohydrate Source

Cell walls are structured by the complex integration of polysaccharides including cellulose, hemicellulose, pectin, and various oligosaccharides as well as lignin and proteins (Taiz & Zeiger, 2010). Among these components, cellulose is the fundamental component of plant structures as it forms microfibrils which function as a "scaffold" of cell wall structure (Hoch, 2007; Taiz & Zeiger, 2010). The commonly accepted model of cellulose synthesis involves plasma membrane-bound cellulose synthase transferring glucose from UDP-glucose to an elongating glucan chain (Verbančič, Lunn, Stitt, & Persson, 2018). UDP-glucose is also the precursor of hemicellulose and pectin (Taiz & Zeiger, 2010) and is supplied via the degradation of sucrose catalyzed by sucrose synthase and UDP-glucose pyrophosphorylase (Dennis & Blakeley, 2000). Lignin is synthesized from Hex-P and TP via phosphoenolpyruvate (PEP) and erythrose 4-phosphate via shikimic acid and pentose phosphate pathway, respectively (Taiz & Zeiger, 2010). Although found in significantly lesser amount compared to polysaccharides, proteins are also important components of cell wall matrix (Taiz & Zeiger, 2010). Protein synthesis and carbohydrate availability are strongly related as the synthetic pathways of 20 standard amino acids are branching from glycolysis and TCA cycle which sources from Hex-P pool and TP (Taiz & Zeiger, 2010).

1.3.9 Carbohydrate Partition and Allocation

In source tissues during the daytime, TP from Calvin-Cycle is either converted into transient starch (section 1.3.3) within the chloroplast or is transported to the cytosol via TP/Pi antiporter (Dennis & Blakeley, 2000; Taiz & Zeiger, 2010). In the cytosol, TP is allocated either to sucrose synthesis or to respiration in source tissues (Dennis & Blakeley, 2000; Taiz & Zeiger, 2010). Towards sucrose synthesis, TP is converted by aldolase into fructose 1,6-bisphosphate (FBP1) which is converted by fructose 1,6-bisphosphatase into F6P (Dennis & Blakeley, 2000; Taiz & Zeiger, 2010). Fructose 6-phosphate is interconverted with G6P and G1P by Hex-P isomerase

and PGM, respectively, constituting a cytosolic Hex-P pool from which F6P and G1P enter sucrose synthesis pathway (section 1.3.7) (Dennis & Blakeley, 2000; Taiz & Zeiger, 2010). Towards respiration in the source tissue, TP is converted to pyruvate which ultimately enters the TCA cycle followed by oxidative phosphorylation in aerobic conditions or enters fermentation reactions in anaerobic conditions (section 1.3.8) (Dennis & Blakeley, 2000; Taiz & Zeiger, 2010).

The allocation of photosynthates among these three major metabolic pathways (transient starch synthesis, sucrose synthesis, and respiration) in source tissues is strictly regulated according to the abundance of TP mediated by fructose 2,6-bisphosphate (Fru-2,6-P₂) functioning as a signalling molecule (Nielsen, Rung, & Villadsen, 2004). In the cytosol, a high concentration of sugar increases TP/Pi ratio as TP accumulates from the phosphorylation of F6P while Pi becomes recycled in ATP synthesis (Taiz & Zeiger, 2010). The high TP/Pi ratio inhibits the synthesis of Fru-2,6- P_2 which inhibits the synthesis of F6P from FBP1; therefore, abundant photosynthates allow the partitioning of carbohydrate towards sucrose synthesis (section 1.3.7) (Nielsen et al., 2004). Also, high TP/Pi ratio in cytosol increases TP in chloroplasts, which stimulates AGPase activity, resulting in greater transient starch accumulation (section 1.3.4) (Geigenberger, 2011). Conversely, low TP/Pi ratio in the cytosol and chloroplast limits sucrose and transient starch synthesis, respectively, while the partitioning of photosynthates towards the respiration and amino acid synthesis within the source tissue is maintained (Nielsen et al., 2004). During the dark period, however, as carbohydrates are supplied from the degradation of transient starch in the chloroplast, TP/Pi ratio in cytosol does affect carbohydrate allocation: the glucose and maltose from the degrading transient starch directly replenish G6P in the Hex-P pool from

which carbohydrate is allocated to both sucrose synthesis and respiration within the source tissue (Nielsen et al., 2004). Additionally, it has been proposed that nitrate functions as a signalling molecule regulating the carbohydrate allocation between sucrose synthesis and amino acid synthesis (Champigny & Foyer, 1992). Nitrate under illumination activates cytosolic protein kinase which activates PEP carboxylase and inactivates sucrose phosphate synthase, which partitions carbohydrate towards amino acid synthesis under high tissue nitrate concentration (Champigny & Foyer, 1992). Photosynthates partitioned to sucrose synthesis in source tissues are allocated to sink tissues via phloem transport throughout the plant structure, and the direction of the translocation is determined by the differences in the relative strength among carbon sinks (Taiz & Zeiger, 2010). However, allocation of carbohydrate may be influenced by various factors in addition to sink strength.

1.3.10 Factors Affecting Photosynthesis and Carbohydrate Partitioning

1.3.10.1 Seasonal Dynamics

The relative sink strength among sink organs varies over the course of the growing season (Pregitzer, 2003). While the demand for energy is highest during the growing season, plants utilize stored carbohydrate even during dormancy for bud development (Loescher, Mccamant, & Keller, 1990) and maintenance respiration (Kozlowski, 1992). Following the bud break, the rapid growth of new shoots is accompanied with the surge of the demand for carbohydrate; therefore, without fully functional foliage, plants need to utilize carbohydrates from the storage (Loescher et al., 1990). The onset of anthesis, even with a fully developed foliage, the rapid consumption of carbohydrate during the reproductive development may require utilization of stored carbohydrate (Loescher et al., 1990). Some species undergo anthesis and flowering before the development of

new leaves, completely relying on the carbohydrate reserve for reproductive development (Loescher et al., 1990). Anthesis and pollination of the apricot tree (*Prunus armeniaca*), for example, occurs before the development of foliage, which appeared to rely on starch reserves in the ovary (Rodrigo, Hormaza, & Herrero, 2000). After the maturation of fruits, storage tissues, such as structural wood and roots become the strongest sink; therefore, the carbohydrate synthesized during this timing is allocated to replenish the carbohydrate storage (Loescher et al., 1990). Throughout the growing season, the amount of newly assimilated carbohydrate supply may not meet the demand at certain periods which may include the period of flowering and fruit development (Loescher et al., 1990) and situation where abiotic stresses reduce photosynthetic capacity (Krasensky & Jonak, 2012; Todaka, Matsushima, & Morohashi, 2000). During such period and situation, the deficit of carbohydrate may be compensated with the supply from degrading starch reserve; therefore, the replenishment of carbohydrate storage prior to entering dormancy is critical to maintaining plant health.

1.3.10.2 Osmotic Stress

Plants under extended periods of drought or saline conditions suffer from osmotic stress which can alter carbohydrate dynamics due to reduced photosynthate production and also altered enzymatic activities (Krasensky & Jonak, 2012; Todaka et al., 2000). Limited water intake reduces turgor pressure, leading to stomatal closure, high stomatal resistance, and low carbon assimilation during drought (Taiz & Zeiger, 2010). Lupine, eucalyptus, sunflower, and grapevine showed a significant reduction of photosynthesis under water stress, which primarily due to the stomatal closure rather than an actual reduction of photosynthetic capacity, except for the grapevine (Quick et al., 1992). In the same study, leaf starch content was significantly reduced in

plants under water stress, while sucrose content was maintained similar or slightly increased compared to the watered plants (Quick et al., 1992). Reduced photosynthesis lowers TP/Pi ratio in the chloroplasts which allosterically inhibits AGPase activity; hence the accumulation of transient starch becomes inhibited (Geigenberger, 2011). Similar results were seen in water-stressed corn plants in which sucrose content was slightly elevated in mature leaves, leaf sheath, young leaves, primary roots, and adventitious roots, while hexose content in all organs showed a marked increase compared to the watered plants (Kim et al., 2000). In the same study, the comparisons of relative activities among cell wall invertase, vacuolar invertase, and cytosolic invertase showed an induced vacuolar invertase activity under the drought stress which degraded sucrose in the vacuole into hexose (Kim et al., 2000). Plants under osmotic stress induced by drought or salt stress may accumulate various osmoprotectants, which include sucrose, fructose, and glucose, to protect cellular components (Krasensky & Jonak, 2012). Osmotic stress also induces starch hydrolysis activity which degrades starch and increases soluble sugar content, thus can deplete starch reserve (Todaka et al., 2000).

1.3.10.3 Temperature Stress

Temperature and maintenance respiration are positively correlated (Adu-Bredu et al., 1997); therefore, the loss of carbohydrate caused by heat stress can be significant as more than 30-60% of the daily carbon assimilates are used for respiration under non-stressed conditions (Kozlowski, 1992; Vries, 1975). Cold stress can also alter carbohydrate allocation: in *Arabidopsis*, cold stress induced the gene expression encoding sucrose synthase, which exhibited a significant increase of hexose to sucrose ratio (Déjardin, Sokolov, & Kleczkowski, 1999).
Either in higher or lower, an extreme temperature change may cause a loss of carbohydrate in storage tissue, as plants increase respiration rate or alter carbohydrate allocation.

1.3.10.4 Nutrient Deficiency

Plants require micro and macro mineral nutrients, and the deficiency of some nutrients directly or indirectly reduces photosynthesis (Marschner, 1988). Magnesium is found in the center of the porphyrin ring of chlorophylls (Farhat et al., 2016) as well as activates Rubisco by modulating the binding site to CO_2 (Jensen, 2000). Iron is required during chlorophyll biosynthesis (Grusak, 2001) and is also found in Cytochrome b₆f complex which catalyzes the transfer of electrons from plastoquinone to plastocyanin on the electron transport chain of thylakoid membrane (Taiz & Zeiger, 2010). Manganese and Cl are required in PSII for splitting water molecules by harvesting electrons (Marschner, 1988). Therefore, deficiency of Mg, Fe, Mn and Cl can directly reduce photosynthetic capacity. Phosphorus, in addition to the central role in nucleic acids and energy transfer, plays a regulatory role in the starch synthesis and translocation of photosynthates (Marschner, 1988). Triose phosphate is exported from chloroplasts to the cytosol via TP/Pi antiporter, and the TP/Pi ratio in the chloroplast influences the AGPase activity (Geigenberger, 2011); therefore, P deficiency can cause accumulation of TP which leads to the high transient starch concentration in the chloroplast (Marschner, 1988). Similarly, Mg deficiency can alter carbohydrate partitioning: Mg binds to ATP and activates H⁺-ATPase in the plasma membrane of sieve tube cells, which enables apoplastic loading of sucrose into the phloem; therefore, Mg deficiency inhibits sucrose transport which causes the accumulation of sucrose in the cytosol and starch in chloroplast (Marschner, 1988). Therefore, P and Mg deficiency can cause accumulation of sugars in source tissues which may lead to a feedback inhibition on photosynthesis

(Goldschmidt & Huber, 2008). Also, the inhibition of sucrose transfer from the source tissues under Mg deficiency prevents translocation of carbohydrate to root, which decreases root/shoot ratio as an early sign of Mg deficiency (Farhat et al., 2016; Hermans et al., 2005), which may further exacerbate the nutrient deficiency and reduce photosynthesis.

1.3.10.5 Cultural Practices

Amount and timing of nitrogen application can affect carbohydrate dynamics in plants. With an excessive rate of nitrogen application, induced shoot growth increases leaf area index, which decreases per capita production of photosynthates due to mutual shading (Marschner, 1988). Leaves grown in shaded areas develop expanded leaf area, and thus such leaves are thinner and have less chlorophyll content compared to light-grown leaves (Marschner, 1988). The reduced photosynthesis during the high rate of carbohydrate utilization induced by the excess tissue nitrogen can result in a depletion of carbohydrate reserves (Marschner, 1988). In the wood of beach-grafted Fuji/M.26 apple trees (*Malus domestica* Borkh), increased tissue nitrogen showed a negative correlation to the total NSC (TNSC) content in the tissue, while the new growth showed an increased leaf area (Cheng & Fuchigami, 2002). Therefore, excessive nitrogen application may cause carbohydrate depletion by allocating more energy to shoot growth and result in unbalanced root/shoot ratio which may further exacerbate the carbohydrate depletion.

Carbohydrate partitioning of horticultural fruit tree crops has been culturally manipulated. Most perennial fruit crops are pruned during dormancy and trained to optimize light interception, crop load, and the balance between vegetative and fruit growth while maintaining a sustainable root/shoot ratio. This canopy management ensures that carbohydrate reserves are available for

fruit growth and remain stable over time. In other cases, pruning is performed to manage crop load to optimize fruit quality.

1.3.11 Remobilization of Secondary Carbohydrate Reserve

During the period of high demand for carbohydrate, plants may utilize carbon sources other than hexose, sucrose, or starch store to support their growth and metabolic activities (Hoch, 2007). Such "secondary" carbohydrate reserve may include lipids, fructans (Chapin, Schulze, & Mooney, 1990), and cell wall materials, which can be degraded to compensate the high carbohydrate demand (Hoch, 2007; Schadel, Blochl, Richter, & Hoch, 2009). Tilia platyphyllos and Pinus Sylvestris contained a significant amount of acylglycerol (neutral lipids) in their stem sapwood; however, unlike NSCs in branch sapwood, the acylglycerol content did not show a seasonal trend (Hoch, Richter, & Korner, 2003). Unlike starch in reserves, neutral lipids require significantly higher energy for the synthesis and degradation, which probably explains the discouraged remobilization of neutral lipids and their more extended storage period than NSCs (Hoch, 2007). Fructans are soluble fructose oligomer and polymers synthesized and stored in vacuoles in some flowering plant species, and studies have indicated that fructans improve plants' tolerance to cold and water stresses (Ritsema & Smeekens, 2003). This indication is supported by the geographic distribution of fructan-accumulating species which inhabit temperate regions experiencing frost or drought seasons. Fructan synthesis is unaffected by low temperature where starch synthesis ceases below 10°C, and therefore, fructan-accumulating species can store photosynthates at the beginning of the season and allocate the carbohydrate to an early growth (Vijn & Smeekens, 1999). Hemicelluloses are matrix polysaccharide produced via the Golgi apparatus and are critical components of both primary and secondary cell wall

(Taiz & Zeiger, 2010). Studies have shown that hemicelluloses in the endosperm of seeds are remobilized and used as a carbon source for germination (Hoch, 2007). In vegetative tissue, however, the evidence is still insufficient to support the notion that cell wall materials can function as carbohydrate storage; however, recent studies indicated a significant reduction of matrix polysaccharides under high demand for carbohydrate (Lee, Matsumura, Soga, Hoson, & Koizumi, 2007; Schadel et al., 2009). Hemicelluloses in the branch sapwood of *Carpinus betulus* decreased following the depletion of starch content prior to bud break but increased following the replenishment of starch content after the development of foliage (Schadel et al., 2009). Gene expression for glycosyl hydrolases in the cell wall of *Arabidopsis thaliana* was induced upon carbohydrate starvation simulated by exogenous sucrose content, under which, pectin, hemicellulose I, and hemicellulose II contents were significantly reduced (Lee et al., 2007). The implication for the degradation of cell wall components may include the loss of structural integrity and the reduced physical resistance to external mechanical stresses.

1.4 NSC Dynamics in Cranberry Plants

1.4.1 Seasonal Trend

Flowering, fruit set, and fruit development are the most resource demanding growth stages in cranberry plants, similar to other perennial fruit trees (Hagidimitriou & Roper, 1994). The overlap of the bud development for the following year and the current year's reproductive development increases the severity of resource limitation (Baumann & Eaton, 1986 as cited by Devetter, Harbut, & Colquhoun, 2013). Previous studies have suggested that the limitation of NSC, among all other essential resources for plant growth, affects crop yield most significantly (Eliezer E. Goldschmidt, 1999; Scholefield, Sedgley, & Alexander, 1985). Seasonal dynamics of

NSC in cranberry plant tissues in vegetative and reproductive uprights, vines, underground stems, and roots have been investigated by Hagidimitriou & Roper (1994) and showed a trend of TNSC concentration in uprights corresponding to the progression of the phenological stages over the course of the growing season. At the beginning of the season, the TNSC concentration in uprights reached the highest point followed by a dramatic decline coinciding with the timing of new growth (Hagidimitriou & Roper, 1994). This sharp decline of the TNSC by the new shoot development continued to decline through the flowering and fruit set stages and reached the lowest point during fruit development in early to mid-August (Hagidimitriou & Roper, 1994). During the current season's flowering and fruit set, inflorescence initiation and bud development for the following season occur simultaneously (Hart et al., 2015); therefore, the difference in TNSC content between vegetative and flowering uprights became significant at the onset of flowering and continued to increase until fruit maturation (Hagidimitriou & Roper, 1994). Although TNSC content started to increase after the fruit maturation, and eventually reached the highest level at the onset of dormancy, the gap in the TNSC content between vegetative and reproductive uprights remained significant at the end of the season (Hagidimitriou & Roper, 1994).

1.4.2 Carbohydrate Allocation

Roper & Klueh (1996) studied the allocation of NSC within and between uprights by tracing the locations of ¹⁴C which was assimilated through photosynthesis, and the results showed that the amount of ¹⁴C assimilated through the acropetal foliage into fruits was significantly higher compared to flowers within the reproductive upright, suggesting that a developing fruit is a stronger carbon sink. However, Roper & Klueh (1996) also found that the ¹⁴C assimilated

through basipetal foliage was not translocated to the fruits or flowers, which may suggest a switching of carbon source from the old to new foliage (Hagidimitriou & Roper, 1995; Roper, Stang, & Hawker, 1992).

1.4.3 Carbohydrate Limitation and Associated Growth Patterns

Cranberry plants exhibit a biennial bearing: yield data has shown alternating seasons with low and high yield (Roper, 2006). A recent study investigated a possible enhancement of return bloom in newly introduced cultivars suggested that the biennial bearing could not simply be explained by the resource limitation (Devetter et al., 2013). Nonetheless, a previous study indicated that the resource limitation, particularly of carbohydrate, during the overlapping timing of current year's reproductive growth and following year's inflorescence initiation and bud development had an impact on the frequency of mix buds formation (Baumann & Eaton, 1986 as cited by Devetter et al., 2013). The relatively greater reduction of TNSC in reproductive uprights after the current season's reproductive development seen in the previous study (Hagidimitriou & Roper, 1994) may suggest that resource limitation prevents flowering uprights from producing berries across consecutive years. Another characteristic which may be associated with carbohydrate limitation is the low percent fruit set. As discussed earlier, only less than 40 to 50 percent of flowers on an upright will set fruit (Hart et al., 2015). Birrenkott & Stang (1990) investigated the cause of acropetal fruiting and the high abortion rate of upper flowers by comparing the percent fruit set of the acropetal flowers after removing two basipetal flowers, and the result showed a significant increase of the percent fruit set in the acropetal flowers compared to the control, suggesting that the resource limitation influenced the percent fruit set within an upright. In a similar study, Brown & Mcneil (2006) showed a consistent result; however, it was

suggested that the acropetal fruit bearing might be an adaptive strategy to maximize reproductive success by increasing pollen with a large number of flower or by producing extra flowers for ensuring fruit set in case of problems with the basipetal flowers.

Chapter 2: Characterization of Soil and Plant Conditions of American Cranberry (*Vaccinium macrocarpon*) in Cranberry Field Decline Syndrome in British Columbia

2.1 Introduction

American cranberry is a low-trailing, perennial, and woody vine naturally inhabiting cool, acidic, and moist environments, such as peat bogs and marshes in temperate regions (Vander Kloet, 1988). The plant structure consists of uprights (vertical shoots), runners (horizontally trailing stolons), stems, underground stems, and fibrous, shallow root system (Bernadine et al., 2002); which collectively form a low-lying, mat-like canopy (Eck, 1990). Primary shoot growth occurs at the apical meristem formed at the tip of uprights but also occurs at axillary positions on runners and vines (Bernadine et al., 2002). Upright density varies in the range of 150-700 uprights per square foot area (\cong 900 cm²) (Bernadine et al., 2002). Uprights and runners accumulate over the existing biomass, which can lead to the formation of a deep canopy. Cranberries tend to be biennial bearing, and therefore uprights typically alternate between vegetative buds, which contain only leaf primordia, and mixed buds, which contain both flower and leaf primordia (Eaton as cited in DeVetter, Colquhoun, Zalapa, & Harbut, 2015). Each upright with a mixed bud can produce 2-7 flowers (Averill et al., 2008), which are formed singly and acropetally along the stem between the previous and current seasons' foliage (Roper, 1997); however, typically only less than 40 to 50 percent of flowers on an upright will set fruit (Hart et al., 2015). The foliage can persist on both flowering and vegetative uprights and functional in photosynthesis for up to two growing seasons (Eck, 1990).

Cranberry production beds can be largely divided into two types of soils: organic soil (peat or muck soil) and sand (DeMoranville, 2008). Cranberry beds are established in peatlands that had been previously harvested, or in constructed sand beds which creates a well-drained, acidic environment (DeMoranville, 2008). A sand-based cranberry bed in Massachusetts contains less than 3.5% of organic matter and approximately 3% clay and silt in the rooting environment (DeMoranville, 2008). Periodic sand application (every 2-5 years) on established cranberry beds is carried out in Massachusetts for both pest management and stimulation of root growth (DeMoranville, 2008). On the other hand, cranberry beds in BC and some areas in Washington State are established directly into the existing organic soil without layering sand over the top (Bernadine et al., 2002).

In recent years, a condition called Cranberry Field Decline (CFD) has developed in several cranberry beds in the Lower Mainland of British Columbia (BC). Affected beds develop patches of stressed vines, reduced upright density, and complete collapse of the canopy. A study of soil characteristics in CFD-affected beds in 2014 (Lavkulich, 2014) and 2015 (Someya & Harbut, 2015) indicated that humification of peat soil might be creating poorly aerated growing conditions for the cranberry roots. Visual assessment of root samples collected from CFD-affected beds showed a lower number of feeder roots and stunted growth of the root tips compared to samples taken from healthy beds (British Columbia Cranberry Marketing Commission, 2014). Moreover, a large mass of canopy was easily peeled off from the soil surface by hand with very little force in the vicinity of CFD-affected areas (*Figure 2-1*). In comparison, the canopy in healthy beds was stable as it was tightly anchored to the soil with healthy roots, suggesting that density and stability of roots were reduced in CFD affected areas.

Characterization of canopy growth in 2015 showed a trend indicating that brown canopy (lower canopy without leaves) depth decreased faster than green canopy (upper canopy retaining leaves) as CFD symptoms progressed (Someya & Harbut, 2015). The objective of the present study was to investigate the mechanisms of CFD. In particular, bed condition was characterized by assessing the differences in soil pH, soil redox potential, root health, upright density, canopy depth, and yield among three levels of CFD conditions.

2.2 Materials and Methods

2.2.1 Site Locations and Descriptions

Four cranberry beds exhibiting CFD symptoms were selected in the Lower Mainland in Southwestern BC. Bed A was located in south Burnaby, Bed B and Bed C were located on the north side of Lulu Island (City of Richmond), and Bed D was located in North Delta. (*Figure* 2-2). According to a study in 2015, average peat depth was over 100cm in Bed A, Bed B and Bed D but was approximately 30cm underlaid with clay-rich soil in Bed C (Someya & Harbut, 2015). The beds were isolated from each other by location and managed by different growers. In response to the manifestation of CFD symptoms, additional drain tiles were installed in the declining areas in Bed D in 2014. Also, in Bed A and Bed B, additional drain tiles were installed parallel to the existing drain tiles in 2016. No additional drain tile was installed in Bed C. Cultivar was Stevens in Bed A, Bed B and Bed D and was Bergman in Bed C.

