GROWTH AND YIELD OF RED RASPBERRIES CULTIVATED UNDER OPEN FIELD CONDITION *VS.* HIGH TUNNEL OR RAIN SHELTER IN THE NORTHERN CANADIAN CLIMATE

Thèse

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Résumé

La culture sous abris avec des infrastructures de type grands tunnels est une nouvelle technologie permettant d'améliorer la production de framboises rouges sous des climats nordiques. L'objectif principal de ce projet de doctorat était d'étudier les performances de ces technologies (grands tunnels *vs.* abris parapluie de type Voen, en comparaison à la culture en plein champ) et leur effets sur le microclimat, la photosynthèse, la croissance des plantes et le rendement en fruits pour les deux types de framboisiers non-remontants et remontants (*Rubus idaeus*, L.). Puisque les pratiques culturales doivent être adaptées aux différents environnements de culture, la taille d'été (pour le cultivar non-remontant), l'optimisation de la densité des tiges (pour le cultivar remontant) et l'utilisation de bâches réfléchissantes (pour les deux types des framboisiers) ont été étudiées sous grands tunnels, abris Voen *vs.* en plein champ.

Les plants cultivés sous grands tunnels produisent en moyenne 1,2 et 1,5 fois le rendement en fruits commercialisables que ceux cultivés sous abri Voen pour le cv. non-remontant 'Jeanne d'Orléans' et le cv. remontant 'Polka', respectivement. Comparativement aux framboisiers cultivés aux champs, le rendement en fruits des plants sous grands tunnels était plus du double pour le cv. 'Jeanne d'Orléans' et près du triple pour le cv. 'Polka'. L'utilisation de bâches réfléchissantes a entrainé un gain significatif sur le rendement en fruits de 12% pour le cv. 'Jeanne d'Orléans' et de 17% pour le cv. 'Polka'. La taille des premières ou deuxièmes pousses a significativement amélioré le rendement en fruits du cv. 'Jeanne d'Orléans' de 26% en moyenne par rapport aux framboisiers non taillés. Des augmentations significatives du rendement en fruits de 43% et 71% du cv. 'Polka' ont été mesurées avec l'accroissement de la densité à 4 et 6 tiges par pot respectivement, comparativement à deux tiges par pot.

Au cours de la période de fructification du cv. 'Jeanne d'Orléans', les bâches réfléchissantes ont augmenté significativement la densité de flux photonique photosynthétique (DFPP) réfléchie à la canopée inférieure de 80% en plein champ et

de 60% sous grands tunnels, comparativement à seulement 14% sous abri Voen. Durant la saison de fructification du cv. ‘Polka’, un effet positif de bâches sur la lumière réfléchie (jusqu’à 42%) a été mesuré seulement en plein champ. Dans tous les cas, les bâches réfléchissantes n’ont présenté aucun effet significatif sur la DFPP incidente foliaire totale et la photosynthèse. Pour le cv. ‘Jeanne d'Orléans’, la DFPP incidente sur la feuille a été atténuée d’environ 46% sous le deux types de revêtement par rapport au plein champ. Par conséquent, la photosynthèse a été réduite en moyenne de 43% sous grands tunnels et de 17% sous abris Voen. Des effets similaires ont été mesurés pour la DFPP incidente et la photosynthèse avec le cv. Polka.

En dépit du taux de photosynthèse des feuilles individuelles systématiquement inférieur à ceux mesurés pour les plants cultivés aux champs, la photosynthèse de la plante entière sous grands tunnels était de 51% supérieure à celle observée au champ pour le cv. ‘Jeanne d’Orléans’, et 46% plus élevée pour le cv. ‘Polka’. Ces résultats s’expliquent par une plus grande (près du double) surface foliaire pour les plants cultivés sous tunnels, qui a compensé pour le plus faible taux de photosynthèse par unité de surface foliaire. Les températures supra-optimales des feuilles mesurées sous grands tunnels (6.6°C plus élevé en moyenne que dans le champ), ainsi que l’atténuation de la DFPP incidente (env. 43%) par les revêtements de tunnels ont contribué à réduire le taux de photosynthèse par unité de surface foliaire. La photosynthèse de la canopée entière était étroitement corrélée avec le rendement en fruits pour les deux types de framboisiers rouges cultivés sous grands tunnels ou en plein champ.

Abstract

Protected culture such as high tunnels is a new technology to improve red raspberry crop production under Northern climates as found in Quebec, Canada. The main objective of this Ph.D. research was to assess the performance of high tunnels *vs.* Voen shelters, a novel umbrella-shaped cover structure, in comparison to open field cultivation, in terms of microclimate, photosynthetic performance, plant growth, and fruit yield for both floricane- and primocane-fruiting types of red raspberries (*Rubus idaeus*, L.). As cultural management practices need to be tailored to the different modified growing environments, relevant practices like summer pruning (for floricane-fruiting cultivar), cane density optimization (for primocane-fruiting cultivar) and reflective mulch (for both fruiting types) were tested under high tunnel and Voen shelter *vs.* open field.

Plants grown under high tunnel produced on average 1.2 and 1.5 times more marketable fruit yield than under Voen shelter for floricane-fruiting cv. 'Jeanne d'Orléans' and primocane-fruiting cv. 'Polka', respectively. Compared to plants grown in open field, the fruit yield of high tunnel-grown plants was more than double for cv. 'Jeanne d'Orléans' and almost three times higher for cv. 'Polka'. The use of reflective mulch had a significant positive effect on fruit yield, namely 12% for cv. 'Jeanne d'Orléans' and 17% for cv. 'Polka'. Pruning the first or second flush of stems from the rhizome significantly improved fruit yield of cv. 'Jeanne d'Orléans' by 26% on average compared to unpruned plants. As cane density increased, the fruit yield of cv. 'Polka' increased significantly, namely by 43% and 71% for a cane density of 4 and 6 canes per pot, respectively, as compared to the standard lower cane density of 2 canes per pot.

During the fruiting period of cv. 'Jeanne d'Orléans', reflective ground cover significantly increased the photosynthetic photon flux density (PPFD) reflected to the lower canopy by 80% in open field and 60% under high tunnel, compared to only 14% under Voen shelter. During the fruiting season of cv. 'Polka', a positive

reflective mulch effect on the reflected light (up to 42%) was only found in open field. In all cases, ground cover had no significant effect on the total leaf PPFD and photosynthesis under any growing conditions. For cv. ‘Jeanne d’Orléans’, the leaf PPFD was attenuated by approx. 46% under both types of protective covering compared to open field. Correspondingly, photosynthesis was on average reduced by 43% under high tunnel and by 17% under Voen shelter. Cultivar ‘Polka’ plants shared a similar growing condition effects on leaf PPFD and photosynthesis.

Despite the fact that lower individual leaf photosynthetic rates were consistently measured in tunnel-grown plants, once leaf-level photosynthesis was scaled up to the whole canopy, the photosynthetic production of tunnel-grown plants was found to be 51% higher than that observed in open field for cv. ‘Jeanne d’Orléans’, and 46% higher for cv. ‘Polka’. This was explained by the greater (nearly twice) leaf area of tunnel-grown plants, which compensated for their lower photosynthetic rate per unit leaf area, the latter being caused by the supra-optimal leaf temperatures found under high tunnel (6.6°C higher on average than in open field) as well as the attenuation of the leaf PPFD (approx. 43%) by the tunnel coverings. Whole-canopy photosynthesis was positively correlated with fruit yield for both fruiting types of red raspberry, whether cultivated under high tunnel or in open field.

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Preface

This thesis initiated in the plant biology doctoral program at Université Laval, consists of six chapters written in English, including a chapter of general introduction and objectives (Chapter 1), and four chapters of results (Chapter 2-5), one chapter of general conclusion (Chapter 6) summarizing the previous four chapters and an opening on the prospects of this work. All chapters of this document were written by the doctoral candidate, with advice and commentary by the director Dr.Yves Desjardins and co-directors Dr. André Gosselin and Dr.Gilbert Ethier.

An increasing number of high tunnels have recently being put up for red raspberry production throughout North America. In Canada, this protected production of raspberry is now expanding rapidly. In order to optimize crop production, an umbrella-shaped structure named Voen shelter was introduced from Germany. This structure requires lower investment and was thus evaluated in our research under Quebec conditions. Microclimate and particularly ambient temperature and light can vary under these different protective coverings, especially for hedgerow plants. Hedgerow-trained red raspberries generally tend to strongly affect light interception and thus result in large light differences between upper and lower canopy. The white reflective mulch was therefore expected to be used as ground cover to counteract the difference by improving canopy light environment in lower portion (Chapter 1). In addition, relevant plant management practices like summer pruning (for floricane-fruiting cultivar) and cane density optimization (for primocane-fruiting cultivar) were also studied in our research.

Accordingly, the fruit yield performance of potted plants grown under both protected structures namely high tunnel and Voen shelter *vs.* open field, with the presence of reflective mulch and plant management practices were studied (Chapter 2); further the effectiveness of reflective mulch under protected growing conditions on fruit yield were assessed by making leaf-level microclimate vs. photosynthetic measurements (Chapter 3); we also investigated in more details the differences between tunnel- and field-grown plants in terms of canopy growth, PPFD distribution and canopy-level photosynthesis and fruit yield throughout the four vertical canopy layers of both fruiting types of red raspberries (Chapter 4 and 5).

This thesis is organized as follows:

Chapter 1. General introduction, hypotheses and objectives

Chapter 2. Fruit size and yield performance of floricane- and primocane-fruiting red raspberries grown under high tunnel and umbrella-shaped structure *vs.* open field

Chapter 3. Microclimate and leaf photosynthesis in floricane- and primocane-fruiting red raspberries cultivated under high tunnel and umbrella-shaped structure *vs.* open field

Chapter 4. Light, plant growth and fruit yield vertical distribution and canopy photosynthesis modeling of floricane-fruiting red raspberry grown under high tunnel *vs.* open field

Chapter 5. Light, plant growth and fruiting yield vertical distribution and canopy photosynthesis modeling of primocane-fruiting red raspberry cultivated under high tunnel *vs.* open field

Chapter 6. General conclusion and further perspectives

Chapter 1: General introduction, hypotheses and objectives

1.1 General introduction

1.1.1 The red raspberry

The red raspberry (*Rubus idaeus* L.) is one of a diverse group of several hundred identified species of *Rubus* spread all over the world (Jennings, 1988). Raspberries were classified within the *Rubus* genus of the family Rosaceae. In North America, ‘bramble’, the term evocating thorniness (Ellis *et al.*, 1991), mainly refers to raspberries and blackberries (Bushway *et al.*, 2008).

Raspberries have been cultivated and grown for up to 500 years in temperate regions of northern hemisphere (Dale, 1989; Bushway *et al.*, 2008). Wild raspberries are growing in the temperate woods or tropic highlands, and were often used in gardens in Europe during the 16th century. Up to the early 19th century, more than 20 cultivars of red raspberry were introduced from England to North America. Subsequently, raspberries rapidly spread all over North America, and were selected and hybridized to produce several improved cultivars.

At present, there are three important areas of raspberry production: Russia, Europe and North America. In Europe, raspberry production is mainly distributed in Germany, Hungary, Poland, Serbia and the UK. In North America, growers started to produce raspberries in New York State as early as 1920s (Bushway *et al*., 2008), mostly for fresh market. Raspberry production is well-developed in British Columbia, Mexico, California, Oregon and Washington. The production in British Columbia, Oregon and Washington State is mostly for processing. For processing industry, fruits are generally harvested mechanically. In Australia, New Zealand and southern hemisphere countries such as Chile, large raspberry productions are grown to meet the fresh market of northern hemisphere countries such as USA and Canada during winter. In both Europe and North America, there are a great number of high tunnels and limited greenhouse raspberry production to supply local markets during winter and spring. High tunnel production of raspberries is extensively used in northern

Europe to extend field season and is becoming popular in North America.

In Canada, British Columbia is the most important province producing raspberries, followed by the province of Quebec. In Quebec, growers produce raspberries in July and August using floricane-fruiting cultivars, and in August and September using early ripening primocane cultivars such as ‘Autumn Britten’ and ‘Polka’.

1.1.1.1 Floricane-fruiting red raspberry

Floricane-fruiting (summer-fruiting) red raspberries have a perennial root system, with above-ground biennial flowering canes system (Crandall, 1995; Dale, 1989; Jennings, 1988). The raspberry plants produce vegetative canes in the first year called primocanes (1-year-old cane), and in the following year, these canes called floricanes are flowering, fruiting and then senesce. Meanwhile, new shoots (primocanes) are growing vegetatively from the same root system during growing season, these primocanes must remain intact for overwintering and fruiting during the growing season till the end of harvest next year.

During the first spring, the plants develop new shoots from basal buds of a previous-year canes or from buds on the rhizomes. In autumn, flower buds develop on the shoots and thereafter produce flower or fruit the following summer. Thus floricane-fruiting raspberry produce flowers or fruits only on 2-year-old canes. After the fruiting period, the floricanes are cut down to the ground, removed and discarded. During growing season, the new emerging primocanes compete for nutrition and light with floricanes. The primocanes must always be kept intact and are overwintered without any pruning to produce fruit the following growing season. Progress through these phases depends partially on internal factors and partially on the effects of the environment. For instance, plant in juvenile stage cannot induce flowering until they reach a certain amount of vegetative growth or a certain number of nodes (Williams, 1960).

1.1.1.2 Primocane-fruiting red raspberry

Primocane-fruiting (fall-fruiting, fall-bearing, tip-fruiting) red raspberry, which are also referred to as everbearing raspberry, produce raspberries on 1-year-old canes (primocanes) from late summer to late autumn. Most of raspberries are produced from the top of the cane down.

If the primocanes are kept and overwintered, flowering and fruiting will occur again on the lowest part of these 2-year-old canes during early summer of the following year. However, these berries may not be as large and may not meet commercial standards, in comparison with either autumn primocane crop from 1-year-old canes or the summer crop of floricane-fruiting types. Also, it is very difficult to harvest these berries in early summer since new shoots from the root system grow among the fruiting canes, resulting in a very dense canopy. Likewise, the autumn primocane crop may be affected negatively by fruiting of 2-year-old canes. Thus the profitability is far lower with the 2-year-old-cane fruiting. Consequently, commercial growers prefer managing the primocane-fruiting raspberries as an annual autumn primocane crop. Generally raspberry fruits are produced on the terminal 1/3 to 1/2 portion of the primocane and are harvested from late summer till late autumn (Crandall, 1995; Jennings, 1998).

This growth habit and cultivation management have triggered great interest to the progressive commercial producers in the red raspberry industry, since pruning costs of the following year after early-summer fruiting are avoided by mowing canes mechanically after the end of the fruiting season. Therefore, the decrease of diseases pressure and insect damage such as cane blight, aphid and some beetles will reduce the frequency of pesticides use. Fertilization will be easier, and winter injury to canes will not be a major concern.

Raspberry fruits are highly nutritious, containing much soluble fiber, vitamins, minerals, and high amounts of antioxidants such as polyphenols, which can prevent inflammatory chronic diseases, resulting in strong market demand and high prices. However, supply of fresh market raspberry fruits is often lower because raspberry can be difficult to grow and the fruits are very perishable. Therefore, utilization of appropriate production methods to improve raspberry fruit yield and produce high quality fruit requires more attention.

1.1.2 Protected production of red raspberry

1.1.2.1 High tunnel production

High tunnels or plastic hoop houses are normally installed directly onto the ground, and designed to help commercial producers to extend the growing season so that they can intensify production and then improve the profitability of their farms (Blomgren et al, 2007; http://www.hightunnels.org/). Plastic cover allows photosynthetically active radiation (PAR) to penetrate while preventing infrared radiation to escape to the sky. High tunnels offer minimal control over the microclimate (temperature and humidity), which can only be controlled by closing or opening the side-walls or doors of the ends of the tunnels. Due to the absence of heating system, lights or any sources of power, it could also be called 'passive solar structures' (Bushway *et al.*, 2008), thus the cost of constructing high tunnels is much lower than that of greenhouses which are built with heating system, ventilation and even lighting equipments. These systems allow growers to combine floricane- and primocane-fruiting raspberry varieties to extend the season to produce raspberries from early summer to late autumn. High tunnels also protect raspberry plants from thigmomorphogenetic pressure such as strong winds, stormy rain, and occasional hail, and thereby favour taller plants with larger leaf area (Chehab *et al.*, 2009; Jaffe and Forbes, 1993). Additionally, raspberry cultivation under high tunnel can reduce disease and pest pressure (Pritts, 2006; Demchak, 2009). With appropriate cultivars, cultivation and management, high tunnel system can highly prolong the harvest season, and then greatly improve raspberry productivity.

High tunnel production of raspberry is rapidly and widely being adopted throughout

Canada and United States (Pritts, 2006; Allen and Raffle, 2000). An increasing number of growers are now producing raspberry under high tunnels. In Canada, high tunnel production of raspberry is just beginning. Research has indicated that high tunnels can produce over twice, almost three times the yields of primocane-fruiting varieties (Goulart and Demchak, 1999) and can provide a 40% return on investment annually.

Figure 1.1 The structures of high tunnel (A) and umbrella-shaped structure (Voen shelter) (B)

1.1.2.2 Umbrella-shaped structure production

Although high tunnel gives high fruit yield, the structures are also expensive to construct and operate. Recently, Canadian researchers have introduced a lower cost ‘umbrella-shaped structure’ system manufactured by a German company called VOEN Vöhringer GmbH & Co. KG, which has similar benefits and is also referred to as ‘Voen shelter’ or ‘Voen tunnel’ (Figure 1.1). These shelters are resistant against strong winds, heavy rain, hail, frost, birds and also offer a good cost-performance ratio. The assembly and dismantling are relatively easy, even in hilly landscape with steep slope as is the case in Switzerland and Norway orchards or berries farms. These cultivation areas can be installed with varying widths, because the framework can be custom designed (http://www.voen.eu).

Umbrella-shaped structure (Voen shelter) production has been already used in many countries and regions. In Germany and the Netherlands, Voen tunnels are used to protect crops from severe stormy winds nearby the coast. In South Africa and Croatia, ‘Voen’ covers are used to prevent hail and avoid sunburn. In Australia, Voen cover system provides better ventilation, which result in lower temperature for the orchards of dry areas around Sydney. In United States and Canada, Quebec in particular, progressive growers started to use this umbrella-shaped structure for crop production (http://www.voen.de/en.html).

Voen shelters are less expensive than high tunnel for protected cultivation and also give higher fruit yield than open field. Only limited research has investigated the ‘Voen’ tunnel production. A variety of stone fruits such as sweet cherries (Rubauskis *et al.*, 2013), apricots, plums, table grapes, red currants and berries such as blueberries and raspberries are grown under the Voen system, to varying degrees, with increased fruit size and yield, improved fruit quality such as fruit coloring uniformity and reduced of fruiting cracking. However, for red raspberries no research has yet been reported. Therefore, the production system really requires different recommendations from various areas for the cultivation management, such as irrigation, soil and fertilizer management, spraying technology, disease, insect and mite scouting, trellising and pruning. These may well vary depending on the climate in the various environments across Canada. Also, at this stage, few cultivars are adapted to this system and have the required fruit quality, production and pest and disease attributes needed to maximize the benefits of the system.

1.1.3 Cultural practices

1.1.3.1 Appropriate pruning

Pruning is necessary for maintaining red raspberries quality and productivity during the growing and dormant seasons. Appropriate pruning allows producers to manipulate cane vigor and have a positive effect on cane growth rate, fruit quantity and size, disease susceptibility, spraying and harvesting efficiency (Bushway *et al.*, 2008).

Floricane-fruiting raspberry canopies can be very dense because both fruit-bearing floricanes and newly emerged vegetative primocanes are growing together from the same root system. They therefore mutually shade themselves and compete for water and nutrients. Especially in lower canopy, leaves can only receive a fraction of incident sunlight, and therefore photosynthesis decreased, resulting in a reduction of fruit yield (Goulart and Demchak, 1993). This shading also interferes with cultural management such as spraying, and affects harvesting efficiency (Stile, 1995; Nehrbas and Pritts, 1988).

Under this condition, after the first few years, normally, there are two main means to control dense canopy, one is pruning at different periods such as at first or second stem flush, then the fruit will be larger and less susceptible to disease. The other means is using reflective mulch, which can improve the efficiency of sunlight (Toye, 1995) and enhance plant microclimate so as to favour crop production.

1.1.3.2 The use of reflective mulch

Extenday reflective covers (Extenday New Zealand Ltd., Auckland, N.Z.) are white, woven plastic material which are widely used in certain parts of the world and can positively affect the light in the inner and lower canopy and improve productivity of various crops. Previous researches carried out on the effect of reflective mulches on various fruit species such as kiwifruit (Costa *et al.*, 2003; Thorp *et al.*, 2000), apple (Green *et al.*, 1995; Andris *et al.*, 1998; Ju *et al.*, 1999) and sweet cherry (Whiting *et al.*, 2008) showed that they could modulate the plants microclimate and particularly canopy light relations, leading to better fruit yield and quality (Tarara, 2000).

In persimmon, Thorp *et al.* (2000) showed that reflective mulches advanced the fruit maturity in the lower portion of canopy. In apples and cherries, fruits from trees grown with reflective mulch were larger compared to those grown without mulch. In sweet cherries, an increase in soluble solids content was observed when reflective mulch was applied (Widmer, 2001). However, there were few research projects on raspberry.

Raspberry plants, in general, are light limited. Shading occurs most markedly in the interior portion of lower canopies (Landry, 2011) and can result in lower fruit yield (Wright and Waister, 1984, 1986; Raymond-Bayne, 2012). Therefore, it is important to study the effects of reflective mulch on growth and marketable fruit yield of raspberry grown under protected structure systems compared with open field plantings.

1.1.3.3 Optimizing cane density

The amounts and quality of fruiting of red raspberries can be affected by the cane densities (Crandall *et al.*, 1974) and competition between them (Buszard 1986; Waister *et al.* 1977). Wood *et al.* (1961) were the first to study the effects of cane densities on yield. Crandall *et al.* (1974) and Oydvin (1986) indicated that fruit yield per linear meter increased as cane density increased (using 2.5 m row spacing). Martin and Nelson (1986) found that among all yield components, cane density was the most correlated to the fruit yield. Lower cane density increased total plant dry weight, while higher cane density decreased cane length, basal diameter and fruit yield per cane (Oliveira *et al.*, 2007).

In Quebec, Granger (1972) indicated that there was a linear increase in fruit yield when increasing cane numbers from 10 to 20 canes per linear meter. Raymond-Bayne (2012) obtained similar results over a wider range from 12 to 30 canes per linear meter, but Evans (1974) found no significant differences over a similar range in Ontario. Fejer (1979) concluded that different cane densities of raspberries were not completely decisive over the years. Buszard (1986) reported that cane vigor was affected by climatic environments and genetic potential, and that the optimum cane number was about 15 canes per linear meter. This recommendation is currently followed by raspberry growers in Ontario and Quebec (Vanden Heuvel, 1999).

For primocane-fruiting red raspberries, producers prefer managing canes as a single annually late-summer primocane crop for keeping optimum cane density and improving harvesting efficiency by cutting down the primocanes to the ground after harvesting. Unlike denser floricane-fruiting raspberry plants (simultaneous occurrence of primocanes and floricanes), therefore for primocane-fruiting raspberries, optimizing cane density can greatly improve plant productivity.

1.1.3.4 Soilless cultivation

Soilless systems have been successfully used for many horticultural plants (such as tomatoes and strawberry) for many years and are gaining in popularity, particularly for production under protected structures like greenhouses (Treftz and Omaye, 2015). Compared to traditional cultivation in soil, soilless growing systems can provide several environmental benefits such as reduction of water and fertilizer amounts as well as pesticide use (Lamack and Niemiera, 1993). These advantages allow soilless systems to address several environmental issues while still providing sustainable systems in arid or urban regions (Ibrahim *et al.* 1989).

Container size can be a serious factor limiting plant development particularly when the plant population must be optimized for a limited costly space. In raspberry production, a strategy recently proposed to increase yields while reducing production cost per square meter is to grow long canes at high linear density using smaller containers (Sønsteby *et al.,* 2013). In most cases, optimum plant densities for different caneberry varieties and growing conditions (field *vs.* protected structures) have not yet been clearly established, particularly with regards to soilless culture.

1.1.4 Leaf gas exchange on red raspberries

Photosynthesis is a biological process that converts solar energy into chemical energy, in the form of large carbon compounds such as sucrose, starch and some other energy containing substances. The energy accumulated in these large carbon compounds can then be used to fuel cellular metabolism and tissue growth. Plant growth is dependent on the balance between carbon gain in photosynthesis and carbon loss during respiration (Dutton *et al.*, 1988; McCree, 1986). It is therefore important to characterize the changes in carbon gain *vs.* carbon loss under various cultural practices.

However, crop productivity is frequently limited as a result of unfavorable environment. Quantifying the response of net carbon assimilation and leaf gas exchange to several main environmental factors such as PPFD, temperature, CO_2 concentration and humidity, contributes to explain how to maximize plant growth and yield potential and may assist in the development of management strategies. There are some research projects that have focused on competition between floricane and primocane and the effect on light penetration (Braun *et al.*, 1989; Palmer *et al.*, 1987) and dry matter partitioning (Waister and Wright, 1989). The four main factors affecting leaf gas exchange are PPFD, CO_2 concentration, temperature and humidity (Cameron *et al.*, 1993; Stafne *et al.*, 2001).

1.1.4.1 Photosynthetic photon flux density (PPFD)

When discussing photosynthetic responses to radiation, the term ‘light intensity’ usually refers to the more specific photosynthetic photon flux density (PPFD) rather than total radiation. The short-term asymptotic photosynthetic light response curve is well known and is similar for fruit trees and other C_3 crops. Three points on the light response curve are worthy of note: the maximum rate, the saturation point in terms of PPFD, and the light compensation point.

As PPFD increases under light-limited conditions, leaf photosynthesis usually follows in linear fashion, then eventually becomes saturated under high light. Thus Thornley (1998) used a non-rectangular hyperbola model to describe the overall photosynthetic light response. In general, dense hedgerow raspberry canopies are light limited (Pritts *et al.*, 2002). Low light conditions, which occur mostly in the autumn and in the inner and lower canopies under high tunnel (Landry, 2011; Raymond-Bayne, 2012), can result in lower leaf photosynthesis and stomatal conductance, consequently leading to lower fruit yield (Wright and Waister, 1984, 1986; Goulart and Demchak, 1999). Generally, the light intensity required to saturate photosynthesis in raspberries is considered relatively low (Pritts *et al.*, 2002). For example, Fernandez and Pritts (1994) measured a light saturation of 500 to 700 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for floricane-fruiting cv. 'Titan'. Similarly, for primocane-fruiting cultivar 'Autumn Britten', Landry (2011) reported a photosynthetic light saturation from 500 to 750 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PPFD.

A slight change in PPFD in the lowest canopies or leaves can have a profound effect on photosynthesis, while at levels higher than saturation, it may have very little effect. This has important practical implications related to cultural practices which might improve PPFD at leaf level. Reflective ground covers can be used to enhance light availability in the lower canopies by reflecting light that would otherwise be absorbed by the ground. The increased photosynthesis stimulates crop production (Bowen and Freyman, 1995). Furthermore, reflective mulch is more effective under direct light than under diffuse light on cloudy days (Raymond-Bayne, 2012; Toye, 1995). Although not often reported, higher PPFD beyond saturation, especially on shade leaves, may result in a decrease in photosynthesis. This was attributed to photo inhibition (Powles, 1984) and may occur under field conditions. For the sun leaves, at very high PPFD, chlorophyll may be damaged and lead to the depression of net photosynthesis.

Diffused light can reduce shadows and allows the plants to get a more uniform light distribution during the day, which may stimulate photosynthesis especially in lower canopy. Despite reducing the incident PPFD by around 30%, high tunnel covers can increase diffused light and accelerate plant growth and the onset of fruiting in raspberry (Prive *et al.*, 1997; Takeda and Perkin, 2009). Therefore, it can be advantageous to utilize different types of covers, such as plastic or Voen covers, to increase diffusing light.

1.1.4.2 CO_2 concentration

Carbon dioxide diffuses from the atmosphere into leaves, first through stomata, then inside the leaf through the intercellular air spaces into chloroplasts, which are the sites where carboxylation takes place. An increase in the CO_2 concentration results in higher photosynthesis, generally the photosynthesis continues to increase until limited by some other factor (e.g. the presence of adequate amounts of light) (Percival *et al.*, 1996).

Carbon dioxide in the atmosphere is usually at quite low concentrations, thus artificial CO_2 enrichment can increase photosynthesis rapidly to reach maximal rates of CO_2 fixation. Mochizuki *et al.* (2010) reported that CO_2 enrichment increased yield and fruit size of field-grown red raspberry under high tunnels, and greatly increased photosynthesis (Percival *et al.*, 1996).

1.1.4.3 Temperature

In the photosynthesis process, the reactions are catalyzed by various enzymes. As the enzymes approach optimum temperatures, the overall rate increases. It approximately doubles for every 10 °C increase in temperature. Once beyond the optimum temperature, photosynthesis declines.

In raspberry, warm temperature (25 to 30 °C) resulted in more rapid vegetative growth, advanced flowering and increased photosynthesis (Carew *et al.*, 2003). Privé *et al.* (1997) also showed that high photosynthesis could be achieved at warm temperatures (25 to 30 °C) in potted primocane-fruiting cv. ‘Autumn Bliss’. However, Fernandez and Pritts (1994) indicated that photosynthesis decreased in the leaves on both type canes (floricane and primocane) of potted floricane-fruiting raspberry cv. ‘Titan’ as temperature increased above 25 °C, and leaves on primocane were keeping higher photosynthesis at each temperature level.

In Quebec, among many protected environments, high tunnels are frequently utilized to improve the microclimate so as to increase structure interior air temperature in late autumn, extending the growing season of primocane-fruiting raspberry (Raymond-Bayne, 2012; Landry, 2011).

1.1.4.4 Vapor pressure deficit (VPD)

Photosynthetic temperature response curves are often produced without considering other factors such as the leaf-air vapor pressure deficit (VPD). Some research (Berry and Bjorkman, 1980) attempted to eliminate this effect by using a constant relative humidity, but this does not maintain constant VPD. Once constant VPD temperature response curves were produced, it became possible to measure the true temperature responses of photosynthesis (although in natural conditions the leaf-air VPD rarely remains constant as temperatures change). Photosynthetic temperature optima and response curve vary with species and prior environmental conditions (Berry and Bjorkman, 1980).

In a comparative study, Moon *et al.* (1987 a, b) evaluated gas exchange responses of commercial blueberry cultivars, wild species and their progeny. Temperature optima differed with species and appeared to be heritable. In this study, VPD was held constant by varying the cuvette inlet humidity as temperature increased so that the temperature effect could be separated from a VPD response.

Many researches indicated that low VPD increased stomatal conductance and photosynthesis, whereas high VPD often encountered under field condition restricts photosynthesis in many species (Bunce, 1993). Photosynthesis in raspberry is both temperature and VPD sensitive (Percival *et al.*, 1996; Fernandez and Pritts, 1994). Privé *et al.* (1997) reported that leaves could maintain the highest photosynthesis at relatively warm temperatures and low VPD in primocane-fruiting red raspberry cv. ‘Autumn Bliss’. However, Percival *et al.* (1996) reported that whole-plant potted primocane-fruiting cv. ‘Heritage’ had the optimum photosynthesis at cool air temperature (17°C), and low VPD (0.25 kPa).

1.1.5 Carbon allocation

Photoassimilates translocation may be acropetal or basipetal depending on the proximity and relative strength of the various plant carbon sinks. During the early stages of plant growth, expanded leaves export most of their photoassimilates acropetally to younger developing leaves (Hale and Weaver, 1962; Hansen, 1971). During anthesis, most of the leaves on a shoot have already changed from a sink to a source and divert a large portion of their assimilates to reproductive organs. In primocane-fruiting raspberry, leaves that develop nearest to fruiting lateral portions supply their assimilates to young developing fruits (Privé *et al.*, 1994).

Fernandez and Pritts (1994) found that the floricanes and primocanes of 'Titan' floricane-fruiting raspberries do not compete for carbohydrates, though they compete for trophic resources like sunlight, water and nutrient. Similar results were reported by Drake (2003) in blackberries. Further studies reported that 'Titan' was resistant to reduction in carbon supply, which indicated that raspberries store a large amount of carbohydrate in the root system that can be used when the current photosynthetic source does not meet the plant sink demand (Fernandez and Pritts, 1996). Likewise, artificial defoliation (up to 2/3 of the leaf area) of primocane-fruiting raspberry varieties did not significantly affect fruit yield (Privé *et al.*, 1994). These studies suggest that raspberry plants are more sink- than source-limited (Waister and Wright, 1989; Privé *et al.*, 1994).

1.2. Hypotheses and objectives

1.2.1 Hypotheses

Cultural management must be tailored to the growth habit of both fruiting types of red raspberry (floricane- and primocane-fruiting) and various growing environments such as under open field conditions and protected structures. High tunnel and Voen shelter (an umbrella-shaped structure) were involved in our experiment to modify environmental factors and expected to create a proper microclimate for both types of red raspberry.

For floricane-fruiting raspberry, canopies can be extremely dense since a large number of primocanes are growing from the same roots during floricanes flowering and fruiting. Both primocanes and floricanes mutually shade themselves. Especially in the lower canopy, leaves only receive little sunlight. In order to improve light availability in the dense canopies, two main practices can be used, summer pruning and reflective mulches. Therefore, a first hypothesis was (I) summer pruning of new shoots and the addition of reflective mulches improve the productivity of floricane-fruiting red raspberry grown under protected structures (high tunnel and Voen shelter) compared to those grown in open field.

For primocane-fruiting raspberry, unlike floricane-fruiting cultivar with simultaneous occurrence of primocanes and floricanes, producers prefer managing canes as a single annually autumn-crop for keeping optimum cane density and improving harvesting efficiency by the means of cutting down the primocanes to the ground after harvesting. Thus as our second hypothesis, (II) we expect that optimizing cane density and the use of reflective mulches have positive effects on fruit yield of primocane-fruiting red raspberry grown under protected structure *vs.* open field.

For both floricane- and primocane-fruiting red raspberries, previous studies have shown that tunnel-grown plants generally produce higher fruit yields than open field-grown plants. Therefore, as our third hypothesis, (III) we expected that the photosynthetic capacity of tunnel-grown (or Voen shelter-grown) plants would be superior to open field-grown plants.

1.2.2 Objectives

1.2.2.1 General objective

This study mainly focuses on the performance of floricane-fruiting and primocane-fruiting red raspberry under the cool northern climate conditions in Quebec, Canada. In order to improve the productivity, we modified the microclimate by using different protected structures and cultural practices (reflective ground cover, pruning or cane density). Thus the aims of this study were to determine and compare the effects of growing environments (high tunnel, Voen shelter or open field), white reflective mulch (absence or presence) and date of pruning or densities on plant productivity of floricane- or primocane-fruiting red raspberries.

1.2.2.2 Specific objectives

For floricane-fruiting cultivar, experiments were conducted to meet the following objectives:

1) Determine crop yield of floricane-fruiting cultivar grown with the presence or absence of reflective mulches in high tunnel, Voen shelter or open field under Quebec climate condition (2012-2013);
2) Identify the best cropping system of canes to ensure high annual and uniform production (2012-2013);
3) By measuring leaf photosynthesis under the prevailing microclimate and then evaluating canopy photosynthesis, further explain how the higher productivity in floricane-fruiting cultivar occurs under protected structure systems, and determine the contribution of different plant parts to growth and fruit yields through gas exchange or carbon partitioning analysis (2013-2014).

For primocane-fruiting cultivar, experiments were designed to achieve the following objectives:

1) Determine the productivity of a primocane-fruiting cultivar grown with or without reflective mulches in high tunnel, Voen shelter or open field under

Quebec climate condition (2012-2013);

2) Identify the best cropping system including optimum cane density for optimizing fruit yield and plant growth (2012-2013);
3) Use combined photosynthesis-microclimate measurements around canopies to explain variation in productivity under different growing environments namely high tunnel, Voen shelter or open field during cool autumn season in Quebec (2013-2014).

Chapter 2: Fruit size and yield performance of floricane- and primocane-fruiting red raspberries grown under high tunnel and rain shelter *vs.* open field

2.1 Abstract

An experiment was conducted from 2012 to 2013 in Quebec City, Canada to determine the effects of growing environments, white reflective ground cover and summer pruning on marketable fruit yield of floricane-fruiting red raspberry variety 'Jeanne d'Orleans' (*Rubus idaeus* L.). High tunnel significantly increased fruit yield by 2.1 and 2.4 times as measured in open field in 2012 and 2013 respectively. Whereas Voen shelter significantly improved 1.6 and 2.3 times more fruit yield than open field in the two years respectively. There is no significant difference between high tunnel and Voen shelter in terms of fruit yield. The use of reflective mulch had a significant positive effect on fruit yield by 13.9% in 2012 and 10.3% in 2013 compared with their control without mulch respectively. Both pruning the first and second flush improved fruit yield by 13.7% compared with unpruned treatments. In 2013, an interaction showed that plants grown under protected structures with pruning new shoots produced higher fruit yield.

For primocane-fruiting red raspberry variety 'Polka'(*Rubus idaeus* L.), an experiment was carried out during 2012 and 2013 to determine the influence of growing conditions, white reflective mulch and cane densities on marketable fruit yield and fruit size of soilless, pot grown raspberry. The results indicated that high tunnel significantly increased fruit yield by 28.9% and 61.5% compared to Voen shelter, and 1.8 and 3.4 times higher than open field in 2012 and 2013, respectively. The presence of reflective mulch had a significant positive effect on fruit yield, increasing this variable by 18.3% and 15.8% compared with the absence mulch in 2012 and 2013, respectively. As cane density increased, fruit yield increased significantly by approx. 55.3% in density of 4 canes per pot and 84.0% in density of 6 canes per pot compared to the low density of 2 canes per pot. In both 2012 and 2013, there was an interaction between growing environments and pruning, which showed that plants grown at density of 4 or 6 canes per pot under high tunnel and at a density of 6 canes per pot under Voen shelter had the highest fruit yield in 2012, whereas in 2013, plants with density of 6 canes per pot under high tunnel produced the highest fruit yield.

2.2 Introduction

The production of red raspberries (*Rubus idaeus* L.) under protected structures, high tunnel in particular, is rapidly and widely adopted throughout Canada and United States (Pritts, 2006; Bushway *et al.*, 2008). In Canada, more progressive producers are now producing raspberries by using high tunnels to extend growing season from early summer to late autumn (Wien and Pritts, 2009). Other researchers indicated that high tunnels can produce over twice and sometimes three times the marketable fruit yield of floricane-fruiting varieties such as 'Nova' and 'Canby' (Hanson *et al.*,2011) and primocane-fruiting varieties (Goulart and Demchak, 1999). High tunnels are used to maximize production by reducing wind damage, protecting the plants from rain and frost (Pritts, 2006; Demchak, 2009) and further reducing disease pressure.

High tunnels can produce higher fruit yield, but are also expensive to build and operate. Recently, our research group have introduced a lower investment 'umbrella-shaped structure system' namely Voen tunnel or Voen shelter (http://www.voen.de/en.html) from Germany, which can be resistant against wind, rainfall, hail and frost and thus offer a good cost-performance ratio. This new production system requires a new set of recommendations for raspberry cultural management, such as branch training, trellising system, optimising cane density, etc. In addition, at this stage, few cultivars are adapted to these systems and have the required fruit quality, production and pest and disease attributes needed to maximize the benefits of the system.

Low light conditions, which occur mostly in the inner and lower canopies or in autumn (Landry, 2011; Raymond, 2012), can result in lower fruit yield (Wright and Waister, 1984, 1986; Goulart and Demchak, 1999). Floricane-fruiting raspberry canopies can be very dense since, during floricane flowering and fruiting, primocanes are growing from the same root system and compete for trophic resources like light, water and nutrient. Especially in lower canopy, leaves can only receive a fraction of incident sunlight, and therefore photosynthesis decreased, then resulting in a reduction on fruit yield (Goulart and Demchak, 1993). This shading also interferes with cultural management such as spraying, and affects harvesting efficiency (Stiles, 1995; Nehrbas and Pritts, 1988).

Reflective mulch can be used to enhance plant microclimate and favour crop production, since it improves the efficiency by reflecting the light that would be absorbed back into the canopy (Raymond-Bayne, 2012; Toye, 1995). Pruning out new shoots in summer at different periods such as at first or second flush, can reduce mutual shading, and improve penetration of sunlight in canopy of floricane-fruiting red raspberries. In Canada, producers prefer managing canes of primocane-fruiting varieties as a single annually late-summer crop to improve harvest efficiency by cutting down primocanes to the ground after harvest in previous year. Thus optimizing cane density can greatly improve plant productivity of the fruiting type.

This project was initiated to determine the effects of cultivation methods such as summer pruning for floricane-fruiting red raspberry, cane density optimization for primocane-fruiting and reflective ground cover for both fruiting types, grown under high tunnel, Voen shelter *vs.* open field, respectively.

2.3 Materials and methods

2.3.1 Experimental site

The experiment was conducted in 2012 and 2013 under high tunnels, Voen shelter and open field at 'Les Fraises de Ile d'Orleans Inc.' (71°01′W, 46°52′), located in Québec, Canada. One common tunnel size is 8.5 m wide, 4.5 m high and 70.0 m long and polyethylene coverings with corresponding size from Industries Harnois (http://www.harnois.com). Temperature, relative humidity and ventilation under can be controlled by closing or opening the side walls or doors. An umbrella-shaped structure (Voen shelter), wooden framework system (in height of 3.6 m) was used (in width of 1.8 m) (see Figure 1.1).

2.3.2 Management of plant materials

In the spring of 2011, two varieties (‘Jeanne d’Orleans’and ‘Polka’) were planted directly into 10-litre black plastic pots containing Fafard® Sphagnum Peat Moss substrate, the natural soil conditioner can improve water retention and aeration and be available in Eastern Canada and United States (http://www.fafard.com/). A hedgerow type trellising system was used to support the canes. Plants were allowed to grow for one year before establishing the treatments.

‘Jeanne d’Orleans’ is a floricane-fruiting or summer-fruiting red raspberry, and harvesting normally occurred during mid-July to late-August. The plants were thinned in the spring of 2012 to keep 3 uniform floricanes (2-year-old canes) per pot to make sure uniform fruit yield every year. After harvest, the floricanes senesced and were cut at soil level and removed, the current-year new shoots (primocanes) were kept in the pot with required pruning to overwinter.

‘Polka’ is a primocane-fruiting or autumn-fruiting red raspberry, and harvest period is usually from mid-August to early October. The fruiting period of this cultivar is considered of medium length compared with other cultivars. At the end of the harvest season, all primocanes were cut at pot level and removed. The following spring, new shoots were trained to keep 2, 4, or 6 canes per pot respectively and were also cut and removed at the end of harvest season.

Pests and weeds were controlled according to local standard cultural practices. Plants were irrigated by using a drip irrigation system with 2 drippers in each pot. Fertilization was achieved by automatically incorporating soluble fertilizers in the irrigation water. During the whole growing season, the substrate pH was kept between 6.0 and 6.5. A higher electrical conductivity (EC, 1.2 µS/cm) and nitrogen contents (NO_3, 150 ppm) were applied with fertigation till the beginning of flowering and thereafter a lower EC (1.0 µS/cm) and N (NO_3, 100 ppm) were supplied according to local recommendations.

2.3.3 Experimental design

The experiments of floricane-fruiting variety ‘Jeanne d’Orléans’ and primocane-fruiting variety ‘Polka’ were designed as a 3×2×3 factorial and arranged as a split-split plot design with 4 replications. Growing environments, namely high tunnel, Voen shelter or open field, was the main factor; white reflective mulch, namely absence or presence, was the sub-plot; pruning primocanes, namely at the first flush, second flush or unpruned, was the sub-sub-plot for ‘Jeanne d’Orléans’, whereas cane densities, namely 2 canes, 4 canes and 6 canes per pot, was a sub-sub-plot for ‘Polka’, and resulting in 18 treatments respectively. Reflective mulches were arranged with absence alternately between hedgerows. The absence or presence of mulch corresponds to nine pots of plants as sub-plots that are divided into three equal parts treated by pruning as sub-sub-plots. Rows were divided into different treatments separated from each other by a 1m long buffer zone.

2.3.4 Data collected and statistical analysis

The climatic data were cumulated for the entire growing season. Under each growing condition, air temperature and relative humidity (at 1 m high above ground under high tunnel and Voen shelter, and 0.7 m tall in open field) as well as root zone temperatures (at 0.1 m below substrate level) were measured by 6 HOBO data loggers (U12-013, Onset Corp., Bourne, MA, USA). In addition, a specific meteorological station (U30, Onset Corp., Bourne, MA, USA) was installed in the open field to monitor temperature, relative humidity, light, wind speed and direction of the whole research site all year round.

For both floricane-fruiting cv. ‘Jeanne d’Orléans’ and primocane-fruiting cv. ‘Polka’, fruits of each plot were harvested three times a week and classified as marketable or non-marketable then counted and weighted respectively. The harvesting periods started on July 10 and finished on August 15 for ‘Jeanne d’Orléans’ and from August 10 to October 10 for ‘Polka’ during 2012 and 2013. The fruit size (average fruit weight) was determined for marketable fruit. Fruits affected by a disease, an insect, mechanical injury, fruit too small, distorted, crumbling, etc. are automatically downgraded. Cane height from the base of the cane to the terminal bud was measured during plant growth and development. Dry weight of canes was measured at the end of harvest for ‘Polka’.

Analysis of variance was completed using the GLIMMIX procedure of SAS (SAS Institute, Cary, N.C.). Multiple comparisons of means were adjusted by Tukey at the $P = 0.05$ probability level.

2.4 Results

2.4.1 Microclimate under high tunnel and Voen shelter (2012 and 2013)

The monthly air temperatures were the highest under high tunnel for each month during growing season of red raspberry in 2012 or 2013, followed by those under Voen shelter, and in open field with lowest temperatures. The temperature in September and October under the Voen shelter were nearly similar to those in open field. The temperatures between 2012 and 2013 were very similar (Figure 2.1).

The average air temperature in July reached nearly 25.0°C, 23.0°C, and 21.5°C for both year under high tunnel, Voen shelter and open field, respectively. Whereas the maximum temperature could reach 39.5°C, 33.5°C and 29.0°C respectively under high tunnel, Voen shelter and open field. In September, the minimum temperatures were less than 10°C under each environment during each year, while the maximum temperatures under Voen shelter and open field were just over 20°C, and it reached nearly 30°C under high tunnel (Figure 2.1).

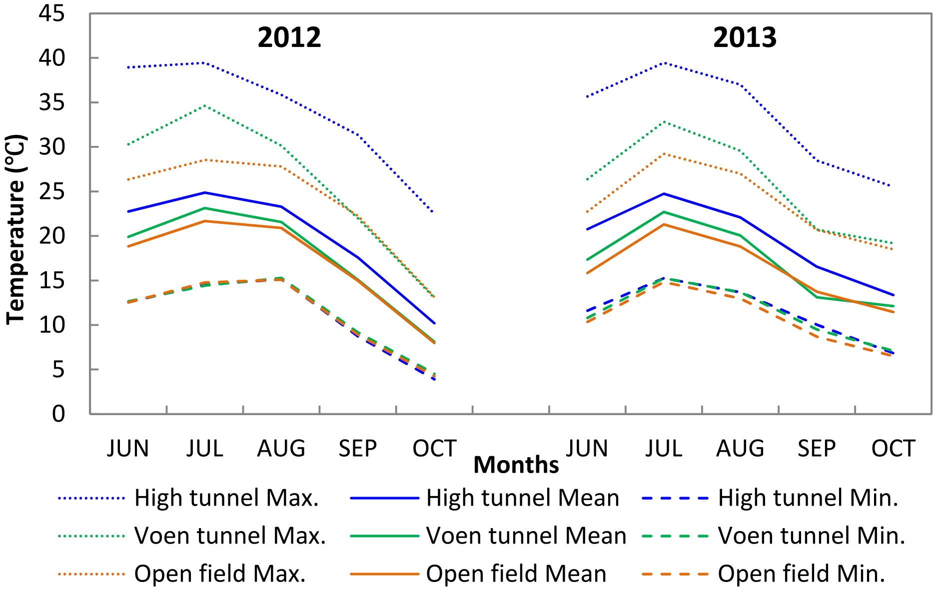

Figure 2.1 The monthly air temperatures under high tunnel, Voen shelter and open field during the growing season in 2012 and 2013 in Québec, Canada.