2.2.2 Sampling Locations

In each bed, three areas were identified by visually assessing the canopy density to determine the severity of CFD symptoms: declining, transitional, and normal (*Figure 2-3*). Declining areas

were characterized by a substantial reduction in canopy density and a complete collapse of the canopy in the center. Samples from declining areas were taken at the areas adjacent to the declining edge as there was no living plant tissue to collect in the center of the declining area. A transitional area was defined as the area between the declining edge and a parallel line measured 50 cm away from the declining edge. Samples from transitional areas were taken along this parallel line. A normal area was defined as the area that was ≥ 10 m away from the closest declining patch and showed no CFD symptoms. One exception was in Bed A, where declining and normal areas were a maximum of 5 m apart due to the severity of CFD in this bed.

2.2.3 Data Collection

2.2.3.1 Soil Characteristics

Soil samples were collected using a soil probe (diameter = 2 cm) from the surface to 10 cm into the soil, yielding approx. 20 cm³ of soil for each sample. Sampling was replicated three times and carried out for each CFD condition in each bed in 2016 for redox potential and 2017 for pH. The measurements were carried out in the lab. For pH, each sample was homogenized, of which approximately 10 g was subsampled, added with the 20 mL of distilled water, stirred vigorously, left at room temperature for 1 hour, and measured for pH (InLab® Expert Pro-ISM, pH/Ion meter S220, Mettler Toledo). For redox potential, each soil sample was mixed with 40 mL of distilled water, stirred vigorously in a container, sealed with plastic film, and left at room temperature for 2 hours. An ORP sensor was placed in each sample and left for 5 min before the measurement was taken. Redox potential was measured using a portable ORP meter (CDS107, OMEGA Engineering, Inc.).

2.2.3.2 Root health

Root health was estimated with a new method called a "pull-test" which approximates the unrooted volume under the canopy (UVC). At each sampling location, the plant canopy was grabbed from the soil surface by hand and pulled up perpendicular to the soil surface. The height of the pull (H) was measured in centimetres with a ruler. Stake flags were placed at four points (P, Q, R, and S) to define the extent of the pulled area, and the distance of PR and QS were measured in centimetres (*Figure 2-4*). The approximated UVC was then calculated as: UVC $[cm^3] = (PR * QS * H) / 4$. The UVC measurement was replicated three times and carried out for normal and transitional areas in each bed in 2016 and 2017. Additionally, three UVC measurements were taken every month from May to October in both 2016 and 2017, except for Bed B in September 2016 and Bed D in 2016 (data not collected). The UVC was not measured in declining areas as the canopy density was too low for the test.

2.2.3.3 Upright Density

At each sampling location, a 30 cm square quadrat was placed, and its position was marked in the bed with two stake flags at the two corners on the top. Upright density was measured by counting the number of uprights within the quadrat for total and flowering uprights. All the uprights were counted regardless of their growth level, developmental stage, or health, except for the dead ones. The flowering upright ratio was calculated from dividing flowering upright density by total upright density. The upright density was measured in all beds in early to mid-August in 2016 and mid-June in 2017. The stake flags were left in the beds throughout the season until the completion of harvest for yield analysis.

2.2.3.4 Canopy Depth

At each sampling location, total and brown canopy depth were measured using a ruler inserted in the canopy perpendicular to the soil surface. Green canopy depth was obtained by subtracting brown canopy depth from the total canopy depth. Total canopy depth was defined as the distance from the soil surface to the approximated average height of the canopy within the 30 cm² area of each sampling location. Brown canopy depth was defined as the distance from the soil surface to the position of the canopy where foliage began to appear. The green canopy was defined as the upper portion of the canopy where the foliage was retained on the vine (*Figure 2-5*). The measurements were carried out at the same time as upright density measurements in both years. Additional three measurements were taken for each CFD condition in May, June, and July in 2016 in Bed A, Bed B, and Bed C and June, July, and Aug in 2017 in all beds.

2.2.3.5 Yield Estimate

Prior to commercial harvest, the industry standard procedure to determine yield estimate per acre was followed. A 30 cm square quadrat was placed on previously flagged locations, and berries within the quadrat were harvested to measure yield (total weight) per quadrat for each CFD condition in each bed in each year. Yield per acre was calculated by converting the yield per quadrat into lbs per acre. Yield is reported in the industry standard of barrels per acre (one barrel = 100 lbs).

2.2.4 Statistical Analysis

The data were structured with three levels of fixed factors; CFD condition (3 levels: declining, transitional, and normal), site (4 levels: Bed A, Bed B, Bed C, and Bed D), and year (2 levels:

2016 and 2017), and consisted of 8 dependent variables. Due to the inherent variability and the differing sample size among beds and between years, data were analyzed separately for each bed and each year for all dependent variables. The significance level (α) was set to 0.05. All statistical tests were carried out using statistical program R with appropriate program packages (R Core Team, 2018).

2.2.4.1 Soil Characteristics

Data on soil characteristics consisted of 2 dependent variables, soil pH and redox potential. A one-way analysis of variance (ANOVA) was carried out separately for each bed for each dependent variable with CFD as the independent fixed factor to test the difference among means. Post hoc multiple comparisons among CFD conditions were carried out on the significant differences with Tukey's Honestly Significant Difference (HSD) test.

2.2.4.2 Root Health Estimate

A Two-Sample Wilcoxon Rank Sum Test was carried out for each bed for each year for UVC with CFD condition as the independent variable (2 levels: transitional and normal) to test the difference between medians.

2.2.4.3 Upright Density

Upright density data consisted of 2 dependent variables, total upright density and flowering upright ratio. A One-Way ANOVA was carried out for each bed for each year for each dependent variable with CFD condition as the independent fixed factor to test the difference

among means. Post hoc multiple comparisons among CFD conditions were carried out on the significant differences with Tukey's HSD test.

2.2.4.4 Canopy Depth

Canopy depth data consisted of 2 dependent variables, green and brown canopies. A One-Way ANOVA was carried out for each bed for each year for each dependent variable with CFD condition as the independent fixed factor to test the difference among means. Post hoc multiple comparisons among CFD conditions were carried out on the significant differences with Tukey's HSD test. For the mean differences of brown canopy depth among CFD conditions in Bed A in 2017, Bed C in 2016, and Bed D in 2017, due to the high heteroscedasticity of the residuals, a Weighted Least Square method was used to carry out the ANOVA test.

2.2.4.5 Yield Estimate

A One-Way ANOVA was carried out for each bed and year for yield estimate with CFD condition as the independent fixed factor to test the difference among means. Post hoc multiple comparisons among CFD conditions were carried out on the significant differences with Tukey's HSD test.

2.3 Results

2.3.1 Soil pH and Redox Potential

The mean soil pH among CFD conditions was significantly different in Bed B and Bed D but was similar in Bed A and Bed C. Post hoc multiple comparisons on the significant differences showed that the mean soil pH was lowest in normal areas in Bed B. In Bed D, however, while the mean soil pH was significantly lower in normal areas compared to transitional areas, the difference was insignificant between normal and declining areas (*Table 2-1, Figure 2-6*). The mean soil redox potential among CFD conditions was significantly different in Bed B but was similar in Bed A, Bed C, and Bed D. Post hoc multiple comparisons on the significant differences showed that the mean redox potential was significantly higher in normal areas compared to transitional and declining areas in Bed B. A similar trend was observed (insignificant) in Bed D; however, the trend was inconsistent compared to Bed A and C where redox potential was lowest (insignificant) in normal areas (*Table 2-2, Figure 2-7*).

2.3.2 Root Health

The median of UVC was generally higher in transitional areas compared to normal areas. The difference of the median of UVC was significant in Bed B and Bed C in both years but was insignificant in Bed A and Bed D in both years (*Table 2-3*, *Figure 2-8*).

2.3.3 Upright Density

The mean total upright density was significantly different among CFD conditions in all beds in both years. Post-hoc multiple comparisons indicated that the mean total upright density was significantly lower in declining areas compared to transitional and normal areas in all cases. However, the differences in the mean total upright density between transitional and normal areas were insignificant in all cases, except for Bed A in 2017 and Bed C in 2016 (*Table 2-4, Figure 2-9*). The mean flowering upright ratio among CFD conditions was significantly different in Bed A in 2017, Bed C in 2017, and Bed D in both years. In Bed B and Bed C, the mean flowering upright ratio was mostly similar among CFD conditions. In Bed D, post hoc multiple

comparisons showed that the mean flowering upright ratio was significantly higher in normal and transitional areas compared to declining areas. In Bed A, the mean flowering upright ratio was highest in transitional areas in both years, and the difference was significant in 2017. Post hoc multiple comparisons indicated that the mean flowering upright ratio was highest in transitional areas in Bed A in 2017 (*Table 2-5, Figure 2-10*).

2.3.4 Canopy Depth

In Bed A, Bed B, and Bed C, the mean green canopy depth among CFD conditions was significantly different in both years and showed a trend that the difference in green canopy depth was generally smaller between normal and transitional areas compared to between transitional and declining areas. However, post hoc multiple comparisons showed that the mean green canopy depth was greater in normal areas compared to transitional areas in all cases, except for Bed C in 2016. The mean green canopy depth was significantly lower in declining areas compared to transitional and normal areas in all cases. In Bed D, the mean green canopy depth among CFD conditions was significantly different in 2017, and post hoc multiple comparisons showed that the mean green canopy depth was similar between normal and transitional areas and significantly lower in declining areas compared to transitional and normal areas (Table 2-6, Figure 2-11). In Bed A, Bed B, and Bed C, the mean brown canopy depth among CFD conditions was significantly different in both years and showed a trend that brown canopy depth constantly declined from normal, transitional, to declining areas. Post hoc multiple comparisons showed that the differences between normal and transitional areas and transitional and declining areas were significant in all cases, except for the difference between normal and transitional areas in Bed B in 2016. In Bed D, the mean brown canopy depth was significantly different in

2017, and post hoc multiple comparisons showed that the mean brown canopy depth was similar between normal and transitional areas but was significantly lower in declining areas compared to transitional and normal areas (*Table 2-7*, *Figure 2-11*).

2.3.5 Yield Estimate

The mean yield estimate among CFD conditions was significantly different in Bed A in both years, Bed B in 2017, and Bed D in both years. Post hoc multiple comparisons on the significant differences showed that the mean yield estimate was highest in transitional areas in Bed A in 2017. In the same bed in 2016, although the difference was insignificant, the trend indicated that the mean yield estimate was highest in transitional areas. However, in other beds, the mean yield estimate was either similar among CFD conditions (Bed C in both years) or lowest at declining areas and generally increased towards normal areas (Bed D in both years) (*Table 2-8, Figure 2-12*).

2.4 Discussion

Characterization of CFD-affected beds in the Lower Mainland of British Columbia was carried out for soil condition and plant growth. Neither soil pH nor redox potential showed a distinct or consistent relationship with CFD condition among beds. The UVC showed a strong relationship with CFD condition, suggesting a significant reduction of root health with the increasing severity of CFD. Total upright density was relatively stable from normal to transitional areas but declined sharply from transitional to declining areas. The flowering upright ratio among CFD conditions did not show a distinct or consistent relationship among beds. Brown canopy depth constantly decreased with the severity of CFD; however, green canopy depth declined slowly from normal to transitional areas and sharply from transitional to declining areas. Yield estimate among CFD conditions did not show a consistent trend among beds, which corresponded to the flowering upright ratio.

2.4.1 Soil Characteristics

Soil pH probably has no relationship with CFD conditions as soil pH showed no distinct or consistent trend with CFD condition and was within the optimal range for cranberry plant growth (4.0-5.5) (Hart et al., 2015) in all beds. The lack of relationship between soil redox potential and the severity of CFD may suggest that there is no significant difference in oxygen level among soils in CFD conditions. However, a preliminary study evaluating soil respiration in CFD-affected beds showed that soils in declining areas emitted a greater amount of methane gas compared to the normal areas (personal communications: Dr. Paul Jassal and Dr. T. A. Black, Biometeorology Group, Land and Food Systems, UBC, Vancouver – Unpublished data), indicating that the soils in declining areas were more hypoxic (Fiedler, Vepraskas, & Richardson, 2007). Also, a previous study evaluating the level of soil humification (von Post index) in CFD-affected beds in 2015 indicated a possible relationship between the bed health and soil humification (Someya & Harbut, 2015). As humification of organic soils reduces saturated hydraulic conductivity (K_{sat}) (Verry et al., 2011), soils in CFD-affected beds may generally be in hypoxia.

In the Lower Mainland of British Columbia, the quality of the organic soils may vary significantly among and within beds due to the differences in humification level influenced by the depth of the existing organic soil. Organic soils located deeper in the soil profile are

generally more degraded as the deepest profile of the peat is predominantly composed of an easily decomposable organic residue derived from aquatic organisms overlaid by the profile that is composed of relatively easily decomposable herbaceous vegetation (Verry *et al.*, 2011). As most of the cranberry beds in the Lower Mainland of British Columbia are established over the post-harvest peatland, where the peat had been mined to close to the mineral profile, the existing peat might be highly degraded.

The degree of humification is the most important property of peat as it influences soil porosity and pore sizes (Boelter, 1966; Verry *et al.*, 2011), which influences drainage of beds. Maintaining proper drainage and aeration in cranberry beds is critical for the productivity (Pelletier, Gallichand, Gumiere, & Caron, 2016) as cranberry plants require well-drained beds for healthy root growth (DeMoranville, 2008). Caron et al. (2016) suggested that optimal soil water matrix potential for cranberry plant was between -4.0 and -7.0 kPa in a sand-based bed in Wisconsin, U.S.A. and reported that deviation from the range lowered photosynthesis which resulted in the reduction of yield by up to 57%. A previous study showed that while K_{sat} of moderately humified organic soil (von Post H = 5) was 32cm/h, which is similar to typical beach sand (K_{sat} = 36cm/h) (Brady & Weil, 2010), K_{sat} of highly humified organic soils (von Post H > 7) was reduced to 1.5cm/h (Verry et al., 2011), confirming that highly humified organic soil has very low drainage.

The soil pH and redox potential measured in this study might be influenced by differing management practices such as irrigation and fertilization among farms. Variability in timing and duration of irrigation can result in a substantial difference in soil moisture content among beds at

the time of sampling. The differing degree of vegetation cover among CFD conditions influences evaporation and evapotranspiration, which may further confound the factors influencing soil moisture content. Depending on the chemistry of irrigation water, varying moisture content in the soil samples can affect pH reading. Also, the differing rate of fertilizer application among the farms can alter soil pH as a larger portion of fertilizer applied in declining areas may be left unused by the plants and alter the soil chemistry more than in transitional and normal areas. Redox potential is directly influenced by the presence of electron acceptors including hydrogen ions, to which redox potential is negatively correlated (Fiedler et al., 2007). Therefore, due to the variability in management practices which may alter soil pH among beds, evaluation of the degree of soil aeration in cranberry beds in BC with redox potential may be challenging. Future research may require an alternative approach such as evaluating humification degree based on chemical compositions to compare the degree of aeration in the soils among CFD conditions.

2.4.2 Estimated Root Health under CFD Conditions

The strong relationship between UVC and CFD condition suggested that root health declines with the increasing severity of CFD. A significantly lower UVC in normal areas compared to the transitional areas seen in Bed B and Bed C suggests that root health declines in the early phase of CFD development. The relatively similar UVC between transitional and normal areas in Bed A, which is also similar to transitional areas in Bed B and Bed C, may indicate that the actual CFD condition in normal areas in Bed A is close to transitional areas due to the shorter distance (< 5 m) between transitional areas and the nearest declining edge compared to the other beds. The similar UVC between transitional and normal areas in Bed D, which is similar to the normal areas in Bed B and Bed C, may indicate that the actual CFD condition of transitional areas in Bed B and Bed C, may indicate that the normal areas in Bed B and Bed C, may indicate that the actual CFD condition of transitional areas in Bed B and Bed C, may indicate that the actual CFD condition of transitional areas in Bed B and Bed C, may indicate that the actual CFD condition of transitional areas in Bed B and Bed C, may indicate that the actual CFD condition of transitional areas in Bed B and Bed C, may indicate that the actual CFD condition of transitional areas in Bed B and Bed C, may indicate that the actual CFD condition of transitional areas in Bed B and Bed C, may indicate that the actual CFD condition of transitional areas in

Bed D is similar to normal areas, which might be due to the drain tiles intersecting declining areas installed in 2014. In this bed, excessive soil moisture may have been a part of the cause of CFD, and the improvement of drainage might allow plants to recover from severe CFD symptoms. Additional drain tiles were installed in Bed A and Bed C in 2016 as well; however, the results may show no indication of an impact on UVC, which might be due to the time since the installation until the data collection of present study and the distance between the additional drain tiles and the transitional areas. As to the practicability of the pull-test, its simple procedure will allow growers to carry out the test without additional off-site work. As the results suggested, a strong relationship between UVC and the early phase of CFD development can be useful in diagnosing CFD before the symptoms become advanced. Although the test is subjective, UVC at CFD-affected areas measured by two different research personnel fell within a reasonable range, suggesting that the results would be reproducible given the methodology was thoroughly followed. Overall, the result indicated a low density and weak anchoring points of roots associated with the increasing severity of CFD, which is consistent with the observations that canopy located adjacent to declining areas in CFD-affected beds was peeled off easily by hand with a minimum force.

2.4.3 Impact of CFD on Canopy Structure

The changes of canopy structure in CFD-affected beds are unnoticeable between normal and transitional areas in fields; however, the canopy density declines sharply beyond transitional areas and collapses in declining areas. The results suggest that, during the early phase of CFD development, relatively stable upright density and the relatively slow decline of green canopy depth maintain the apparent health of the upper canopy. In the lower canopy, brown canopy

depth constantly declines from normal to declining areas, which, however, is masked by the seemingly healthy upper canopy. Beyond transitional areas, while brown canopy is continuously and constantly declining, upright density and green canopy depth sharply declines to the level which renders the changes in canopy structure highly conspicuous. Such differences in the canopy structure between pre- and post-transitional areas may be due to carbohydrate deficit caused by reduced carbon assimilation and overutilization of carbohydrate reserve. As previously discussed, CFD development is strongly related to the reduction in root health, which suggests that photosynthesis may be reduced with the increasing severity of CFD. The reduction of carbon assimilation is probably compensated by the utilization of carbohydrate reserve in brown canopy, which can sustain the shoot development and growth between normal and transitional areas. However, beyond transitional areas, the remaining carbohydrate reserve in declining brown canopy may not be able to support shoot development and growth. Therefore, changes in canopy structure in CFD-affected beds are subtle and unnoticeable in the early phase of CFD development as relatively stable shoot development and growth masks declining brown canopy depth; however, the changes become highly visible in fields beyond the threshold as the whole canopy collapses sharply.

2.4.4 Implications for Yield Components

Flowering upright ratios and yield estimates showed no distinctive or consistent relationship with CFD condition among beds; however, there were some recognizable patterns by bed. In Bed A, yield estimate was highest in transitional areas in both years, which may be due to a stress-induced flowering which can be seen in many plant species (Takeno, 2012). Violet variety of *Pharbitis nil*, short-day plants, under long-day and poor-nutrient treatments, for instance,

induced flowering and inhibited vegetative growth (Wada, Yamada, Shiraya, & Takeno, 2010). The other recognizable yield pattern was the possible biennial bearing in normal areas in Bed A and transitional areas in Bed D. As previously discussed, the actual health of normal areas in Bed A may be similar to transitional areas. In this bed, the high yield under the moderate stress from CFD in normal areas in 2016 might have impacted the bud development for the 2017 season. A previous study suggested that the carbohydrate limitation during inflorescence initiation for the following season had an impact on mixed buds formation (Baumann & Eaton, 1986 as cited by Devetter *et al.*, 2013). In other beds, yield generally declined with the severity of CFD, which is due to the proportional reduction of flowering-upright density to the declining total upright density. Additionally, yield in normal areas in Bed D was sustained at a high level in two consecutive years, which is consistent with the canopy characteristics and root health that the normal area in Bed D is significantly healthier than other beds. Overall, yield does not show a consistent trend with the increasing severity of CFD among beds; however, the trends of yield estimate might indicate differences in the stress level of plants among beds.

2.4.5 Cultivar Difference in Growth Characteristics under CFD conditions

The results generally showed a similar trend of UVC, upright density, and canopy depth between Stevens (Bed A, Bed B and Bed D) and Bergman (Bed C) among CFD conditions, which may suggest that these cultivars were equally affected by CFD within the scope of the present study. However, to fully understand cultivar differences in growth characteristics under CFD development, it may require the involvement of other cultivars grown under similar management practices.

2.5 Conclusion

CFD-affected cranberry beds in the Lower Mainland of BC were characterized by the assessment of soil conditions and plant growth. Within the scope of the present study, the results suggested that pH and redox potential had no relationship with the increasing severity of CFD. A strong relationship between UVC and CFD conditions suggested that root health was strongly related to the increasing severity of CFD. From normal to transitional areas, the development and growth of uprights were relatively unaffected, while brown canopy depth constantly declined from normal to declining areas. Beyond transitional areas, upright density and green canopy depth declined abruptly, leading to a complete collapse of the canopy in declining areas. Unlike the vegetative canopy growth, the response of reproductive growth to the CFD conditions did not show a consistent trend among beds.

Advancement of CFD condition beyond the transitional areas can result in the significant loss of yield. As cranberry plants between normal and transitional areas generally appeared to be capable of maintaining the upright density and green canopy depth, alleviation of possible stress factors early in the CFD development may allow the plants to recover. Therefore, it is critical to detect early signs of CFD development, which can be done by understanding the general characteristics of canopy structure and root health.

					Soil pl										
Dal		Decl	ining		Transitional			Nor	mal	ANOVA	Tul	Tukey's HSD (Pr)			
Deu	n	Mean	SE	n	Mean	SE	n	Mean	SE	(Pr)	D-T	D-N	T-N		
А	9	4.262	0.036	9	4.250	0.036	9	4.356	0.067	0.260		-			
В	9	4.369	0.055	9	4.308	0.068	9	4.084	0.058	0.007	0.758	0.008	0.040		
С	9	4.736	0.106	9	4.721	0.089	9	4.783	0.035	0.856		-			
D	9	4.900	0.078	9	4.984	0.083	9	4.688	0.053	0.024	0.695	0.120	0.022		

Table 2-1 Summary statistics of soil pH under CFD conditions: declining (D), transitional (T), and normal (N). n: sample size. SE: standard error of the mean. Pr: probability value. Significance level: *α* = 0.05.

Table 2-2 Summary statistics of soil redox potential (mV) under CFD conditions: declining (D), transitional (T), and normal (N). n: sample size. SE: standard error of the mean. Pr: probability value. Significance level: $\alpha = 0.05$.

	_												
Dal		Declir	ning		Transitional			Nor	mal	ANOVA	Tuk	ey's HSD	(Pr)
Bed	n	Mean	SE	n	Mean	SE	n	Mean	SE	(Pr)	D-T	D-N	T-N
А	3	174.97	2.40	3	176.33	2.05	3	166.53	6.06	0.243		-	
В	3	154.90	3.16	3	164.60	6.60	3	187.63	3.380	0.007	0.366	0.006	0.030
С	3	151.97	4.356	3	151.90	3.75	3	137.37	4.48	0.078		-	
D	3	121.43	6.64	3	132.00	4.90	3	146.60	6.71	0.071		-	

			UV	C (cm ³)		
Vaar	Dad	Tr	ansitional	No	ormal	Wilcoxon Rank Sum Test
rear	Beu	n	Median	n	Median	(Pr)
2016	А	21	1428	20	704	0.058
2017	А	20	2337	21	1189	0.208
2016	В	18	2030	18	264	< 0.001
2017	В	21	1610	21	425	< 0.001
2016	С	21	1054	21	416	0.001
2017	С	21	2504	21	404	< 0.001
2016	D	3	204	3	138	0.400
2017	D	21	297	21	169	0.138

Table 2-3 Summary statistics of volume under the canopy under CFD conditions: transitional and normal. n: sample size. Pr: probability value. Significance level: $\alpha = 0.05$.

Table 2-4 Summary statistics of total upright density (number of uprights / 30 cm square area) under CFD conditions: declining (D), transitional (T), and normal (N). n: sample size. SE: standard error of the mean. Pr: probability value. Significance level: $\alpha = 0.05$.