2.4.2 Marketable fruit yield of floricane-fruiting red raspberry 'Jeanne d'Orléans' (2012 and 2013)

Statistically, combined ANOVA cannot be used to analyze the variation of fruit yield or fruit size over two years 2012 and 2013, since there is an interaction between experimental year and growing environments. Thus we have analysed the variation of fruit yield or size for the two years separately.

In 2012, growing environments (high tunnel, Voen shelter or open field) and white reflective ground cover (absence and presence) respectively influenced marketable fruit yield of the floricane-fruiting red raspberry 'Jeanne d'Orléans' significantly ($P < 0.05$), pruning had no effect on fruit yield, and there was no interaction between treatments (Table 2.1). A significant interaction ($P < 0.05$) between growing conditions and pruning was observed (Table 2.1).

High tunnel increased marketable fruit yield by 26.2% compared with Voen shelter, and 2.1 times the fruit yield as measured in open field. Voen shelter improved 1.6 times fruit yield compared with open field (Table 2.2). Reflective mulch increased fruit yield by 13.9% more than without the mulch (Table 2.3). Though pruning has not significantly (*P* = 0.0662) affected fruit yield, both pruning at the first flush and second flush of raspberry plants had an obvious tendency to improve fruit yield by 12.4% and 15.0% respectively compared to unpruned treated (Table 2.4, Appendix, Figure A.2.1). For fruit size, the interaction between growing environments and pruning indicated that the fruits produced by plants under high tunnel which were pruned at the second flush were biggest (Table 2.5).

In 2013, ANOVA showed that all the three factors namely growing environments, white reflective mulch and pruning, significantly ($P < 0.05$) influenced marketable fruit yield of 'Jeanne d'Orléans' respectively. An interaction ($P < 0.05$) between growing conditions and pruning was observed. Growing conditions and pruning have significant effect ($P < 0.05$) on fruit size, while reflective mulch has no significant effect on fruit size, and no significant interaction between treatments was measured (Table 2.1).

Multiple comparisons indicated that high tunnel improved marketable fruit yield by 5.0% compared with Voen shelter, and by 2.4 times the fruit yield as measured in open field. Voen shelter improved by 2.3 times fruit yield compared with open field (Table 2.2). Reflective mulch increased fruit yield by 10.3% compared with the absence of that (Table 2.3). A significant interaction was observed between pruning and the different protected cultivation treatments for fruit yield; in this case plants grown under protected cultivation and pruned after the first flush of growth gave the best yield. There was no difference between both pruning treatments under each growing condition (Table 2.5). For fruit size, both fruits under Voen shelter and open field were significantly larger than those under high tunnel (Table 2.2). Pruning at second flush increased significantly fruit size compared with unpruned (Table 2.4).

Table 2.1 ANOVA of marketable fruit yield and fruit size of floricane-fruiting cv. 'Jeanne d'Orléans' and primocane-fruiting cv. 'Polka'(2012 and 2013)

Effect	***P*-value (2012)**		***P*-value (2013)**	
	Fruit yield	**Fruit size**	**Fruit yield**	**Fruit size**
'Jeanne d'Orléans'				
Protected cultivation (PC)	**0.0016***	0.6732	**<.0001***	**0.0149***
Mulch (M)	**0.0279***	0.2540	**0.0265***	0.2484
PC*M	0.3368	0.6118	0.6888	0.2783
Pruning (P)	**0.0662**	**0.0002***	**<.0001***	**0.0050***
PC*P	0.4589	**0.0465***	**0.0350***	0.2357
M*P	0.7674	0.8394	0.4152	0.5900
PC*M*P	0.8303	0.6371	0.8724	0.9532
'Polka'				
PC	**0.0018***	0.0601	**<.0001***	**0.0007***
M	**0.0027***	0.1097	**0.0202***	**0.0157***
PC*M	0.1595	0.7415	0.6727	0.8895
Density (D)	**<.0001***	**0.0481***	**<.0001***	**<.0001***
PC*D	**0.0002***	0.9171	**<.0001***	0.9971
M*D	0.7272	0.9444	0.0598	0.5743
PC*M*D	0.5615	0.9840	0.9347	0.9743

The * represents the significance level at $P < 0.05$

Table 2.2 Influence of growing environments namely high tunnel, Voen shelter or open field on marketable fruit yield (g/linear meter) and fruit size (g/fruit) of cv. 'Jeanne d'Orléans' and cv. 'Polka'(2012 and 2013)

Growing environments	**2012**		**2013**	
	Fruit yield	**Fruit size**	**Fruit yield**	**Fruit size**
'Jeanne d'Orléans'				
High tunnel	2333.8 a	3.60	2157.7	2.89 b
Voen shelter	1849.6 a	3.57	2055.0	3.13 a
Open field	1132.5 b	3.64	885.1	3.19 a
'Polka'				
High tunnel	2718.3 a	3.89 a	3201.6	3.71 b
Voen shelter	2108.9 b	4.14 a	1982.1	4.17 a
Open field	1494.8 c	3.97 a	953.9	4.05 a

Values within a column followed by different letters are significantly different at the 5% level of Tukey's multiple range test.

Table 2.3 Influence of reflective mulch on marketable fruit yield (g/linear meter) and fruit size (g/fruit) of cv. ‘Jeanne d’Orléans’ and cv. ‘Polka’ (2012 and 2013)

Mulch	**2012**		**2013**	
	Fruit yield	**Fruit size**	**Fruit yield**	**Fruit size**
‘Jeanne d’Orléans’				
No mulch	1656.8 b	3.58	1616.2 b	3.03
With mulch	1887.1 a	3.63	1782.4 a	3.10
‘Polka’				
No mulch	1931.0 b	3.96	1896.4 b	3.90
With mulch	2283.6 a	4.04	2195.3 a	4.05

Values within a column followed by different letters are significantly different according to Tukey’s multiple range test at 5% level.

Table 2.4 Influence of pruning on marketable fruit yield (g/linear meter) and fruit size (g/fruit) of cv. ‘Jeanne d’Orléans’ (2012 and 2013)

Pruning	**2012**		**2013**	
	Fruit yield	**Fruit size**	**Fruit yield**	**Fruit size**
Unpruned	1623.4 a	3.49	1445.3	2.96 b
Prune at 1st flush	1825.4 a	3.58	1890.4	3.04 ab
Prune at 2nd flush	1867.2 a	3.74	1762.0	3.21 a

Values within a column followed by different letters are significantly different at the 5% level of Tukey’s multiple range test.

Table 2.5 Influence of growing environments and pruning on marketable fruit yield (g/linear meter) and fruit size (g/fruit) of cv. ‘Jeanne d’Orléans’ (2012 and 2013)

Growing environments	**Pruning**	**2012**		**2013**	
		Fruit yield	**Fruit size**	**Fruit yield**	**Fruit size**
High tunnel	**No**	2023.3	3.36 b	1865.7 b	2.75
	1st flush	2466.8	3.60 ab	2399.7 a	2.97
	2nd flush	2511.4	3.83 a	2207.8 ab	2.94
Voen shelter	**No**	1739.2	3.54 ab	1640.9 c	3.00
	1st flush	1886.3	3.48 ab	2319.3 a	3.11
	2nd flush	1923.2	3.70 ab	2204.7 ab	3.28
Open field	**No**	1107.7	3.58 ab	829.3 d	3.12
	1st flush	1123.1	3.65 ab	952.3 d	3.03
	2nd flush	1166.9	3.70 ab	873.7 d	3.41
PC* P interaction		NS	*	*	NS

Values within the column followed by different letters are significantly differed according to Tukey’s multiple range test at 5% level.

2.4.3 Marketable fruit yield of primocane-fruiting red raspberry ‘Polka’ (2012 and 2013)

As for the analysis of the results conducted with the cv. Jeanne d’Orléans, the ANOVA for the two consecutive years was conducted separately. Combined ANOVA cannot be used for analysis of variation of marketable fruit yield and fruit size on primocane-fruiting cv. ‘Polka’ over two years 2012 and 2013. Thus the results of two years were showed separately as follows.

In 2012, white reflective mulch (absence or presence) significantly ($P < 0.05$) influenced marketable fruit yield of ‘Polka’, a significant interaction ($P < 0.05$) between growing conditions and cane densities was measured. Cane density has significant effect ($P < 0.05$) on fruit size (Table 2.1).

High tunnel increased more marketable fruit yield by 28.9% than Voen shelter, and 1.8 times the fruit yield as measured in open field. Voen shelter improved 1.4 times fruit yield compared with open field (Table 2.2). Reflective mulch increased the fruit yield by 18.3% compared with the absence of that (Table 2.3). As cane density increased, fruit yield increased significantly by 43.1% in density of 4 canes per pot and 70.6% in density of 6 canes per pot compared with the low density of 2 canes per pot (Table 2.6). The interaction on fruit yield between growing conditions and cane densities indicated that plants grown with densities of 4 and 6 canes per pot under high tunnel and those grown with density of 6 canes per pot under Voen shelter had the highest fruit yield (Table 2.7). As cane density increased, fruit size decreased. Plants at lowest cane density produced significant larger fruits than those at highest density (Table 2.6).

Table 2.6 Influence of cane density on marketable fruit yield (g/linear meter) and fruit size (g/fruit) of cv.'Polka' (2012 and 2013)

Density	**2012**		**2013**	
(# cane/pot)	**Fruit yield**	**Fruit size**	**Fruit yield**	**Fruit size**
2	1528.3	4.07 a	1320.6	4.13 a
4	2186.5	4.02 ab	2210.3	3.98 b
6	2607.1	3.92 b	2606.6	3.82c

Values within a column followed by different letters are significantly differed according to Tukey's multiple range test at 5% level.

Table 2.7 Influence of growing environments and cane density on marketable fruit yield (g/linear meter) and fruit size (g/fruit) of cv. 'Polka' (2012 and 2013)

Growing environments	**Density (# cane/pot)**	**2012**		**2013**	
		Fruit yield	**Fruit size**	**Fruit yield**	**Fruit size**
High tunnel	2	2088.8 b	3.93	1976.3 cd	3.85
	4	3157.3 a	3.95	3478.7 b	3.71
	6	2908.8 a	3.79	4149.8 a	3.57
Voen shelter	2	1365.8 cd	4.21	1374.8 de	4.33
	4	2016.5 b	4.14	2100.1 c	4.16
	6	2944.3 a	4.08	2471.4 c	4.02
Open field	2	1130.5 d	4.07	610.7 f	4.21
	4	1385.8 bcd	3.96	1052.2 ef	4.06
	6	1968.2 bc	3.88	1198.7 e	3.88
Environments * Densities		*	NS	*	NS

Values within each column followed by different letters are significantly different at the 5% level of Tukey's multiple range test.

In 2013, reflective mulch significantly ($P < 0.05$) influenced fruit yield, all factors namely growing conditions, reflective mulch and cane densities significantly ($P < 0.05$) influenced fruit size of 'Polka' respectively. A significant interaction ($P < 0.05$) on fruit yield was measured between growing conditions and cane densities, but there was no interaction on fruit size between treatments (Table 2.1).

Multiple comparisons indicated that high tunnel increased 1.6 times more marketable fruit yield than Voen shelter, and 3.4 times fruit yield as measured in open field. Voen shelter improved 2.1 times fruit yield compared with open field (Table 2.2). Reflective mulch increased fruit yield by 15.8% compared to no mulch (Table 2.3). As cane density increased, fruit yield increased by 67.4% in density of 4 canes per pot and 97.4% in density of 6 canes per pot compared with low density of 2 canes per pot

(Table 2.6). The interaction on fruit yield indicated that plants grown with highest density under high tunnel obtained the best fruit yield (Table 2.7). For fruit size, under high tunnel it is significantly lower than that under Voen shelter and open field (Table 2.2). As density increased, fruit size decreased. There are significant differences between any two levels of cane density (Table 2.6).

2.5 Discussion

2.5.1 Microclimate under high tunnel and Voen shelter

In general, and as expected, average monthly air temperature under high tunnel is considerably higher than in open field. Medina (2008) and Landry (2011) measured comparable air temperatures under high tunnel. Thus high tunnels allowed early yield of floricane-fruiting raspberry e.g. cv. 'Jeanne d'Orleans' and extended production of primocane-fruiting raspberry such as 'Polka' till late autumn. It is obviously a desirable aspect for extension of raspberry production season in Northern climates such as Québec, Canada. High tunnel is an enclosed system while Voen shelter is open to air circulation. Air temperature under Voen shelter is thus lower than under high tunnel, yet still slightly higher than in open field. During September and October, the air temperatures monitored under Voen shelter and open field were comparable. This suggests that Voen shelter is not best suited for the extension of the growing season of primocane-fruiting (autumn-fruiting) red raspberries.

In the summer, to protect floricane-fruiting raspberry plants from overheating, the air temperature and humidity inside the high tunnel are passively controlled by the manual opening of the tunnel's ends and sides. In autumn, the tunnel openings are kept closed most of the time to warm primocane-fruiting raspberry plants, extend the harvest season, and thereby maximize their production. Compared to high tunnel, the Voen shelter is significantly better ventilated, making it a good choice for summer-fruiting cultivars.

2.5.2 Effects of protected structure on marketable fruit yield of floricane-fruiting red raspberry ‘Jeanne d’Orléans’ and primocane-fruiting red raspberry ‘Polka’

Protected structures, high tunnels in particular, are used extensively for improving the yield and quality of horticultural crops. Our results show that high tunnel significantly increased marketable fruit yield of floricane-fruiting variety ‘Jeanne d’Orléans’ by 2.1 and 2.4 times compared with open field in 2012 and 2013 respectively. Some researchers such as Hanson *et al.* (2011) also indicated that high tunnel can double fruit yield of floricane-fruiting varieties ‘Nova’ and ‘Canby’ in Michigan, USA. Interestingly, Voen shelter also significantly increased fruit yield of ‘Jeanne d’Orléans’ by 1.6 and 2.3 times compared with open field in 2012 and 2013, respectively. Hence, both types of protective structure stimulated fruit yield to a nearly similar extent, thereby suggesting that Voen shelters, being less costly to implement, may be a sound alternative to high tunnels for summer-fruiting raspberry cultivar production.

Similar results were obtained in primocane-fruiting cv. ‘Polka’ plants grown under protected structures, that is high tunnel and Voen shelter caused a significantly higher fruit yield than that of plants grown in open field. Some researchers have also indicated that high tunnel can produce over twice and almost three times the fruit yield of primocane-fruiting varieties (Goulart and Demchak, 1999). However, compared to the aforementioned nearly equivalent protected structure effects found for cv. ‘Jeanne d’Orléans’, marketable fruit yield of cv. ‘Polka’ (autumn-fruiting) grown under high tunnel was clearly better than the yield obtained under Voen shelter. In late autumn, high tunnel created a warmer and better microclimate through passive control, which prolonged the harvest season and ensured sustained fruit ripening. In comparison, the microclimate of the more open Voen shelter remained much more coupled to the climate outside (Figure 2.1). As a result, ‘Polka’ plants grown under Voen shelter produced significantly lower fruit yield than those under high tunnel.

Despite the fact that Voen shelters did not cause a warmer microclimate in the autumn, they still improved the fruit yield by 1.4 times compared to open field conditions. A higher non-marketable fruit ratio occurred in open field because the pressure of strong wind, rainfall, sunburn etc. lowered fruit quality (data not shown). In Voen shelter these natural forces are dampened. In rainy days, the Voen cover prevents rainwater from soaking fruits, leading to better fruit quality. The semi-transparent Voen cover also protects fruits from sunscald. Overall, although the Voen shelter microclimate did not affect the timing of flowering or the fruiting duration compared to open field, it still provided enough protection against thigmomorphogenetic forces to allow plants to grow taller and bear longer fruiting laterals.

2.5.3 Effects of reflective mulch on marketable fruit yield of floricane-fruiting red raspberry ‘Jeanne d’Orléans’ and primocane-fruiting red raspberry ‘Polka’

Reflective mulch has been used in annual field crops like tomato (Nyochembeng *et al.*, 2014) and potato (Campiglia *et al.*, 2009) as well as in perennial fruit crops like grape (Todic *et al.*, 2008). It is used to increase the reflected light from the ground, which is associated with improved crop yields, particularly in lower canopy (Thorp *et al.* 2001). There has been few researches on the effect of reflective mulch under protective covers. In our study, reflective mulch improved marketable fruit yield by approximately 13% under protected structures for both cultivars, and by 8.3% and 37.1% in open field for ‘Jeanne d’Orléans’ and ‘Polka’, respectively. This difference between fruiting types in open field may be due to their inherently different growth habits. At the cane densities used in this study, ‘Jeanne d’Orléans’ plants had a much denser canopy with longer laterals than ‘Polka’ plants. Also, at the start of the growing season, the cv. ‘Polka’ canopy developed from newly emerging canes whereas for cv. ‘Jeanne d’Orléans’ the canopy flushed from already established 1.5 m high floricanes. Hence, the combination of the high fraction of direct radiation in open field with the smaller canopy of cv. ‘Polka’ probably increased the reflective efficiency of the mulch and favoured growth and yield.

The positive effect reflective mulch had on raspberry fruit yield in this study is consistent with previous reports on other perennial fruit crops like vine grapes (Todic *et al.*, 2008; Coventry *et al.* 2005) and apple trees (Privé *et al*, 2008; Grout *et al.*, 2004). Likewise, Bertelsen (2005) reported a 60% increase in pear fruit yield by using reflective mulch. Costa *et al.* (2003) and Thorp *et al.* (2001) observed an increase in yield (15% and 31% respectively) in kiwi production. However, these authors did not obtain similar yield increases during the second year, suggesting the absence of long term effect of the mulch. Comparatively for red raspberry, our results and also those of Raymond-Bayne (2012) showed that the positive effect of reflective mulch on fruit yield extended to at least the second year of culture.

2.5.4 Effects of summer pruning on marketable fruit yield of floricane-fruiting red raspberry 'Jeanne d'Orléans'

The pruning of raspberry canes is one of the most labour-intensive operations in raspberry production, yet appropriate pruning has a significant positive impact on the overall and marketable fruit yield, including larger fruits, control of cane vigor, and harvest of disease-free and high quality fruits (Bushway *et al.*, 2008). In our study, plants from which new shoots were pruned in the first year (2012) tended to produce more fruit yield (13.7%) than unpruned plants ($P = 0.066$), whereas in the subsequent year (2013) the positive effect (26.4%) of pruning new shoots became significant ($P < 0.05$). It therefore appears that pruning biannual raspberry has a long-term effect on marketable yield.

2.5.5 Effects of cane density on marketable fruit yield of primocane-fruiting red raspberry 'Polka'

The effects of cane density on red raspberry have been studied by several researchers (Nes et al., 2008; Vanden Heuvel, 1999; Gundersheim and Pritts, 1991; Nehrbas and Pritts 1988; Crandall, 1980; Crandall et al., 1974). Although some exception can be found (e.g. Evans, 1974), generally speaking, when increasing the number of canes per linear meter, the yield also increases. For example, in Québec, Granger (1972) found that increasing cane numbers from 10 to 20 canes per linear meter lead to proportional increases in fruit yield. Likewise, Raymond-Bayne (2012) obtained similar results over a wider range of 12 to 30 canes per linear meter. Unlike these two studies, our research was conducted on potted plants that may comparatively have a more limited root system, but significant gains in fruit yields were observed over a range of 2 to 6 canes per pot (three pots per linear meter in all cases) (Table 2.6).

Nevertheless, beyond a certain density threshold, the fruit yield reaches a plateau (Waister *et al.*, 1977). There is an optimum cane density at which the fruit yield is maximal (Oliveira, 2004; Buszard, 1986). Oliveira (2004) achieved maximum yield of primocane-fruiting red raspberry ‘Autumn Bliss’ at densities of 16 to 24 canes per linear meter. Landry (2011) reported that primocane-fruiting cv. ‘Autumn Britten’ grown at a density of 25 canes per linear meter produced 10.4% and 8.5% more fruit yield than those cultivated at 15 canes and 30 canes per linear meter, respectively. For such soil-cultivated raspberry, Buszard (1986) reported that optimum cane number is about 15 canes per linear meter and raspberry producers in Ontario and Québec often follow this recommendation now. For pot-grown primocane-fruiting cv. ‘Polka’, the cane density range evaluated in our study did not allow us to determine the actual optimal cane density, yet from a multi-year plant management point of view, we suggest a density of 4 canes per pot as a reasonable operational limit.

Raspberry has the ability to increase fruit size and overall yield per cane to partially offset a decrease in cane density. Such results have repeatedly been observed for raspberry cultivation in soil (Wright and Waister 1982; Lawson and Wiseman, 1983; Van den Heuvel 1999) and are thought to arise from a lessening of inter-cane competition for limited resources (e.g. light, soil water and nutrients). Similar results were found in our study for container-grown primocane-fruiting variety ‘Polka’, that is as cane density increased, both fruit size and fruit yield per cane decreases during 2012 and 2013.

2.6 Conclusion

In summary, the experiments carried out from 2012 to 2013 in Québec, determined the effects of growing environments, white reflective ground cover and summer pruning or cane densities on marketable fruit yield of floricane- or primocane-fruiting red raspberries, 'Jeanne d'Orleans' or 'Polka'. For both varieties, plants grown under high tunnel produced the highest marketable fruit yield during 2012 and 2013, followed by those grown under Voen shelter; those grown in open field gave the lowest fruit yield. Using white reflective mulch significantly improved marketable fruit yield.

Specifically, for floricane-fruiting cv. 'Jeanne d'Orléans', no significant difference on fruit yield was observed between the two protected structures, namely high tunnel and Voen shelter. Plants from which new emerging primocane shoots were removed produced more fruits than unpruned plants, the increase becoming more significant in the second year of culture. This suggests that pruning had long-term (two fruiting years at least) additive effect on marketable fruit yield, possibly by improving the light microclimate of the remaining canopy, and also by lessening the inter-cane competition for soil water and nutrients.

In primocane-fruiting cv. 'Polka', there was a significant difference on marketable fruit yield between the two protected structures (high tunnel being superior), most likely because the high tunnel created a warmer microclimate that sustained fruit ripening for a longer period in autumn, a period during which plants grown under the cooler Voen shelter underwent low temperature-induced slowing down of fruit maturing. Still, despite the Voen shelter microclimate being similar to open field in late summer/autumn, Voen shelter still improved the fruit yield 1.4 times relative to open field, probably due to sufficient buffering against thigmomorphogenetic forces that allowed plants to grow taller canes with longer fruiting laterals than in open field.

With regards to the effect of cane density on fruit yield for primocane-fruiting cv.

‘Polka’, increasing density from 2 to 4 to 6 canes per pot (giving 6 to 12 to 18 canes per linear meter) decreased the marketable fruit size and fruit yield per cane, but this inter-cane competition effect was not important enough to prevent the fruit yield per pot to significantly increase proportionally to cane density.

High tunnel and Voen shelter systems were used successfully for commercial production of floricane- and primocane-fruiting red raspberries under northern Canadian climate as they increased fruit yield by creating a better plant growth microclimate. In order to gain a better understanding of such microclimatic effects on productivity, aboveground biomass accumulation and fruit yield, in the next three chapters the photosynthetic response of red raspberry to light and temperature/VPD will be evaluated at the leaf *vs.* plant-level under protective structures in comparison to open field.

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Chapter 3: Microclimate and leaf photosynthesis in floricane- and primocane-fruiting red raspberries cultivated under high tunnel and rain shelter *vs.* open field

3.1 Abstract

Leaf photosynthetic rate is a direct determinant of crop yield. Variations in photosynthetic responses to different microclimates under protected structures are poorly understood, particularly in red raspberry plants. Therefore the present experiments examined leaf photosynthesis in potted floricane-fruiting cv. 'Jeanne d'Orleans' and primocane-fruiting cv. 'Polka' in response to protective cultivation under high tunnel or Voen shelter (an umbrella-shaped structure) *vs.* open field.

Concerning reflective mulch effects, during the fruiting period of cv. 'Jeanne d'Orléans', white ground cover significantly increased the PPFD reflected to the lower canopy by 80% in open field and 60% under high tunnel, compared to only 14% under Voen shelter. During the fruiting season of cv. 'Polka', a positive reflective mulch effect on the reflected light (up to 42%) was only found in open field. In all cases, ground cover had no significant effect on the total leaf PPFD and photosynthesis under any growing conditions.

With regard to canopy position effects, for cv. 'Jeanne d'Orléans', leaf PPFD decreased by 24% in the lower canopy compared to the upper in open field, but no differences were measured under protected structures. In contrast, for cv. 'Polka', the PPFD reaching the lower canopy was 24% lower than the upper canopy under the both types of protected structures, resulting in a concomitant decrease in photosynthesis of 19%. This inter-varietal performance difference was likely due to the fact that cv. 'Polka' developed appreciably larger leaf canopies than cv. 'Jeanne d'Orléans', resulting in significantly different vertical light gradient patterns between the two cultivars.

Regarding growing condition effects, for cv. 'Jeanne d'Orléans', the leaf PPFD was attenuated by approximately 46% under the both types of protective covering compared to open field. Corresponding photosynthesis was on average reduced by 43% under high tunnel and by 17% under Voen shelter. The effect of the high tunnel and

Voen protective coverings on leaf PPFD and photosynthesis were similar in cv. ‘Polka’. The consistently lower leaf photosynthesis rates measured under high tunnel were most likely due to the significantly higher leaf temperatures prevailing there. Further analysis of pooled leaf photosynthesis *vs.* leaf temperature under the three growing conditions confirmed that the net leaf photosynthetic rates of both cv. ‘Jeanne d’Orléans’ and cv.‘Polka’ fell steeply when leaf temperatures exceed 25°C and 20°C, respectively.

3.2 Introduction

High tunnels are extensively used throughout North America to maximize red raspberries (*Rubus idaeus* L.) production by protecting plants from wind and rain damage and further by reducing disease pressure (Pritts, 2006; Demchak, 2009). Many scientists have reported that high tunnels can produce over twice and sometimes three times the marketable fruit yield of floricane-fruiting varieties such as ‘Nova’, ‘Canby’ (Hanson *et al.*, 2011) or ‘Jeanne d’Orleans’ (Xu *et al.*, 2013) as well as of primocane-fruiting varieties (Goulart and Demchak, 1999).

In recent years, a new type of wooden umbrella-shaped structure called Voen (Vöhringer GmbH & Co. KG, http://www.voen.de/en.html) has been evaluated in Canada. From a cost-performance ratio perspective this Voen shelter represents an economical alternative to high tunnels for red raspberries production. In sweet cherry production such use of Voen umbrella-shaped tunnels resulted in increased fruit size and yield, and improved fruit quality such as uniform fruit color (Rubauskis *et al.*, 2013). For raspberries, limited case studies have been reported.

Compared to the open field climate, the microclimate (light, rain and wind, air temperature and humidity) under protected structures like the high tunnel polyethylene film or the Voen rain-shelter covering is modified considerably. For instance, lower light conditions particularly in the lower canopies of red raspberry row cultures are found under high tunnel (Landry, 2011; Raymond, 2012). Reflective ground mulches have been shown to improve the lower canopy light environment by reflecting light that would otherwise be absorbed by the ground back towards the canopy (Raymond, 2012; Toye, 1995). Air temperatures are known to be significantly increased under high tunnel, a well-recognized advantage for the cultivation of autumn-fruiting raspberry cultivars in cold climates (Landry, 2011; Hanson *et al.*, 2011); but for summer-fruiting cultivars potentially harmful excessive daytime temperatures may develop under high tunnel in the summer, although such heat stress may partially be mitigated by the manual passive ventilation (Blomgren *et al.*, 2007).

Cultivation of raspberry plants under sub-optimal microclimates may result in lower leaf stomatal conductance and photosynthesis, leading to lower biomass production and reduced fruit yield (Wright and Waister, 1984, 1986; Goulart and Demchak, 1993, 1999). Therefore, such parallel assessment of microclimatic conditions and leaf photosynthetic properties under various protected structures will likely benefit our understanding of why a particular protected cultivation practice is more successful than others. Previous studies on the photosynthetic physiology in red raspberries have mostly been conducted in the open field and have focused mainly on seasonal changes (Fernandez and Pritts, 1994) or on differences between floricanes and primocanes in light interception and dry matter partitioning (Palmer *et al.* 1987; Braun *et al.* 1989; Waister and Wright 1989). Recently, Landry (2011) and Raymond (2012) have reported a significant positive effect of reflective ground cover on the fruit yield of primocane-fruiting red raspberry crops grown under high tunnel. However, they did not extend their research to other growing conditions like open field or Voen cover.

The present research examined the interactive effects between tunnel coverings and ground covers on the photosynthesis of floricane- and primocane-fruiting red raspberries. Specifically, our main objective was to determine the influence of the aerial growing environment (namely high tunnel, Voen shelter *vs.* open field) and the presence of reflective ground cover on the microclimate and photosynthesis of lower *vs.* upper canopy leaves during the summer (floricane-fruiting cultivar) and early-autumn (primocane-fruiting cultivar) growing seasons.

3.3 Materials and methods

3.3.1 Research site

Experiments were carried out in 2013 under different growing conditions including high tunnel, Voen shelter and open field at ‘Les Fraises de Ile d’Orleans inc. (71°01'W, 46°52'N) located in Québec, Canada. The high tunnel size used was 8.5 m wide, 4.5 m high, and 70.0 m long with polyethylene coverings from Industries Harnois (http://www.harnois.com). Temperature, relative humidity and ventilation inside the tunnel were partially controlled by passive ventilation consisting in closing or opening the side walls or doors of the tunnels. For the Voen shelter a wooden framework consisting of 3.6 m high posts lined up between rows was used to support umbrellas, each 2.5 m in width and 70.0 m in length (see Figure 1.1). The Voen umbrella covering was made of double-layered woven plastic films manufactured in Germany (http://www.voen.de/en.html).

3.3.2 Plant material

Both mature floricane- and primocane-fruiting potted red raspberry plants were used for the experiment. The floricane-fruiting cv. ‘Jeanne d’Orleans’ plants were thinned in the spring of 2013 to keep three uniform floricanes per pot. After harvest, the floricanes senesced and were cut at the level of the soil. The primocanes were kept intact in pot with required tip pruning (1.5 m for open field and 1.75 m for high tunnel- and Voen shelter-grown plants) to overwinter. The primocane-fruiting cv. ‘Polka’ plants were grown one year before establishing the experiment. In the spring of 2013, new shoots were trained to keep four uniform canes per pot. Hedgerow type trellising system was used to support the canes for both fruiting types.

Pests and weeds were controlled according to Canadian standard cultural practices (Canadian General Standards Board and Standards Council of Canada, 2006). Plants were irrigated by using a drip irrigation system with two drippers in each pot. Plants were fertilized by automatically incorporating soluble fertilizers in the irrigation water according to local recommendations (Tellier, 2007).

3.3.3 Experimental design

For both floricane-fruiting ‘Jeanne d’Orléans’ and primocane-fruiting ‘Polka’ varieties, the experiments were designed as 3×2 factorials and set up in a split-plot design with the three growing conditions (high tunnel, Voen shelter and open field) as the main plots and reflective mulch (presence or absence) as the sub-plots, resulting in six treatments. The six treatments were established in a single plant row and were replicated four times. Reflective ground cover sub-plots alternated with ‘no mulch’ sub-plots in pairwise fashion. Reflective mulches were installed in alternation with the ‘no mulch’ sub-plots of a same row. Plants were grown in pots using a total of nine pots per sub-plot and separated from the next sub-plot in line by four additional pots as buffer zones between adjacent treatments within the row. In order to determine the effects of growing conditions on the photosynthesis of leaves from the upper and lower canopy regions, the experimental designs were set as 3×2 factorials with three growing conditions and two canopy levels for both fruiting types of cultivars, resulting in six treatments.

3.3.4 Data collected

3.3.4.1 Microclimate

Microclimate data were collected in each growing environment at different plant canopy heights throughout the entire 2013 growing season (i.e. from early June to early October). Measurements of average root zone temperature at 10 cm below soil level and average air temperature and relative humidity at 0.5, 1.0 and 1.5 m above ground were recorded every 15 minutes with HOBO data loggers (U12-013, Onset Corp., Bourne, MA, USA).

The incident and reflected photosynthetic photon flux density (PPFD) just outside the periphery of the row crop canopy (sunny side) was monitored at the lower (0.6 m) *vs.* upper (1.2 m) canopy levels using 2 quantum sensors (LI-190R, Li-Cor Inc., Lincoln, NE, USA) per plot. Each quantum sensor pair had one sensor oriented skywards while the other sensor pointed towards the ground. A weather station (U30, Onset Corp., Bourne, MA, USA) was also installed in the open field to provide reference climate data for the whole research site.

3.3.4.2 Leaf photosynthesis

Leaf gas exchange rates were measured with a portable photosynthesis system (LI-6400XT, Li-Cor Inc. Lincoln, NE, USA) equipped with a 6 cm^2 leaf chamber with integrated red-blue light-emitting diode (LED) light source (LI-6400-02B, Li-Cor). Prior to clamping the leaf chamber onto a target leaf, the ambient CO_2 and water vapour concentrations were recorded with the LI-6400XT, the abaxial leaf temperature was measured with an infrared thermometer (AR330, Starmeter Instruments Co., Canton, Guangzhou, China), and the two-sided PPFD of the leaf (i.e. incident on the upper side + reflected on the underside) was measured with a quantum sensor oriented parallel to the leaf inclination plane. The aforementioned leaf microclimate conditions were subsequently reproduced inside the leaf chamber via the LI-6400XT environmental control system. Thus, the net CO_2 assimilation rate (A), stomatal conductance (g_s) and intercellular CO_2 concentration (C_i) of each target leaf were recorded under their own particular current microclimate. Photosynthesis measurements were taken between 08h00 and 16h00 on leaves selected from the outer half of fruiting laterals located around the mid-height of the lower (approx. 0.4-0.5 m) and of the upper (approx. 1.2-1.5 m) canopy portions.

Gas exchange measurements were made under predominantly clear days or otherwise uniform sky conditions throughout the approximate 2-hour period required to sample all three growing environments (i.e. paired measurements made on one mature leaf from two randomly selected plants in the high tunnel, Voen shelter, and open field, respectively). Sub-plots (ground cover or canopy position) were paired-sampled in different 2-hour block periods, that is once each in the morning (i.e. a total of 4 hours) and once more each in the afternoon. Hence, four 2-hour measurement blocks were completed per day. A total of 36 replicate leaves were eventually sampled for each treatments, that is 12 replicates per measurement cycle repeated three times over the fruit harvest period of ‘Jeanne d’Orléans’ (mid-July to late-Aug) and ‘Polka’ (mid-Aug to early-Oct) respectively.

At the beginning of the experiments, in order to verify potential differences among leaflets of trifoliate or pentafoliate leaves (Appendix, Figures A.3.1 and A.3.2), the photosynthesis of 9 trifoliate and 15 pentafoliate leaflets from both cultivars were measured on July 15 ('Jeanne d'Orléans') and August 10 ('Polka'). The different leaflets of trifoliate and pentafoliate leaves were tagged either 1 to 3 or 1 to 5 and were analyzed according to their relative position. No significant difference (P = 0.254, > 0.05) was found between leaflet position of a same leaf (data not shown); thus all subsequent gas exchange measurements were made on randomly selected leaflets.

3.3.5 Statistical analysis

Analysis of variance was completed using the GLIMMIX procedure of SAS (SAS Institute, Cary, N.C.). Multiple comparisons of means were adjusted by Tukey at the P = 0.05 probability level. Data transformations were made when necessary to ensure the validity of the assumptions of normality of errors and homogeneity of variance.

3.4 Results

3.4.1 Seasonal changes in air temperatures under high tunnel and Voen shelter

The highest daily temperatures occurred under high tunnel throughout the entire growing season in 2013, followed by those under Voen shelter. Compared to Voen shelter and open field respectively, the average daily high tunnel temperature was 3.4 and 4.9°C higher in early summer (June in Quebec) and 1.6 and 2.2°C in late autumn (Figure 3.1A). During mid-summer, the time when the cv. 'Jeanne d'Orléans' fruited, the daily maximum temperatures averaged 38.0°C and 31.4°C under high tunnel and Voen shelter, respectively, compared to 27.9°C in open field (Figure 3.1B). Compared to daytime temperatures, daily minimum temperatures occurring during night-time were about the same for all three growing environments, falling below 10°C in mid-September for the latter half of cv. 'Polka's growing season (Figure 3.1C). During that period, the daytime temperatures under the Voen shelter were also quite similar to those in open field (Figure 3.1A and 3.1B).

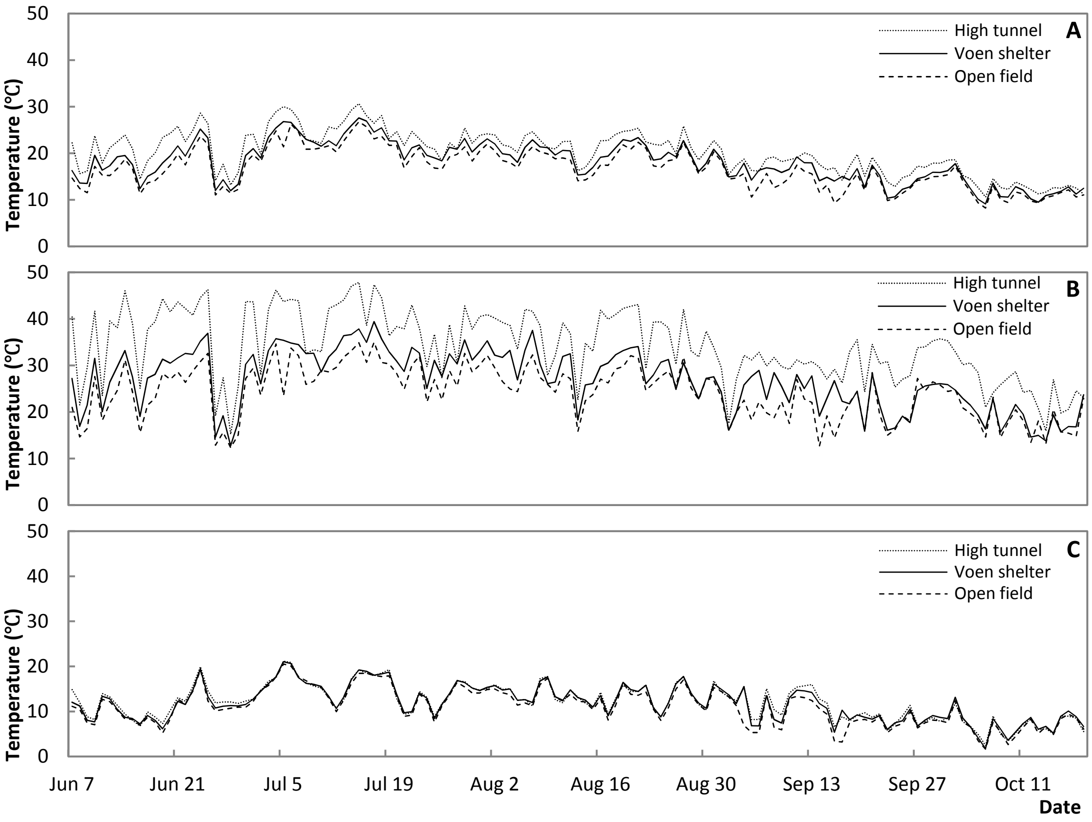

Figure 3.1 Daily A) average, B) maximum, and C) minimum air temperatures under high tunnel, Voen shelter and open field during the 2013 growing season of floricane- and primocane-fruiting red raspberries. Values are the averages of the three sensors installed at upper, middle and lower canopy under each growing condition respectively.

3.4.2 Photosynthesis of floricane-fruiting red raspberry 'Jeanne d'Orléans' grown under various growing conditions: effect of the ground cover

We previously hypothesized that the presence of white reflective mulches on the ground between hedgerows could improve the light environment of the plant canopy, especially in the lower portion. Figure 3.2D shows that the reflective mulch increased the PPFD reflected to the lower canopy by 80.5% and 60.3% under open field and high tunnel, respectively, whereas it only increased it by 14.3% in the Voen shelter.

In comparison, the total leaf PPFD (incident plus reflected) in the lower canopy was not significantly ($P > 0.05$) affected by the presence of reflective mulch under any growing conditions (Figure 3.2C and Appendix, Table A.3.1). Similarly, the photosynthetic activity of the leaves located in the lower canopy was not significantly ($P > 0.05$) affected by the presence of mulch in any growing environments (Figure 3.2A, Appendix, Table A.3.1). Under both high tunnels and Voen shelter, the photosynthesis of leaves located in the lower canopy was 43.0% and 17.6% lower than in open field, respectively. Comparatively, leaf temperature was highest under high tunnel, followed by Voen shelter, and lowest open field (the latter two being 12% and 22% lower than under high tunnel, respectively). This indicates that the net leaf photosynthetic rate of 'Jeanne d'Orléans' was inversely related to leaf temperature above 25°C (Figure 3.4).

In the upper canopy, the presence of white mulch had a significant positive effect on the reflected leaf PPFD only in open field (Figure 3.3D), but the contribution of the reflected PPFD to the total leaf PPFD was too small (5%) to produce a significant change in the latter, or to leaf photosynthesis (Figure 3.3A and 3.3C). There was no significant difference in leaf temperature between the upper and lower leaf canopy notwithstanding the presence or absence of a reflective ground cover (Figures 3.2B and 3.3B, Appendix, Table A.3.2).

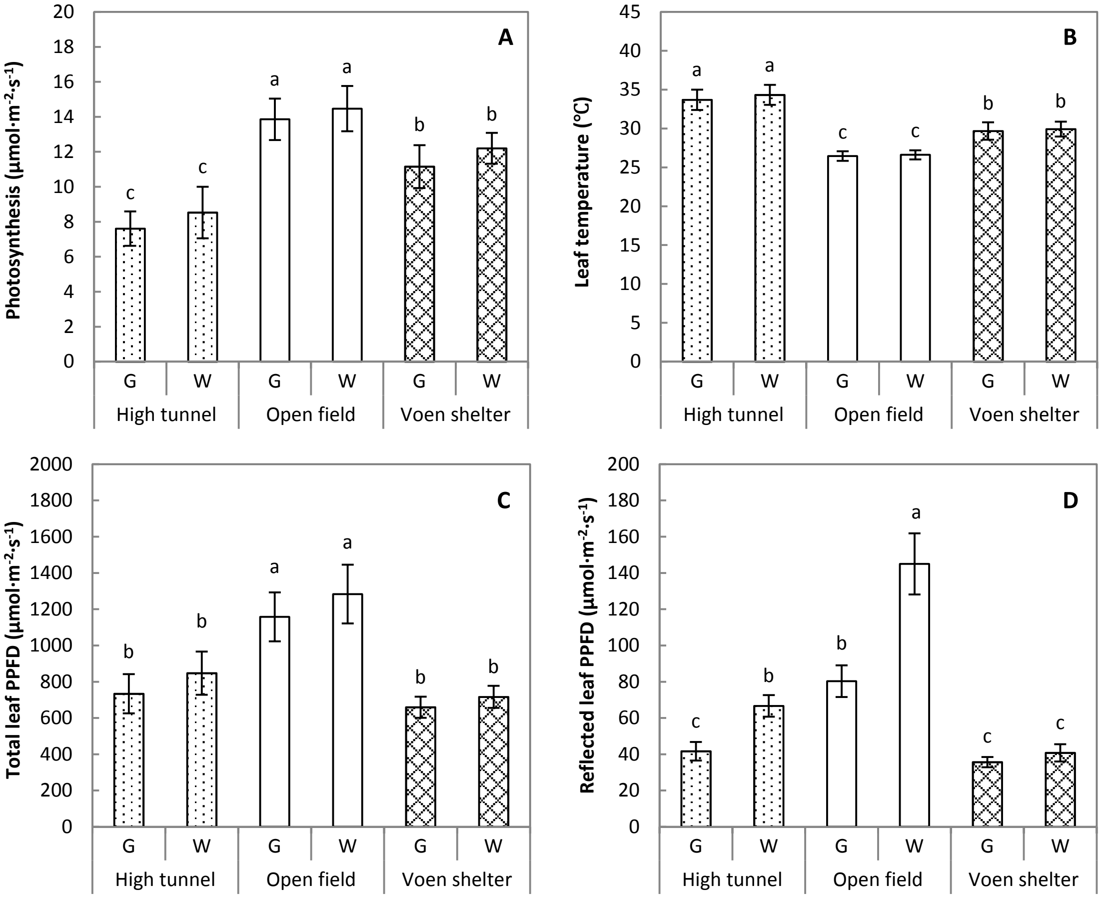

Figure 3.2 Effects of growing conditions (high tunnel, Voen shelter or open field) and reflective mulch (G, absence (natural ground vegetation) or W, presence) on: A) leaf photosynthesis, B) leaf temperature, C) total and D) reflected leaf PPFD in the **lower canopy** of floricane-fruiting cv. '**Jeanne d'Orléans**'. Mean value columns followed by different letters are significantly different according to Tukey's multiple range test at 5% level.

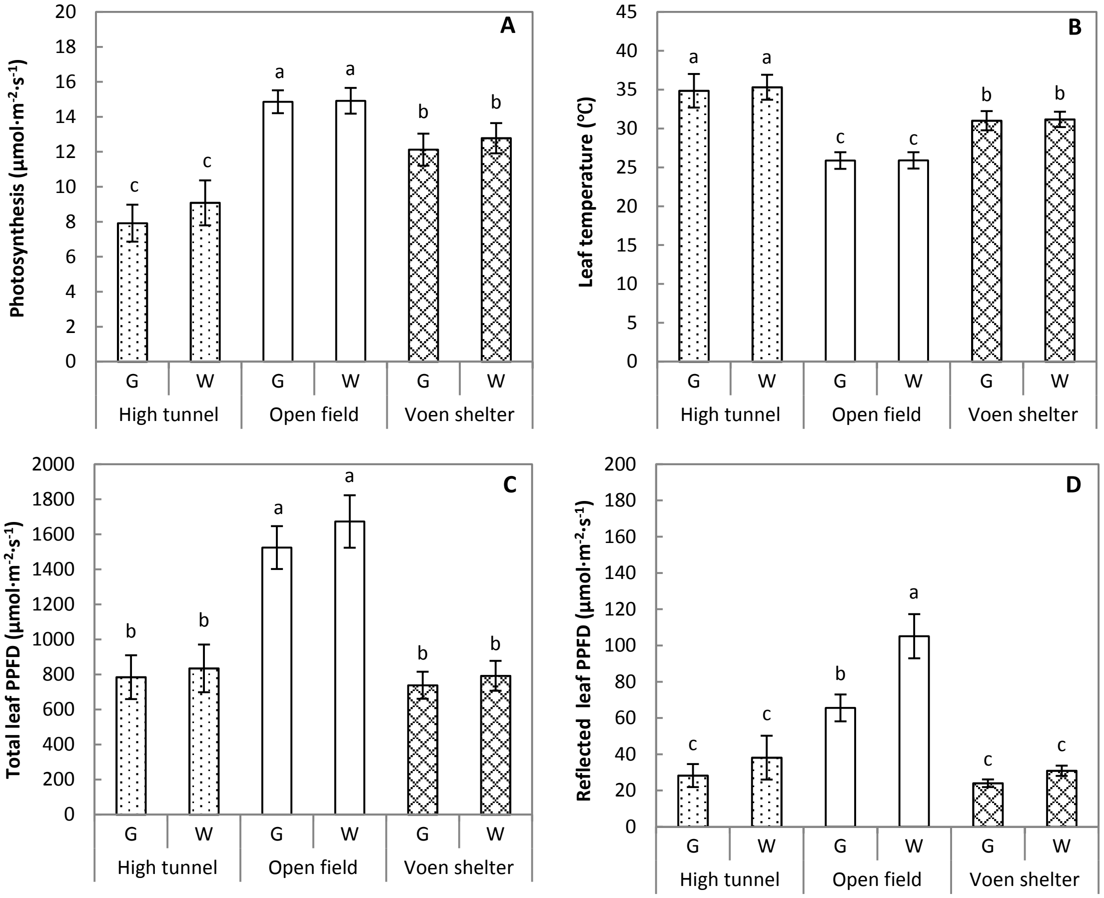

Figure 3.3 Effects of growing conditions (high tunnel, Voen shelter or open field) and reflective mulch (G, absence (natural ground vegetation) or W, presence) on: A) leaf photosynthesis, B) leaf temperature, C) total and D) reflected leaf PPFD in the **upper canopy** of floricane-fruiting cv. '**Jeanne d'Orléans**'. Mean value columns followed by different letters are significantly different according to Tukey's multiple range test at 5% level.