			Tot	tal uprigh	t density	y (number	of uprig	,hts / [900						
Veen	Dad		Decli	ning		Transi	tional		Nor	mal	ANOVA	Tuk	ey's HSD (P	r)
rear	веа	n	Mean	SE	n	Mean	SE	n	Mean	SE	(Pr)	D-T	D-N	T-N
2016	А	3	105.0	12.3	3	496.3	33.6	3	564.0	33.7	< 0.001	< 0.001	< 0.001	0.284
2017	А	3	152.7	10.3	3	440.3	38.8	3	597.3	17.6	< 0.001	< 0.001	< 0.001	0.011
2016	В	3	161.7	13.0	3	558.3	19.2	3	641.3	72.0	0.001	0.002	0.001	0.425
2017	В	3	144.0	11.6	3	514.0	41.6	3	568.0	21.4	< 0.001	< 0.001	< 0.001	0.411
2016	С	3	178.7	16.6	3	405.0	37.5	3	572.3	36.2	< 0.001	0.006	< 0.001	0.022
2017	С	3	229.7	33.8	3	685.7	31.3	3	751.0	25.9	< 0.001	< 0.001	< 0.001	0.349
2016	D	3	152.0	20.1	3	472.7	35.3	3	460.3	15.9	< 0.001	< 0.001	< 0.001	0.937
2017	D	3	144.3	34.7	3	637.7	28.9	3	567.0	39.9	< 0.001	< 0.001	< 0.001	0.383

					Flo	wering upr								
V	Dad		Decli	ning		Transi	tional		Nor	mal	ANOVA	Tuk	ey's HSD	(Pr)
rear	веа	n	Mean	SE	n	Mean	SE	n	Mean	SE	(Pr)	D-T	D-N	T-N
2016	А	3	0.28	0.03	3	0.38	0.1	3	0.28	0.08	0.576			
2017	А	3	0.24	0.04	3	0.43	0.03	3	0.11	0.04	0.001	0.016	0.070	0.001
2016	В	3	0.22	0.07	3	0.19	0.06	3	0.23	0.05	0.875			
2017	В	3	0.34	0.01	3	0.32	0.03	3	0.32	0.06	0.921			
2016	С	3	0.14	0.03	3	0.11	0.01	3	0.13	0.02	0.570			
2017	С	3	0.16	0.01	3	0.11	0.02	3	0.23	0.01	0.005	0.112	0.063	0.004
2016	D	3	0.06	0.03	3	0.38	0.06	3	0.34	0.05	0.007	0.010	0.016	0.885
2017	D	3	0.01	0.01	3	0.22	0.02	3	0.37	0.02	< 0.001	0.001	< 0.001	0.004

Table 2-5 Summary statistics of flowering upright ratios (flowering / total upright density) under CFD conditions: declining (D), transitional (T), and normal (N). n: sample size. SE: standard error of the mean. Pr: probability value. Significance level: $\alpha = 0.05$.

Table 2-6 Summary statistics of green canopy depth under CFD conditions: declining (D), transitional (T), and normal (N). n: sample size. SE: standard error of the mean. Pr: probability value. Significance level: $\alpha = 0.05$.

					Green	canopy d	epth (cm	ı)						
Voor	Pad		Declining			Transi	tional		Nor	mal	ANOVA	Tu	key's HSD ((Pr)
Teal	Beu	n	Mean	SE	n	Mean	SE	n	Mean	SE	(Pr)	D-T	D-N	T-N
2016	А	12	6.00	0.37	12	7.67	0.41	12	11.25	0.41	< 0.001	0.015	< 0.001	< 0.001
2017	А	12	5.68	0.22	12	11.38	0.30	12	13.03	0.20	< 0.001	< 0.001	< 0.001	< 0.001
2016	В	15	7.13	0.39	15	9.27	0.57	15	11.20	0.69	< 0.001	0.027	< 0.001	0.050
2017	В	12	5.97	0.26	11	10.12	0.39	12	11.97	0.22	< 0.001	< 0.001	< 0.001	< 0.001
2016	С	12	6.92	0.45	12	14.25	0.46	12	13.92	0.58	< 0.001	< 0.001	< 0.001	0.886
2017	С	15	6.22	0.33	15	10.95	0.20	14	12.01	0.21	< 0.001	< 0.001	< 0.001	0.015
2016	D	3	NA	NA	3	11.33	0.88	3	8.00	0.58	0.034		-	
2017	D	9	7.11	0.37	12	10.95	0.37	12	10.81	0.45	< 0.001	< 0.001	< 0.001	0.964

		_			Brow	n canopy d	lepth (cm	l)						
Veen	Dad		Declining			Transi	tional		Nor	mal	ANOVA	Tu	key's HSD ((Pr)
rear	веа	n	Mean	SE	n	Mean	SE	n	Mean	SE	(Pr)	D-T	D-N	T-N
2016	А	12	3.67	0.36	12	7.25	0.52	12	12.58	0.57	< 0.001	< 0.000	< 0.000	< 0.000
2017	А	12	3.86	0.21	12	8.18	0.41	12	11.85	0.58	< 0.001	< 0.000	< 0.000	< 0.000
2016	В	15	6.20	0.28	15	9.93	0.46	15	11.13	0.57	< 0.001	< 0.000	< 0.000	0.159
2017	В	12	6.93	0.28	11	9.36	0.23	12	10.93	0.28	< 0.001	< 0.000	< 0.000	< 0.000
2016	С	12	5.33	0.38	12	11.50	0.60	12	16.25	1.16	< 0.001	< 0.000	< 0.000	< 0.000
2017	С	15	5.74	0.42	15	11.35	0.35	14	15.85	0.44	< 0.001	< 0.000	< 0.000	< 0.000
2016	D	3	NA	NA	3	8.67	0.67	3	9.33	0.33	0.422		-	
2017	D	9	3.32	0.68	12	11.43	0.48	12	10.15	0.19	< 0.001	< 0.000	< 0.000	0.109

Table 2-7 Summary statistics of brown canopy depth under CFD conditions: declining (D), transitional (T), and normal (N). n: sample size. SE: standard error of the mean. Pr: probability value. Significance level: $\alpha = 0.05$.

Table 2-8 Summary statistics of yield estimate under CFD conditions: declining (D), transitional (T), and normal (N). n: sample size. SE: standard error of the mean. Pr: probability value. Significance level: $\alpha = 0.05$.

					Yield	estimate	(bbl/acre)							
Vaar	Dad		Declining			Trans	ition		Nor	mal	ANOVA	Tuk	ey's HSD ((Pr)
rear	Бей	n	Mean	SE	n	Mean	SE	n	Mean	SE	(Pr)	D-T	key's HSD (D-N 0.098 0.951 0.028 - - 0.003 < 0.000	T-N
2016	А	3	93.7	33.4	3	600.7	44.3	3	341.7	106.3	0.006	0.005	0.098	0.085
2017	А	3	100.7	27.0	3	452.0	41.6	3	84.0	45.5	0.001	0.002	0.951	0.001
2017	В	3	94.0	27.5	3	301.0	51.0	3	352.7	67.6	0.026	0.066	0.028	0.766
2016	С	3	33.0	6.4	3	123.3	62.7	3	111.7	20.3	0.268		-	
2017	С	3	73.7	14.3	3	93.0	29.5	3	186.3	51.3	0.129		-	
2016	D	3	21.0	11.1	3	484.3	84.1	3	476.3	44.6	0.002	0.003	0.003	0.994
2017	D	3	1.7	0.9	3	117.3	14.1	3	431.7	52.1	0.000	0.087	< 0.000	0.001



Figure 2-1 Poorly rooted cranberry canopy peeled off from the soil. The photo is taken in a CFD-affected bed.



Figure 2-2 Location map of the beds selected for the CFD characterization. The red dots in the main map show the locations of beds (Bed A, Bed B, Bed C, and Bed D) (Global Administrative Areas, 2012; Google, n.d.-b; Kahle & Wickham, 2013)



Figure 2-3 Sampling arrangement in a cranberry bed for CFD characterization, under three different levels of CFD development: declining, transitional, and normal. Three sampling locations were randomly selected within each area: near the declining edge (red line) for declining areas (red stars), on the parallel (yellow) line to the declining edge (red line) for transitional areas, and within an area more than 10 m away (beyond green line) from the declining edge (red line) for normal areas. The normal areas in Bed A were maximum 5 m apart from the declining edge.



Figure 2-4 Diagram of unrooted volume under the canopy (UVC) measurement for CFD characterization. The red allow indicates the pulling direction of the canopy. First, measure the pulled height (H), and mark the 4 points (P, Q, R, and S) as shown in the diagram in such way that the line PR and QS intersect at right angle. Measure the distance PR and QS. UVC, the approximated pulled volume was calculated as: UVC (cm³) = (PR x QS x H) / 4.



Figure 2-5 Canopy structure of cranberry plants, depicting total, green, and brown canopy.



Figure 2-6 The mean soil pH measured in each CFD condition in each bed in 2017. Colours of bars indicate the CFD conditions: red = declining (D), yellow = transitional (T), and green = normal (N). Error bars indicate standard error of the mean. Bars with the same letters are not significantly different based on the Tukey's HSD test. Significance level: $\alpha = 0.05$.



Figure 2-7 The mean soil redox potential measured in each CFD condition in each bed in 2017. Colour of bars indicate the CFD conditions: red = declining (D), yellow = transitional (T), and green = normal (N). Error bars indicate standard error of the mean. Bars with the same letters are not significantly different based on the Tukey's HSD test. Significance level: $\alpha = 0.05$.



Figure 2-8 Boxplot of unrooted volume under the canopy (UVC) for in each CFD condition in each bed in 2016 and 2017. Colours of bars indicate the CFD conditions: yellow = transitional (T) and green = normal (N). Higher values indicate lower root health and vice versa. Boxes show interquartile range (from the top, 75th, 50th [median], and 25th percentile). The medians between CFD conditions in Bed B and Bed C are significantly different in both years.



Figure 2-9 The mean total upright density in each CFD condition in each bed in 2016 and 2017. Colours of bars indicate the CFD conditions: red = declining (D), yellow = transitional (T), and green = normal (N). Error bars indicate standard error of the mean. Bars with the same letters are not significantly different based on the Tukey's HSD test. Significance level: $\alpha = 0.05$.



Figure 2-10 The mean flowering upright ratio (flowering upright density / total upright density) in each CFD condition in each bed in 2016 and 2017. Colours of bars indicate the CFD conditions: red = declining (D), yellow = transitional (T), and green = normal (N). Error bars indicate standard error of the mean. Bars with the same letters are not significantly different based on the Tukey's HSD test. Significance level: $\alpha = 0.05$.



Figure 2-11 The mean green and brown canopy depth in each CFD condition in each bed in 2016 and 2017. Colour of bars indicate the CFD conditions: red = declining (D), yellow = transitional (T), and green = normal (N). Error bars indicate standard error of the mean. Bars with the same letters are not significantly different based on the Tukey's HSD test. Significance level: $\alpha = 0.05$.



Figure 2-12 The mean yield estimates in each CFD condition in each bed in 2016 and 2017, except for Bed B missing data in 2016. Colors of bars indicate the CFD conditions: red = declining (D), yellow = transitional (T), and green = normal (N). Error bars indicate standard error of the mean. Bars with the same letters are not significantly different based on the Tukey's HSD test. Significance level: $\alpha = 0.05$.

Chapter 3: Carbohydrate Dynamics in American Cranberry (*Vaccinium macrocarpon*) in Cranberry Field Decline Syndrome in British Columbia

3.1 Introduction

Carbohydrates are an essential resource for plant growth and survival and are stored as nonstructural carbohydrates (NSC) in their perennial tissues (Loescher et al., 1990). Among the various type of NSCs, glucose, fructose, sucrose, and starch are commonly found across plant taxa (Kozlowski, 1992). Glucose and fructose are found in the phosphorylated forms and constitute the hexose phosphate (Hex-P) pool in the cytosol (Taiz & Zeiger, 2010). Sucrose is synthesized from Hex-P in the cytosol and is the most common form of sugar that is translocated from source to sink tissues via phloem transport (Taiz & Zeiger, 2010). Hexose and sucrose are soluble sugars that are generally stored in vacuoles and readily available for plant metabolisms and exhibit an immediate effect on cellular functionality (Dietze et al., 2014). On the other hand, starch is insoluble and osmotically and metabolically inactive, and found in chloroplasts and amyloplast (Yasunori Nakamura, 2015; Smirnova et al., 2015). However, starch is also a critical part of NSC as it is by far the dominant carbohydrate reserve in higher plants and is an essential energy source for the plants' survival (Oliveira & Priestley, 1988; Taiz & Zeiger, 2010).

Carbohydrate reserves, generally composed of starch, sucrose, and other secondary compounds including fructans and lipids, depending on species (Chapin et al., 1990), compensate for periodic carbohydrate deficiency in plants throughout the year (Martínez-Vilalta et al., 2016). Early in the season, the foliage development of deciduous trees completely relies on the
carbohydrate reserve stored in the previous season (Oliveira & Priestley, 1988). In some deciduous tree species, reproductive development occurs before new foliage becomes fully functional, relying almost completely on carbohydrate reserve (Loescher et al., 1990). Even with fully functional foliage, the high carbohydrate demand during flowering and fruit set may surpass the rate of photosynthesis and utilize the reserve (Oliveira & Priestley, 1988). In fruit trees, a developing fruit is a strong carbon sink among the plant organs, and the competition for carbohydrates remains high from fruit set until maturation (Kozlowski, 1992). After the cessation of shoot growth and fruit development, studies have shown that surplus NSC is allocated to various storage tissues, maintenance respiration, secondary growth, and root growth (Oliveira & Priestley, 1988). During the dormant period, bud development and maintenance respiration rely completely on the carbohydrates reserve (Loescher et al., 1990). Therefore, ensuring sufficient amounts of carbohydrate reserve by the end of each growing season is critical for the survival and development of many perennial plant species.

Carbohydrate reserve is generally replenished by the end of each season (Martínez-Vilalta et al., 2016); however, environmental stresses can alter the carbohydrate allocation and deplete the reserve. Temperature is positively correlated with the maintenance respiration, which occurs to maintain the functionality of the existing biomass (Kozlowski, 1992). The loss of carbohydrate on maintenance respiration under heat stress can be significant as more than 30-60% of daily carbon assimilates are allocated to respiration (Kozlowski, 1992). Cold stress induced the expression of sucrose synthase-encoding gene in *Arabidopsis*, which exhibited a significant increase of hexose to sucrose ratio (Déjardin et al., 1999). Drought stress reduces photosynthates by closing stomata, which limits leaf starch content (Quick et al., 1992), while stress-induced

vacuolar invertase activity degrades sucrose, which elevates hexose content (Kim et al., 2000). While cold and drought stresses may not change the total NSC (TNSC), the stress-induced accumulation of soluble sugar reduces starch content (Maguire & Kobe, 2015).

Depletion of carbohydrate reserve may cause various physiological dysfunctions and can result in reduced structural resilience. Although starch is osmotically and metabolically inactive (Smirnova et al., 2015), it accounts for the majority of carbohydrate reserve and is utilized for compensating carbon deficiency and carrying out secondary metabolism to cope with abiotic stresses (Thalmann & Santelia, 2017). The relationship between carbohydrate depletion and plant structural integrity has not been fully investigated; however, recent studies have indicated a significant reduction of matrix polysaccharides under high carbohydrate demand (Schadel et al., 2009). Therefore, overutilization of carbohydrate reserve and depletion of starch storage may indirectly reduce plant structural resilience against mechanical stresses.

In recent years, several cranberry beds in the Lower Mainland of British Columbia (BC) have been exhibiting significant canopy decline resulting in large dead patches. This condition, called Cranberry Field Decline (CFD), has been under investigation for the last few years to develop a better understanding of the cause of the disorder. Characterization of canopy architecture in CFD-affected beds indicated a possible relationship between the depth of brown canopy (lower and nonphotosynthetic) and CFD development (Chapter 2). Abrupt reduction of canopy density at a certain point of CFD development was thought to be caused by carbohydrate depletion in the storage tissue of brown canopy. In the present study, the contents of NSCs in uprights and stems were assessed with respect to the CFD development. In particular, it was hypothesized that starch

content in stems was different among the varying levels of CFD development. Additionally, NSC dynamics in stems and uprights were characterized under three levels of CFD development.

3.2 Materials and methods

3.2.1 Site Locations

Four cranberry beds exhibiting CFD symptoms were selected in the Lower Mainland in Southwestern BC. Bed A was located in south Burnaby, Bed B and C were located on the north side of Lulu Island (City of Richmond), and Bed D was located in North Delta. (*Figure 3-1*). In response to the manifestation of CFD symptoms, additional drain tiles were installed in the declining areas in Bed D by the farm in 2014. Also In Bed A and Bed B, additional drain tiles were installed parallel to the existing drain tiles in 2016 by the farms. No additional drain tile was installed in Bed C. Cultivar was Stevens in Bed A, Bed B and Bed D and was Bergman in Bed C.

3.2.2 Sampling

In each bed, three areas were identified by visually assessing the canopy density to determine the severity of CFD symptoms: declining, transitional, and normal (*Figure 3-2*). Declining areas were characterized by a substantial reduction in canopy density and a complete collapse of the canopy in the center. Samples from declining areas were taken at the areas adjacent to the declining edge as there was no living plant tissue to collect in the center of the declining area. A transitional area was defined as the area between the declining edge and a parallel line measured 50 cm away from the declining edge. Samples from transitional areas were taken along this parallel line. A normal area was defined as the area that was ≥ 10 m away from the closest

declining patch and showed no CFD symptoms. One exception was in Bed A, where declining and normal areas were a maximum of 5 m apart due to the severity of CFD in this bed. Three sampling locations were randomly selected for each CFD condition. Throughout the growing season, vine samples were collected in May (between late May and early June), July, August, and after the commercial harvest (between late Oct and early November). Sampling was carried out in all beds in both years, except for Bed D in 2016. At each sampling location, a batch of vines (10-20 vines) were cut approximately 40 cm from the top of the uprights so that each vine would contain a sufficient length of stems for analysis. Uprights contained tissues of current and previous years' growth, and stems contained 3-year-old growth or older. Samples were collected in paper bags and stored in a cooler with ice packs to suppress the respiration during transportation. The available length of vines was limited at the declining areas in Bed D, as the dead vines had been cleared by the farmers.

3.2.3 Processing Samples

Vine samples were rinsed in tap water to remove soil particles and other organic materials. Each sample was separated into uprights and stems and placed into separate paper bags (W x D x H: 13 x 8 x 7 cm). Samples in the paper bags were dried in a dryer at 80°C for at least 48 hours (to constant weight). The dried samples were ground into powder, packed in separate paper envelopes, and stored in a semi-airtight plastic container with silica-gel to keep the samples dry. Silica-gel was rejuvenated with microwave every 5-7 days.

3.2.4 Carbohydrate Analysis

Samples were sent to the Analytical Chemistry Services Laboratory, Ministry of Environment and Climate Change Strategy in Victoria, BC. In the lab, samples were ground before the chemical extraction. Soluble sugars (glucose, fructose, and sucrose) were extracted from each ground sample with 10 mL of hot ethanol (80%, 80°C) 3 times. The extracts were filtered and analyzed by High-Performance Liquid Chromatography. The residue from the soluble sugar extraction was analyzed for starch content. The residue was treated with alpha-Amylase and Amyloglucosidase to convert starch into glucose. The starch content was measured in glucose equivalent using an Agilent UV-Vis Spectrophotometer at 450 nm. A subset of samples from July in Bed C were excluded from this analysis, due to budget limitation.

3.2.5 Statistical Analysis

Differences in mean NSC content among CFD conditions were assessed by performing one-way analysis of variance (ANOVA). Data were structured with three fixed factors: CFD condition (3 levels: declining, transitional, and normal), site (4 levels: Bed A, B, C, and D), and year (2 levels: 2016 and 2017), and consisted of 7 dependent variables (starch content in uprights [U_Sta], starch content in stems [S_Sta], hexose content in uprights [U_Hex], hexose content in stems [S_Hex], sucrose content in uprights [U_Suc], sucrose content in stems [S_Suc], and total NSC in whole vines [W_TNSC]). Hexose content was calculated by summing glucose and fructose contents for uprights and stems separately, and W_TNSC was calculated by summing all NSCs from both uprights and stems combined. The site was considered a fixed factor as the beds were chosen for the existence of the CFD symptoms. As beds were isolated from each other and managed differently by different farmers, the data contained inherent variability among beds.

Therefore, ANOVA was carried out separately for each bed per month per year with CFD condition as the independent variable. Significant results ($\alpha = 0.05$) were further analyzed by carrying out post hoc multiple comparisons with Tukey's Honestly Significant Difference (HSD) test.

Relationships among the NSCs (glucose, fructose, sucrose, and starch) in uprights and stems with CFD conditions and growth stages (vegetative growth and pre-bloom [VG/PB], bloom and fruit set [BL/FS], fruit development [FD], ripening [RP], post-harvest [PH]) were assessed with Principal Component Analysis (PCA). The top two components were chosen. Rotations and observations were plotted on 2-dimensional scales to generate a covariance biplot. A 95% probability ellipse was drawn for each CFD condition and growth stage. The results of the PCA analysis were visually assessed for the correlation and the distribution of the observations concerning CFD development and growth stage. Carbohydrate data of Bed D in 2017 were excluded from PCA as growth characteristics, such as upright density, canopy depth and root health (Chapter 2), as well as S_Sta in the present study indicated a strong improvement of plants' health in transitional areas in response to the drain tile installation in 2014.All the statistical tests were carried out using statistical program R with appropriate program packages (R Core Team, 2018).

3.3 Results

3.3.1 Starch Content

The mean U_Sta overall showed an increasing trend with CFD severity from early to midseason, except for Bed D which showed an opposite trend. Post hoc multiple comparisons carried out on the significant differences indicated that the mean U Sta was significantly higher in declining areas than normal areas in May in Bed A, May and August in Bed B, and August in Bed C in 2016; however, the differences were insignificant in other cases in early and midseason. For Bed D, post hoc multiple comparisons indicated that the mean U_Sta was lower in declining areas followed by transitional and normal areas. After harvest, the mean U Sta was similar among CFD conditions with no significant difference in most cases in both years (Table 3-1, Figure 3-3 A). The mean S_Sta in both 2016 and 2017 was consistently higher in normal areas compared to declining areas, and transitional areas were generally in-between. Except for Bed B in August 2016 and May 2017, the differences of the mean S_Sta among CFD conditions were significant throughout the season in all beds in both years. Post hoc multiple comparisons carried out on the significant differences indicated that the mean S_Sta was significantly higher in normal areas compared to declining areas in all cases, except for after harvest in Bed D in 2017. The mean S_Sta in transitional areas generally fell between the normal and declining areas in Bed A, B, and C throughout the seasons; however, the differences between normal and transitional areas and between transitional and declining areas were often not significant. In Bed D in 2017, the mean S Sta was similar between normal and transitional areas from May to August (Table 3-1, Figure 3-3 B).

3.3.2 Hexose Content

The mean U_Hex in both 2016 and 2017 was generally higher in declining areas compared to normal areas throughout the growing season, except for Bed D; however, the differences were not always significant. Post hoc multiple comparisons carried out on the significant differences indicated that the mean U_Hex was significantly higher in declining areas than normal areas (

Table 3-2, Figure 3-4 A). The mean S_Hex in both 2016 and 2017 was generally similar among CFD conditions with a slightly higher amount in declining areas compared to normal areas in some cases. Post hoc multiple comparisons on the significant differences indicated that the mean S_Hex in declining areas was significantly higher than normal areas in most cases (*Table 3-2, Figure 3-4 B*).

3.3.3 Sucrose Content

The mean U_Suc in both 2016 and 2017 was generally similar among CFD conditions particularly during mid-season, and the differences were mostly insignificant. However, early and late in the season, the mean U_Suc in declining areas was slightly lower and higher compared to normal areas, respectively, in most cases, but the differences were not always significant (*Table 3-3, Figure 3-5 A*). The mean S_Suc in both 2016 and 2017 was similar among CFD conditions in most of the growing season. Although post hoc multiple comparisons on the significant differences indicated that the mean S_Suc was higher in declining areas compared to normal areas in some cases, the trend was inconsistent among beds and years (*Table 3-3, Figure 3-5 B*).