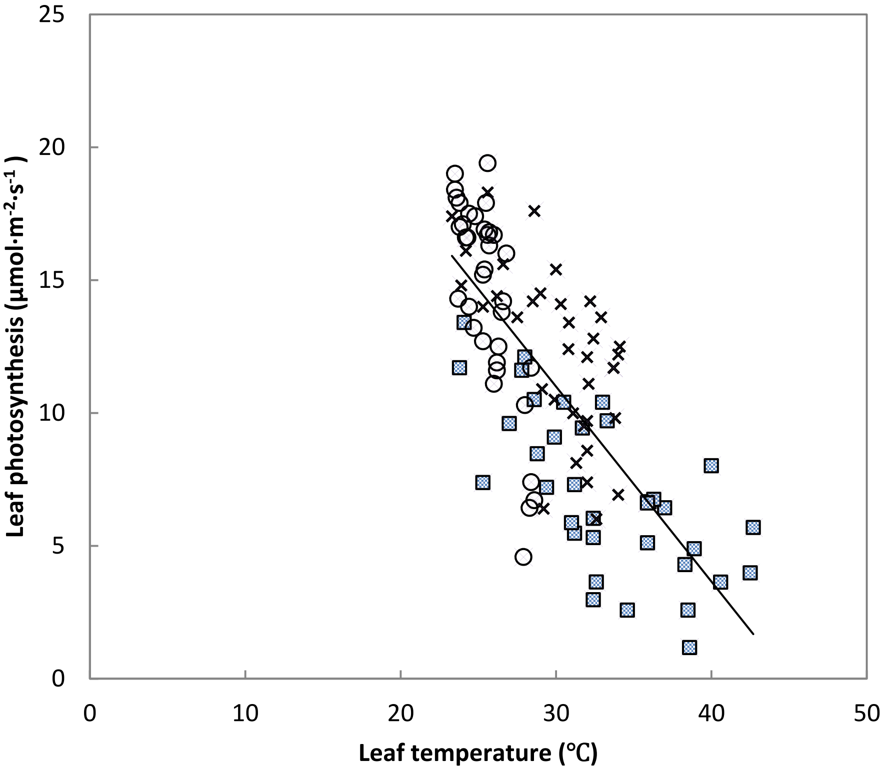

Figure 3.4 Effects of leaf temperature on net leaf photosynthesis in floricane-fruiting cv. '**Jeanne d'Orléans**' during the growing season (namely in the three sampling days, July19, Aug 6 and 18, respectively) under high tunnel (▨), Voen shelter (×**),** and open field (○). The equation for the overall linear regression line shown is y = -0.74x + 33.01, $R^2 = 0.57$.

3.4.3 Photosynthesis of floricane-fruiting red raspberry 'Jeanne d'Orléans' grown under various growing conditions: effect of canopy position

There were no significant differences in leaf PPFD between the upper and lower canopy layers under high tunnel and Voen shelter, whereas in open field the upper canopy leaf PPFD exceeded that in the lower canopy by approx. 30% (Figure 3.5C). Compared to open field, the leaf PPFD was on average reduced by 46% under protective coverings (Figure 3.5C). However, leaf photosynthesis was similar between both canopy layers under each growing condition (Figure 3.5A). This was in part due to the absence of a significant thermal stratification between the two reference canopy heights around which leaf gas exchange measurements were taken (Figure 3.5B), but also to the fact that the PPFD incident on target leaves from the outer portion of branch laterals was in all treatments near or above the photosynthetic light saturation point of 'Jeanne d'Orléans', which is around 700 μmol quanta m^{-2} s^{-1} (see Chapter 4).

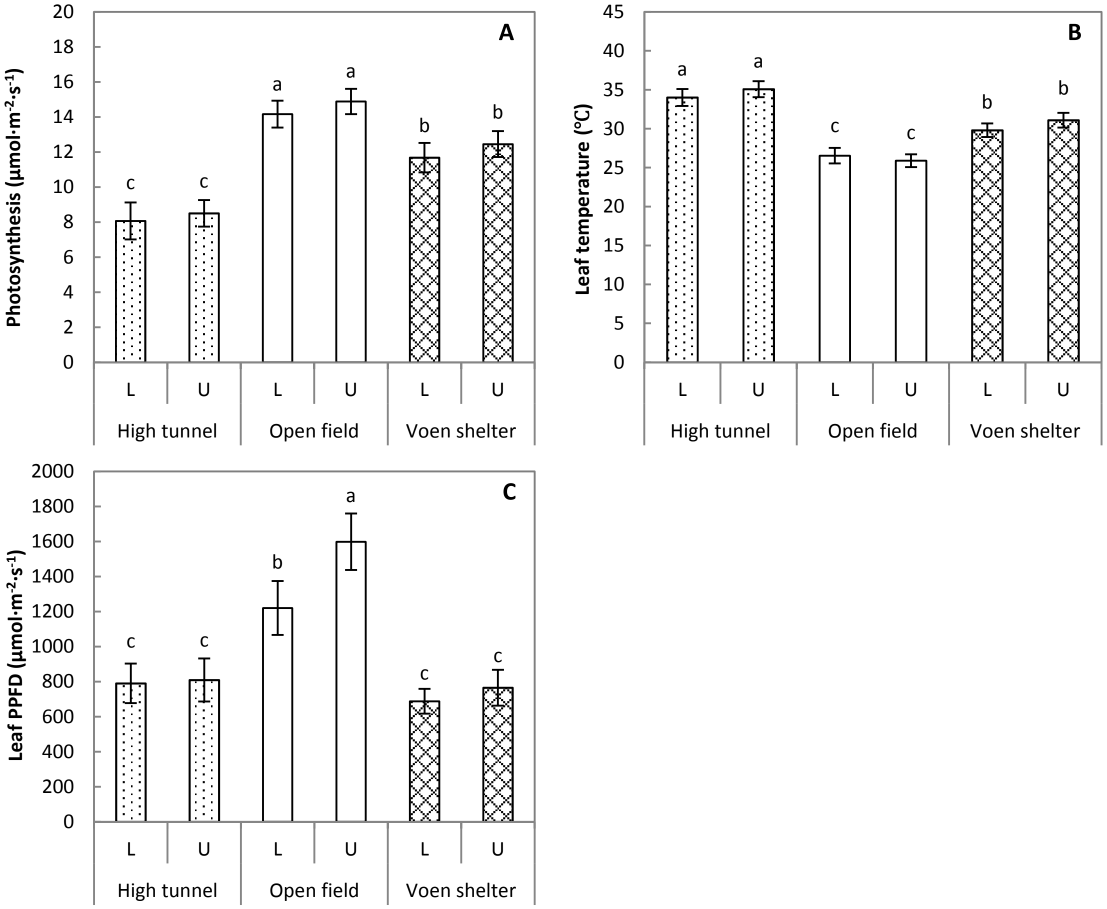

Figure 3.5 Effects of growing conditions (high tunnel, Voen shelter or open field) and leaf positions (U, upper canopy and L, lower canopy) on: A) leaf net photosynthesis, B) leaf temperature and C) leaf PPFD in floricane-fruiting cv. '**Jeanne d'Orléans**'. Mean value columns followed by different letters are significantly different according to Tukey's multiple range test at 5% level.

3.4.4 Photosynthesis of primocane-fruiting red raspberry ‘Polka’ grown under various growing conditions: effect of ground cover

In the lower canopy (Figure 3.6), reflective mulch significantly increased the reflected light (by up to 42%) under open field condition. No significant difference was measured under protected structures (Figure 3.6D). In terms of total leaf PPFD, there was no significant difference between ground cover types in any growing conditions (Figure 3.6C). Compared to open field, the total leaf PPFD at the lower canopy level was significantly reduced under protective covers, namely by 42% under high tunnel and 56.5% under Voen shelter (Figure 3.6C). As for the floricane-fruiting cv. ‘Jeanne d’Orléans’, leaf photosynthesis of primocane-fruiting cv. ‘Polka’ was inversely correlated to the leaf temperature among growing environments (Figures 3.6A, 3.6B and 3.9), with no significant difference detected between ground cover types (Figure 3.6A).

In the upper canopy, the leaf microclimate and leaf photosynthesis followed very similar patterns as observed in the lower canopy (Figure 3.7). With the exception of reflected PPFD under open field conditions, significant difference occurred in lower canopy due to ground cover but no difference was measured in upper canopy.

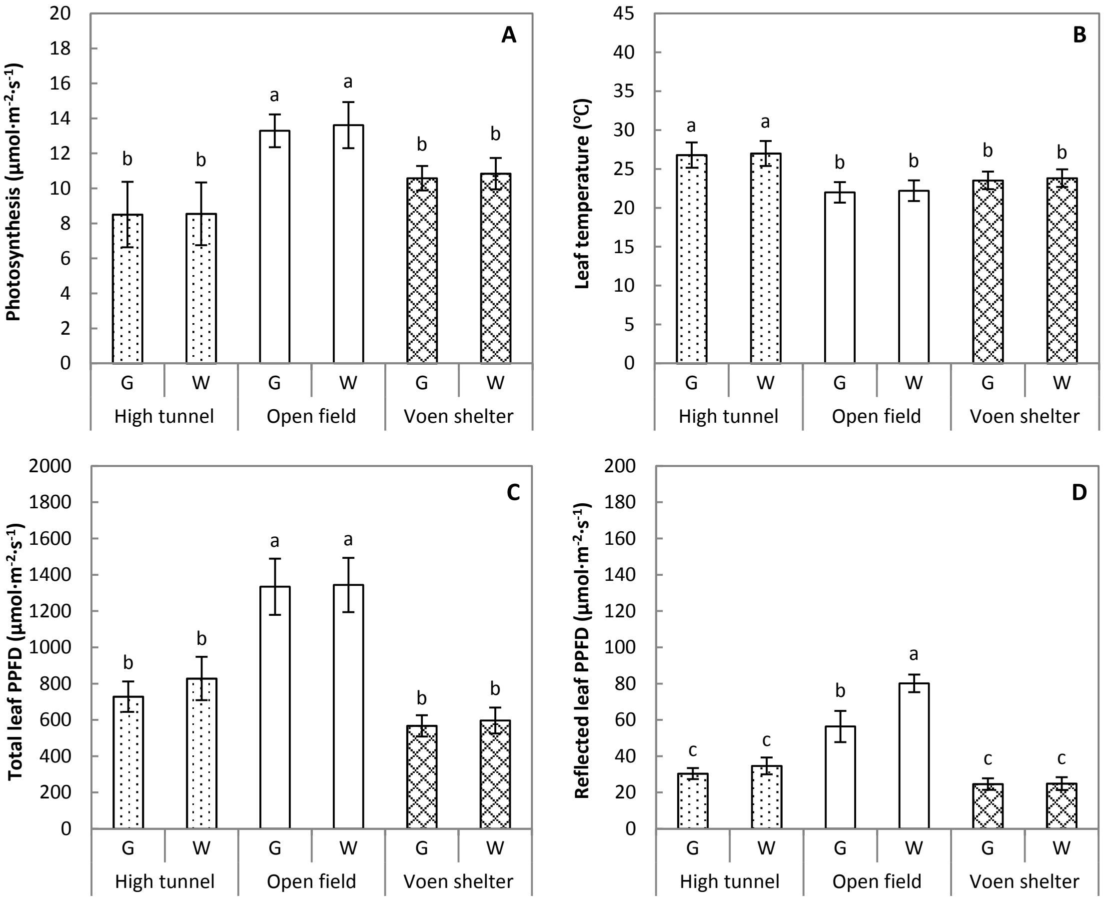

Figure 3.6 Effects of growing conditions (high tunnel, Voen shelter or open field) and reflective mulch (G, absence (natural ground vegetation) or W, presence) on: A) leaf photosynthesis, B) leaf temperature, C) total and D) reflected leaf PPFD in the **lower canopy** of primocane-fruiting cv. '**Polka**'. Mean value columns followed by different letters are significantly different according to Tukey's multiple range test at 5% level.

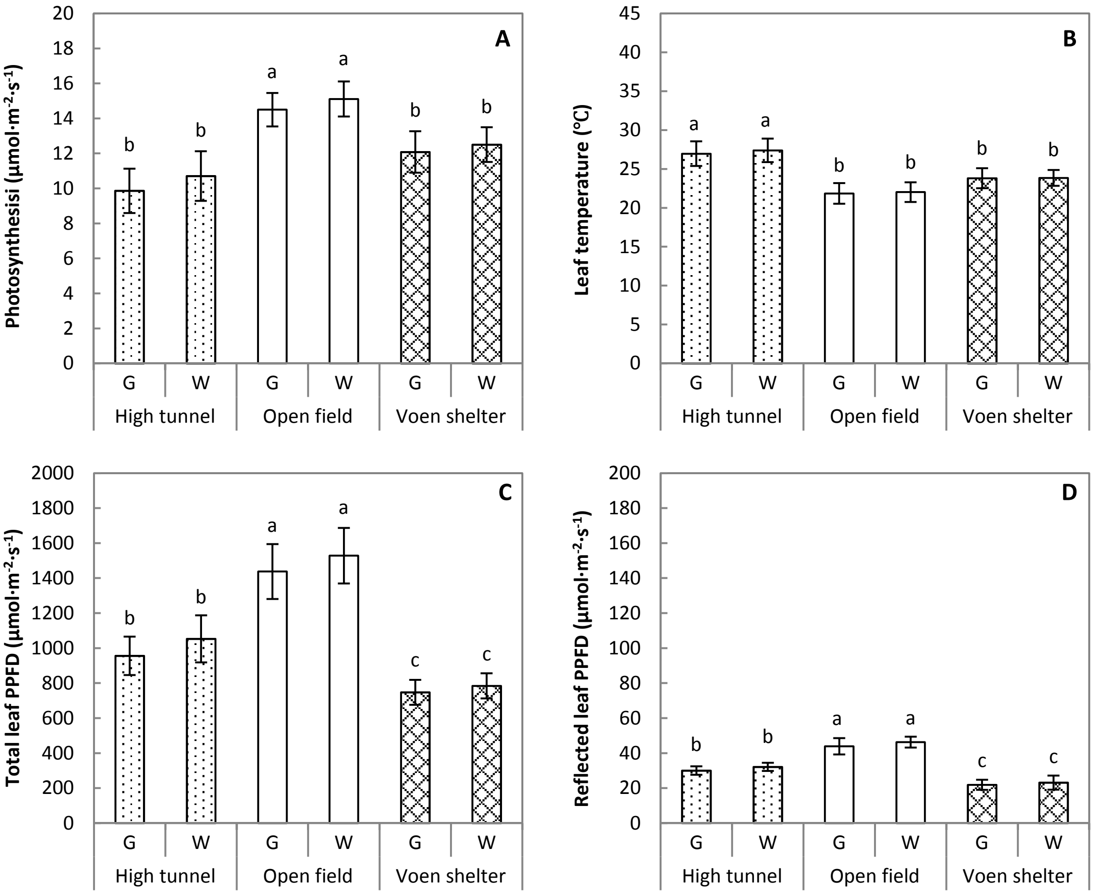

Figure 3.7 Effects of growing conditions (high tunnel, Voen shelter or open field) and reflective mulch (G, absence (natural ground vegetation) or W, presence) on: A) leaf photosynthesis, B) leaf temperature, C) total and D) reflected leaf PPFD in the **upper canopy** of primocane-fruiting cv. '**Polka**'. Mean value columns followed by different letters are significantly different according to Tukey's multiple range test at 5% level.

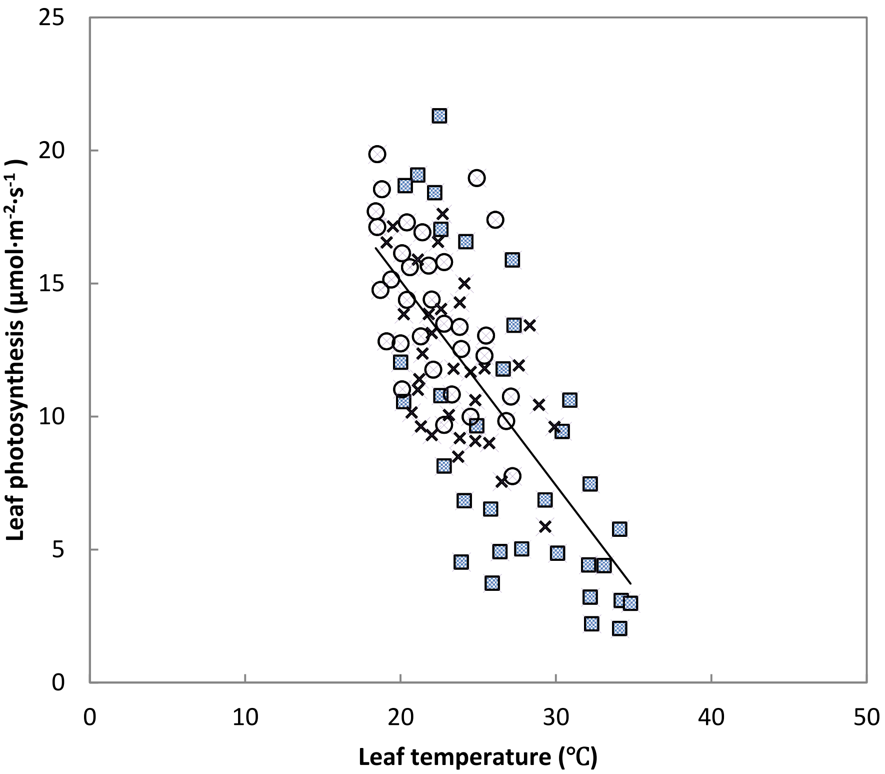

Figure 3.8 Effects of leaf temperature on net leaf photosynthesis in primocane-fruiting cv. '**Polka**' during the growing season under high tunnel (▨), Voen shelter (×**),** and open field (○). The equation for the overall linear regression line shown is $y = -0.77x + 30.48$, $R^2 = 0.50$.

3.4.5 Photosynthesis of primocane-fruiting red raspberry 'Polka' under various growing conditions: effect of canopy position

Contrary to what we observed previously with the floricane-fruiting cv. 'Jeanne d'Orléans' (see section 3.4.3), significant differences in leaf PPFD between the upper and lower canopy levels were present with the primocane-fruiting cv. 'Polka' grown under protected structures, whereas no significant difference was measured in open field (Figure 3.9C).

Under the both types of protected structures, the PPFD reaching the lower canopy was 24% lower than the upper canopy (Figure 3.9C). This lower light caused a concomitant decrease in photosynthesis of 20.4% and 17.3% under high tunnel and Voen shelter, respectively (Figure 3.9A). Compared to open field, the leaf PPFD was on average attenuated by 39.3% under high tunnel and by 52.6% under Voen shelter (Figure 3.9C). Because the leaf temperatures were the same in open field and under Voen shelter (Figure 3.9B), the aforementioned relative leaf PPFD attenuation under Voen shelter may have been significant to the corresponding 18.6% reduction of leaf photosynthesis between these two growing environments. For high tunnel, the significantly higher leaf temperature is likely responsible for the additional photosynthetic depression relative to open field (Figures 3.8 and 3.9B).

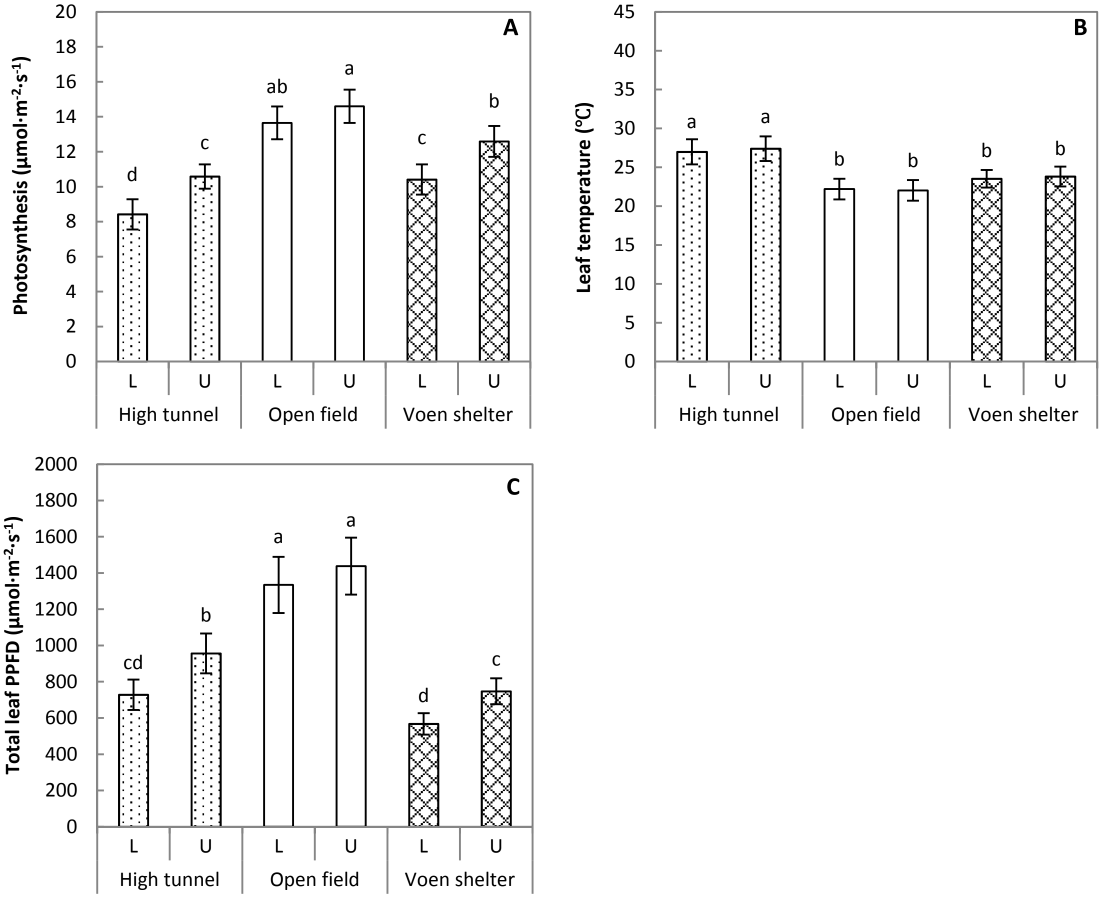

Figure 3.9 Effects of growing conditions (high tunnel, Voen shelter or open field) and leaf positions (U, upper canopy and L, lower canopy) on: A) leaf net photosynthesis, B) leaf temperature and C) leaf PPFD in primocane-fruiting cv. '**Polka**'. Mean value columns followed by different letters are significantly different according to Tukey's multiple range test at 5% level.

3.5 Discussion

3.5.1 Seasonal microclimate under protective coverings: influence of leaf temperature on photosynthesis rates

Daily temperatures are normally found to be higher under high tunnel than in open field. Although inside the tunnel the microclimate follows the natural fluctuations of the climate in outside, greater temperature differentials generally develop between high tunnel and open field around midday. This is indeed what we monitored in 2013 (Figure 3.1B), and such trend was also observed in the three previous years (Raymond-Bayne, 2012). Compared to high tunnel, the Voen shelter maintained a microclimate that was on average 2.4°C cooler over the whole growing season. But by mid-September the average Voen shelter air temperature was not different than in open field (Figure 3.1). Because the Voen shelter is an open system with good air ventilation, and also due to the lower radiation load of the mid-September/October months, air temperatures under this type of cover were well coupled with the temperatures outside. Thus the Voen shelter does not appear to be ideal to favor seasonal extension of primocane-fruiting red raspberries in autumn.