3.3.4 Total Nonstructural Carbohydrate in Whole Vines

The mean W_TNSC in both 2016 and 2017 was very similar among CFD conditions, and the differences were insignificant throughout most of the growing season in all beds, except for Bed D in 2017 (*Table 3-4, Figure 3-6*).

3.3.5 Principal Component Analysis

The component 1 and 2 of the PCA analysis collectively explained 66.9% of the total variance among glucose, fructose, sucrose, and starch in both uprights and stems. A covariance biplot indicated a strong negative correlation between S_Sta and U_Frc and between S_Sta and U_Glc. On the other hand, the result showed a minimal correlation between S_Sta and U_Suc or between S_Sta and S_Suc (*Figure 3-7*). The 95% probability ellipses indicating the distribution pattern of data points regarding both CFD conditions (*Figure 3-7 A*) and growth stages (*Figure 3-7 B*) were largely overlapping; however, the result showed trends indicating the development of CFD condition along with the increase of U_Glc/S_Sta and U_Frc/S_Sta ratios (*Figure 3-7 A*), while growth stage was more strongly related with U_Suc and S_Suc compared to S_Sta, U_Glc, or U_Frc (*Figure 3-7 B*).

3.4 Discussion

The results of this study suggest that the abrupt canopy collapse resulting from CFD is due to the carbohydrate starvation caused by the gradual and steady decline of the carbohydrate reserve in the stem. Carbohydrates are depleted until they become too low to support continued plant growth and maintenance. The results showed that S_Sta was significantly different among CFD conditions in almost all observations throughout the growing season for two consecutive years in all beds, supporting the hypothesis. The results also showed that S_Sta content decreased from normal, transitional, to declining areas consistently in almost all observations, suggesting a correlation of S_Sta and the level of CFD development.

Additionally, the contents of other NSCs, namely U_Hex, S_Hex, U_Suc, S_Suc, as well as U_Sta, were measured to characterize NSC dynamics in relation to CFD. The result showed that U_Hex was generally higher in declining areas than normal areas throughout the growing season; however, the differences were not always significant. The PCA indicated that U_Hex content was negatively correlated to S_Sta, and the U_Hex/S_Sta ratio appeared to increase with the increasing severity of CFD, while W_TNSC did not differ among CFD conditions. U_Sta was generally higher in declining areas in the beginning, slightly higher in the middle and similar at the end of the season. U_Suc showed a slight difference in the beginning and end of the season. However, U_Suc and U_Sta, as well as other NSCs (S_Suc and S_Hex), showed no correlation with U_Hex, S_Sta, or the levels of CFD development.

3.4.1 Reduction of Starch in Stems under CFD Influence

The significant reduction of S_Sta content in CFD-affected plants might be partly caused by an excessive utilization of carbohydrate reserve in compensation of carbohydrate deficit. Characterization of CFD estimated that the root health was severely reduced in transitional areas (Chapter 2), which suggested that the cranberry shoots under the influence of CFD had a significant reduction in photosynthesis throughout the growing season, and hence a severe carbon deficit. To compensate for this deficit, plants may utilize S_Sta to meet the carbon demand for growth and maintenance, particularly during the period of rapid growth. A previous study investigating the seasonal trend of NSCs in cranberry plants showed that the starch content declined not only in uprights but also in woody vines and underground stems during new foliage development, flower induction, and fruit set (Hagidimitriou & Roper, 1994). The present study

suggests that such utilization of starch storage during the peak period might be increased under the influence of CFD.

In addition to the compensation of carbon deficit, cranberry plants under the influence of CFD appear to exhibit a stress-induced mobilization of soluble sugar, which enhances the degradation of starch in stems. With reduced root health (Chapter 2), CFD-affected plants may exhibit symptoms of drought stress. In general, plants under drought or salt stress experience osmotic stress, which leads to the accumulation of various osmoprotectants including sucrose, glucose, and fructose to maintain the osmotic pressure (Krasensky & Jonak, 2012). Under osmotic stress, starch hydrolysis activity is induced, which degrades starch and increases soluble sugar content (Todaka et al., 2000). In the present study, the elevated U_Hex content in conjunction with the significantly reduced S_Sta in declining areas is consistent with the drought-induced accumulation of soluble sugar. In water-stressed corn plants, a marked increase of hexose content was detected in all organs along with a slight increase in sucrose content (Kim et al., 2000). In the same study, a comparison of relative invertase activities among various plant structures showed induction of vacuolar invertase activity which degrades sucrose into Hex-P (Kim et al., 2000). Moreover, PCA results indicated a strong, negative correlation between U_Hex and S_Sta and an increase of U_Hex/S_Sta ratio with CFD development, which suggests that the accumulation of soluble sugar was enhanced at more severe CFD conditions.

The compensation of carbohydrate deficit under the influence of CFD, however, might only have a limited impact on the reduction of starch storage; rather, the significant reduction of S_Sta content in the present study might be largely due to the stress-induced mobilization of soluble sugars. As indicated in the characterization of CFD (Chapter 2), upright density and green canopy depth showed a gradual decline along the CFD development. Such trends could be a result of the downregulation of growth due to reduced photosynthesis leading to a sink limitation and proportional decline of demand for NSC (Sala, Woodruff, & Meinzer, 2012). On the other hand, the degradation of starch and mobilization of soluble sugars might constantly occur in response to stress (Kim et al., 2000; Krasensky & Jonak, 2012; Todaka et al., 2000). This idea is further supported by the lack of relationship between U_Hex or S_Sta and growth stages and the stable TNSC content among CFD conditions. If the utilization of S_Sta is strongly driven by the compensation of carbon deficit, a correlation between U_Hex/S_Sta ratio and growth stage would be expected as development and growth of plant structure increase the carbon demand. Similarly, TNSC content would have been lower in declining areas compared to normal areas as compensation of carbon deficit implies the consumption of carbohydrate through respiration. A study investigating the effect of drought and shade treatment on carbohydrate allocation in four tree species found that seedlings of three drought tolerant species under drought stress showed a marked increase in soluble sugar and decrease in starch but no change in TNSC content (Maguire & Kobe, 2015). On the other hand, in the same study, the seedlings of the same tree species under shade treatment did not increase soluble sugar content but decreased TNSC content (Maguire & Kobe, 2015), demonstrating the differences between a carbon deficit by limited-photosynthesis and stress-induced soluble sugar accumulation regarding the impact on NSC allocation. Therefore, in the present study, the marked reduction of S_Sta was probably dominantly driven by the stress-induced mobilization of soluble sugar.

3.4.2 Implications of Starch Depletion for Structural Resilience

Constant reduction of photosynthesis and exposure to stresses under the influence of CFD probably prevented the cranberry plants from recovering S_Sta back to normal levels and reduced S_Sta further down to a threshold beyond which the structural resilience of secondary growth might be severely compromised. The loss of S Sta in declining and transitional areas in 2016, which was probably carried over from the previous season, mostly remained through the rest of the year and resulted in substantially lower S_Sta in declining and transitional areas at the beginning of 2017 season. Although S_Sta was not completely depleted, the magnitude of reduction relative to normal areas may have been severe enough to prevent the plants from returning to normal levels of growth and maintenance. A study investigating the relationships between tree mortality and carbohydrate depletion showed that Norway Spruce which died from drought-induced carbon starvation did not deplete starch in the above-ground storage tissue (Hartmann, Ziegler, & Trumbore, 2013). Similarly, a meta-analysis investigating NSC dynamics of terrestrial plants indicated that trees rarely deplete NSCs completely and generally retain more than 40% of maximum capacity throughout the growing season (Martínez-Vilalta et al., 2016). In our results, there were several observations in which S_Sta in declining areas fell below 40% of the highest S_Sta in normal areas. Constant reduction of S_Sta in the stems may cause utilization of other potential carbohydrate reserves including hemicelluloses in cell-wall matrix. Hemicelluloses in the branch sapwood of *Carpinus betulus* decreased following the depletion of starch prior to bud break but increased following the replenishment of starch after the development of foliage (Schadel et al., 2009). Degradation of hemicelluloses in cell-wall matrix can reduce the quality of secondary growth which may lower the structural resilience of woody

tissues. Therefore, the stems with severely and constantly reduced S_Sta may break easily upon mechanical pressure from routine farming operations regardless of the time of the year.

3.4.3 Accumulation of NSCs in Green Canopy

The differences in the contents of NSCs in uprights other than U_Hex and S_Sta among CFD conditions were relatively small and mostly insignificant; however, the trends were influenced by the seasonality. Starch in uprights in 2016 was generally higher in declining areas early to mid-season, but differences among CFD conditions diminished at the end of the season. This is possibly due to an elevated triose phosphate (TP) content in chloroplasts supplied from the interconversion of elevated U_Hex content in source cells. The increased TP/Pi ratio in chloroplasts stimulated the activity of adenosine diphosphate glucose pyrophosphorylase (AGPase) (Geigenberger, 2011), resulting in an accumulation of U_Sta in declining areas despite having a reduced supply of photosynthates. The increased U_Sta content in declining areas was maintained by the elevated U_Hex until the diminishing rate of photosynthesis downregulated starch synthesis by inactivating the modulation of AGPase. Modulation upregulates reactivity of AGPase to allosteric effectors such as TP (Geigenberger, 2011; Tetlow et al., 2015). As a result, the conversion of U_Hex to U_Sta declined towards the end of the season and the difference in U_Sta content among CFD conditions diminished. As to sucrose content, both U_Suc and S_Suc were generally similar among CFD conditions and showed a consistent seasonal trend. Sucrose content was increased by cold acclimation at the end of the season and decreased by deacclimation early in the season. The perpendicular intersection of vectors representing U_Suc and S_Suc to U_Hex, S_Sta, and the CFD development seen in the results of PCA suggest that

sucrose content was predominantly influenced by the seasonality and unaffected by the stress associated with CFD in the present study.

3.4.4 Cultivar Difference in Carbohydrate Characteristics under CFD conditions

The results generally showed a similar trend of each NSC between Stevens (Bed A and Bed B in 2016) and Bergman (Bed C in 2016) among CFD conditions, which may suggest that these cultivars were equally affected by CFD within the scope of the present study. However, to fully understand cultivar differences in carbohydrate characteristics under CFD development, it may require the involvement of other cultivars grown under similar management practices.

3.5 Conclusion

The present study tested the hypothesis that S_Sta differed among three levels of CFD development. Other common NSCs were also measured, and the impact of CFD on NSC dynamics was assessed. The results showed that S_Sta declined with the development of CFD, which supported the hypothesis. The decrease of S_Sta corresponded to the increase of U_Hex and the U_Hex/S_Sta ratio was correlated to CFD development, which was probably more dominantly caused by stress-induced mobilization of soluble sugars in shoots than the compensation of carbon deficit. Regarding other NSCs, an increase of U_Sta early to mid-season was probably due to the elevated U_Hex, which has a strong correlation with CFD development; however, the diminishing difference in U_Sta at the end of the season and the result of PCA suggested U_Sta was more strongly influenced by seasonality than CFD. Similarly, neither U_Suc nor S_Suc showed a clear trend with CFD. The clear and consistent trends of sucrose content driven by cold acclimatization for both uprights and stems showed that sucrose in

cranberry plants was generally free from the impact of stresses associated with CFD but was more strongly influenced by seasonality.

Understanding the dynamics of NSC content in plants under biotic and abiotic disorders may help to discover the hidden or inconspicuous signs of poor plant health, which may inform strategies for maintaining healthy plants. As demonstrated in the present study, analysis of NSC content, particularly S_Sta and U_Hex, may be used to infer stress levels of cranberry plants and can assist with early detection of the CFD development. Understanding the levels of NSC content may also inform canopy management strategies that focus on maintaining optimal rootstem-upright ratios to improve NSC availability, which may improve various yield components limited by NSC reserves. In future research, identification of stress factors may be necessary for further dissecting the mechanism altering the NSC dynamics under CFD to link the research results more closely to applicable management practices. As well, identifying more accessible, cost-effective indices that are closely correlated to the changes in U_Hex/S_Sta ratio may help improve the applicability of the present and future research on CFD.

				Starch in Uprights				Starch in Stems			
V	Bed	Month	DOM	ANOVA (Pr) T		ukey's HSD (Pr)		ANOVA (Pr)	Tukey's HSD (Pr)		
rear			DOY	D-T-N	D-T	D-N	T-N	D-T-N	D-T	D-N	T-N
	А	May	153	0.010*	0.134	0.008 **	0.112	0.017 *	0.993	0.024 *	0.028*
		Jul	207	0.153				0.001 **	0.761	0.001 **	0.002 **
		Aug	243	0.821				0.001 **	0.005 **	0.001 **	0.117
		Oct	318	0.262				0.009 **	0.009 **	0.034*	0.516
	В	May	152	0.011 *	0.084	0.010 **	0.231	0.024 *	0.320	0.020*	0.141
2016		Jul	201	0.058 *				0.002 **	0.042 *	0.001 **	0.036*
		Aug	241	0.018*	0.083	0.016*	0.395	0.058			
		Oct	318	0.940				0.002 **	0.005 **	0.002 **	0.753
	С	May	158	0.443				0.031 *	0.194	0.026*	0.305
		Aug	236	0.026*	0.042 *	0.037*	0.992	0.012 *	0.158	0.010 **	0.124
		Oct	311	0.149				0.003 **	0.015 *	0.003 **	0.280
	А	May	143	0.814				0.002 **	0.007 **	0.002 **	0.338
		Jul	204	0.920				0.023 *	0.324	0.019*	0.131
		Aug	237	0.076				0.047 *	0.331	0.039*	0.279
		Oct	322	0.298				0.001 **	0.084	0.001 **	0.011*
		May	143	0.607				0.133			
2017	В	Jul	207	0.521				0.001 **	0.002 **	0.001 **	0.572
		Aug	242	0.649				0.001 **	0.021 *	< 0.001 ***	0.012*
		Oct	319	0.006 **	0.220	0.037*	0.005 **	< 0.001 ***	0.259	< 0.001 ***	0.002 **
	D	May	144	0.017 *	0.087	0.014*	0.349	0.006 **	0.014 *	0.007 **	0.784
		Jul	213	0.014*	0.128	0.012*	0.197	0.002 **	0.003 **	0.005 **	0.827
	D	Aug	237	< 0.001	0.001 **	< 0.001 ***	0.092	0.001 **	0.003 **	0.002 **	0.783
		Oct	319	0.944				< 0.001 ***	< 0.001 ***	0.150	0.002 **

Table 3-1 Summary statistics of starch content in uprights (U_Sta) and stems (S_Sta) under CFD conditions: declining (D), transitional (T), and normal (N). DOY: day of the year. Pr: probability value. Significance mark: '***' Pr ≤ 0.001 ; '**' $0.001 < Pr \leq 0.01$; '*' $0.01 < Pr \leq 0.05$. Significance level: $\alpha = 0.05$.

				Hexose in Uprights				Hexose in Stems				
Veen	D . 1	Month	DOV	ANOVA Tukey's HSD (Pr)		ANOVA Tuke		ıkey's HSD (P	key's HSD (Pr)			
rear	Бец		DOT	D-T-N	D-T	D-N	T-N	D-T-N	D-T	D-N	T-N	
		May	153	0.488				0.255				
	А	Jul	207	0.026*	0.061	0.028 *	0.799	0.563				
		Aug	243	0.004 **	0.013 *	0.004 **	0.553	0.557				
		Oct	318	0.012*	0.030*	0.014 *	0.772	0.933				
		May	152	0.357				0.004 **	0.011*	0.004 **	0.650	
2016	П	Jul	201	0.394				0.140				
	D	Aug	241	0.011 *	0.508	0.010*	0.039*	0.032*	0.091	0.031*	0.671	
		Oct	318	0.001 **	0.001 **	0.001 ***	0.978	0.839				
	С	May	158	0.086				0.022 *	0.054	0.023*	0.773	
		Aug	236	0.102				0.209				
		Oct	311	< 0.001 ***	0.001 **	< 0.001 ***	0.320	0.105				
		May	143	0.002 **	0.009 **	0.001 **	0.196	0.137				
	А	Jul	204	0.007 **	0.015 *	0.009 **	0.889	0.042 *	0.268	0.036*	0.311	
		Aug	237	0.002 **	0.015 *	0.002 **	0.179	0.095				
		Oct	322	0.106				0.121				
		May	143	0.588				0.542				
2017	р	Jul	207	0.020*	0.080	0.018 *	0.467	0.017 *	0.376	0.015*	0.086	
2017	D	Aug	242	0.325				0.232				
-		Oct	319	0.071				0.032*	0.027 *	0.303	0.204	
		May	144	0.121				0.165				
	D	Jul	213	0.178				0.070				
	U	Aug	237	0.256				0.212				
		Oct	319	0.284				0.001 **	0.192	0.001 **	0.005 **	

Table 3-2 Summary statistics of hexose content in uprights (U_Hex) and stems (S_Hex) under CFD conditions: declining (D), transitional (T), and normal (N). DOY: day of the year. Pr: probability value. Significance mark: '***' Pr ≤ 0.001 ; '**' $0.001 < Pr \leq 0.01$; '*' $0.01 < Pr \leq 0.05$. Significance level: $\alpha = 0.05$.

				Sucrose in Uprights				Sucrose in Stems				
Vaar	D 1	Manuf	DOV	ANOVA	Tukey's HSD (Pr)			ANOVA	Tukey's HSD (Pr)			
rear	Бец	Month	DOT	D-T-N	D-T	D-N	T-N	D-T-N	D-T	D-N	T-N	
2016		May	153	0.391				0.020*	0.071	0.019*	0.539	
	А	Jul	207	0.003 **	0.010 **	0.003 **	0.487	0.103				
		Aug	243	0.051				0.064				
		Oct	318	0.004 **	0.009 **	0.005 **	0.809	0.023 *	0.031 *	0.037 *	0.989	
		May	152	0.013*	0.797	0.015*	0.031 *	0.204				
	р	Jul	201	0.020*	0.019*	0.070	0.544	0.031*	0.049 *	0.044 *	0.996	
	В	Aug	241	0.093				0.007 **	0.008 **	0.016*	0.831	
		Oct	318	0.003 **	0.030*	0.003 **	0.117	0.774				
	С	May	158	0.405				0.046*	0.370	0.039*	0.247	
		Aug	236	0.028*	0.035 *	0.053	0.937	0.553				
		Oct	311	0.675				0.237				
	А	May	143	0.240				0.577				
		Jul	204	0.406				< 0.001 ***	< 0.000 ***	0.001 **	0.408	
		Aug	237	0.072				0.003 **	0.021 *	0.002 **	0.163	
		Oct	322	0.283				0.200				
		May	143	< 0.001 ***	0.005 **	< 0.000 ***	< 0.000 ***	0.046*	0.753	0.046*	0.117	
2017	р	Jul	207	0.181				0.063				
	D	Aug	242	0.625				0.868				
		Oct	319	0.384				0.364				
	D	May	144	0.023 *	0.408	0.021 *	0.110	0.001 **	0.003 **	< 0.001 ***	0.102	
		Jul	213	0.575				0.093				
	U	Aug	237	0.396				0.011 *	0.010*	0.049*	0.406	
		Oct	319	0.004 **	0.005 **	0.013*	0.609	0.682				

Table 3-3 Summary statistics of sucrose content in uprights (U_Suc) and stems (S_Suc) under CFD conditions: declining (D), transitional (T), and normal (N). DOY: day of the year. Pr: probability value. Significance mark: '***' Pr ≤ 0.001 ; '**' $0.001 < Pr \leq 0.01$; '*' $0.01 < Pr \leq 0.05$. Significance level: $\alpha = 0.05$.

					Total NSC in Whole Vines						
X 7	D 1	Month	DOY	ANOVA	Tuke						
Year	Bed			D-T-N	D-T	D-N	T-N				
		May	153	0.111							
	٨	Jul	207	0.038 *	0.042 *	0.868	0.080				
	A	Aug	243	0.988							
		Oct	318	0.351							
		May	152	0.636							
2016	р	Jul	201	0.221							
	D	Aug	241	0.219							
		Oct	318	0.008 **	0.031*	0.007 **	0.434				
		May	158	0.890							
	С	Aug	236	0.318							
		Oct	311	0.879							
		May	143	0.673							
	٨	Jul	204	0.709							
	A	Aug	237	0.729							
		Oct	322	0.612							
		May	143	0.571							
2017	P	Jul	207	0.943							
2017	Б	Aug	242	0.553							
		Oct	319	0.110							
		May	144	0.004 **	0.027 *	0.003 **	0.185				
	D	Jul	213	0.006 **	0.011*	0.010 **	0.998				
	D	Aug	237	< 0.001 ***	< 0.000 ***	< 0.000 ***	0.205				
		Oct	319	0.356							

Table 3-4 Summary statistics of total nonstructural carbohydrate content in whole vines (W_TNSC) under CFD conditions: declining (D), transitional (T), and normal (N). DOY: day of the year. Pr: probability value. Significance mark: '***' Pr ≤ 0.001 ; '**' $0.001 < Pr \leq 0.01$; '*' $0.01 < Pr \leq 0.05$. Significance level: $\alpha = 0.05$.



Figure 3-1 Location map of the beds selected for the carbohydrate analysis. The red dots in the main map show the locations of beds (Bed A, Bed B, Bed C, and Bed D) (Global Administrative Areas, 2012; Google, n.d.-b; Kahle & Wickham, 2013)



Figure 3-2 Sampling arrangement in a cranberry bed for carbohydrate analysis, under three different levels of CFD development: declining, transitional, and normal. Three sampling locations were randomly selected within each area: near the declining edge (red line) for declining areas (red stars), on the parallel (yellow) line to the declining edge (red line) for transitional areas, and within an area more than 10 m away (beyond green line) from the declining edge (red line) for normal areas. The normal areas in Bed A were maximum 5 m apart from the declining edge.



Figure 3-3 The mean starch (Sta) content in (A) uprights (U_Sta) and (B) stems (S_Sta) under CFD conditions in May, July, Aug, and postharvest (Oct or Nov) in Bed A, B, C in 2016 (except for Bed C missing data in Jul) and Bed A, B, D in 2017. Line colors indicate the CFD conditions: red = declining (D), yellow = transitional (T), and green = normal (N). The error bars indicate the standard error of the mean (SE). Means with the same letter are not significantly different according to Tukey's HSD test. Significant level: $\alpha = 0.05$.



Figure 3-4 The mean hexose content in (A) uprights (U_Hex) and (B) stems (S_Hex) under CFD conditions in May, July, Aug, and postharvest (Oct or Nov) in Bed A, B, C in 2016 (except for Bed C missing data in Jul) and Bed A, B, D in 2017. Line colors indicate the CFD conditions: red = declining (D), yellow = transitional (T), and green = normal (N). The error bars indicate the standard error of the mean (SE). Means with the same letter are not significantly different according to Tukey's HSD test. Significant level: $\alpha = 0.05$.



Figure 3-5 The mean sucrose content in (A) uprights (U_Suc) and (B) stems (S_Suc) under CFD conditions in May, July, Aug, and postharvest (Oct or Nov) in Bed A, B, C in 2016 (except for Bed C missing data in Jul) and Bed A, B, D in 2017. Line colors indicate the CFD conditions: red = declining (D), yellow = transitional (T), and green = normal (N). The error bars indicate the standard error of the mean (SE). Means with the same letter are not significantly different according to Tukey's HSD test. Significant level: $\alpha = 0.05$.



Figure 3-6 The mean total nonstructural carbohydrate content in whole vines (W_TNSC) under CFD conditions in May, July, Aug, and postharvest (Oct or Nov) in Bed A, B, and C in 2016 (except for Bed C missing data in Jul) and Bed A, B, and D in 2017. Line colors indicate the CFD conditions: red = declining (D), yellow = transitional (T), and green = normal (N). The error bars indicate the standard error of the mean (SE). Means with the same letter are not significantly different according to Tukey's HSD test. Significant level: $\alpha = 0.05$.