During the fruiting period of the floricane-fruiting cv. ‘Jeanne d’Orleans’ (early July to late August), the closed tunnel microclimate was excessively warm during midday for this type of cultivar production, so it was necessary to ventilate to protect the plants from overheating. However, it can be seen by comparing Figures 3.1 and 3.4 that despite the opening of tunnel ends and side doors the elevated air temperatures inside the tunnel reduced photosynthesis considerably. A similar phenomenon was also observed under high tunnel during the fruiting period of primocane-fruiting cv. ‘Polka’ (late Aug to early October), suggesting that the lower high tunnel air temperatures in late summer/early fall were still significantly above the temperature optimum for photosynthesis in this cultivar (Figure 3.8). This contrasts with the findings of Privé *et al.* (1997) and Carew *et al.* (2003) who reported higher photosynthetic rates under warm temperatures (25 to 30°C) in potted primocane-fruiting cv. ‘Autumn Bliss’. However, our results for floricane-fruiting cv. ‘Jeanne d'Orleans' are consistent with that of Fernandez and Pritts (1994) who reported decreases in photosynthesis in leaves of both types of canes (floricane and primocane) in potted floricane-fruiting raspberry cv. 'Titan' as temperature increased above 25°C.

Surprisingly, the photosynthetic reduction taking place under high tunnel was not reflected in the fruit yields. On the contrary, yields of cv. 'Polka' for the 2013 season were significantly greater under high tunnel than under Voen cover or in open field (1.6 and 3.4 times greater, respectively – see Chapter 2), showing the benefits of extending the fruit harvest period of cv. 'Polka' by partially or fully closing the tunnel openings to raise its temperature inside (~2°C on average above ambient, see Figure 3.1A). Carew *et al.* (2003) similarly found that higher temperatures (25 to 30°C) resulted in faster vegetative growth and advanced flowering in primocane-fruiting cv. 'Autumn Bliss'. In Chapters 4 and 5, the positive effect of warmer growing conditions on the overall leaf area of both fruiting types of red raspberry will be discussed in detail.

During summer the temperature-induced photosynthetic reduction of floricane-fruiting cv. 'Jeanne d'Orleans' under high tunnel was also not detrimental to its overall fruit yield since the latter was twice that obtained in open field (see Chapter 2). In this case, the warming effect of the high tunnel may have been more beneficial during the early growing season to stimulate vegetative growth and flower bud development (Bushway *et al.*, 2008), thereby favouring an earlier beginning of fruit harvest (Hanson *et al.*, 2011).

3.5.2 The influence of canopy positions on leaf photosynthesis under various growing conditions

Contrary to what we observed with the floricane-fruiting cv. 'Jeanne d'Orléans', significant differences in leaf PPFD between the upper and lower canopy levels were measured for primocane-fruiting cv. 'Polka' grown under protected structures, while no significant difference was measured in open field. Under protective coverings where plants were protected perfectly from natural forces like wind and rainfall, the row leaf area index of cv. ‘Polka’ grew significantly larger than that of cv. ‘Jeanne d’Orléans” (10.4 *vs.* 7.1, respectively), resulting in a considerable reduction in sunflecks and light transmissivity in the lower canopy. In contrast, under open field condition the plants underwent a strong thigmomorphogenetic response to wind pressure that resulted in reduced foliage size, as well as shortened cane height and fruiting lateral length, thus leading to a reduction of canopy size and thereby creating a more uniform PPFD distribution down the more exposed peripheral portion of the row crop canopy.

The differences in light environment between the upper and lower peripheral canopy regions were reflected in corresponding relative changes in photosynthesis between canopy positions. For instance, for primocane-fruiting cv. ‘Polka’, there was a 24 % reduction in leaf PPFD from the upper to the lower canopy under protected structures, resulting in a corresponding 19% reduction in photosynthesis. Whereas in open field condition, no significant difference in leaf PPFD or leaf photosynthesis was found between the upper and lower canopy (Figure 3.9A and 3.9C). This is consistent with the findings of Privé *et al.* (1997) who reported that under uniform open field conditions all healthy, fully expanded leaves along the primocane length of primocane-fruiting cv. ‘Autumn Bliss’ had a similar photosynthetic potential.

For the sparser canopy of cv. ‘Jeanne d’Orléans’, the lack of significant photosynthetic differentiation between the upper and lower peripheral canopy regions can be explained by the fact that the leaf PPFD measured around both canopy layers remained near or above the photosynthetic light saturation point estimated for this cultivar (~700 μmol quanta m^{-2} s^{-1}) (Figure 3.5).

3.5.3 The influence of reflective mulch on leaf photosynthesis under various growing conditions

During the fruiting period of ‘Jeanne d’Orléans’, i.e. mid-July to late August, reflective ground cover increased the reflected lower canopy leaf PPFD by 80.5% and 60.3% under open field and high tunnel respectively, which is appreciably more than the 28.7% increase observed under Voen shelter. This may be attributed to the greater proportion of direct-beam light under high tunnel and open field, which improves the reflection efficiency of the white mulch in comparison to under the doubled-layered woven polyester covering of the Voen shelter.

During the fruiting period of ‘Polka’, i.e. mid-August to early October, the larger canopy size combined with the greater reflectivity of the high tunnel and Voen shelter coverings at decreasing solar elevations likely caused the decrease of leaf PPFD to sub-saturating levels in the lower canopy under these growing environments. Under both protective coverings, more diffuse light and less direct-beam light caused relatively lower reflection from reflective mulch, thereby reducing the differences in reflected leaf PPFD between the absence and presence of mulch (Figure 3.6D). Comparatively in open field condition, the high proportion of direct-beam light led to an increase of 42% in reflected PPFD with the reflective ground cover.

Landry (2011) has reported that the Extenday™ reflective mulch installed under high tunnel allowed 5.4 and 3.6 times more light reflection at two peripheral canopy levels of primocane-fruiting cv. ‘Autumn Britten’, namely 0.5 and 1.0 meter above ground, respectively. This discrepancy between Landry (2011) and our results can be explained by the fact that we measured the reflected PPFD only during the fruiting period when the fully mature canopy had developed a larger leaf area and longer laterals, leading to more shading between hedgerows (alleyway) and thereby lowering the reflection efficiency of the reflective mulch. In comparison Landry (2011) made her measurements only during vegetative growth when the canopy was lower and sparser, which most likely allowed a significantly greater canopy light transmissivity.

In addition, it was observed that cv. ‘Polka’ generally has a growth habit with larger individual leaf compared to cv. ‘Autumn Britten’, which further affects the light environment in lower canopy.

For both fruiting types, total leaf PPFD was not significantly affected by adding reflective mulch under any growing condition. A similar result was obtained by Landry (2011) on primocane-fruiting cv. ‘Autumn Britten’ grown under high tunnel condition. Since the contribution of reflected PPFD to the total leaf PPFD was only about 10% for cv. ‘Jeanne d’Orléans’ and 5% for cv. ‘Polka’ on average during the fruiting period, it was evidently too low to significantly affect the total PPFD under each growing condition. Consequently, overall plant photosynthesis was likewise probably not significantly affected by the presence of reflective ground cover in all growing conditions. Similar conclusions were reached by Privé *et al.* (2008) for an apple tree culture. However, others have suggested that the presence of reflective mulch increased photosynthesis in other fruit row cultures such as by 25% for kiwi plants (Costa *et al.* 2003) and by 50% for cherry (Whiting *et al.*, 2008). With respect to red raspberry culture, our results confirm those of Landry (2011) and Raymond-Bayne (2012) who also did not find any photosynthetic difference between natural ground and the mulch treatment. Nevertheless, it is likely that the positive effect reflective mulch had on the fruit yield of both ‘Jeanne d’Orléans’ and ‘Polka’ cultivars (12% and 17% increases, respectively – see Chapter 2) came from the greater proportion of reflected light occurring particularly in the earlier stages of growth when the leaf canopies were less dense (and shorter in the case of cv. ‘Polka’). The added radiation may have benefited leaf and/or flower development, and in doing so may have marginally increased the overall canopy photosynthesis, thereby resulting in accumulated reserves for the longer term. Additionally, although the lower canopy layers of cv. ‘Polka’ do not contribute to fruit yield (see Chapter 5), their photosynthetic production during the reproductive stage may have a positive impact on sugar reserves stored in the roots (the proximal carbon sink) for subsequent vegetative growth (Williams, 1960; Williams and Martinson, 2003). For the biennial floricane-fruiting cv. ‘Jeanne d’Orléans’, improving the reflected PPFD in the first year might have positively affected plant growth and development in the following year.

3.6 Conclusion

In comparison to open field light conditions, available light above the raspberry canopy was attenuated by approx. 30% (Figure 4.6) by tunnel polyethylene films and by 35% under Voen coverings. It was therefore expected that the use of reflective ground cover could increase leaf photosynthesis rates by improving the light environment of the plant canopy under the protected structures, particularly in the lower canopy portion.

For reflective mulch effects, during the fruiting period of cv. ‘Jeanne d’Orléans’, reflective ground cover produced a significant positive effect on the PPFD reflected from the ground to the lower canopy under high tunnel and open field. No such effect was found under Voen shelter, which likely was due to the significantly greater proportion of diffuse light produced by the special Voen coverings. Comparatively for the primocane-fruiting cv. ‘Polka’, a significant positive effect of white mulch on reflected PPFD to the lower canopy was only observed in open field. In all cases, the use of reflective mulch had no significant effect on the total leaf PPFD under any growing conditions due to the fact that reflective mulch increased the total leaf PPFD in the fruiting canopy region by only about 10% for cv. ‘Jeanne d’Orléans’ and 5% for cv. ‘Polka’. The reflective mulch thus hardly benefits photosynthesis accumulation on the short time scale (as shown during the fruiting period), but potentially more so when cumulated over the whole growing season (i.e. when the added photosynthetic contribution of the developing vegetative/flowering canopy is taken into account).

Secondly, concerning canopy position effects, for cv. ‘Jeanne d’Orléans’ the leaf PPFD increased by 30% from lower to upper canopy in open field, but no differences were found under protected structures. In contrast, for cv. ‘Polka’ leaf PPFD increased by a similar 31.5% from lower to upper canopy under both protected structures, with concomitant photosynthetic increases of 25.7% and 20.9% under high tunnel and Voen shelter, respectively. This inter-varietal performance difference was likely due to the fact that cv. 'Polka' developed appreciably larger leaf canopies than cv. 'Jeanne d'Orléans', resulting in significantly different vertical light gradient patters between the two cultivars.

Thirdly, with respect to growing condition effects, for cv. 'Jeanne d'Orléans', the leaf PPFD was attenuated by approximately 46% under the both type of protective coverings compared to open field. Corresponding leaf photosynthesis was on average reduced by 43% under high tunnel and by 17% under Voen shelter. Cultivar 'Polka' plants shared similar growing condition effects on leaf PPFD and photosynthesis. The consistently lower leaf photosynthesis rates observed under high tunnel were most likely caused by the significantly higher air temperature under this growth environment. Further analysis of pooled leaf photosynthesis vs. temperature data under the three different growing conditions confirmed that the net leaf photosynthetic rates of both cv. 'Jeanne d'Orléans' and 'Polka' fell steeply when leaf temperatures exceeded 25°C and 20°C, respectively.

In summary, compared with open field-grown plants, higher-yielding cultures were obtained under protected structures (see Chapter 2), yet with consistently lower photosynthesis per unit leaf area. To better explain this inverse relationship and reconcile fruit yields with estimated photosynthetic production, next we set up to scale individual leaf photosynthesis measurements up to the total leaf area of the canopy for the two most contrasting growing conditions: high tunnel *vs.* open field (see Chapters 4 and 5).

3.7 Acknowledgements

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Chapter 4: Light, plant growth and fruit yield vertical distribution and canopy photosynthesis modeling of floricane-fruiting red raspberry grown under high tunnel *vs.* open field

4.1 Abstract

For the floricane-fruiting red raspberry ‘Jeanne d’Orleans’, despite consistently lower leaf photosynthesis (Pn) rates, fruit yields during the previous 2013 cropping year were significantly higher under high tunnel than in open field (see Chapter 3). To better address the question of why tunnel-grown raspberry plants gave the highest fruit yield but the lower leaf Pn, for the 2014 field season we set to estimate photosynthesis at the whole-plant level by integrating leaf-level Pn rates to the entire canopy leaf area. To do so, the plant canopy was divided into four layers and the average photosynthetic light response of leaves in each layer was applied across its distribution of photosynthetic photon flux density (PPFD) then summed over the layer’s leaf area. The relationship between canopy photosynthesis and plant biomass accumulation and fruit yield of ‘Jeanne d’Orleans’ cultivated under high tunnel compared to. open field was then evaluated.

Plants grown under high tunnel produced 1.9 times more leaf area (1.6 times more dry biomass), 1.5 times more overall canopy photosynthesis and 3.0 times more fruit yield than plants grown in the open field. Under high tunnel, approximately 85% of the productivity mentioned above was distributed in the upper three layers, while in open field the vertical distribution of dry biomass, leaf area and canopy Pn showed a ‘bell-shaped’ curve, peaking at mid-canopy height. In the open field, the four canopy layers contributed equally to fruit yield.

Seasonal changes in dry biomass, leaf area and canopy Pn were measured or modeled five times repeatedly during the growing season. Under high tunnel, dry weight and leaf area increased linearly until fruit harvest then curvilinearly at a decreasing rate afterwards. Comparatively, canopy Pn ceased to increase upon reaching the peak harvest period. In open field, plants ceased growth concurrently to canopy Pn reaching its peak at the beginning of the harvest, after which a slight decrease in canopy Pn took place until the end of the harvest.

Canopy Pn was positively correlated to dry biomass, leaf area and fruit yield under both growing conditions. Under high tunnel, crop fruit yield per unit canopy photosynthesis or accumulated biomass was notably higher possibly due to a combination of warmer growth temperatures in the early vegetative and flowering stages, as well as the absence of thigmomorphogenetic stress.

4.2 Introduction

In general, it is agreed that marketable fruit yield of floricane-fruiting cv. 'Jeanne d'Orleans' grown under high tunnel is significantly higher than in open field (Xu *et al.*, 2013). However, when we compared the net photosynthesis rates per unit leaf area of plants grown under high tunnel to that of plants cultivated in open field, we observed that photosynthesis was consistently higher in open field. To better understand the paradox that lower photosynthetic rates under high tunnel culminated in greater fruit yields (see Chapter 3), we wished to evaluate if scaling up the leaf-level photosynthesis measurements to the whole raspberry canopy would reveal a direct relationship between overall photosynthetic production and fruit harvest.

Leaf area has a significant effect on solar radiation transmission and consequently affects much photosynthesis and plant productivity (Goudriaan and Van Laar, 1994). Many researchers have indicated the importance of leaf area in assessing crop growth rate, fruit yield potential and light use efficiency (Williams and Martinson, 2003). It is also recognized that leaf area measurements are necessary to evaluate the effectiveness of trellising systems, pruning and training treatments, as well as to model canopy photosynthetic productivity (Gutierrez and Lavin, 2000). In raspberry cultivation, a hedgerow type trellising system is typically used for supporting the plants. Under this type of training, leaves in the inner (central) canopy region are significantly shaded by those located at the crown periphery, although around midday the canopy light gradients are expected to be predominantly vertical. To reliably model canopy photosynthesis under such complex horizontal and vertical canopy light gradients, it is therefore essential to determine the spatial distribution of leaf area.

At the leaf level, the photosynthetic light response is best described as non-rectangular hyperbola (Thornley, 1998). A typical photosynthetic light response (A-Q) curve is usually constructed going from higher to lower incident PPFD values in a range between 2000 and 0 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Thus parameterized, the non-rectangular hyperbola model can then be used to estimate net photosynthesis at any given incident PPFD between full sunlight and darkness. It is known that A-Q curves are sensitive to environmental conditions, such as light intensity and direction (Ögren, 1993). Moreover, age-related intrinsic factors such as leaf mass per area (LMA), leaf nitrogen (N) content also affect the parameters of the A-Q curve (Lachapelle and Shipley, 2012). Therefore, to properly integrate crop canopy photosynthesis model it is important to account for the A-Q curve parameter variation both in space (various canopy layers) and in time (repeated determinations throughout the growing season). Even on a diurnal basis, environmental factors such as air temperature and relative humidity will modulate some of the parameters of the photosynthetic light response. Hence, to obtain a more faithful reproduction of the diurnal variation of canopy photosynthetic capacity, it was recommended to monitor the PPFD distribution and A-Q curve variation repeatedly throughout the day.

The objectives of this study were: 1) to determine the vertical distribution of PPFD, leaf area and dry biomass under tunnel- and field-grown floricane-fruiting red raspberry; 2) to generate A-Q curves to parameterize a leaf photosynthesis model and scale it up to canopy level (four canopy layers) over the entire growing season; 3) to describe the relationship between PPFD distribution, plant growth or fruit yield and canopy photosynthetic accumulation.

4.3 Materials and methods

4.3.1 Experimental site

The experiment was carried out under high tunnels and open field at 'Les Fraises de Ile d'Orleans Inc.' (71°01′W, 46°52′N), located in Québec, Canada. The tunnel size was 8.5 m wide, 4.5 m high and 70.0 m long with polyethylene coverings from Industries Harnois (http://www.harnois.com). Air temperature, relative humidity and ventilation under the tunnel were passively controlled by closing or opening the side walls and end doors.

4.3.2 Plant material

Floricane-fruiting red raspberry cv. ‘Jeanne d’Orleans’ was first introduced by Agriculture and Agri-Food Canada, and Horticulture Research and Development Center (Khanizadeh *et al.*, 2010). Two year old potted plants cultivated in a previous experiment (see Chapter 3) were chosen for the present study. In spring of 2014, plants were thinned to keep two uniform floricanes per pot. Fruits were harvested from mid-July to late August. After harvest, the floricanes senesced and then were removed at pot level, the primocanes were kept intact with required pruning to overwinter and produce fruits over the next year. A hedgerow type trellising system was used to support the canes.

Crop pest, pathogens and weeds were controlled according to Canadian standard organic management practices (CGSB and SCC, 2006). Plants were irrigated by using a drip irrigation system and fertilized by automatically incorporating soluble fertilizers in the irrigation water. Higher electrical conductivity (1.2 mS/cm) and nitrogen (N) contents (3.0 kg/ha per week) were provided till the beginning of the flowering and then lowered thereafter to EC (1.0 mS/cm) and N (1.5 kg/ha per week) was supplied according to local recommendations (Raymond-Bayne, 2012).

4.3.3 Experimental design

From the fruit yield results of the previous study conducted in 2013 (see Chapter 2, Table 2.5, 2.3), the best cropping system for ‘Jeanne d’Orléans’, which consisted in growing plants in high tunnel with a ground reflective mulch and in allowing pruning new primocane shoots, was adopted for the 2014 experiment as a comparative to a corresponding open field cropping system. The canopy was separated into 4 horizontal layers (Figure 4.1) (corresponding to different plant heights whether under high tunnel or in open field) to determine the contribution of each layer to growth, marketable fruit yield and canopy photosynthetic accumulation.

The experiment was designed as a two-stage nested ANOVA design with 2 growing conditions (high tunnel and open field) as the main plots and 4 equal canopy layers (layer 1, 2, 3 and 4, in sequence from uppermost to lowermost) as sub-plots, resulting in 8 treatments. The treatments were replicated 4 times. There were buffer zones within a row between adjacent treatments.

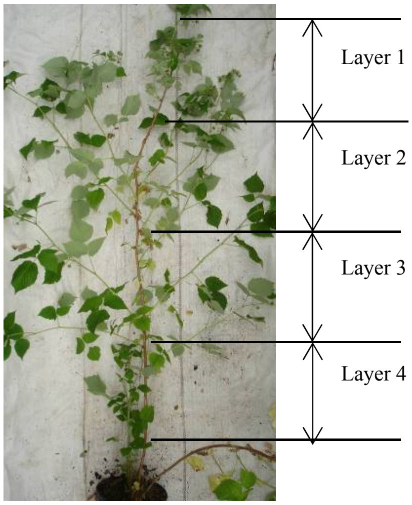

Figure 4.1 Four canopy layers in terms of cane height of floricane-fruiting red raspberry ‘Jeanne d’Orléans’

4.3.4 Data collected

4.3.4.1 Microclimate under high tunnel and open field

Climate data were collected at canopy height during the whole growing season in 2014 that is from June 1 to the end of harvest in late August. Air temperatures, relative humidity as well as root zone temperature (at 10 cm below substrate level) were monitored by HOBO data loggers (U12-013, Onset Corp., Bourne, MA, USA) under high tunnel and open field. Additionally, a standard meteorological station (U30, Onset Corp., Bourne, MA, USA) was installed at ‘Les Fraises de Ile d’Orleans Inc.’ in the open field to monitor the air temperature, relative humidity, incident PPFD and horizontal wind speed and direction of the whole research site all year round.

4.3.4.2 Fruit yield and plant growth

The harvest period started on mid-July and finished on late-August 2014. Fruits in each sample plot were harvested three times a week and separated as marketable *vs.* non-marketable, weighted, then counted. Fruits affected by disease, insect, mechanical injury, fruit too small, distorted, crumbling, etc. were automatically downgraded. The fruit size (average fruit weight) was determined for marketable fruits.

Plant dry biomass and leaf area in each of four canopy layers were determined destructively, repeatedly in five blocking times during the growing season (June 18, 30, July 13, 27 and August 14). Leaf area was measured using a LI-3100C Leaf Area Meter (Li-Cor Inc., Lincoln, NE, USA). Leaf area index was estimated by one-sided leaf area per unit ground surface area. Other plant parts such as stem and laterals were also sampled, oven dried at 65°C and weighed separately from the leaves. The plant leaf area and dry biomass cumulative growth curves were then determined from the five repeated sampling times during the growing season.

4.3.4.3 Determination of PPFD distribution

The incident *vs.* reflected horizontal PPFD distributions at the mid-point of each of the four canopy layers were measured every 1.5 hours from 8:30 am to 4:30 pm on clear sunny days using a SunScan canopy analysis system (Delta-T Devices Ltd., Cambridge, UK). To measure incident PPFD, the SunScan ceptometer was oriented skywards, whereas to measure the reflected PPFD from the ground mulch the ceptometer's orientation was reversed. The reference incoming PPFD was measured 0.2 m above the plant canopy. These diurnal PPFD measurements were repeated in five blocking times during the growing season of cv. 'Jeanne d'Orléans' (T1, June 20-23; T2, July 2-5; T3, July 19-22; T4, August 1-4; T5, August 10-13).

4.3.4.4 Photosynthetic light-response curves measurements

Concurrently to the horizontal PPFD distribution measurements, photosynthetic light response curves were made on three replicate fully expanded (i.e. greater than 9 cm^2) healthy sunlit leaves from each of the four canopy layers under high tunnel and open field. Net photosynthesis measurements were made using a portable gas exchange system (LI-6400XT, Li-Cor Inc. Lincoln, NE, USA) equipped with a 6 cm^2 leaf chamber with integrated red-blue light-emitting diode (LED) light source (LI-6400-02B, Li-Cor). The leaf chamber CO_2 and H_2O mole fractions were maintained fixed to ambient levels throughout the A-Q curve, and the leaf temperature was controlled to the average canopy layer. Leaf temperature was previously determined from infrared thermometer (AR330, Starmeter Instruments Co., Canton, Guangzhou, China) measurements made on three sunlit and three shaded leaves. Leaves were first measured under their current incident PPFD level before initiating the A-Q curve, ramping PPFD levels from 1800 µmol quanta m^{-2} s^{-1} down to zero light. Like the ceptometer horizontal PPFD distribution measurements, the A-Q curve measurements were repeated on the same treatments (using a different sub-plot block) every 1.5 hours from 8:30 am to 4:30 pm, and were repeated in five blocking times. Environmental conditions during these measurements ranged from 16 to 39°C (leaf temperature), 0.8 to 2.7 kPa (VPD), 381 to 417 µmol mol^{-1} (CO_2) and 0 to 2200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (PPFD).

4.3.5 Computation and statistical analysis

Photosynthetic light response curve measurements were fitted to the non-rectangular hyperbola model of Thornley (1998):

$$P_n = -R_d + \frac{\alpha \cdot PPFD + P_{max} - \sqrt{(\alpha \cdot PPFD + P_{max})^2 - 4\theta \cdot \alpha \cdot PPFD \cdot P_{max}}}{2\theta} \quad (1)$$

where R_d is dark respiration, θ is the scaling constant for curvature (which determines the sharpness of the inflection of the A-Q curve), α is light-limited quantum efficiency (i.e. the initial slope of the light response curve), P_{max} is the maximum (that is light saturated) gross photosynthetic rate. Equation 1 was fitted to the A-Q curve data using the non-linear fitting procedure NLIN in SAS (SAS Institute Inc. 9.3, Cary, NC). Resulting A-Q curve parameters from the triplicate measurements of each canopy layer were averaged to give a representative mean A-Q curve for each layer at each sampling time and date. To scale up the leaf level P_n measurements in each canopy layer to the whole-layer P_n sum, the ceptometer incident PPFD (2-sided, top + underside of the leaf) histogram (64 individual 2-sided measurements across the whole canopy layer width) was used as the independent driving variable for Eqn 1 (using the canopy layer's averaged A-Q curve parameters mentioned above) assuming an equal distribution of leaf area across the ceptometer length.

Analysis of variance of fruit yield, leaf area, dry weight, PPFD distribution and modeled canopy photosynthesis was completed using the Glimmix procedure of SAS. Multiple comparisons of means were adjusted by Tukey t-test at the $P = 0.05$ probability level. The normality of a model was tested with univariate procedure of SAS.

4.4 Results

4.4.1 Microclimate under high tunnel and open field (2014)

During the growing season (from late May to late August), the daytime air temperature under high tunnel was on average 3.8°C higher than in open field, with maximal differences reaching up to 7.2°C (Figure 4.2). The fruiting period of 'Jeanne d'Orléans' was from early July to late August, with daily temperatures averaging 25.4 and 22.2°C under high tunnel and open field, respectively, during that period (Figure 4.2).

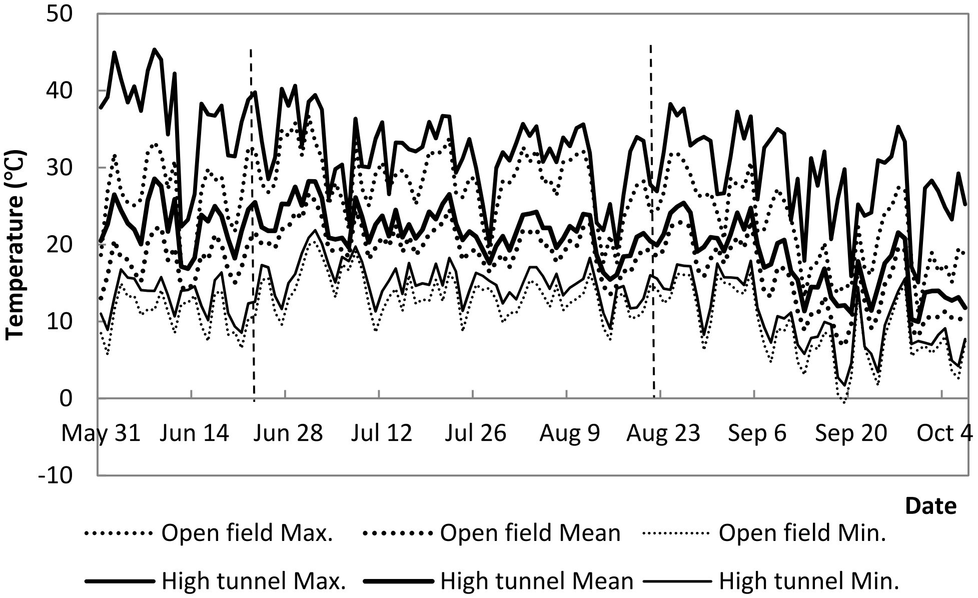

Figure 4.2 The daily air temperature under high tunnel and open field during the growing season of floricane-fruiting cv. 'Jeanne d'Orléans' in 2014 in Québec, Canada. Time range between the two dotted lines represents reproductive period of cv. 'Jeanne d'Orléans'.

4.4.2 Marketable fruit yield in different canopy layers

In order to determine the contribution of different plant canopy layers, whole canopy was separated into 4 zones vertically according to plant height for fruits harvesting. Growing conditions (high tunnel and open field) and layers nested under their growing condition significantly affected marketable fruit yield and fruit number of floricane-fruiting cv. 'Jeanne d'Orléans' (Table 4.1).

Plants grown under high tunnel displayed 3.0 times more marketable fruit yield and 3.7 times more fruit number than in open field. Under high tunnel, fruit yield decreased significantly from uppermost (L1) to lowermost canopy layer (L4). Layer 1 produced 37.8% of the whole-canopy fruit yield. The two middle layers, L2 and L3 produced equal fruit yields, accounting for 24.4% for each. Only 13.4% of the fruit yield was obtained in L4. Comparatively in open field, the fruit yield was equally distributed throughout the four canopy layers (Figure 4.3).

Table 4.1 ANOVA of marketable fruit yield, plant growth and modeled canopy photosynthesis during the fruiting period of floricane-fruiting cv. 'Jeanne d'Orléans'

Effect	**Fruit yield**	**Fruit number**	**Dry weight**	**Leaf area**	**Canopy Pn**
Protected cultivation (PC)	**<.0001**	**<.0001**	**<.0001**	**<.0001**	**<.0001**
Layer (PC)	**<.0001**	**<.0001**	**0.0015**	**0.0001**	**0.0004**

Layer (PC), canopy layers nested under their corresponding growing environments namely high tunnel or open field. *P*-values < 0.05 indicate significant differences.

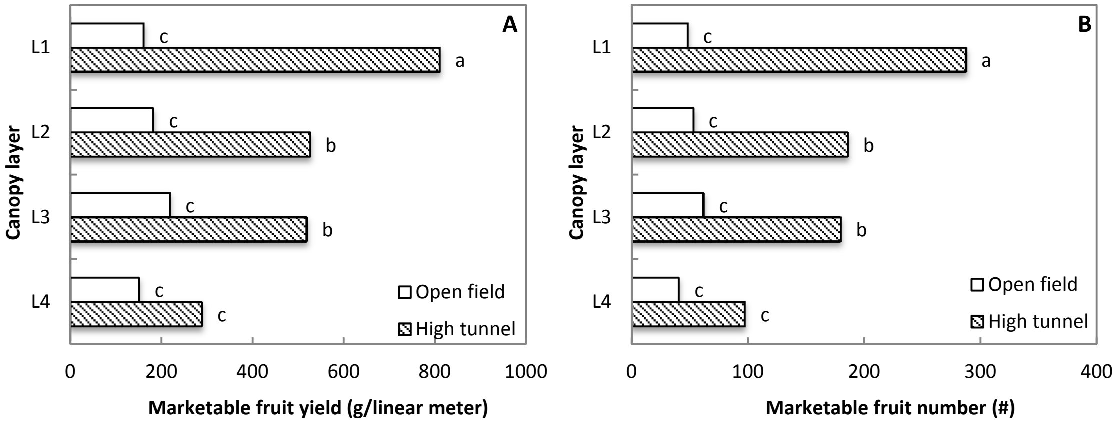

Figure 4.3 Influence of growing conditions (high tunnel and open field) and canopy layers (L1, L2, L3 and L4, from upper to lower) on A) marketable fruit yield and B) fruit number of floricane-fruiting cv. 'Jeanne d'Orléans'. Horizontal bars followed by different letters are significantly different according to Tukey's multiple range test at 5% level.

4.4.3 Dry biomass accumulation in different canopy layers and whole-canopy

Growing conditions (high tunnel and open field) and layers nested in their growing condition significantly affected canopy layer dry weight in the fruiting period (e.g. July 27) (Table 4.1).

During the fruiting period, the canopy layers, L1, L2, L3 and L4, accumulated 32.2%, 27.5%, 25.6% and 14.7% of the whole-canopy dry biomass, respectively. In comparison in open field, the top and bottom layers (L1 and L4) produced less biomass (18.9% of whole-canopy dry biomass each) than the two middle layers (31.2% of whole-canopy dry biomass each) (Figure 4.4A).

Plants grown under high tunnel accumulated approximately 1.6 times more dry weight than those in open field during the fruiting period: beginning of harvest (July 13), harvest peak (July 27) and end of harvest (August 14). ‘Jeanne d’Orléans’ plants grown in open field ceased growth at the beginning of harvest, approximately one month earlier than those cultivated under high tunnel (Figure 4.4B).

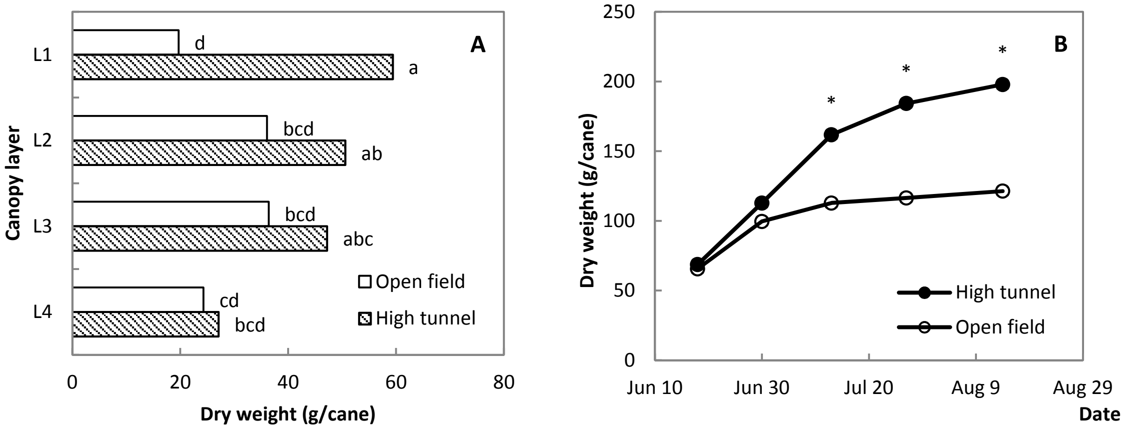

Figure 4.4 Influence of growing conditions (high tunnel or open field) on A) the dry biomass accumulated during the fruiting period in each of the four canopy layers (L1, L2, L3 and L4 from upper to lower layers) and B) the cumulative whole-canopy dry biomass increment over the growing season of floricane-fruiting cv. ‘Jeanne d’Orléans’. In A), horizontal bars followed by different letters are significantly different according to Tukey’s multiple range test at 5% level, while in B) significant differences in dry weight between high tunnel and open field are indicated by a * sign.

4.4.4 Leaf area accumulation in different canopy layers and whole-canopy

Growing conditions (high tunnel and open field) and layers nested under their growing condition significantly influenced layered-canopy leaf area. in the fruiting period (e.g. July 27) (Table 4.1).

Under high tunnel, the leaf area of the three upper layers (L1, L2 and L3) was uniformly distributed and was on average 2.2 times greater than in the bottom layer (L4) where only 12.9% of leaf area was produced. In open field, the leaf area peaked in the middle two layers, which contributed approximately 32% of the whole-canopy leaf area each, whereas L1 and L4 each contributed only 18.0% of the total leaf area (Figure 4.5A).

Looking at the cumulative whole-canopy leaf area growth over the entire growing season, plants grown under high tunnel cumulated 1.9 times more leaf area than in open field. As indicated above, 'Jeanne d'Orléans' plants ceased leaf growth at the beginning of harvest in open field; in high tunnel the whole-canopy leaf area kept increasing throughout the whole growing season, but the rate of increase was significantly less after the beginning of harvest (July 13) (Figure 4.5B).

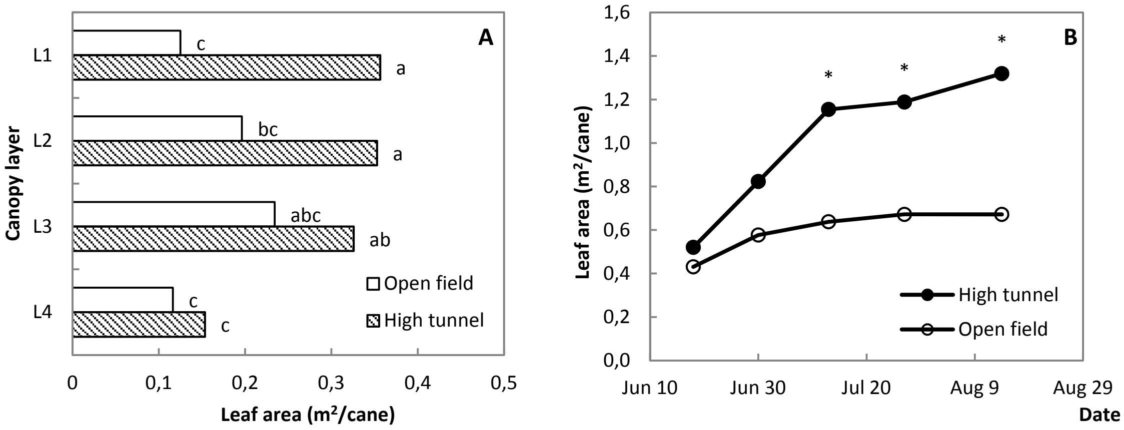

Figure 4.5 Influence of growing conditions (high tunnel or open field) on A) the leaf area accumulated during the fruiting period in each of the four canopy layers (L1, L2, L3 and L4 from upper to lower layers) and B) the cumulative whole-canopy leaf area growth over the growing season of floricane-fruiting cv. 'Jeanne d'Orléans'. In A), horizontal bars followed by different letters are significantly different according to Tukey's multiple range test at 5% level, while in B) significant differences in canopy leaf area between high tunnel and open field are indicated by a * sign.

4.4.5 Light vertical distribution throughout different canopy layers

The average incident PPFD above and inside the canopy was significantly lower under high tunnel than in open field (Figure 4.6). Around midday (11:00 am to 1:00 pm) in both high tunnel and open field conditions, the PPFD decreased gradually from the uppermost to the lowermost layer, while earlier in the morning or later in the afternoon the PPFD distribution was more uniform throughout the four-layered canopy (Figure 4.6).

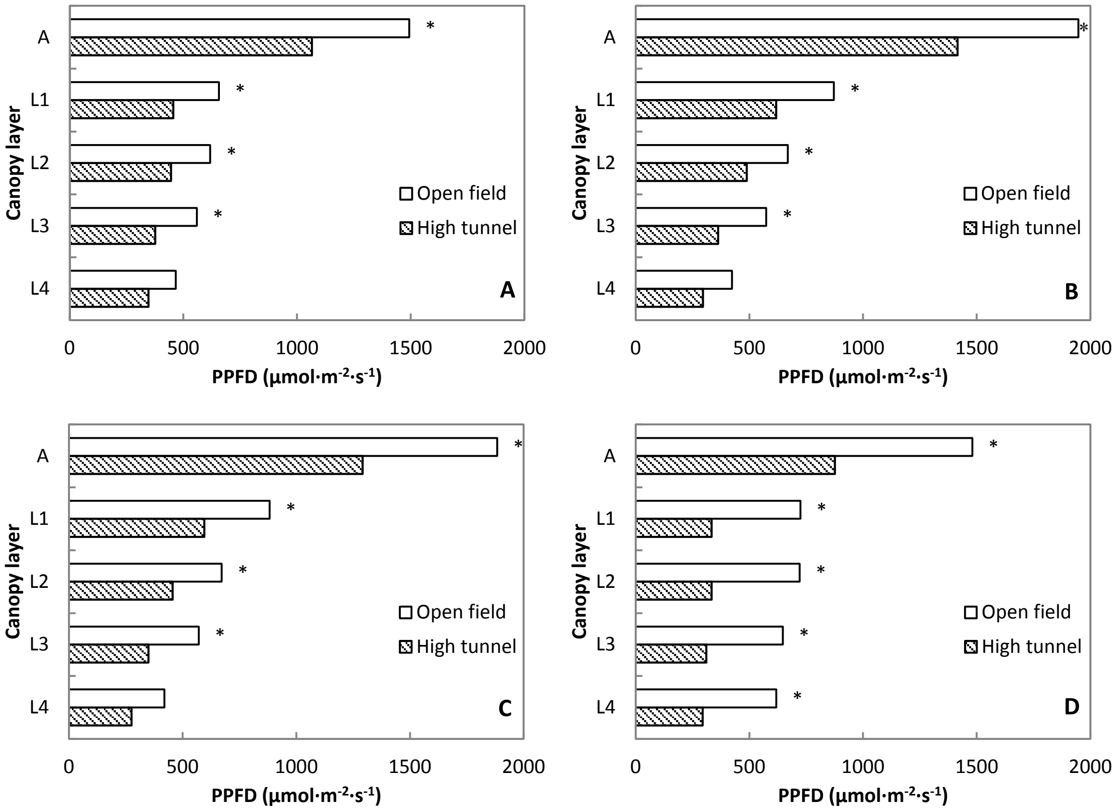

Figure 4.6 Diurnal variations in the vertical distribution of the average incident PPFD among canopy layers (A: above canopy, L1: uppermost, L2: middle, L3: middle and L4: lowermost layer) of floricane-fruiting cv. ‘Jeanne d’Orléans’ grown under high tunnel and open field on a typical sunny day (July 20 2014): A) 9:00 am, B) 11:00 am, C) 1:00 pm, D) 3:00 pm. Significant difference ($P < 0.05$) in average PPFD between high tunnel and open field are indicated by a * sign.

When looking at the horizontal PPFD distribution across the various canopy layers, PPFD readings on the sunlit side of the canopy (i.e. the east side of the plant canopy in the morning, changing to the west side in the afternoon) were always higher in open field than under high tunnel, whereas on the shaded side the differences were less marked (Appendix, Figure A.4.1).

Correspondingly, photosynthetic light response curve measurements taken concurrently on the same experimental unit demonstrated that the higher available light in open field resulted in higher photosynthetic capacity (P_{max}) (see Appendix, Figure A.4.2).

4.4.6 Photosynthetic accumulation in canopy layers and whole-canopy

Growing conditions (high tunnel and open field) and layers nested under their growing condition significantly affected canopy layer photosynthetic carbon fixation during the fruiting period (Table 4.1).

Indeed, plants grown under high tunnel cumulated 2.8, 1.8 and 1.7 times more integrated canopy layer photosynthesis in the three upper canopy layers (L1, L2 and L3, respectively) than plants cultivated in open field (Figure 4.7A). As for bottom layer (L4), similar cumulative photosynthesis occurred between high tunnel and open field. Under high tunnel, cumulative photosynthesis decreased vertically among the four canopy layers, which accounted for 33.2%, 28.3%, 25.8% and 12.6% of the total whole-canopy photosynthesis, respectively. In comparison in open field, L1 and L4 displayed a similar canopy layer photosynthesis, accounting for 21.7% of the total whole-canopy photosynthesis each, markedly lower than the 28.3% measured in both middle layers (Figure 4.7A). Adding the photosynthetic gains of the four layers together for each of the five blocking times of the whole growing season indicated that plants growing under high tunnel cumulated approximately 1.5 times more whole-canopy photosynthesis than in open field, with most of the difference taking place during the fruiting period (Figure 4.7B).

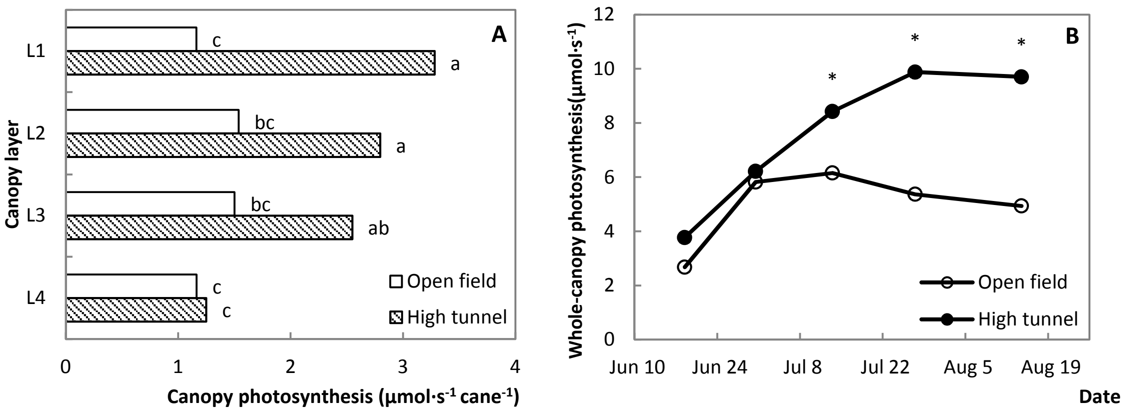

Figure 4.7 Influence of growing conditions (high tunnel or open field) on A) the net photosynthetic gain cumulated during the fruiting period in each of the four canopy layers (L1, L2, L3 and L4 from upper to lower layers) and B) the whole-canopy net photosynthetic gain over the whole growing season of floricane-fruiting cv. 'Jeanne d'Orléans'. In A), horizontal bars followed by different letters are significantly different according to Tukey's multiple range test at 5% level, while in B) significant differences in whole-canopy photosynthesis between high tunnel and open field are indicated by a * sign.

4.5 Discussion

4.5.1 The effects of high tunnel coverings on microclimate

The agricultural region of Québec is at similar latitude as that of Ontario, but it nevertheless experiences a cooler growing season climate. Thus it may be profitable to use high tunnels in Québec to increase the growing season air temperature and protect plants from weather damages, thereby potentially improve fruit yield and quality of floricane-fruiting red raspberry 'Jeanne d'Orléans'.

Daily temperature is usually higher under high tunnel than in open field. Although inside the tunnel the microclimate follows the natural fluctuations of the climate in outside, greater temperature differentials generally develop between high tunnel and open field around midday. This is indeed what we monitored in 2014, and such trend was also observed in the three previous years (Raymond-Bayne, 2012). During the fruiting period, normally from mid-July to late August, the closed tunnel microclimate was excessively warm for floricane-fruiting cultivar production, so it was necessary to open the tunnel ends and side doors to protect the plants from overheating.

Compared with open field, during the fruiting period, the PPFD above the canopy was reduced by 30% under high tunnel due to the presence of polyethylene films. This caused a corresponding decrease in light within each canopy layer under high tunnel. Under both growing conditions, when the sun was directly above the canopy around noon (11:00 am to 1:00 pm), the sunlight beam penetrated the hedgerow plant canopy predominantly from the top layer, so less light could reach the lower canopy layers, thereby establishing a steeper vertical PPFD gradient inside the canopy (Figure 4.6). Whereas in the morning (e.g. 9:00 am) or afternoon (e.g. 3:00 pm), the sun beam was obliquely incident to the plant canopy and thus penetrated the hedgerows from their outer periphery thereby resulting in a more uniform vertical PPFD distribution through canopy layers. All in all, despite its high temperatures and lower light levels, which together contributed to decrease photosynthetic rates per unit leaf area, the high tunnel could apparently create a stimulating microclimate for raspberry biomass/leaf area growth and fruit.

4.5.2 The effects of growing conditions and canopy layers on plant growth

Plant grown under high tunnel had nearly twice as more leaf area and accumulated 1.6 times more dry biomass than in open field. Plants growing in the open windy field adapted to the harsher conditions by reducing canopy size, that is by shortening cane height and fruiting lateral length, thus leading to a corresponding decrease in leaf area and plant dry biomass accumulation. The adaptation is a typical thigmomorphogenetic response to wind, rain or other natural forces touching plants (Chehab *et al.*, 2009).

Plants grown under high tunnel were protected from any thigmomorphogenetic stimuli, while in open field the upper plant parts were strongly touched by wind and rain, and frequently knocked against the trellising system, which induced a strong thigmomorphogenetic response in the upper canopy. Consequently, under high tunnel quite similar leaf area or dry biomass was distributed among the three upper canopy layers, whereas in open field the leaf area and dry weight vertical distribution followed a more typical ‘bell shape’. Moreover, ‘Jeanne d’Orléans’ plants ceased growth earlier (at the beginning of the fruiting period) in open field than in high tunnel, likely due to the thigmomorphogenetic pressure experienced by the apical meristem in the terminal growing points.

4.5.3 The effects of growing conditions and canopy layers on marketable fruit yield

The contribution of four canopy layers to fruit yield was determined by computing each layer fruit yield as a percentage of whole-canopy. Under high tunnel, fruit yield in layer 1 (uppermost), 2, 3 and 4 (lowermost) accounted for 37.8%, 24.4%, 24.4% and 13.4% of the overall whole-canopy yield, respectively. Most fruits were concentrated in the three upper layers where there were more fruiting laterals. This growth habit might be caused by the vertical attenuation of PPFD and leaf area, which led to a steady decrease in canopy photosynthesis from top to bottom layers, thereby likely resulting in a similar-trend in fruit yield.