Figure 3-7 Covariance biplot generated by principle component analysis (PCA) of the nonstructural carbohydrate data of cranberry plant tissue. Components 1 and 2 were plotted on the x and y-axis, respectively, and together explain 66.9% of the total variance. The length and the angle of the vectors indicate the relative strength and degree of correlation between the variables, respectively (smaller angles indicate stronger positive correlations and vice versa). The 95% probability ellipses were colour-coded to identify the distribution characteristics of the observations grouped by (A) CFD conditions (D: declining, T: transitional, N: normal) and (B) phenological stages (VG/PB: vegetative growth and pre-bloom, BL/FS: bloom and fruit set, FD: fruit development, RP: ripening, PH: post-harvest). U_Sta: starch content in uprights. S_Sta: starch content in stems. U_Glc: glucose content in uprights. S_Glc: glucose content in uprights. S_Suc: sucrose content in stems. The overlapping variable names are U_Suc and S_Suc.

Chapter 4: Evaluating the effects of Sanding on the Growth and Yield of American Cranberry (*Vaccinium macrocarpon*)

4.1 Introduction

American cranberry (*Vaccinium macrocarpon* Ait) is a low-trailing, perennial, woody vine adapted to cool, acidic, and moist environments, such as bogs and marshes (Vander Kloet, 1988). The first cultivation of *V. macrocarpon* started in Cape Cod, Massachusetts in 1816, upon discovery of superior vine growth in an area receiving sand blown from a nearby dune (Caruso et al., 2000). Today, in eastern North America, cranberries are planted into constructed sand beds, and sand is applied to the bed every 2-5 years (DeMoranville, 2008). Sand-based cranberry beds in Massachusetts contain less than 3.5% of organic matter and approximately 3% clay and silt in the rooting environment (DeMoranville, 2008). On the other hand, cranberry beds in British Columbia (BC) and some areas in Washington State are established directly into the existing organic soil without layering sand over the top (Bernadine et al., 2002).

Sand-based beds create a well-drained environment (DeMoranville, 2008; Eck, 1990) which is similar to the natural habitat of cranberries in dryer sections of a bog, such as the herbaceous layer of bog vegetation (Andreas & Bryan, 1990; DeMoranville, 2008). Peat, however, may exhibit poor drainage depending on the degree of decomposition (DeMoranville, 2008). In the Lower Mainland of BC, the quality of the organic soil may vary significantly within and between beds. Most of the beds in BC were established in the post-harvest peatland where peat was mined close to the underlying mineral soil horizon, and hence, the existing peat might be highly

degraded as the degree of humification increases with depth (Verry *et al.*, 2011). The degree of humification is the most important property of peat as it influences soil porosity and pore sizes (Boelter, 1966; Verry *et al.*, 2011). This, in turn, influences soil drainage and aeration, which is a challenge in many BC cranberry beds.

The structures of *V. macrocarpon* consists of uprights (vertical shoots), runners (horizontally trailing stolons), underground stems, and fibrous root (Bernadine et al., 2002), which collectively form a low-lying, mat-like canopy (Eck, 1990). Every year, 5-10 cm of upright growth is added to the canopy (Bernadine et al., 2002), which, if not properly managed, can result in the formation of a deep, poorly rooted brown canopy, leading to low root/shoot ratio. Periodic sanding can contribute to the maintenance of an appropriate canopy depth, preventing the development of a deep canopy and allows younger vines to root which is necessary to renew the root system (DeMoranville, 2008; Eck, 1990).

In recent years, a condition known as Cranberry Field Decline (CFD) has developed in several cranberry beds in the Lower Mainland of BC. Affected beds develop patches of stressed vines, reduced upright density, and complete collapse of the canopy. Previous studies suggested a possible link between the peat humification and CFD (Lavkulich, 2014; Someya & Harbut, 2015), and observations on root health near the patches of severely declining canopy density indicated a greater reduction of the feeder roots, stunted growth of the root tips, and poorly anchored canopy to the soil (British Columbia Cranberry Marketing Commission, 2014). Although occasional sanding within limited areas of a bed has become more common for

rehabilitating such conditions under CFD, it is uncommon to apply sand across an entire bed in BC.

The slow adoption of sanding as a management practice may be due to the uncertainty of application practices and efficacy. Although several studies conducted in the US suggested that sanding can rejuvenate the cranberry plant by inducing root growth (DeMoranville & Sandler, 2008), the effect of sanding may vary depending on different factors. Previous studies indicated that heavy sanding may reduce yield (Davenport & Schiffhauer, 2000; Strik & Poole, 115995; Suhayda, DeMoranville, Sandler, Autio, & Vanden Heuvel, 2009), while moderate to light sanding showed no effect to a slight increase in yield (Davenport & Schiffhauer, 2000; Strik & Poole, 1995; Suhayda et al., 2009). The variable response to the depth of sanding may be due to differences in bed age and structure (Strik & Poole, 1995).

The impact of sanding and the optimal amount (depth) of sand required to effectively rejuvenate canopy health or improve yield components on peat-based cranberry beds in BC has not been well defined. This study aims to provide information on the effects of sanding at three different depth on the canopy characteristics and yield in a commercial cranberry bed in BC.

4.2 Materials and Methods

4.2.1 Site Locations

Two cranberry beds (Bed F and Bed G) were selected for the sanding trials in the Lower Mainland of BC. The beds were located on the east side of Lulu Island (City of Richmond) (*Figure 4-1*); however, they were isolated and managed by different farms. In Bed F, the current

plantings were planted in 2012, and the bed was sanded in 2013. In Bed G, the current plantings were 12^+ years old, and the section of the bed subject of the present study was never sanded. The cultivars of both beds were Stevens.

4.2.2 Experimental Design

A Randomized Complete Block (RCB) design was used to test the effect of sanding. In each cranberry bed, two sets of 3 x 4 grids were established, yielding 8 blocks per bed. Each grid contained 12 plots (1 plot = 1 m x 1 m square) which were separated with 50 cm wide buffer strips (*Figure 4-2*). Three treatments of sand application (0, 1.3, and 2.5 cm in depth) were randomly assigned to the plots in each block (a row of the grids). The volume of sand required for each treatment was calculated based on the area of the plot and the depth for each treatment. The sand was applied by hand evenly across the surface of the canopy within each plot, and the canopy was shaken to settle the sand on the soil surface. The establishment of the experimental plots and application of treatments were completed in late May 2016.

4.2.3 Data Collection

4.2.3.1 Upright Density

A 30 cm square quadrat was randomly placed at three locations in each plot. The upright density was measured by counting the number of uprights within the quadrat for total and flowering uprights. The number of vegetative uprights within the quadrat was obtained by subtracting the number of flowering uprights from the number of total uprights. All the uprights were counted regardless of their height, growth level, or health, except for the dead ones. The upright density was measured in early July in Bed F and mid-July in Bed G in 2017.

4.2.3.2 Canopy Depth

Within each plot, total and brown canopy depth were measured using a ruler inserted in the canopy perpendicular to the soil surface. Total canopy depth was defined as the distance from the soil surface to the approximated average height of the canopy. Brown canopy depth was defined as the distance from the soil surface to the position of the canopy where foliage began to appear. Green canopy depth was obtained by subtracting brown canopy depth from the total canopy depth. The green canopy was defined as the upper portion of the canopy where the foliage was retained on the vine (*Figure 4-3*). Canopy depth measurements were carried out at the same time as upright density (early to mid-July in 2017).

4.2.3.3 Estimation of Root Health

Root health was estimated by measuring the unrooted volume under the canopy (UVC). At the center of each plot, the plant canopy was grabbed by hand at the bottom and pulled up perpendicularly to the soil surface. The pulled height of canopy (H) was measured in centimetres with a ruler. Stake flags were placed at four points (P, Q, R, and S) to define the extent of the pulled area (*Figure 4-4*). The distance of PR and QS were measured in centimetres. The approximated UVC was then calculated as UVC $[cm^3] = (PR * QS * H) / 4$. Measurements of UVC were carried out at the same time as upright density (early to mid-July in 2017).

4.2.3.4 Yield Estimate

Prior to commercial harvest, the industry standard procedure to determine yield estimate per acre was followed. A 30 cm square quadrat was randomly placed within each plot, and berries within the quadrat were harvested to measure yield (total weight) per quadrat for each sample. Yield per acre was calculated by converting the yield per quadrat into lbs per acre. Yield is reported in the industry standard of barrels per acre (One barrel = 100 lbs). Berries were harvested in early October 2017.

4.2.4 Statistical Analyses

Data were structured with treatments (3 levels: 0, 1.3, and 2.5 cm of sanding) as the fixed factor and bed (2 levels: Bed F and Bed G) as a random factor, and contained six dependent variables (total, vegetative, and flowering upright density; flowering upright ratio [flowering upright density / total upright density]; green and brown canopy depth; UVC; and yield estimate). A twoway analysis of variance (ANOVA) was carried out to test the interaction between the effects of treatment and bed and to evaluate the differences between beds. Upon detection of significant interactions or the effects of bed for most variables further analysis was carried out for each bed separately with RCB ANOVA. Following the detection of a significant mean difference in RCB ANOVA, post hoc multiple comparisons were carried out with Tukey's Honestly Significant Difference (HSD) test. The UVC was transformed with common logarithm (log₁₀) to satisfy the assumption of ANOVA. The rest of the variables were analyzed without transformation. All the statistical tests were carried out using statistical program R with appropriate program packages (R Core Team, 2018).

4.3 Results

The interaction between the effect of sanding (main effect) and the effect of bed was significant for total upright density and vegetative upright density. The interaction was insignificant for flowering upright density, flowering upright ratio, green canopy depth, brown canopy depth, UVC, and estimated yield per acre, all of which showed a significant effect of bed, except for green canopy depth (*Table 4-1*). The mean total upright density among treatments was not significantly different in Bed F but was significantly different in bed G. Post hoc multiple comparisons indicated that the mean total upright density was significantly lower in control compared to 1.3 cm and 2.5 cm of sand in Bed G, but was not significantly different between 1.3 cm and 2.5 cm of sand (Table 4-2, Figure 4-5). The mean vegetative upright density among treatments was not significantly different in Bed F but was significantly different in bed G. Post hoc multiple comparisons indicated that the mean vegetative upright density was significantly lower in control compared to 2.5 cm of sand, but was not significantly different between the other treatments (Table 4-2, Figure 4-5). The mean flowering upright density was slightly higher in 1.3 cm of sand compared to the control and lower in 2.5 cm compared to 1.3 cm of sand in Bed G. The mean flowering upright density in Bed F was similar among the treatments (*Table* 4-2, Figure 4-5). The mean flowering upright ratio was slightly lower in 2.5 cm compared to the control and 1.3 cm of sand in Bed G. The mean flowering upright ratio did not differ significantly among treatments in Bed F (Table 4-3, Figure 4-6). The mean green and brown canopy depth were similar among treatments in each bed (Table 4-4, Figure 4-7). The mean log₁₀UVC was similar among treatments in each bed (*Table 4-5*, *Figure 4-8*). The mean yield estimate was slightly lower in 2.5 cm compared to the control and 1.3 cm of sand in Bed G. The mean yield estimate was not significantly different among the treatments in Bed F (Table 4-6, Figure 4-9).

4.4 Discussion

Sanding of cranberry beds has been shown to benefit cranberry production and is commonly used in the eastern US and Canada. However, in BC cranberry beds, effects of sanding on growth characteristics and yield have not been well-defined. In the present study, the growth characteristics of the cranberry plant treated with three different depths of sanding (0, 1.3, and2.5 cm) were evaluated in two commercial cranberry beds in BC. The results showed that sanding with any depth did not affect growth characteristics or yield in Bed F. However, in Bed G, vegetative upright density increased as sand depth increased, and flowering upright ratio and yield decreased slightly with 2.5 cm of sand. Similar responses in growth characteristics to the sanding were also seen in previous studies in other regions. Strik & Poole (1995) investigated the impact of sanding at 0, 1.3, and 2.5 cm depths on various growth characteristics and yield at cranberry beds in Oregon, which were established on peat and had never received a sanding, and the result showed a general increase in vegetative upright density with the sanding. In the same study, Strik & Poole (1995) also reported that the cumulative yield over the three years following the treatments showed a small increase with 1.3 cm of sand in one of the beds and small to moderate reduction with 2.5 cm of sand in both beds. It was noted that the age of plantings and bed construction might influence the impact of the sanding on yield components (Strik & Poole, 1995). Davenport & Schiffhauer (2000) reported that vegetative upright density increased with sanding in the first year but decreased in the third year for both Early Black and Stevens varieties. Davenport & Schiffhauer (2000) also reported that 1.3 cm of sanding did not affect yield, while 2.5 cm of sanding negatively impacted yield for both cultivars. Suhayda et al. (2009) used four levels of sanding depths (0, 1.5, 3.0 and 4.5 cm), and concluded that 1.5 cm of sand increased total vegetative upright density and maintained the flowering upright ratio similar to

control, which increased yield. Suhayda et al. (2009) also reported that sand depth greater than 1.5 cm reduced upright density and flowering upright ratio, which reduced yield. Although the levels and significance of differences vary in the effect of sanding among previous studies, the results generally agree that sanding greater than moderate depth (> 1.3 ~ 1.5 cm) have a negative impact on yield, while moderate sanding increases vegetative upright density (Davenport & Schiffhauer, 2000; Strik & Poole, 1995; Suhayda et al., 2009). However, it has also been pointed out that differences in bed condition may influence the effect of sanding (Strik & Poole, 1995).

4.4.1 Effects of Sanding Influenced by Bed Condition

The significant interaction between the effect of sanding and bed on total and vegetative upright density may suggest that bed condition influences the effectiveness of sanding. The significant effect of bed without interaction with treatment on UVC, yield, and brown canopy depth indicates the differences in bed condition. As UVC was identified as a potential diagnostic index of the degree of CFD development (Chapter 2), the lower UVC indicates healthier plant growth and vice versa. Therefore, the significantly lower UVC in Bed F suggests healthier plants in Bed F compared to Bed G, which is supported by the greater yield estimate in Bed F compared to Bed G. The less healthy plants in Bed G might have a greater margin for improvement for upright density in response to 2.5 cm sanding compared to the healthier plants in Bed F.

Deep brown canopies may reduce the effectiveness of sanding as the bottom of the deep canopy may predominantly consist of very old vines which might have a reduced potential for root regeneration compared to younger vines. As a cranberry bed ages, woody vines accumulate as the stems of uprights and runners undergo secondary growth, which, without proper canopy management, leads to the formation of a deep brown canopy system (DeMoranville, 2008; Eck, 1990). In the present study, while plantings were older in Bed G (12^+ years old) compared to Bed F (4 years old), brown canopy depth was shallower in Bed G compared to Bed F. This contradiction is probably due to differences in canopy management between the farms. The shallower brown canopy in Bed G likely indicates that young stems are located near the soil, while in Bed F young stems may be too far from the soil. While a few centimetres of sanding may only bury the older vines at the bottom of deeper brown canopy in Bed F, the same treatment may bury the younger vines in a shallower brown canopy in Bed G. The latter case may result in greater impact by the sanding on the shoot growth as younger vines are probably more capable of root regeneration (Browse, 2011). A study investigated on the formation of the adventitious root (AR) of cuttings of Pinus elliottii x P. caribaea hybrid at different ages found that 15-week-old cuttings grew AR faster and produced a greater amount of AR compared to 9year-old cuttings (Rasmussen & Hunt, 2010). Such difference may be because mature tissue of older cuttings has lower sensitivity to endogenous auxin which plays a central role in the development and growth of AR (Pacurar, Perrone, & Bellini, 2014). Conversely, a heavy sanding to a shallow brown canopy may smother young uprights and auxiliary buds, which may reduce upright density and yield, while the same treatment to a deeper brown canopy may have no impact on upright density or yield. Strik & Poole (1995) showed that 2.5 cm of sanding reduced yield by 50% in the first and third year in an 8 years old bed, while the same treatment had no impact in a 24 years old bed. The accumulation of vines was probably greater in the older bed as both beds never received a sanding before the experiment (Strik & Poole, 1995). The results suggest that the effectiveness of sanding is influenced by the canopy depth which is probably due
to the differences in the age of the stems near the soil as younger stems may have a greater potential for regenerating roots.

Furthermore, the effectiveness of sanding may vary depending on the quality of peat and the presence or absence of past sanding. In the present study, neither Bed F nor G was tested for peat humification levels; however, a previous study characterizing BC cranberry beds indicated differences in peat humification among beds in the Lower Mainland (Someya & Harbut, 2015). Many cranberry beds in the Lower Mainland of BC were established on the post-harvest peat bogs, and peat in the deeper horizon is generally more humified than the ones in the shallower horizon, due to the differences in botanical components of the parent material. Same depth of sanding may have a greater impact on a bed with highly humified peat than a bed with less humified peat as less humified organic soil has greater drainage capacity (DeMoranville, 2008). Verry et al. (2011) reported that saturated hydraulic conductivity (K_{sat}) was 32 cm/h in moderately humified organic soils (von Post H = 5) but decreased to 1.5 cm/h in highly humified organic soils (von Post H > 7)). As K_{sat} of ordinary beach sand is approximately 36 cm/h (Brady & Weil, 2010), sanding of highly humified organic soil may result in greater improvement in drainage and aeration in the rooting environment. In addition to the quality of peat soil, the presence or absence of past sanding may influence the effectiveness of successive sanding. Sanding in Bed F in 2013 might substantially impact K_{sat}, and the additional sanding after 3 years in the present study might not have a significant impact on the drainage capacity and aeration in the rooting environment. On the other hand, Bed G was never sanded, and therefore, the sanding for the first time might substantially increase K_{sat} and improve the condition in the rooting environment. The effectiveness of sanding on cranberry canopy may be influenced by the

humification level of the peat soil and the presence or absence of past sanding as sanding improves drainage and aeration in the rooting environment.

4.5 Conclusion

Sand application is known to improve the growth and productivity of cranberry plants in the eastern US and Canada; however, the effect of the treatment has not been studied in BC cranberry beds. The present study evaluated the effects of sanding at three depth levels. The results showed a significant interaction between sanding treatment and bed on total and vegetative upright density, suggesting the effectiveness of sanding was influenced by bed condition. A significant effect of bed on UVC, yield, and brown canopy depth indicated differences in plant health and rooting capacity between the beds. In the bed with less healthy plant growth and shallower brown canopy depth, sanding at 2.5 cm depth significantly increased total and vegetative upright density compared to the control but slightly reduced yield. These results generally agreed with previous studies that showed light to moderate sanding increased vegetative growth but heavy sanding reduced yield. In the bed with healthier plant growth and deeper brown canopy depth, however, sanding at any depth did not affect plant growth. The results showed the impact of sanding on growth characteristics but also indicated the influence of bed condition on the effectiveness of sanding.

Nevertheless, overwhelming evidence suggests that sanding improves growth and yield of cranberry beds. In BC cranberry beds, the sanding can improve drainage and aeration in degrading peat and prevent excessive accumulation of vines. Therefore, despite the varying impact of sanding between the beds seen in the results of the present study, BC cranberry beds

can benefit from sanding. However, as indicated in the present study, the efficacy of sanding might be largely determined by the bed conditions. In future studies, a greater number of beds with known differences may provide a better understanding of how different factors influence the impact of sanding.

Table 4-1 Summary results of two-way analysis of variance for sanding experiment, showing an interaction between sand depth (main effect) and bed for total and vegetative upright density. The effect of bed was shown only for variables with an insignificant interaction between sand depth and bed. Significance level: $\alpha = 0.05$.

Variable	Interact	ion (sand dep	th x bed)		Effect of b	bed
variable	df	Fv	Pr	df	Fv	Pr
Total Upright Density	2, 39	5.18	0.010		-	
Vegetative Upright Density	2, 39	4.73	0.014		-	
Flowering Upright Density	2, 39	0.93	0.40	1, 39	65.42	< 0.001
Flowering Upright Ratio	2, 39	1.45	0.25	1, 39	30.07	< 0.001
Green Canopy Depth	2, 39	1.38	0.26	1, 39	3.10	0.086
Brown Canopy Depth	2, 39	0.20	0.82	1, 39	37.47	< 0.001
UVC	2, 39	0.28	0.76	1, 39	25.96	< 0.001
Yield	2, 39	1.53	0.23	1, 39	33.11	< 0.001

				Densit	ty (num	ber of up	rights / 90	0 [cm ²])				T	ukay's HSD	(\mathbf{Dr})
Upright	D 1]	Depth = 0	(cm)	D	epth $= 1.3$	(cm)	D	epth = 2.5	(cm)	RCB	Combi	nation of dep	oths (cm)
type	Bed	n	Mean	SE	n	Mean	SE	n	Mean	SE	ANOVA (Pr)	0-1.3	0-2.5	1.3-2.5
Total	F	8	575.6	25.2	8	584.6	28.4	8	542.9	20.6	0.153		-	
Total	G	7	410.4	28.8	7	508.1	31.4	7	551.9	27.9	0.005	0.042	0.005	0.455
Vecetation	F	8	367.4	29.0	8	386.8	29.4	8	337.8	23.3	0.075		-	
vegetative	G	7	301.3	19.6	7	378.9	31.7	7	445.6	36.8	0.004	0.100	0.003	0.167
Florensing	F	8	208.3	15.0	8	196.6	6.7	8	205.1	12.4	0.667		-	
Flowering	G	7	109.1	16.1	7	129.3	16.5	7	106.3	12.1	0.347		-	

Table 4-2 Summary statistics of total, vegetative, and flowering upright density under sanding treatment at three different depths (0, 1.3, and 2.5 cm). The density was determined by counting the number of uprights per 30 x 30 cm square area (900 cm²). Significance level: $\alpha = 0.05$. n: sample size. SE: standard error of the mean. Pr: probability value.

Table 4-3 Summary statistics of flowering upright ratio under sanding treatment at three different depths (0, 1.3, and 2.5 cm). The ratio was calculated by dividing flowering upright density by total upright density. Significance level: $\alpha = 0.05$. n: sample size. SE: standard error of the mean. Pr: probability value.

				Flov	vering upri	ght ratio				
D - J		Sand $= 0 c$	m		Sand = 1.3	cm		Sand = 2.5	cm	RCB ANOVA
Bed	n	Mean	SE	n	Mean	SE	n	Mean	SE	(Pr)
F	8	0.37	0.03	8	0.34	0.02	8	0.38	0.02	0.171
G	7	0.26	0.03	7	0.26	0.03	7	0.20	0.03	0.196

Table 4-4 Summary statistics of green and brown canopy depth (cm) under sanding treatment at three different depths (0, 1.3, and 2.5 cm). Significance level: $\alpha = 0.05$. n: sample size. SE: standard error of the mean. Pr: probability value.

					Ca	nopy dept	h (cm)				
Concern Torres	Ded		Depth = 0	cm]	Depth $= 1.3$	3 cm]	Depth = 2.5	5 cm	RCB ANOVA
Canopy Type	Bed	n	Mean	SE	n	Mean	SE	n	Mean	SE	(Pr)
Crean Canony	F	8	11.94	0.11	8	12.16	0.14	8	12.16	0.13	0.310
Green Canopy	G	7	11.96	0.40	7	12.41	0.22	7	13.03	0.46	0.196
Deserve Cara serve	F	8	13.86	0.74	8	13.46	0.58	8	13.04	0.63	0.057
Бтоwп Сапору	G	7	10.29	0.64	7	9.50	0.63	7	9.97	0.97	0.605

Table 4-5 Summary statistics of log-transformed unrooted volume under the canopy (UVC) under sanding treatment at three different depths (0, 1.3, and 2.5 cm). Significance level: $\alpha = 0.05$. n: sample size. SE: standard error of the mean. Pr: probability value.

					Log ₁₀ (UV	C)				
D - J		Depth = 0	em		Depth = 1.3	cm		Depth = 2.5	cm	RCB ANOVA
Bed	n	Mean	SE	n	Mean	SE	n	Mean	SE	(Pr)
F	8	1.89	0.02	8	1.90	0.13	8	1.95	0.09	0.884
G	7	2.62	0.21	7	2.42	0.16	7	2.51	0.20	0.663

Table 4-6 Summary statistics of yield estimate (bbl/acre) under sanding treatment at three different depths (0, 1.3, and 2.5 cm). One bbl (barrel) weighs 100 lbs. Significance level: $\alpha = 0.05$. n: sample size. SE: standard error of the mean. Pr: probability value.

				Yiel	d estimate (l	obl/acre)				
Dal		Depth = 0 d	cm		Depth = 1.3	cm		Depth = 2.5	cm	RCB ANOVA
Bed	n	Mean	SE	n	Mean	SE	n	Mean	SE	(Pr)
F	8	471.5	40.1	8	430.4	41.6	8	478.9	38.7	0.458
G	7	310.3	42.3	7	308.7	27.4	7	227.7	31.0	0.133



Figure 4-1 Location map of the beds selected for the sanding experiment. The red dots in the main map show the locations of beds (Bed F and Bed G) (Global Administrative Areas, 2012; Google, n.d.-a; Kahle & Wickham, 2013)



Figure 4-2 Arrangement of grid system for sanding experiment, depicting a 3 x 4 grid containing 12 plots which are separated with 50 cm buffer strips. Each plot measures 1m x 1m square.



Figure 4-3 Canopy structure of cranberry plant, depicting total, green, and brown canopy.



Figure 4-4 Diagram of unrooted volume under the canopy (UVC) measurement. The red allow indicates the pulling direction of the canopy. First, measure the pulled height (H), and mark the 4 points (P, Q, R, and S) as shown in the diagram in such way that the line PR and QS intersect at right angle. Measure the distance PR and QS. UVC, the approximated pulled volume was calculated as: UVC (cm^3) = (PR x QS x H) / 4.



Figure 4-5 Mean upright density under sanding treatment, showing the impact of sand application at three different depths (0, 1.3, and 2.5 cm) on total, vegetative, and flowering upright density per 30 cm square quadrat in two cranberry beds (Bed F and Bed G). Bars with the same letters are not significantly different based on the Tukey's HSD test. Significance level: $\alpha = 0.05$. Differences were insignificant for flowering upright density. Error bars indicate the standard error of the mean.



Figure 4-6 Mean flowering upright ratio under sanding treatment, showing the impact of sand application at three different depths (0, 1.3, and 2.5 cm) on flowering upright density to total upright density ratio in two cranberry beds (Bed F and Bed G). Differences were insignificant. Error bars indicate the standard error of the mean.



Figure 4-7 Mean canopy depth under sanding treatment, showing the impact of sand application at three different depths (0, 1.3, and 2.5 cm) on green and brown canopy depth in two cranberry beds (Bed F and Bed G). Differences were insignificant for both canopy types. Error bars indicate the standard error of the mean.



Figure 4-8 Mean log-transformed unrooted volume under the canopy (log₁₀UVC) under sanding treatment, showing the impact of sand application at three different depths (0, 1.3, and 2.5 cm) on UVC in two cranberry beds (Bed F and Bed G). Differences were insignificant. Error bars indicate the standard error of the mean.



Figure 4-9 Mean yield estimate under sanding treatment, showing the impact of sand application at three different depths (0, 1.3, and 2.5 cm) on yield in two cranberry beds (Bed F and Bed G). Differences were insignificant. One bbl (barrel) weighs 100 lbs. Error bars indicate the standard error of the mean.

Chapter 5: Conclusion

In recent years, several cranberry beds in the Lower Mainland in BC have exhibited symptoms of a condition called cranberry field decline (CFD) which include severe reduction of canopy density and complete collapse of the canopy. In the present study, four CFD-affected cranberry beds in the Lower Mainland of BC were characterized by the assessment of soil chemistry, plant growth, and carbohydrate status in the canopy. Soil pH, soil redox potential, root health, total upright density, flowering upright ratio, green and brown canopy depth, and yield estimate were compared among three levels of CFD condition. Glucose, fructose, sucrose, and starch contents in uprights and stems were analyzed for their dynamics among CFD conditions. It was hypothesized that starch content in stems (S_Sta) was different among CFD conditions. In addition, the effectiveness of sanding on cranberry beds to rehabilitate stressed vines was evaluated by comparing total, vegetative, and flowering upright density, green and brown canopy depth, root health, and yield estimate among three levels of sand depth.

The results of CFD characterization showed no distinctive or consistent trend between soil pH or redox potential and CFD conditions among beds, suggesting that soil chemistry may not be related to CFD development. Plant growth, on the other hand, showed distinctive and mostly consistent trends with the increasing severity of CFD; however, this was not found for the yield estimate. The unrooted volume under the canopy (UVC) showed a strong relationship with the increasing severity of CFD from normal to transitional areas, suggesting that root health declines in the early phase of CFD. From normal to transitional areas, brown canopy depth steadily declined, while green canopy depth and upright density declined slower and insignificantly,

respectively. However, all the canopy structures, such as brown canopy, green canopy, and upright density, sharply declined beyond transitional areas and collapsed completely towards declining areas. Also, carbohydrate analysis showed a significant reduction of S_Sta with the increasing severity of CFD, supporting the hypothesis. Moreover, carbohydrate dynamics showed that hexose in uprights (U_Hex) to S_Sta ratio increased with the CFD development, while total nonstructural carbohydrate (W_TNSC: the sum of all nonstructural carbohydrates [NSCs] measured in the present study) was similar among CFD conditions.

These results suggest that the stress-induced alteration of carbohydrate allocation under reduced photosynthesis may explain the changes in canopy structure with the increasing severity of CFD. During the early phase of CFD, the reduction of root health and density reduces photosynthesis in the upper canopy, leading to a carbohydrate deficiency. Under such condition, it was thought that plants might utilize S_Sta to maintain the upright development and growth, which corresponds to the relatively stable upright density and minimal reduction of green canopy depth. However, with the increasing severity of CFD, sugars from the degrading S_Sta are translocated to uprights and mainly accumulated as hexose rather than compensating the carbohydrate deficit for development or growth as W_TNSC showed no difference among CFD conditions. Therefore, the reduction of S_Sta is probably predominantly driven by the stress-induced translocation of carbohydrate. The declining S_Sta may not be fully replenished by the reduced photosynthesis by the end of the season, leading to a depletion of S_Sta which may reduce maintenance respiration and structural resilience in stems. Prolonged depletion of S_Sta may lead to a steady reduction of brown canopy depth with the increasing severity of CFD. After reaching transitional areas, the remaining starch reserve in stems is insufficient to support growth or maintenance of plant structures, leading to a sharp collapse of the whole canopy in declining areas.

The results of the sanding experiment showed that sanding increased upright density moderately and significantly with 1.3 and 2.5 cm of sand, respectively, while 2.5 cm of sand slightly decreased yield. These impacts of sanding, however, were only seen in a bed with lower root health and shallower brown canopy depth, which may suggest that the effectiveness of sanding is highly influenced by the health and age of plantings.

Characterization of CFD provides BC cranberry farmers with information and tools needed to manage and prevent the symptoms of CFD. According to the results of CFD characterization, it is critical to monitor brown canopy depth and root health, as an assessment of plant health only visually with upright density and green canopy depth might result in a late diagnosis of CFD. The pull-test, in particular, has been shown to be capable of diagnosing CFD in its early phase and is a practical in-field diagnostic tool for its simplicity, which allows growers to identify the symptoms of CFD before the condition advances to the declining stage. Analysis of the carbohydrate dynamics, particularly the relationship between U_Hex/S_Sta ratio and the increasing severity of CFD, may contribute to more accurate and early diagnosis of CFD conditions. Understanding the levels of NSC content may also contribute to the establishment of canopy management strategies aiming to improve various yield components limited by NSC reserve. Additionally, understanding the interaction of bed condition and the effectiveness of sanding may inform optimal timing and level of sanding as a part of canopy management practices.

The involvement of multiple cranberry beds operated under separate management practices in the present study provided both strengths to the applicability and limitations to the analyses. The characterization of CFD in each of four beds showed the variability among beds; therefore, the results of the analyses can be more widely applied to other CFD-affected cranberry beds in BC compared to an analysis on a single bed. However, the involvement of multiple beds reduced the amount of data collected per CFD condition per bed, which potentially reduced the statistical power to detect differences in the parameters among CFD conditions in each bed. Also, the potential differences in management practices among beds, particularly in the rate and timing of fertilization and irrigation, may have rendered the analysis of soil chemistry among CFD conditions challenging.

In future research, further investigation of CFD may be carried out in both differing soil conditions and plant growth. The relationship between soil humification and CFD development may be assessed by comparing a field-wide humification measurement to a mapping of CFD conditions. Also, identification of stress factors associated with CFD symptoms by investigating the correlation between the hexose in upright to starch in stem ratio, and various biotic and abiotic factors among CFD conditions may provide information to address the cause of CFD. As well, finding more cost-effective and simpler parameters corresponding to the results of carbohydrate analysis could diagnose CFD more accurately. Finally, investigating the relationship between age and rooting capacity of cranberry stems may inform an optimal canopy depth of cranberry plant and sanding frequency on the canopy for maximum effect of sanding.

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Appendices

Appendix A Detailed Data of CFD Characterization

A.1 Summary Statistics of Soil Characteristics under CFD influence

Table A.1-1 Soil pH in distilled water in comparison among CFD conditions.

Soil	pН		Declini	ng		Transit	ion		Norma	al		ANOVA	A	Tul	key's HSD	(Pr)
Bed	Year	n	Mean	SE	n	Mean	SE	n	Mean	SE	df	Fv	Pr	D-T	D-N	T-N
А	2017	9	4.262	0.036	9	4.250	0.036	9	4.356	0.067	2, 24	1.42	0.260		-	
В	2017	9	4.369	0.055	9	4.308	0.068	9	4.084	0.058	2, 24	6.11	0.007	0.758	0.008	0.040
С	2017	9	4.736	0.106	9	4.721	0.089	9	4.783	0.035	2, 24	0.16	0.856		-	
D	2017	9	4.900	0.078	9	4.984	0.083	9	4.688	0.053	2, 24	4.40	0.024	0.695	0.120	0.022

Table A.1-2 Soil oxidation reduction potential (ORP [mV]) in comparison among CFD conditions.

Soil OR	P (mV)		Declinir	ng		Transitio	on			Norma	1		ANOV	A	Tuk	ey's HSD) (Pr)
Bed	Year	n	Mean	SE	n	Mean	SE	n	l	Mean	SE	df	Fv	Pr	D-T	D-N	T-N
А	2016	3	174.97	2.40	3	176.33	2.05	9	;	166.53	6.06	2, 6	1.81	0.243		-	
В	2016	3	154.90	3.16	3	164.60	6.60	3	;	187.63	3.38	2,6	13.05	0.007	0.366	0.006	0.030
С	2016	3	151.97	4.35	3	151.90	3.75	3	;	137.37	4.48	2,6	4.01	0.078		-	
D	2016	3	121.43	6.63	3	132.00	4.90	3	;	146.60	6.71	2,6	4.24	0.071		-	

Field Condition	рН	Eh (mV)	OM (%)	H ₂ O (%)	Ex, NH ₄ (g/kg)	Ex, NO _x (g/kg)	TDS (%)	EC (μs/m)	Flux N2O (µmol/m²/hr)	Flux CO2 (µmol/m²/s)	Flux CH4 (µmol/m²/hr)
Declining	4.4	157	88	392	28.9	0.82	94	143	31.2	20	16.1
Healthy	3.8	166	70	294	58.0	0.38	95	138	71.5	4.8	1.1
Rehabilitated	3.9	173	68	340	33.2	0.45	101	154	43.3	9.0	0

Table A.1-3 Soil chemistry and soil gas flux in cranberry beds under the influence of CFD in British Columbia (Lavkulich, 2017)

A.2 Summary Statistics of Plant Canopy Characteristics under CFD influence

The table below provides the results of two-sample t-test on log-transformed UVC data.

Table A.2-1 Log-transformed unrooted volume under the canopy (log₁₀UVC) in comparison among CFD conditions

Log ₁₀	UVC		Transition	ı		Normal			t-test	
Bed	Year	n	Mean	SE	n	Mean	SE	df	t	Pr
А	2016	21	3.186	0.076	20	2.966	0.110	39	-1.65	0.107
А	2017	21	3.296	0.096	21	3.102	0.086	40	-1.50	0.142
В	2016	18	3.257	0.088	18	2.369	0.085	34	-7.25	< 0.001
В	2017	21	3.322	0.081	21	2.718	0.059	40	-6.05	< 0.001
С	2016	21	2.980	0.070	21	2.620	0.079	40	-3.42	0.002
С	2017	21	3.386	0.047	21	2.640	0.049	40	-10.98	< 0.001
D	2016	3	2.109	0.267	3	1.928	0.218	4	-0.52	0.628
D	2017	21	2.446	0.082	21	2.261	0.085	40	-1.57	0.125

TtlUp [#/.	30cm sq.]		Declini	ng		Transiti	on		Norma	ıl		ANOV	A	Tuk	ey's HSD	(Pr)
Bed	Year	n	Mean	SE	n	Mean	SE	n	Mean	SE	df	Fv	Pr	D-T	D-N	T-N
А	2016	3	105.0	12.3	3	496.3	33.6	3	564.0	33.7	2, 6	76.36	< 0.001	< 0.001	< 0.001	0.284
А	2017	3	152.7	10.3	3	440.3	38.8	3	597.3	17.6	2, 6	79.50	< 0.001	< 0.001	< 0.001	0.011
В	2016	3	161.7	13.0	3	558.3	19.2	3	641.3	72.0	2, 6	34.43	0.001	0.002	0.001	0.425
В	2017	3	144.0	11.6	3	514.0	41.6	3	568.0	21.4	2, 6	68.77	< 0.001	< 0.001	< 0.001	0.411
С	2016	3	178.7	16.6	3	405.0	37.5	3	572.3	36.2	2, 6	39.12	< 0.001	0.006	< 0.001	0.022
С	2017	3	229.7	33.8	3	685.7	31.3	3	751.0	25.9	2, 6	86.72	< 0.001	< 0.001	< 0.001	0.349
D	2016	3	152.0	20.1	3	472.7	35.3	3	460.3	15.9	2, 6	51.96	< 0.001	< 0.001	< 0.001	0.937
D	2017	3	144.3	34.7	3	637.7	28.9	3	567.0	39.9	2, 6	58.72	< 0.001	< 0.001	< 0.001	0.383

Table A.2-2 Total upright density (TtlUp [# / 30 cm sq.]) in comparison among CFD conditions

Table A.2-3 Vegetative upright (VgtUp [# / 30 cm sq.]) density in comparison among CFD conditions

VgtUp [#/3	30cm sq.]	-	Declini	ng		Transiti	on	-	Norma	ıl		ANOVA	Ą	Tuk	ey's HSD	(Pr)
Bed	Year	n	Mean	SE	n	Mean	SE	n	Mean	SE	df	Fv	Pr	D-T	D-N	T-N
А	2016	3	75.3	9.3	3	312.3	66.1	3	410.7	65.5	2,6	10.19	0.012	0.048	0.011	0.451
А	2017	3	116.0	10.3	3	252.3	21.8	3	531.7	19.9	2,6	137.98	< 0.001	0.004	< 0.001	< 0.001
В	2016	3	126.3	17.3	3	452.0	40.0	3	492.0	73.6	2,6	16.51	0.004	0.008	0.005	0.839
В	2017	3	95.7	7.5	3	349.3	24.8	3	386.7	33.0	2,6	42.65	< 0.001	0.001	< 0.001	0.554
С	2016	3	153.7	18.4	3	358.7	28.0	3	496.3	22.7	2,6	54.53	< 0.001	0.002	< 0.001	0.014
С	2017	3	192.7	29.4	3	610.0	33.0	3	580.7	18.7	2,6	70.82	< 0.001	< 0.001	< 0.001	0.745
D	2016	3	143.0	21.2	3	294.0	30.0	3	304.3	34.8	2,6	9.55	0.014	0.025	0.019	0.966
D	2017	3	142.0	33.7	3	497.3	32.5	3	360.3	37.8	2, 6	26.59	0.001	0.001	0.010	0.071

FlwUp (# /	30 cm sq.)		Declini	ng	_	Transiti	on		Norma	ıl		ANOV	A	Tuke	ey's HSD	(Pr)
Bed	Year	n	Mean	SE	n	Mean	SE	n	Mean	SE	df	Fv	Pr	D-T	D-N	T-N
А	2016	3	29.7	5.2	3	184.0	43.3	3	153.3	40.4	2, 6	5.67	0.042	0.044	0.096	0.809
А	2017	3	36.7	5.5	3	188.0	23.2	3	65.7	23.0	2,6	17.67	0.003	0.003	0.563	0.010
В	2016	3	35.3	10.2	3	107.3	35.5	3	149.3	27.8	2,6	4.66	0.060		-	
В	2017	3	48.3	4.4	3	164.7	27.4	3	181.3	31.7	2,6	8.88	0.016	0.034	0.019	0.881
С	2016	3	25.3	5.4	3	46.3	9.5	3	75.7	13.9	2,6	6.15	0.035	0.374	0.030	0.185
С	2017	3	37.0	5.3	3	75.7	13.8	3	170.3	11.3	2,6	40.54	< 0.001	0.097	< 0.001	0.002
D	2016	3	9.0	3.2	3	179.0	39.1	3	156.0	18.9	2,6	13.47	0.006	0.007	0.014	0.801
D	2017	3	2.3	1.9	3	140.3	10.9	3	206.7	2.7	2, 6	250.75	< 0.001	< 0.001	< 0.001	0.001

Table A.2-4 Flowering upright density (FlwUp [# / 30 cm sq.]) in comparison among CFD conditions

Table A.2-5 Flowering upright ratio (FlwRto) relative to the total upright count in comparison among CFD conditions

Flw	Rto	_	Declinir	ng		Transitio	on		Norma	1		ANOV	A	Tuk	ey's HSD	(Pr)
Bed	Year	n	Mean	SE	n	Mean	SE	n	Mean	SE	df	Fv	Pr	D-T	D-N	T-N
А	2016	3	0.28	0.03	3	0.38	0.10	3	0.28	0.08	2, 6	0.60	0.576		-	
А	2017	3	0.24	0.04	3	0.43	0.03	3	0.11	0.04	2,6	23.43	0.001	0.016	0.070	0.001
В	2016	3	0.22	0.07	3	0.19	0.06	3	0.23	0.05	2,6	0.14	0.875		-	
В	2017	3	0.34	0.01	3	0.32	0.03	3	0.32	0.06	2,6	0.08	0.921		-	
С	2016	3	0.14	0.03	3	0.11	0.01	3	0.13	0.02	2,6	0.62	0.570		-	
С	2017	3	0.16	0.02	3	0.11	0.02	3	0.23	0.01	2,6	14.17	0.005	0.112	0.063	0.004
D	2016	3	0.06	0.03	3	0.38	0.06	3	0.34	0.05	2,6	12.35	0.007	0.010	0.016	0.885
D	2017	3	0.01	0.01	3	0.22	0.02	3	0.37	0.02	2, 6	89.56	< 0.001	0.001	< 0.001	0.004

GrnC	p (cm)		Declinin	g		Transitio	n		Normal			ANOVA		Tuk	ey's HSD	(Pr)
Bed	Year	n	Mean	SE	n	Mean	SE	n	Mean	SE	df	Fv	Pr	D-T	D-N	T-N
А	2016	12	6.00	0.37	12	7.67	0.41	12	11.20	0.41	2, 33	45.30	< 0.001	0.015	< 0.001	< 0.001
А	2017	12	5.68	0.22	12	11.38	0.30	12	13.03	0.20	2, 33	250.37	< 0.001	< 0.001	< 0.001	< 0.001
В	2016	15	7.13	0.39	15	9.27	0.57	15	11.20	0.69	2, 42	13.10	< 0.001	0.027	< 0.001	0.050
В	2017	12	5.97	0.26	11	10.12	0.39	12	11.97	0.22	2, 32	112.97	< 0.001	< 0.001	< 0.001	< 0.001
С	2016	12	6.92	0.45	12	14.25	0.46	12	13.92	0.58	2, 33	67.85	< 0.001	< 0.001	< 0.001	0.886
С	2017	15	6.22	0.33	15	10.95	0.20	14	12.01	0.21	2, 41	147.84	< 0.001	< 0.001	< 0.001	0.015
D	2016	3	NA	NA	3	11.33	0.88	3	8.00	0.58	1,4	10.00	0.034		-	
D	2017	9	7.11	0.37	12	10.95	0.37	12	10.81	0.45	2, 30	25.92	< 0.001	< 0.001	< 0.001	0.964

Table A.2-6 Green canopy depth (GrnCp [cm]) in comparison among CFD conditions

Table A.2-7 Brown canopy depth (BrnCp [cm]) in comparison among CFD conditions

BrnC	p (cm)		Declinin	g		Transitio	on		Norma	1	_	ANOVA		Tuk	ey's HSD (H	Pr)
Bed	Year	n	Mean	SE	n	Mean	SE	n	Mean	SE	df	Fv	Pr	D-T	D-N	T-N
А	2016	12	3.67	0.36	12	7.25	0.52	12	12.58	0.57	2, 33	83.19	< 0.001	< 0.001	< 0.001	< 0.001
А	2017	12	3.86	0.21	12	8.18	0.41	12	11.85	0.58	2, 33	111.36	< 0.001	< 0.001	< 0.001	< 0.001
В	2016	15	6.20	0.28	15	9.93	0.46	15	11.13	0.57	2, 42	32.31	< 0.001	< 0.001	< 0.001	0.159
В	2017	12	6.93	0.28	11	9.36	0.23	12	10.93	0.28	2, 32	59.45	< 0.001	< 0.001	< 0.001	0.001
С	2016	12	5.33	0.38	12	11.50	0.60	12	16.25	1.16	2, 33	67.45	< 0.001	< 0.001	< 0.001	< 0.001
С	2017	15	5.74	0.42	15	11.35	0.36	14	15.85	0.44	2, 41	155.20	< 0.001	< 0.001	< 0.001	< 0.001
D	2016	3	NA	NA	3	8.67	0.67	3	9.33	0.33	1,4	0.80	0.422		-	
D	2017	9	3.32	0.68	12	11.43	0.48	12	10.15	0.19	2, 30	53.18	< 0.001	< 0.001	< 0.001	0.109

Yld (bbl/a)		Declinin	g		Transitic	n	_	Norma	.1	_	ANOVA		Tuk	ey's HSD	(Pr)
Bed	Year	n	Mean	SE	n	Mean	SE	n	Mean	SE	df	Fv	Pr	D-T	D-N	T-N
А	2016	3	93.7	33.4	3	600.7	44.3	3	341.7	106.3	2,6	13.41	0.006	0.005	0.098	0.085
А	2017	3	100.7	27.0	3	452.0	41.6	3	84.0	45.5	2,6	28.65	0.001	0.002	0.951	0.001
В	2016	3	94.0	27.5	3	301.0	51.0	3	352.7	67.6	2,6	7.10	0.026	0.066	0.028	0.766
С	2016	3	33.0	6.4	3	123.3	62.7	3	111.7	20.3	2,6	1.65	0.268		-	
С	2017	3	73.7	14.3	3	93.0	29.5	3	186.3	51.3	2,6	2.94	0.129		-	
D	2016	3	21.0	11.1	3	484.3	84.1	3	476.3	44.6	2,6	22.96	0.002	0.003	0.003	0.994
D	2017	3	1.7	0.9	3	117.3	14.1	3	431.7	52.1	2,6	50.95	0.000	0.087	< 0.001	0.001

Table A.2-8 Yield estimate (Yld) in barrel per acre (bbl/a) in comparison among CFD conditions

Appendix B Detailed Data of Carbohydrate Analysis

Table B.1-1 Starch content in uprights (U_Sta [% d.w.]) of cranberry plants. DOY: day of the year. SE indicates standard error of the mean. U Sta (% d.w.) Declining Transition Normal ANOVA Tukey's HSD (Pr) Mean SE SE Mean SE df Fv Pr D-T Year Bed Month DOY n Mean D-N n n 0.134 2016 153 3 10.966 0.900 7.950 1.333 4.749 0.163 11.09 0.010 0.008 А May 3 3 2,6 5.893 2.700 2016 207 3 1.489 0.497 0.797 А Jul 3 3 3.646 2,6 2.60 0.153 0.822 2016 Α 243 3 5.011 1.346 3 5.175 1.207 3 4.261 0.488 2,6 0.20 Aug -2016 А Oct 318 3 4.409 0.321 3 3.700 0.332 3 3.903 0.152 2,6 1.69 0.262 . 9.683 7.918 0.511 6.684 0.012 0.084 2016 В 152 3 0.314 3 3 0.550 2,6 10.30 0.010 0.231 May 0.964 3.768 0.058 2016 В Jul 201 3 6.119 3 3.481 0.611 3 0.152 2,6 4.74 4.157 2016 В 3 6.400 0.533 4.933 0.388 3 0.148 2,6 8.53 0.018 0.084 0.016 0.395 Aug 241 3 В 3 3.005 3.152 0.940 2016 318 0.194 3 3.040 0.281 3 0.410 2,6 0.06 Oct -2016 С 158 3 8.613 2.296 5.635 6.017 3 1.365 3 1.139 2,6 0.93 0.443 May 0.836 4.102 С 2016 236 3 6.905 3 4.202 0.471 3 0.381 2,6 7.12 0.026 0.042 0.037 0.992 Aug С 2.877 2.842 0.300 3.412 2016 Oct 311 3 0.133 3 3 0.087 2,6 2.65 0.150 2017 А 143 3 13.933 2.040 12.918 0.204 12.819 1.072 2,6 0.21 0.814 May 3 3 2017 Α Jul 204 3 3.764 0.538 3 4.121 0.991 3 4.051 0.019 2,6 0.08 0.920 6.241 2017 А Aug 237 3 0.822 3 5.448 0.195 3 3.933 0.545 2,6 4.08 0.076 -2017 322 3 1.377 0.224 1.455 0.147 1.912 0.310 2,6 0.298 А Oct 3 3 1.49 3 11.907 2.479 10.506 2017 В 143 12.768 0.472 3 0.910 2,6 0.54 0.607 May 3 2017 В 207 3 7.972 2.239 5.691 1.154 5.970 0.198 2,6 0.73 0.521 Jul 3 3 -1.015 3 2017 В 242 5.046 3 4.803 0.471 3 4.022 0.769 2,6 0.47 0.649 Aug 0.897 1.606 0.037 2017 В Oct 319 3 1.155 0.128 3 0.089 3 0.060 2,6 13.90 0.006 0.220

Summary Statistics of Nonstructural Carbohydrate Content under CFD influence **B.1**

0.005

T-N

0.112

U_Sta	(% d.	.w.)			Declini	ng	_	Transiti	ion		Norm	al		ANOV	ΥA	Tuk	ey's HSD	(Pr)
Year	Bed	Month	DOY	n	Mean	SE	n	Mean	SE	n	Mean	SE	df	Fv	Pr	D-T	D-N	T-N
2017	D	May	144	3	5.493	1.245	3	9.761	1.371	3	12.229	0.738	2,6	8.77	0.017	0.087	0.014	0.349
2017	D	Jul	213	3	1.729	0.191	3	3.420	0.515	3	4.863	0.702	2,6	9.31	0.015	0.128	0.012	0.197
2017	D	Aug	237	3	2.188	0.165	3	4.048	0.212	3	4.763	0.208	2,6	46.02	< 0.001	0.001	< 0.001	0.092
2017	D	Oct	319	3	1.773	0.178	3	1.840	0.394	3	1.710	0.180	2,6	0.06	0.944		-	

S_Sta	(% d.	w.)			Declin	ing		Transit	ion	_	Norm	al	_	ANOV	/A	Tuke	y's HSD (Pr)
Year	Bed	Month	DOY	n	Mean	SE	n	Mean	SE	n	Mean	SE	df	Fv	Pr	D-T	D-N	T-N
2016	А	May	153	3	4.410	0.197	3	4.477	0.686	3	6.562	0.075	2,6	8.71	0.017	0.993	0.024	0.028
2016	А	Jul	207	3	2.200	0.136	3	2.550	0.150	3	5.578	0.559	2,6	29.24	0.001	0.761	0.001	0.002
2016	А	Aug	243	3	2.466	0.263	3	4.622	0.384	3	5.619	0.211	2,6	29.87	0.001	0.005	0.001	0.117
2016	А	Oct	318	3	4.626	0.216	3	7.425	0.525	3	6.713	0.494	2,6	11.21	0.009	0.009	0.034	0.516
2016	В	May	152	3	6.646	0.144	3	8.025	0.819	3	9.973	0.662	2,6	7.42	0.024	0.320	0.020	0.141
2016	В	Jul	201	3	3.969	0.283	3	5.914	0.465	3	7.939	0.505	2,6	21.40	0.002	0.042	0.001	0.036
2016	В	Aug	241	3	5.698	0.346	3	6.880	0.315	3	8.259	0.906	2, 6	4.74	0.058		-	
2016	В	Oct	318	3	3.920	0.266	3	7.537	0.173	3	8.042	0.779	2, 6	21.43	0.002	0.005	0.002	0.753
2016	С	May	158	3	4.233	0.542	3	6.158	0.847	3	7.728	0.619	2, 6	6.60	0.031	0.194	0.026	0.305
2016	С	Aug	236	3	3.453	0.314	3	4.913	0.715	3	6.502	0.279	2, 6	10.15	0.012	0.158	0.010	0.124
2016	С	Oct	311	3	4.083	0.046	3	6.027	0.378	3	6.828	0.433	2, 6	17.95	0.003	0.015	0.003	0.280
2017	А	May	143	3	4.713	0.336	3	7.406	0.146	3	8.265	0.574	2, 6	22.22	0.002	0.007	0.002	0.338
2017	А	Jul	204	3	1.885	0.383	3	2.942	0.629	3	4.484	0.361	2,6	7.62	0.023	0.324	0.019	0.131
2017	А	Aug	237	3	2.792	0.366	3	4.495	0.577	3	6.356	1.149	2, 6	5.33	0.047	0.331	0.039	0.279
2017	А	Oct	322	3	2.367	0.186	3	3.052	0.184	3	4.181	0.178	2, 6	25.12	0.001	0.084	0.001	0.011
2017	В	May	143	3	7.248	0.864	3	8.693	0.126	3	8.894	0.285	2, 6	2.87	0.133		-	
2017	В	Jul	207	3	3.338	0.385	3	7.304	0.198	3	7.986	0.660	2, 6	30.34	0.001	0.002	0.001	0.572
2017	В	Aug	242	3	4.240	0.812	3	6.921	0.294	3	9.959	0.057	2, 6	32.78	0.001	0.021	< 0.001	0.012
2017	В	Oct	319	3	2.003	0.347	3	2.699	0.281	3	5.228	0.186	2, 6	37.02	< 0.001	0.259	< 0.001	0.002
2017	D	May	144	3	3.500	1.297	3	8.159	0.246	3	8.922	0.388	2,6	13.64	0.006	0.014	0.007	0.784
2017	D	Jul	213	3	2.411	0.331	3	7.110	0.864	3	6.622	0.382	2,6	19.97	0.002	0.003	0.005	0.827
2017	D	Aug	237	3	2.576	0.204	3	5.769	0.291	3	6.152	0.593	2,6	24.19	0.001	0.003	0.002	0.783
2017	D	Oct	319	3	2.571	0.273	3	5.262	0.267	3	3.283	0.105	2,6	37.10	< 0.001	< 0.001	0.150	0.002

Table B.1-2 Starch content in stems (S_Sta [% d.w.]) of cranberry plants. DOY: day of the year. SE indicates standard error of the mean.

U_He	x (% d	.w.)			Declin	ing		Transit	ion		Norm	al		ANOV	/A	Tuk	ey's HSD	(Pr)
Year	Bed	Month	DOY	n	Mean	SE	n	Mean	SE	n	Mean	SE	df	$\mathbf{F}\mathbf{v}$	Pr	D-T	D-N	T-N
2016	А	May	153	3	3.142	0.130	3	2.361	0.736	3	2.714	0.096	2,6	0.81	0.488		-	
2016	А	Jul	207	3	3.227	0.277	3	2.419	0.093	3	2.238	0.175	2,6	7.18	0.026	0.061	0.028	0.799
2016	А	Aug	243	3	3.142	0.024	3	2.045	0.245	3	1.762	0.201	2,6	15.78	0.004	0.013	0.004	0.553
2016	А	Oct	318	3	2.397	0.283	3	1.472	0.130	3	1.286	0.093	2,6	10.08	0.012	0.030	0.014	0.772
2016	В	May	152	3	3.056	0.264	3	2.747	0.043	3	2.688	0.154	2,6	1.23	0.357		-	
2016	В	Jul	201	3	2.450	0.029	3	2.357	0.259	3	2.127	0.089	2,6	1.09	0.394		-	
2016	В	Aug	241	3	2.702	0.088	3	2.463	0.103	3	1.797	0.209	2,6	10.62	0.011	0.508	0.010	0.039
2016	В	Oct	318	3	3.528	0.116	3	2.357	0.043	3	2.323	0.169	2,6	32.31	0.001	0.001	0.001	0.978
2016	С	May	158	3	3.170	0.300	3	3.067	0.226	3	2.349	0.130	2,6	3.79	0.086		-	
2016	С	Aug	236	3	3.124	0.315	3	2.541	0.246	3	2.150	0.226	2,6	3.42	0.102		-	
2016	С	Oct	311	3	4.125	0.248	3	1.970	0.212	3	1.449	0.234	2,6	37.46	< 0.001	0.001	< 0.001	0.320
2017	А	May	143	3	3.614	0.304	3	2.382	0.119	3	1.847	0.044	2,6	22.69	0.002	0.009	0.002	0.196
2017	А	Jul	204	3	4.760	0.278	3	2.924	0.409	3	2.716	0.231	2,6	12.73	0.007	0.015	0.009	0.889
2017	А	Aug	237	3	3.065	0.142	3	2.188	0.097	3	1.746	0.199	2, 6	19.54	0.002	0.015	0.002	0.179
2017	А	Oct	322	3	3.258	0.523	3	2.122	0.207	3	2.356	0.081	2,6	3.34	0.106		-	
2017	В	May	143	3	2.475	0.354	3	2.478	0.089	3	2.194	0.063	2,6	0.58	0.588		-	
2017	В	Jul	207	3	4.006	0.378	3	2.970	0.206	3	2.486	0.194	2,6	8.12	0.020	0.080	0.018	0.467
2017	В	Aug	242	3	3.565	0.553	3	2.763	0.429	3	2.181	0.757	2, 6	1.36	0.325		-	
2017	В	Oct	319	3	3.872	0.356	3	4.471	0.293	3	3.319	0.147	2,6	4.25	0.071		-	
2017	D	May	144	3	2.039	0.228	3	1.667	0.183	3	2.269	0.071	2,6	3.06	0.121		-	
2017	D	Jul	213	3	3.141	0.273	3	3.098	0.371	3	2.391	0.125	2,6	2.34	0.178		-	
2017	D	Aug	237	3	2.672	0.549	3	1.896	0.104	3	2.693	0.215	2, 6	1.72	0.256		-	
2017	D	Oct	319	3	1.957	0.184	3	2.161	0.068	3	2.318	0.155	2, 6	1.56	0.284		-	

Table B.1-3 Hexose content in uprights (U_Hex [% d.w.]) of cranberry plants. DOY: day of the year. SE: standard error of the mean.

S_Hex	x (% d.	w.)			Declini	ng		Transiti	ion		Norm	al		ANOVA	A	Tuke	y's HSD	(Pr)
Year	Bed	Month	DOY	n	Mean	SE	n	Mean	SE	n	Mean	SE	df	Fv	Pr	D-T	D-N	T-N
2016	А	May	153	3	0.543	0.045	3	0.626	0.101	3	0.431	0.067	2,6	1.73	0.255		-	
2016	А	Jul	207	3	0.639	0.166	3	0.641	0.094	3	0.478	0.069	2,6	0.63	0.563		-	
2016	А	Aug	243	3	0.538	0.075	3	0.455	0.059	3	0.549	0.056	2,6	0.65	0.557		-	
2016	А	Oct	318	3	0.787	0.006	3	0.814	0.076	3	0.821	0.094	2,6	0.07	0.933		-	
2016	В	May	152	3	0.617	0.049	3	0.417	0.024	3	0.375	0.009	2,6	16.15	0.004	0.011	0.004	0.650
2016	В	Jul	201	3	0.657	0.038	3	0.727	0.142	3	0.450	0.028	2,6	2.78	0.140		-	
2016	В	Aug	241	3	0.524	0.065	3	0.347	0.032	3	0.287	0.041	2,6	6.50	0.032	0.091	0.031	0.671
2016	В	Oct	318	3	1.272	0.081	3	1.309	0.037	3	1.222	0.154	2,6	0.18	0.839		-	
2016	С	May	158	3	0.528	0.059	3	0.324	0.059	3	0.276	0.005	2,6	7.76	0.022	0.054	0.023	0.773
2016	С	Aug	236	3	0.716	0.100	3	0.594	0.036	3	0.518	0.056	2,6	2.06	0.209		-	
2016	С	Oct	311	3	0.977	0.075	3	0.824	0.067	3	0.741	0.052	2,6	3.35	0.105		-	
2017	А	May	143	3	1.175	0.214	3	1.190	0.121	3	0.764	0.041	2,6	2.82	0.137		-	
2017	А	Jul	204	3	1.243	0.165	3	0.992	0.047	3	0.759	0.044	2,6	5.61	0.042	0.268	0.036	0.311
2017	А	Aug	237	3	0.469	0.091	3	0.430	0.047	3	0.235	0.052	2,6	3.57	0.095		-	
2017	А	Oct	322	3	1.381	0.195	3	1.761	0.184	3	1.236	0.013	2,6	3.07	0.121		-	
2017	В	May	143	3	0.745	0.043	3	0.710	0.028	3	0.666	0.065	2,6	0.68	0.542		-	
2017	В	Jul	207	3	0.762	0.100	3	0.627	0.052	3	0.382	0.015	2,6	8.59	0.017	0.376	0.015	0.086
2017	В	Aug	242	3	1.762	0.789	3	0.637	0.173	3	0.653	0.098	2,6	1.88	0.232		-	
2017	В	Oct	319	3	1.111	0.240	3	1.878	0.049	3	1.460	0.092	2,6	6.46	0.032	0.027	0.303	0.204
2017	D	May	144	3	0.864	0.179	3	0.761	0.069	3	1.121	0.072	2,6	2.47	0.165		-	
2017	D	Jul	213	3	0.614	0.084	3	0.682	0.044	3	0.460	0.014	2,6	4.28	0.070		-	
2017	D	Aug	237	3	0.360	0.057	3	0.514	0.056	3	0.482	0.059	2,6	2.03	0.212		-	
2017	D	Oct	319	3	0.757	0.081	3	0.949	0.003	3	1.451	0.085	2,6	27.91	0.001	0.192	0.001	0.005

Table B.1-4 Hexose content in stems (S_Hex [% d.w.]) of cranberry plants. DOY: day of the year. SE: standard error of the mean.

U_Su	e (% d	.w.)			Declin	ing		Transit	ion		Norm	al		ANOV	A	Tu	key's HSD	O (Pr)
Year	Bed	Month	DOY	n	Mean	SE	n	Mean	SE	n	Mean	SE	df	Fv	Pr	D-T	D-N	T-N
2016	А	May	153	3	0.809	0.128	3	1.096	0.190	3	0.843	0.121	2,6	1.10	0.391		-	
2016	А	Jul	207	3	1.216	0.124	3	0.645	0.084	3	0.490	0.042	2,6	18.08	0.003	0.010	0.003	0.487
2016	А	Aug	243	3	1.328	0.141	3	0.849	0.045	3	0.661	0.218	2,6	5.11	0.051		-	
2016	А	Oct	318	3	4.273	0.440	3	2.579	0.081	3	2.347	0.052	2, 6	16.38	0.004	0.009	0.005	0.809
2016	В	May	152	3	0.859	0.063	3	0.911	0.059	3	1.187	0.046	2,6	9.74	0.013	0.797	0.015	0.031
2016	В	Jul	201	3	0.350	0.043	3	0.187	0.017	3	0.233	0.023	2,6	8.09	0.020	0.019	0.070	0.544
2016	В	Aug	241	3	0.866	0.148	3	0.597	0.021	3	0.554	0.036	2,6	3.62	0.093		-	
2016	В	Oct	318	3	2.778	0.207	3	3.440	0.099	3	3.896	0.041	2, 6	17.42	0.003	0.031	0.003	0.117
2016	С	May	158	3	1.366	0.063	3	1.226	0.326	3	0.952	0.127	2,6	1.05	0.405		-	
2016	С	Aug	236	3	1.152	0.129	3	0.729	0.047	3	0.772	0.070	2,6	6.84	0.028	0.035	0.053	0.937
2016	С	Oct	311	3	2.883	0.290	3	2.779	0.239	3	2.597	0.093	2,6	0.42	0.675		-	
2017	А	May	143	3	2.655	0.519	3	3.336	0.240	3	3.503	0.060	2,6	1.83	0.240		-	
2017	А	Jul	204	3	0.217	0.048	3	0.155	0.019	3	0.167	0.019	2,6	1.05	0.406		-	
2017	А	Aug	237	3	1.244	0.194	3	1.062	0.134	3	0.670	0.074	2,6	4.23	0.072		-	
2017	А	Oct	322	3	4.999	0.647	3	3.988	0.330	3	4.152	0.187	2,6	1.57	0.283		-	
2017	В	May	143	3	2.349	0.041	3	2.592	0.041	3	3.177	0.006	2,6	161.07	< 0.001	0.005	< 0.001	< 0.001
2017	В	Jul	207	3	0.306	0.136	3	0.101	0.012	3	0.323	0.035	2,6	2.30	0.181		-	
2017	В	Aug	242	3	0.645	0.186	3	0.303	0.134	3	0.639	0.416	2,6	0.51	0.625		-	
2017	В	Oct	319	3	6.426	0.447	3	6.057	0.564	3	5.545	0.047	2,6	1.13	0.384		-	
2017	D	May	144	3	1.555	0.151	3	2.182	0.177	3	3.289	0.505	2,6	7.48	0.023	0.408	0.021	0.110
2017	D	Jul	213	3	0.083	0.003	3	0.397	0.330	3	0.287	0.130	2,6	0.61	0.575		-	
2017	D	Aug	237	3	0.665	0.440	3	1.083	0.143	3	0.553	0.034	2,6	1.09	0.396		-	
2017	D	Oct	319	3	7.163	0.046	3	5.839	0.295	3	6.090	0.085	2, 6	15.43	0.004	0.005	0.013	0.609

Table B.1-5 Sucrose content in uprights (U_Suc [% d.w.]) of cranberry plants. D DOY: day of the year. SE: standard error of the mean.

S_Suc	: (% d.	w.)			Declin	ing		Transit	ion		Norm	al		ANOV	VΑ	Tukey	y's HSD	(Pr)
Year	Bed	Month	DOY	n	Mean	SE	n	Mean	SE	n	Mean	SE	df	Fv	Pr	D-T	D-N	T-N
2016	А	May	153	3	1.367	0.080	3	0.977	0.135	3	0.821	0.070	2,6	8.10	0.020	0.071	0.019	0.540
2016	А	Jul	207	3	1.386	0.182	3	0.907	0.058	3	1.381	0.175	2,6	3.39	0.103		-	
2016	А	Aug	243	3	1.281	0.111	3	0.886	0.056	3	1.011	0.108	2,6	4.50	0.064		-	
2016	А	Oct	318	3	2.693	0.215	3	1.977	0.082	3	2.007	0.107	2,6	7.63	0.023	0.032	0.037	0.989
2016	В	May	152	3	1.290	0.135	3	1.131	0.011	3	1.060	0.039	2,6	2.10	0.204		-	
2016	В	Jul	201	3	1.246	0.087	3	0.948	0.072	3	0.939	0.033	2,6	6.56	0.031	0.049	0.044	0.996
2016	В	Aug	241	3	1.373	0.087	3	1.020	0.013	3	1.065	0.029	2,6	12.84	0.007	0.008	0.016	0.831
2016	В	Oct	318	3	3.589	0.342	3	3.446	0.067	3	3.655	0.074	2,6	0.27	0.774		-	
2016	С	May	158	3	1.380	0.082	3	1.140	0.141	3	0.844	0.117	2,6	5.35	0.046	0.370	0.039	0.247
2016	С	Aug	236	3	1.387	0.043	3	1.242	0.126	3	1.340	0.086	2,6	0.65	0.553		-	
2016	С	Oct	311	3	2.347	0.128	3	2.329	0.271	3	1.728	0.333	2,6	1.85	0.237		-	
2017	А	May	143	3	3.079	0.467	3	3.143	0.227	3	2.706	0.088	2,6	0.60	0.577		-	
2017	А	Jul	204	3	0.840	0.029	3	0.450	0.017	3	0.511	0.041	2,6	46.29	< 0.001	< 0.001	0.001	0.408
2017	А	Aug	237	3	1.399	0.049	3	1.108	0.054	3	0.945	0.059	2,6	18.05	0.003	0.021	0.003	0.163
2017	А	Oct	322	3	3.789	0.348	3	3.347	0.358	3	2.929	0.106	2,6	2.13	0.200		-	
2017	В	May	143	3	2.688	0.173	3	2.826	0.061	3	3.276	0.139	2,6	5.35	0.046	0.753	0.046	0.117
2017	В	Jul	207	3	0.834	0.185	3	0.362	0.023	3	0.619	0.047	2,6	4.54	0.063		-	
2017	В	Aug	242	3	0.774	0.341	3	0.662	0.165	3	0.605	0.097	2,6	0.15	0.868		-	
2017	В	Oct	319	3	3.866	0.038	3	4.043	0.091	3	4.062	0.139	2,6	1.20	0.364		-	
2017	D	May	144	3	1.129	0.120	3	2.478	0.055	3	3.080	0.264	2,6	34.37	0.001	0.003	0.001	0.102
2017	D	Jul	213	3	0.426	0.032	3	0.511	0.054	3	0.685	0.103	2,6	3.61	0.093		-	
2017	D	Aug	237	3	0.858	0.106	3	1.294	0.051	3	1.159	0.018	2,6	10.47	0.011	0.010	0.049	0.406
2017	D	Oct	319	3	5.041	0.547	3	4.664	0.226	3	5.050	0.077	2, 6	0.41	0.682		-	

Table B.1-6 Sucrose content in stems (S_Suc [% d.w.]) of cranberry plants. DOY: day of the year. SE: standard error of the mean.

U_SSg	g (% d.	w.)			Declini	ng		Transiti	on		Norm	al		ANOV	4	Tuke	y's HSD	(Pr)
Year	Bed	Month	DOY	n	Mean	SE	n	Mean	SE	n	Mean	SE	df	Fv	Pr	D-T	D-N	T-N
2016	А	May	153	3	3.952	0.228	3	3.457	0.591	3	3.557	0.127	2,6	0.49	0.634		-	
2016	А	Jul	207	3	4.444	0.375	3	3.064	0.083	3	2.728	0.210	2,6	12.93	0.007	0.020	0.007	0.638
2016	А	Aug	243	3	4.470	0.123	3	2.894	0.285	3	2.423	0.170	2,6	27.55	0.001	0.004	0.001	0.304
2016	А	Oct	318	3	6.670	0.564	3	4.051	0.164	3	3.634	0.120	2,6	22.61	0.002	0.004	0.002	0.687
2016	В	May	152	3	3.914	0.207	3	3.658	0.048	3	3.875	0.184	2,6	0.72	0.523		-	
2016	В	Jul	201	3	2.800	0.071	3	2.544	0.267	3	2.361	0.081	2,6	1.77	0.249		-	
2016	В	Aug	241	3	3.569	0.141	3	3.060	0.123	3	2.351	0.228	2,6	12.91	0.007	0.167	0.006	0.058
2016	В	Oct	318	3	6.306	0.296	3	5.798	0.136	3	6.218	0.169	2,6	1.65	0.269		-	
2016	С	May	158	3	4.535	0.350	3	4.293	0.542	3	3.301	0.206	2,6	2.80	0.139		-	
2016	С	Aug	236	3	4.275	0.397	3	3.269	0.286	3	2.922	0.296	2,6	4.53	0.063		-	
2016	С	Oct	311	3	7.008	0.333	3	4.749	0.211	3	4.046	0.295	2,6	29.67	0.001	0.003	0.001	0.264
2017	А	May	143	3	6.269	0.323	3	5.718	0.357	3	5.350	0.101	2,6	2.65	0.150		-	
2017	А	Jul	204	3	4.977	0.238	3	3.079	0.426	3	2.883	0.216	2,6	14.10	0.005	0.011	0.007	0.896
2017	А	Aug	237	3	4.310	0.052	3	3.250	0.099	3	2.416	0.270	2,6	31.61	0.001	0.010	0.001	0.030
2017	А	Oct	322	3	8.257	1.014	3	6.110	0.529	3	6.508	0.187	2,6	2.91	0.131		-	
2017	В	May	143	3	4.823	0.384	3	5.071	0.129	3	5.372	0.058	2,6	1.35	0.327		-	
2017	В	Jul	207	3	4.312	0.511	3	3.071	0.213	3	2.809	0.182	2,6	5.69	0.041	0.089	0.045	0.851
2017	В	Aug	242	3	4.209	0.459	3	3.067	0.315	3	2.819	0.341	2,6	3.86	0.084		-	
2017	В	Oct	319	3	10.298	0.448	3	10.527	0.856	3	8.864	0.194	2,6	2.51	0.161		-	
2017	D	May	144	3	3.594	0.377	3	3.849	0.255	3	5.558	0.524	2,6	7.10	0.026	0.897	0.031	0.053
2017	D	Jul	213	3	3.223	0.270	3	3.495	0.688	3	2.678	0.090	2,6	0.94	0.442		-	
2017	D	Aug	237	3	3.337	0.130	3	2.979	0.081	3	3.246	0.249	2,6	1.22	0.360		-	
2017	D	Oct	319	3	9.120	0.230	3	8.000	0.361	3	8.408	0.222	2,6	4.14	0.074		-	

Table B.1-7 Total soluble sugar content uprights (U_SSg [% d.w.]) of cranberry plants. DOY: day of the year. SE: standard error of the mean. SSg is a sum of glucose, fructose, and sucrose content.
S_SSg	(% d.	w.)			Declini	ng		Transit	ion		Norm	al		ANOV	4	Tuke	y's HSD	(Pr)
Year	Bed	Month	DOY	n	Mean	SE	n	Mean	SE	n	Mean	SE	df	Fv	Pr	D-T	D-N	T-N
2016	А	May	153	3	1.910	0.077	3	1.603	0.101	3	1.251	0.032	2,6	18.95	0.003	0.064	0.002	0.038
2016	А	Jul	207	3	2.024	0.347	3	1.548	0.038	3	1.859	0.233	2,6	1.00	0.423		-	
2016	А	Aug	243	3	1.820	0.166	3	1.341	0.103	3	1.560	0.141	2,6	2.97	0.127		-	
2016	А	Oct	318	3	3.480	0.220	3	2.792	0.057	3	2.828	0.181	2,6	5.31	0.047	0.062	0.075	0.987
2016	В	May	152	3	1.907	0.165	3	1.548	0.021	3	1.435	0.031	2,6	6.35	0.033	0.090	0.033	0.708
2016	В	Jul	201	3	1.903	0.123	3	1.675	0.214	3	1.389	0.022	2,6	3.24	0.111		-	
2016	В	Aug	241	3	1.897	0.152	3	1.368	0.040	3	1.353	0.035	2,6	11.15	0.010	0.016	0.014	0.993
2016	В	Oct	318	3	4.861	0.416	3	4.756	0.049	3	4.876	0.194	2,6	0.06	0.941		-	
2016	С	May	158	3	1.908	0.124	3	1.463	0.124	3	1.120	0.123	2,6	10.18	0.012	0.097	0.010	0.203
2016	С	Aug	236	3	2.103	0.074	3	1.835	0.104	3	1.858	0.104	2,6	2.43	0.169		-	
2016	С	Oct	311	3	3.324	0.127	3	3.153	0.208	3	2.469	0.311	2,6	3.93	0.081		-	
2017	А	May	143	3	4.254	0.679	3	4.333	0.343	3	3.470	0.053	2,6	1.17	0.372		-	
2017	А	Jul	204	3	2.084	0.151	3	1.443	0.029	3	1.269	0.076	2,6	18.78	0.003	0.009	0.003	0.476
2017	А	Aug	237	3	1.868	0.057	3	1.538	0.100	3	1.181	0.103	2,6	14.80	0.005	0.089	0.004	0.067
2017	А	Oct	322	3	5.170	0.164	3	5.108	0.527	3	4.166	0.093	2,6	3.03	0.123		-	
2017	В	May	143	3	3.432	0.131	3	3.536	0.064	3	3.942	0.106	2,6	6.69	0.030	0.771	0.031	0.074
2017	В	Jul	207	3	1.596	0.103	3	0.989	0.054	3	1.001	0.061	2,6	20.72	0.002	0.003	0.004	0.993
2017	В	Aug	242	3	2.536	0.459	3	1.299	0.021	3	1.258	0.037	2,6	7.45	0.024	0.038	0.034	0.994
2017	В	Oct	319	3	4.978	0.250	3	5.921	0.140	3	5.523	0.149	2,6	6.44	0.032	0.027	0.178	0.352
2017	D	May	144	3	1.993	0.297	3	3.238	0.117	3	4.201	0.208	2,6	25.24	0.001	0.017	0.001	0.049
2017	D	Jul	213	3	1.040	0.107	3	1.193	0.048	3	1.144	0.091	2,6	0.83	0.479		-	
2017	D	Aug	237	3	1.218	0.052	3	1.808	0.066	3	1.641	0.043	2,6	31.54	0.001	0.001	0.004	0.154
2017	D	Oct	319	3	5.798	0.516	3	5.614	0.224	3	6.501	0.138	2,6	1.96	0.221		-	

Table B.1-8 Total soluble sugar content in stems (S_SSg [% d.w.]) of cranberry plants. DOY: day of the year. SE: standard error of the mean. SSg is a sum of glucose, fructose, and sucrose content.

U_TN	U _TNSC (% d.w.) Year Bed Month DO'				Declini	ng		Transiti	on		Norma	ıl		ANOV	4	Tuke	y's HSD	(Pr)
Year	Bed	Month	DOY	n	Mean	SE	n	Mean	SE	n	Mean	SE	df	Fv	Pr	D-T	D-N	T-N
2016	А	May	153	3	14.918	0.855	3	11.407	1.879	3	8.306	0.228	2,6	7.61	0.023	0.177	0.019	0.239
2016	А	Jul	207	3	10.337	1.376	3	5.764	0.500	3	6.374	1.006	2,6	5.86	0.039	0.045	0.076	0.908
2016	А	Aug	243	3	9.481	1.467	3	8.069	1.484	3	6.684	0.576	2,6	1.25	0.351		-	
2016	А	Oct	318	3	11.079	0.871	3	7.751	0.495	3	7.537	0.197	2,6	11.36	0.009	0.017	0.013	0.964
2016	В	May	152	3	13.597	0.221	3	11.576	0.465	3	10.559	0.734	2,6	8.93	0.016	0.073	0.014	0.403
2016	В	Jul	201	3	8.920	0.911	3	6.025	0.429	3	6.129	0.106	2,6	7.89	0.021	0.030	0.034	0.991
2016	В	Aug	241	3	9.968	0.408	3	7.993	0.496	3	6.508	0.097	2,6	21.43	0.002	0.023	0.002	0.070
2016	В	Oct	318	3	9.311	0.484	3	8.838	0.312	3	9.370	0.256	2,6	0.64	0.558		-	
2016	С	May	158	3	13.149	2.180	3	9.928	1.895	3	9.318	1.345	2,6	1.25	0.351		-	
2016	С	Aug	236	3	11.180	1.037	3	7.471	0.729	3	7.025	0.481	2,6	8.49	0.018	0.036	0.022	0.916
2016	С	Oct	311	3	9.886	0.464	3	7.591	0.510	3	7.457	0.289	2,6	10.00	0.012	0.022	0.017	0.974
2017	А	May	143	3	20.203	1.719	3	18.636	0.234	3	18.169	1.067	2,6	0.82	0.484		-	
2017	А	Jul	204	3	8.741	0.323	3	7.200	1.161	3	6.934	0.230	2,6	1.90	0.230		-	
2017	А	Aug	237	3	10.550	0.772	3	8.698	0.232	3	6.349	0.802	2,6	10.30	0.012	0.194	0.010	0.098
2017	А	Oct	322	3	9.633	1.029	3	7.565	0.384	3	8.420	0.497	2,6	2.23	0.189		-	
2017	В	May	143	3	16.731	2.238	3	17.839	0.444	3	15.878	0.961	2,6	0.47	0.645		-	
2017	В	Jul	207	3	12.284	1.870	3	8.761	1.354	3	8.779	0.068	2,6	2.32	0.180		-	
2017	В	Aug	242	3	9.255	1.001	3	7.869	0.566	3	6.841	1.086	2,6	1.76	0.250		-	
2017	В	Oct	319	3	11.453	0.320	3	11.424	0.793	3	10.471	0.254	2,6	1.18	0.370		-	
2017	D	May	144	3	9.087	1.587	3	13.610	1.593	3	17.787	0.953	2,6	9.52	0.014	0.137	0.011	0.171
2017	D	Jul	213	3	4.952	0.339	3	6.915	0.972	3	7.541	0.776	2,6	3.30	0.108		-	
2017	D	Aug	237	3	5.525	0.295	3	7.027	0.283	3	8.009	0.158	2,6	24.49	0.001	0.013	0.001	0.075
2017	D	Oct	319	3	10.894	0.158	3	9.841	0.512	3	10.118	0.114	2, 6	2.97	0.127		-	

Table B.1-9 Total nonstructural carbohydrate content in uprights (U_TNSC [% d.w.]) of cranberry plants. DOY: day of the year. SE: standard error of the mean. TNSC is a sum of glucose, fructose, sucrose, and starch content.

S_TN	S_TNSC (% d.w.) Year Bed Month DOY				Declin	ing	_	Transiti	on	_	Norma	al		ANOV	'A	Tuk	ey's HSD	(Pr)
Year	Bed	Month	DOY	n	Mean	SE	n	Mean	SE	n	Mean	SE	df	Fv	Pr	D-T	D-N	T-N
2016	А	May	153	3	6.321	0.272	3	6.081	0.683	3	7.814	0.083	2, 6	4.83	0.056		-	
2016	А	Jul	207	3	4.224	0.314	3	4.098	0.140	3	7.437	0.758	2, 6	15.51	0.004	0.981	0.008	0.006
2016	А	Aug	243	3	4.285	0.300	3	5.963	0.281	3	7.178	0.322	2, 6	23.19	0.002	0.018	0.001	0.066
2016	А	Oct	318	3	8.106	0.436	3	10.217	0.513	3	9.541	0.671	2,6	3.86	0.084		-	
2016	В	May	152	3	8.553	0.278	3	9.573	0.813	3	11.408	0.631	2,6	5.52	0.044	0.510	0.039	0.168
2016	В	Jul	201	3	5.873	0.163	3	7.589	0.256	3	9.328	0.514	2,6	25.13	0.001	0.029	0.001	0.027
2016	В	Aug	241	3	7.595	0.444	3	8.248	0.315	3	9.611	0.882	2,6	2.95	0.128		-	
2016	В	Oct	318	3	8.781	0.199	3	12.293	0.217	3	12.918	0.620	2,6	31.66	0.001	0.002	0.001	0.540
2016	С	May	158	3	6.141	0.666	3	7.621	0.958	3	8.849	0.741	2,6	2.89	0.132		-	
2016	С	Aug	236	3	5.555	0.386	3	6.748	0.819	3	8.36	0.368	2,6	6.23	0.034	0.358	0.029	0.188
2016	С	Oct	311	3	7.407	0.126	3	9.179	0.585	3	9.297	0.670	2, 6	4.16	0.073		-	
2017	А	May	143	3	8.966	0.954	3	11.739	0.371	3	11.735	0.586	2,6	5.52	0.044	0.063	0.064	1.000
2017	А	Jul	204	3	3.969	0.238	3	4.384	0.638	3	5.753	0.426	2,6	4.06	0.077		-	
2017	А	Aug	237	3	4.659	0.390	3	6.033	0.477	3	7.536	1.143	2,6	3.68	0.091		-	
2017	А	Oct	322	3	7.536	0.350	3	8.160	0.465	3	8.346	0.267	2,6	1.32	0.336		-	
2017	В	May	143	3	10.68	0.733	3	12.229	0.063	3	12.836	0.284	2,6	5.96	0.038	0.115	0.036	0.636
2017	В	Jul	207	3	4.933	0.450	3	8.293	0.252	3	8.987	0.637	2,6	20.99	0.002	0.006	0.002	0.583
2017	В	Aug	242	3	6.776	1.247	3	8.220	0.274	3	11.217	0.093	2,6	9.40	0.014	0.407	0.013	0.064
2017	В	Oct	319	3	6.981	0.133	3	8.620	0.387	3	10.75	0.315	2,6	40.28	< 0.001	0.019	< 0.001	0.006
2017	D	May	144	3	5.493	1.594	3	11.397	0.243	3	13.123	0.592	2,6	16.29	0.004	0.013	0.004	0.480
2017	D	Jul	213	3	3.451	0.401	3	8.303	0.908	3	7.766	0.469	2,6	17.62	0.003	0.004	0.007	0.826
2017	D	Aug	237	3	3.794	0.222	3	7.577	0.267	3	7.794	0.575	2,6	33.68	0.001	0.001	0.001	0.919
2017	D	Oct	319	3	8.369	0.787	3	10.876	0.404	3	9.784	0.215	2, 6	5.72	0.041	0.035	0.218	0.369

Table B.1-10 Total nonstructural carbohydrate content in stems (S_TNSC [% d.w.]) of cranberry plants. DOY: day of the year. SE: standard error of the mean. TNSC is a sum of glucose, fructose, sucrose, and starch content.

W_TN	NSC (%	% d.w.)		Declining n Mean SE				Transitio	onal		Norma	al		ANOV	νA	Tuke	y's HSD (Pr)
Year	Bed	Month	DOY	n	Mean	SE	n	Mean	SE	n	Mean	SE	df	Fv	Pr	D-T	D-N	T-N
2016	А	May	153	3	21.239	0.811	3	17.488	2.396	3	16.120	0.310	2,6	3.24	0.111		-	
2016	А	Jul	207	3	14.561	1.081	3	9.861	0.554	3	13.811	1.321	2,6	5.94	0.038	0.042	0.868	0.080
2016	А	Aug	243	3	13.767	1.735	3	14.032	1.229	3	13.862	0.355	2,6	0.01	0.988		-	
2016	А	Oct	318	3	19.185	1.085	3	17.968	0.935	3	17.078	0.791	2,6	1.25	0.351		-	
2016	В	May	152	3	22.151	0.308	3	21.149	0.601	3	21.967	1.137	2,6	0.49	0.636		-	
2016	В	Jul	201	3	14.792	0.941	3	13.614	0.318	3	15.457	0.587	2,6	1.96	0.221		-	
2016	В	Aug	241	3	17.563	0.182	3	16.241	0.531	3	16.119	0.810	2,6	1.98	0.219		-	
2016	В	Oct	318	3	18.092	0.648	3	21.130	0.118	3	22.289	0.846	2,6	12.27	0.008	0.031	0.007	0.434
2016	С	May	158	3	19.290	2.691	3	17.549	2.842	3	18.167	2.082	2,6	0.12	0.890		-	
2016	С	Aug	236	3	16.736	0.874	3	14.219	1.530	3	15.385	0.553	2,6	1.40	0.318		-	
2016	С	Oct	311	3	17.293	0.406	3	16.770	1.093	3	16.754	0.885	2,6	0.13	0.879		-	
2017	А	May	143	3	29.169	0.774	3	30.375	0.305	3	29.903	1.388	2,6	0.42	0.673		-	
2017	А	Jul	204	3	12.710	0.496	3	11.584	1.766	3	12.687	0.197	2,6	0.36	0.709		-	
2017	А	Aug	237	3	15.210	1.138	3	14.731	0.300	3	13.885	1.635	2,6	0.33	0.729		-	
2017	А	Oct	322	3	17.170	1.348	3	15.725	0.849	3	16.766	0.763	2,6	0.53	0.612		-	
2017	В	May	143	3	27.411	2.784	3	30.068	0.411	3	28.714	0.819	2,6	0.62	0.571		-	
2017	В	Jul	207	3	17.218	2.192	3	17.054	1.336	3	17.766	0.690	2,6	0.06	0.943		-	
2017	В	Aug	242	3	16.031	2.149	3	16.089	0.622	3	18.058	1.051	2,6	0.65	0.554		-	
2017	В	Oct	319	3	18.434	0.429	3	20.044	1.169	3	21.221	0.504	2,6	3.25	0.110		-	
2017	D	May	144	3	14.580	3.075	3	25.007	1.615	3	30.910	0.777	2,6	16.19	0.004	0.027	0.003	0.186
2017	D	Jul	213	3	8.4030	0.735	3	15.218	1.219	3	15.307	1.241	2,6	13.20	0.006	0.011	0.010	0.998
2017	D	Aug	237	3	9.3190	0.131	3	14.604	0.518	3	15.803	0.531	2,6	62.99	< 0.001	< 0.001	< 0.001	0.205
2017	D	Oct	319	3	19.263	0.755	3	20.717	0.813	3	19.902	0.250	2, 6	1.23	0.356		-	

Table B.1-11 Total nonstructural carbohydrate content in whole vines (W_TNSC [% d.w.]) of cranberry plants. DOY: day of the year. SE: standard error of the mean. W_TNSC is a sum of glucose, fructose, sucrose, and starch content in uprights and stems combined.

B.2 Results of PCA of Carbohydrate Analysis

Table B.2-1 Principle components listed in the order	of the Importance (proportion of the v	variance explained)
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	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
Standard deviation	1.88	1.347	1.0639	0.85684	0.72454	0.3546	0.28908	0.22515
Proportion of Variance	0.4418	0.2268	0.1415	0.09177	0.06562	0.01572	0.01045	0.00634
Cumulative Proportion	0.4418	0.6686	0.8101	0.90188	0.9675	0.98322	0.99366	1



Figure B.2-1 Scree plot showing proportion of variances explained by each component in the principle components analysis.

Appendix C Detailed Data of Sanding Experiment

C.1 Summary Statistics of Plant Growth Characteristics under Sand Application (Chapter 4)

TtlUp (# / 30 cm sq.)		Depth=0	cm		Depth=1.3	Scm		Depth=2.5	Scm	RC	B ANO	VA	Tuk	ey's HSI	O (Pr)
Bed	n	Mean	SE	n	Mean	SE	n	Mean	SE	df	Fv	Pr	0-1.3	0-2.5	1.3-2.5
F	8	575.6	25.2	8	584.6	28.4	8	542.9	20.6	2, 14	2.16	0.153		-	
G	7	410.4	28.8	7	508.1	31.4	7	551.9	27.9	2, 12	8.40	0.005	0.042	0.005	0.455

Table C.1-1 Total upright count per 30cm sq. quadrat (TtlUp [#/30cm sq.])

Table C.1-2 Vegetative upright count per 30cm sq. quadrat (VgtUp [#/30cm sq.])

VgtUp (# / 30 cm sq.)		Depth=00	em]	Depth=1.3	Bcm		Depth=2.5	Scm	 RC	B ANO	VA	Tuk	ey's HSI	O (Pr)
Bed	n	Mean	SE	n	Mean	SE	n	Mean	SE	df	Fv	Pr	0-1.3	0-2.5	1.3-2.5
F	8	367.4	29.0	8	386.8	29.4	8	337.8	23.3	2, 14	3.13	0.075		-	
G	7	301.3	19.6	7	378.9	31.7	7	445.6	36.8	2, 12	8.91	0.004	0.100	0.003	0.167

Table C.1-3 Flowering upright count per 30cm sq. quadrat (FlwUp [#/30cm sq.])

FlwUp (# / 30 cm sq.)	_	Contro	1]	Depth=1.3	Bcm		Depth=2.5	ōcm		RC	B ANO	VA	Tuk	key's HSI	O (Pr)
Bed	n	Mean	SE	n	Mean	SE	n	Mean	SE		df	Fv	Pr	0-1.3	0-2.5	1.3-2.5
F	8	208.3	15.0	8	196.6	6.7	8	205.1	12.4	2	2, 14	0.42	0.667		-	
G	7	109.1	16.1	7	129.3	16.5	7	106.3	12.1	2	2, 12	1.16	0.347		-	

FlwRto	Depth=0cm		m		Depth=1.3	cm	_	Depth=2.5	cm	RC	B ANOV	/A	Tu	key's HSE) (Pr)
Bed	n	Mean	SE	n	Mean	SE	n	Mean	SE	df	Fv	Pr	0-1.3	0-2.5	1.3-2.5
F	8	0.37	0.03	8	0.34	0.02	8	0.38	0.02	2, 14	2.01	0.171		-	
G	7	0.26	0.03	7	0.26	0.03	7	0.20	0.03	2, 12	1.87	0.196		-	

Table C.1-4 Flowering upright ratio per 30cm sq. quadrat (FlwRto)

Table C.1-5 Green canopy depth (GrnCp [cm])

GrnCp (cm)	GrnCp (cm) Depth=0cm		m		Depth=1.3	cm		Depth=2.5	cm	R	CB ANO	VA	Tul	key's HSI	O (Pr)
Bed	n	Mean	SE	n	Mean	SE	n	Mean	SE	df	Fv	Pr	0-1.3	0-2.5	1.3-2.5
F	8	11.94	0.11	8	12.16	0.14	8	12.16	0.13	2, 14	1.27	0.310		-	
G	7	11.96	0.40	7	12.41	0.22	7	13.03	0.46	2, 12	1.88	0.196		-	

Table C.1-6 Brown canopy depth (BrnCp [cm])

BrnCp (cm)	BrnCp (cm) Depth = 0 cm		cm	D	Depth $= 1.3$	3 cm	Ι	Depth = 2.3	5 cm	RC	B ANO	VA	Tuk	ey's HSD (l	Pr)
Bed	n	Mean	SE	n	Mean	SE	n	Mean	SE	df	Fv	Pr	0-1.3	0-2.5	1.3-2.5
F	8	13.86	0.74	8	13.46	0.58	8	13.04	0.64	2, 14	3.53	0.057		-	
G	7	10.29	0.64	7	9.50	0.63	7	9.97	0.97	2, 12	0.52	0.605		-	

Table C.1-7 Root health estimate in a log-transformed unrooted volume under the canopy (Log₁₀UVC)

Log ₁₀ UVC	Depth = 0 cm			Depth = 1.3 cm			Ι	Depth = 2.5 cm			RCB ANOVA			Tukey's HSD (Pr)		
Bed	n	Mean	SE	n	Mean	SE	n	Mean	SE	df	Fv	Pr	0-1.3	0-2.5	1.3-2.5	
F	8	1.89	0.02	8	1.90	0.13	8	1.95	0.09	2, 14	0.12	0.884		-		
G	7	2.62	0.21	7	2.42	0.16	7	2.51	0.20	2, 12	0.42	0.663		-		

Yld (bbl/acre)	Depth=0cm			Depth=1.3cm			Depth=2.5cm			RCB ANOVA			Tukey's HSD (Pr)		
Bed	n	Mean	SE	n	Mean	SE	n	Mean	SE	df	Fv	Pr	0-1.3	0-2.5	1.3-2.5
F	8	471.5	40.1	8	430.4	41.6	8	478.9	38.7	2, 14	0.83	0.458		-	
G	7	310.3	42.3	7	308.7	27.4	7	227.7	31.0	2, 12	2.40	0.133		-	

Table C.1-8 Yield estimate (Yld [bbl/acre])