In open field the contributions to fruit yield were quite uniform among the four canopy layers. Although in open field there was also a general decrease in PPFD distribution from the upper to the lower canopy, similar canopy photosynthesis or fruit yield occurred among the four layers owing to the fact that less leaf area was produced in the upper layers (L1 and L2), likely due to the aforementioned thigmomorphogenetic response to wind, rain, etc. In short, the vertical distribution of fruit yield among the four canopy layers was largely dependent on plant growth habits, which in turn was under strong influence from environmental factors (i.e. vertical PPFD distribution, air temperature, wind and rain, etc.)

4.5.4 The relationship between canopy photosynthesis and plant growth and fruit yield

The relationship between leaf-level photosynthesis and grain/fruit yield has been discussed extensively in the past in relation to various annual field crops (rice, soybean, spring wheat and etc.) (Buttery *et al.*, 1981; Fischer *et al.* 1981; Kumar *et al.*, 1998; Sharma *et al.*, 1982) as well as several vegetable and fruit crops like tomato (Zhu *et al.*, 2012), grapevine (Medrano *et al.*, 2003) and apple (Palmer *et al.*, 1997). Through it all, there has been ongoing uncertainty concerning the relevance of leaf photosynthesis measurements with regards to plant growth and yield (Kruger & Violin, 2006). Many have noted the absence of an empirical relationship between plant biomass/fruit yield and leaf photosynthesis (Moss, 1976; Elmore, 1980; Gifford, 1987; Nelson, 1988). Certainly, the results of the present study (see also Chapter 3) lead support to such a viewpoint (i.e. higher photosynthetic rates measured in open field, but greater fruit yields obtained under high tunnel).

On the other hand, many studies have reported a significant relationship between leaf photosynthesis and grain/fruit yield. For example, Medrano *et al.* (2003) and Palmer *et al.* (1997) observed that the correlation between leaf photosynthesis per unit area and fruit yield or crop load was significantly positive in grape cv. ‘Tempranillo’ and ‘Braeburn’/M.26 apple trees. Moreover, Zhu *et al.* (2012) described that a significantly quadratic correlation existed between leaf-level photosynthesis and tomato fruit yield, due to the fact that more photosynthates were allocated to vegetative organs than to reproductive organs, leading to low fruit yield when leaf photosynthesis was higher than a certain value.

Given all that, it should be noted that the studies mentioned above referred to individual leaf-level photosynthesis measurements, which represent instantaneous

CO_2 exchange rates per unit area and time, whereas crop yield is the result of biomass partitioning and accumulation during the vegetative, flowering, and fruiting periods; it is a long-term effect of photosynthetic assimilation. In general, it is recognized that attempting to establish a correlation between instantaneous and accumulative variables is problematical. It is therefore not so surprising that a positive, negative, or no correlation between individual leaf photosynthesis rates and crop yield have been found over the years in various agricultural crops and horticultural cultivars. This led Evans (1992) to affirm that there were no evidences that increasing photosynthesis per unit area would necessarily result in an improvement of crop yield potential in crop breeding and cultivation improvement programs.

Consequently, canopy-level photosynthesis, preferably time-integrated, rather than average instantaneous leaf-level photosynthesis, should be used as a correlate to crop yield. Most canopy-level photosynthesis researches to date have focused on agricultural crops like barley (Biscoe *et al.* 1975), maize (Hu *et al.*, 1993), soybean (Harrison *et al.*, 1981; Wells *et al.*, 1986), cotton (Wells *et al.*, 1982), etc.. Limited work has been done on fruit trees and other horticultural crops, including red raspberries. Our results indicated that during the fruiting period of the floricane-fruiting cv. 'Jeanne d'Orléans', there was a significantly positive correlation between canopy photosynthesis and total/marketable fruit yield under high tunnel (r = 0.958/0.970, $P < 0.05$) and in open field (r = 0.975/0.973, $P < 0.05$) (Figure 4.8). In apple ('Braeburn'/M.26 apple trees grown in a New Zealand orchard), which come from the same botanical family (*Rosaceae*) as raspberries, whole-canopy gas exchange also correlated linearly to crop loads (Wünsche and Lakso, 2000; Wünsche *et al.*, 2000).

In our study, canopy photosynthesis was estimated by scaling-up the average individual leaf photosynthetic light response of a given canopy layer to the whole-layer leaf area using the PPFD distribution across that layer, then summing up over all canopy layers. Since ultimately all plant biomass accumulation is created by canopy photosynthesis, the relationship between canopy photosynthesis and plant biomass or total leaf area can only be a positive one (see Appendix Figure A.4.3). It is not surprising then that in our study the raspberry crop fruit yield correlated positively with canopy photosynthesis in both high tunnel and open field conditions (Figure 4.8). However, judging from the differing slope of the linear relationships between total fruit yield and canopy photosynthesis (Figure 4.8A), it is clear that a greater proportion of the photosynthate was allocated to fruit production under high tunnel. A combination of warmer growth temperatures at the early stages of growth and flower bud initiation, as well as the absence of any thigmomorphogenetic stress under high tunnel throughout the growing season, are the likely environmental factors contributing to the significantly greater leaf area, canopy photosynthesis, and fruit yield of the tunnel-grown 'Jeanne d'Orléans' raspberry crop.

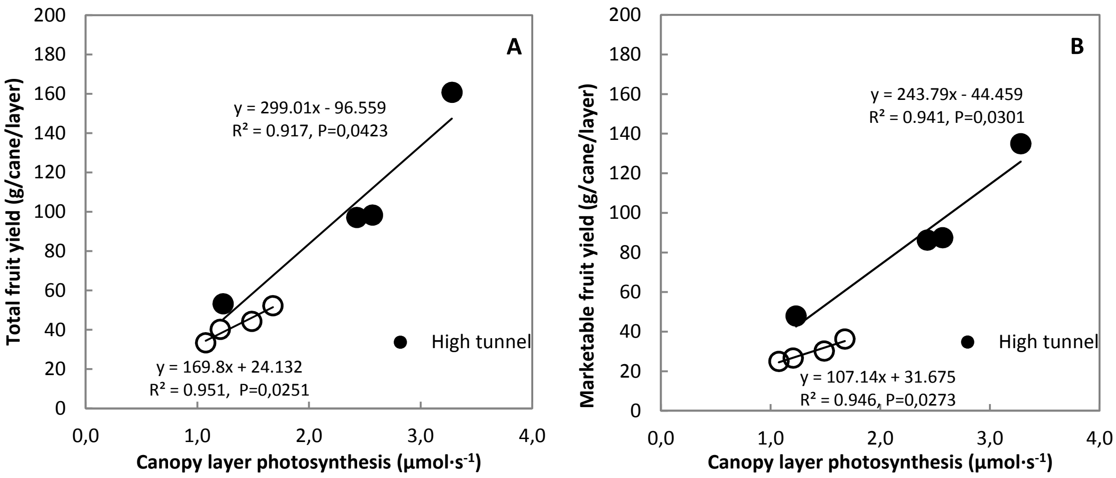

Figure 4.8 The relationship between canopy photosynthesis and (A) total or (B) marketable fruit yield for floricane-fruiting cv. 'Jeanne d'Orléans' grown under high tunnel and open field.

4.6 Conclusion

This experiment was aimed to determine the influence of growing season conditions (high tunnel *vs.* open field) and the contribution of different canopy layers on plant growth, PPFD distribution, canopy photosynthesis, and fruit yield in floricane-fruiting red raspberry 'Jeanne d'Orleans'.

High tunnel effects

High tunnel increased ambient air temperature by 3.8/7.2°C (mean/max.) relative to open field during the 2014 growing season. Compared to open field-grown plants, plants grown under high tunnels produced 1.6 times more dry biomass, 1.9 times more leaf area, 1.5 times more whole-canopy photosynthesis, which taken together translated into 3.0 times more fruit yield.

Canopy layer effects

Under high tunnel, approximately 85% of the whole-canopy dry biomass, leaf area, canopy photosynthesis, and fruit yield were distributed in the upper three layers while in open field the vertical distribution of dry biomass, leaf area and canopy layer photosynthesis followed a 'bell-shaped' variation. As for fruit yield in the open field, all four canopy layers contributed equally.

Seasonal effects

Under high tunnel, leaf area and dry weight increased linearly during the vegetative growth period, and curvilinearly at a much lesser rate during fruiting period. In open field, plants ceased their vegetative growth at the beginning of fruiting period. Canopy photosynthesis increased until harvest peak under high tunnel, whereas in open field it reached its maximum at the beginning of harvest, then a slight decrease occurred until the end of harvest.

Relationship between canopy photosynthesis and plant growth or fruit yield

Canopy photosynthesis was positively correlated with dry biomass, leaf area and fruit yield under both growing conditions. Despite consistently lower photosynthesis rates at the leaf level, the overall whole-canopy photosynthetic production of high tunnel-grown plants exceeded that of open field-grown plants by 51%, due to the fact that plants grown under high tunnel produced on average 1.9 times more leaf area than those grown in open field (thereby overcompensating for the leaf-level photosynthetic depression either caused by lower leaf PPFD or high leaf temperature). Under high tunnel, crop fruit yield per unit canopy photosynthesis or accumulated biomass was notably higher possibly due to a combination of warmer growth temperatures in the early vegetative and flowering stages, as well as the absence of thigmomorphogenetic stress.

4.7 Acknowledgements

The author wishes to thank Agriculture and Agri-Food Canada, The Conseil Canadien de l'Horticulture, Natural Sciences and Engineering Research Council of Canada, Les Fraises de l'Île d'Orléans Inc., Fafard et Frères ltd. and Pépinière Luc Lareault inc. for the technical and financial support.

Chapter 5: Light, plant growth and fruit yield vertical distribution and canopy photosynthesis modeling of primocane-fruiting red raspberry cultivated under high tunnel *vs.* open field

5.1 Abstract

Similar to floricane-fruiting cv. ‘Jeanne d’Orleans’, lower leaf photosynthesis rates vs. higher fruit yields also occurred in high tunnel-grown cv. ‘Polka’ (primocane-fruiting) in comparison to those cultivated in open field. To credibly explain the relationship between photosynthetic accumulation and fruit harvest during the 2014 growing season, an experiment was conducted to determine whole canopy photosynthesis by scaling individual leaf-level photosynthetic rates up to the total canopy leaf area. To do this the plant canopy was separated in 4 vertical layers and the light interception and photosynthesis of each layer was evaluated both diurnally and seasonally. The relationship between cumulative canopy layer photosynthesis and fruit yield was then evaluated for the whole fruiting season.

High tunnel-grown plants presented 1.6 times more leaf area (1.4 times more dry biomass), 1.5 times more canopy photosynthesis, and 2.8 times more fruit yield than plants cultivated in the open field. Under both growing conditions, approximately 82% of the total dry biomass, 88% of the total leaf area, 90% of the whole-canopy Pn, and 100% of the total fruit yield was distributed in the three upper layers. In addition, dry biomass vertical distribution showed a ‘bell-shaped’ variation, namely higher biomass accumulation at two middle canopy layers. No raspberry fruits were found in the lowermost layer in the cv. ‘Polka’.

For seasonal effects, under each growing condition, dry weight, leaf area and canopy photosynthesis increased linearly until the fruit harvest, and then reached a maximum and remained constant afterwards, except for a slight decrease of canopy photosynthesis in open field at the end of harvest due to the leaf senescence likely caused by cold temperature in late autumn. Canopy photosynthesis was positively correlated to dry biomass, leaf area and fruit yield under both growing conditions. The photosynthetic crop efficiency gain (gram fruit per unit photosynthesis) under high tunnel relative to open field of cv. ‘Polka’ was found to be greater than that of cv. ‘Jeanne d’Orléans’.

5.2 Introduction

In our previous study conducted in 2013, high tunnel-grown cv. 'Polka' (primocane-fruiting) plants produced significantly more (3.4 times) marketable fruit yield than plants cultivated in open field (see Chapter 2). In the same year, individual leaf photosynthesis measurements were made and indicated that tunnel-grown plants presented significantly lower (33%) photosynthetic rates than field-grown plants (see Chapter 3). As outlined in Chapter 4, similar results were obtained with summer-grown floricane-fruiting cv. 'Jeanne d'Orléans', and parallel to what was done in that study to try reconcile the measured lower leaf-level photosynthetic rates of tunnel-grown plants with their greater fruit yield, we hypothesized that once scaled up to the level of the whole raspberry canopy leaf area under high tunnel *vs.* open field could address this discrepancy, and a direct relationship between overall photosynthetic production and fruit yield performance would reveal itself positive and significant.

Leaf area and absorbed PPFD are essential for modeling canopy photosynthesis (Gutierrez and Lavin, 2000). The distribution of leaf area in a crop canopy has a significant effect on the PPFD interception and consequently influences canopy photosynthesis, plant growth and yield (Bhatt and Chanda, 2003; Stewart *et al*., 2002). In hedgerow-trained plant canopies like grapevine (Dokoozlian and Kliewer, 1995) and raspberry (Wright and Waister, 1985), shading is most preeminent in the inner portion of the lower canopy where PPFD is significantly attenuated by upper and/or peripheral canopy leaves. To properly model hedgerow canopy photosynthesis, both the horizontal and vertical distribution of leaf area and PPFD throughout the canopy should be evaluated .

According to the non-rectangular hyperbola photosynthesis of Thornley (1998), the photosynthetic rate of a leaf is dependent on its inherent photosynthetic light efficiency (quantum yield) under limiting PPFD and on its maximal photosynthetic capacity ($P_{\max}$) under saturating PPFD. In this study, we parameterized the Thornley model at the leaf level to estimate net leaf photosynthesis at any given incident PPFD between full sunlight and darkness. The parameters of the Thornley model are sensitive to environmental factors even on a diurnal basis (Ögren and Evans, 1993), thus in our study we chose to replicate the light response curve measurements required to parameterize the photosynthesis model both in space (vertical in canopy) and in time (seasonal and diurnal) (see also in Chapter 4).

In parallel to Chapter 4, the objectives of the current study were: 1) to determine the vertical distribution of PPFD, leaf area and dry biomass under tunnel- and field-grown primocane-fruiting cv. 'Polka'; 2) to generate A-Q curves to parameterize a leaf photosynthesis model and scale it up to canopy level (four canopy layers) over the entire growing season; 3) to describe the relationship between PPFD distribution, plant growth or fruit yield and canopy photosynthetic accumulation; 4) to compare the fruit yield gain (relative to open field cultivation) of tunnel-grown primocane-fruiting cv. 'Polka' to that of floricane-fruiting cv. 'Jeanne d'Orléans'. Because the warming effect of the high tunnel was expected to be most beneficial under cooler late-summer/autumn climate, we hypothesized that the relative photosynthetic and fruit yield gain of tunnel-grown cultivation would be most notable for autumn-fruiting cv. 'Polka'.

5.3 Materials and methods

5.3.1 Research site

The experiment was conducted under high tunnels *vs.* open field at 'Les Fraises de Ile d'Orleans Inc.' (71°01′W, 46°52′N), in Québec, Canada. One common tunnel size was 8.5 m wide, 4.5 m high and 70.0 m long with polyethylene coverings from Industries Harnois (http://www.harnois.com). Air temperature, relative humidity and ventilation under the tunnel were passively controlled by closing or opening the side walls and end doors.

5.3.2 Plant material

Primocane-fruiting red raspberry cv. ‘Polka’ potted plants were successively used for the 2014 experiment. In spring, new shoots were trained to keep four uniform canes per pot. Fruits were harvested from mid-August to early October. After harvest, all the primocanes were cut down and removed at pot level. A hedgerow type trellising system was used to support the canes. Crop pest, pathogens and weeds were controlled according to Canadian standard organic management practices (CGSB and SCC, 2006). Fertigation for plants was according to local recommendations (Tellier, 2007).

5.3.3 Experimental design

The best cropping system in terms of fruit yield for ‘Polka’, including cultivated plants under high tunnel with a reflective ground cover and in a density of 12 canes per linear meter (4 canes per pot) (see Chapter 2, Table 2.7), was used for the 2014 experiment in comparison to open field cropping pattern. Similar to cv. ‘Jeanne d’Orléans’ (Figure 4.1), cv. ‘Polka’ plant canopy was also divided into 4 zones vertically according to cane height to determine the contribution of each layer to growth, fruit yield and canopy photosynthesis.

The experiment was set up as a two-way nested ANOVA design with 2 growing conditions (high tunnel and open field) as the main plots and 4 equal canopy layers (layer 1, 2, 3 and 4, in sequence from upper to lower) as sub-plots, resulting in 8 treatments. The treatments were replicated 4 times. Buffer zones were arranged within a row between adjacent treatments.

5.3.4 Data collected

5.3.4.1 Microclimate under high tunnel and open field

Climate data were cumulated at different canopy heights during the 2014 growing season. Air temperatures, relative humidity were monitored by HOBO data loggers

(U12-013, Onset Corp., Bourne, MA, USA) under high tunnel and open field. A standard weather station (see Chapter 4) was installed in the open field to collected more detailed climate data of the whole research site all year round.

5.3.4.2 Fruit yield and plant growth

The harvest season was from mid-August and to early October 2014. Fruits in each treatment were picked three times a week and selected as marketable *vs.* non-marketable, counted and weighted. Fruits impacted by disease, insect, mechanical injury, fruit too small, distorted, crumbling, etc. were downgraded. The fruit size (average fruit weight) was determined for marketable fruits. Plant dry biomass and leaf area in each of four canopy layers were determined on June 18, July 10, August 8 and 30 and September 22, respectively. The corresponding cumulative growth curves were then determined from the five repeated sampling times during the growing season. Leaf area was measured using a Li-3100C Area Meter (see Chapter 4).

5.3.4.3 Determination of light distribution

The incident *vs.* reflected horizontal PPFD distributions in each canopy layer were monitored every 1.5 hours from 8:30 am to 4:30 pm on clear sunny days using a SunScan canopy analysis system (see Chapter 4). The incoming PPFD was paired measured 0.2 m above the plant canopy. These diurnal PPFD measurements were repeated in five sampling times during the growing season namely T1, June 18; T2, July 10-11; T3, August 7-10; T4, August 30-September 2; T5, September 21-24.

5.3.4.4 Photosynthetic light-response curves measurements

Concurrently to the horizontal PPFD distribution measurements, photosynthetic light response (A-Q) curves were made on three replicate fully expanded healthy sunlit leaves from each of the four canopy layers under high tunnel and open field. Net photosynthesis measurements were made using a LI-6400XT portable gas exchange system as described in Chapter 4. The leaf chamber CO_2 and H_2O mole fractions were maintained fixed to ambient levels throughout the A-Q curve, and the leaf temperature was set to the average canopy layer leaf temperature estimated from infrared thermometer measurements made on three sunlit and three shaded leaves (see Chapter 4). Leaves were first measured under their current incident PPFD level before initiating the A-Q curve from PPFD = 1800 µmol quanta m^{-2} s^{-1} down to zero light. The above-mentioned measurements were repeated on the same treatments (using a different sub-plot block) every 1.5 hours from 8:30 am to 4:30 pm, and were repeated in five blocking times.

5.3.5 Computation and statistical analysis

Photosynthetic light response curve measurements were fitted (non-linear fitting procedure NLIN in SAS; SAS Institute Inc.) to the non-rectangular hyperbola model of Thornley (1998):

$$P_n = -R_d + \frac{\alpha \cdot PPFD + P_{max} - \sqrt{(\alpha \cdot PPFD + P_{max})^2 - 4\theta \cdot \alpha \cdot PPFD \cdot P_{max}}}{2\theta} \quad (1)$$

where R_d is dark respiration, θ is the scaling constant for curvature, α is light-limited quantum efficiency, and P_{max} is the light saturated gross photosynthetic rate. Resulting A-Q curve parameters from the triplicate measurements of each canopy layer were averaged to give a representative mean A-Q curve for each layer at each sampling time and date. To scale up the leaf level P_n measurements in each canopy layer to the whole-layer P_n sum, the ceptometer incident 2-sided PPFD histogram was used as the independent driving variable for Eqn 1 (hence giving 64 individual P_n estimates) assuming an equal distribution of leaf area across the ceptometer length.

Analysis of variance of fruit yield, leaf area, dry weight, PPFD distribution and modeled canopy photosynthesis was completed using the GLIMMIX procedure of SAS. Multiple comparisons of means were adjusted by Tukey t-test at the $P = 0.05$ probability level. The normality of a model was tested with univariate procedure of SAS.

5.4 Results

5.4.1 Microclimate under high tunnel and open field (2014)

During the growing season (from early June to early October), air temperature under high tunnel was 3.2°C/6.8°C (mean/max.) higher than in open field (Figure 5.1). The fruiting period of 'Polka' was from mid-August to early October, with daily temperatures averaging 21.2 and 19.2°C under high tunnel and open field, respectively. Moreover, after early September, the daily mean temperature dropped rapidly from 20.6/18.0°C to 14.7/12.1°C under high tunnel and open field, respectively (Figure 5.1).

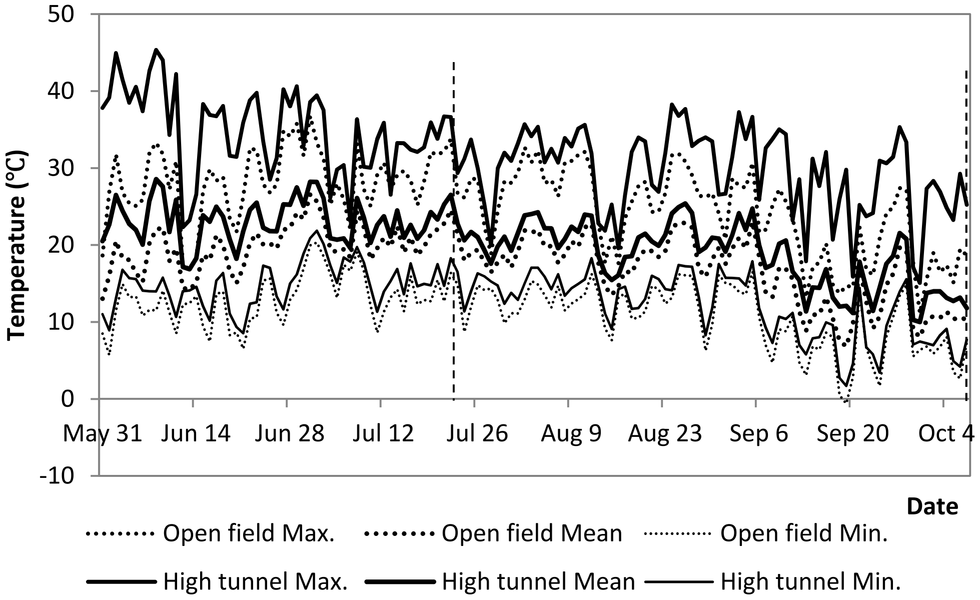

Figure 5.1 The daily air temperature under high tunnel and open field during growing season of primocane-fruiting cv. 'Polka' in 2014 in Québec, Canada. Time range between the two dotted lines represents reproductive period of cv. 'Polka'.

5.4.2 Marketable fruit yield in different canopy layers

Growing conditions (high tunnel and open field) and layers nested in their growing condition significantly influenced marketable fruit yield and fruit number of primocane-fruiting cv. 'Polka' (Table 5.1).

Plants cultivated under high tunnel produced 2.8 times more marketable fruit yield and 3.0 times more fruit number than in open field. Under each growing condition, the two upper canopy layers (L1 and L2) had equal fruit yields and fruit numbers, approximately 9.5 and 7.9 times higher than in the lower layer (L3), respectively. No fruits were harvested in the lowermost layer (L4) (Figure 5.2).

Table 5.1 ANOVA of marketable fruit yield, plant growth and modeled canopy photosynthesis during the fruiting period of primocane-fruiting cv. 'Polka'

Effect	Fruit yield	Fruit number	Dry weight	Leaf area	Canopy Pn
Protected cultivation (PC)	**<.0001**	**<.0001**	**<.0001**	**<.0001**	**0.0013**
Layer (PC)	**<.0001**	**<.0001**	**<.0001**	**<.0001**	**<.0001**

Layer (PC), canopy layers nested under their corresponding growing environments namely high tunnel or open field. *P*-values < 0.05 indicate significant differences.

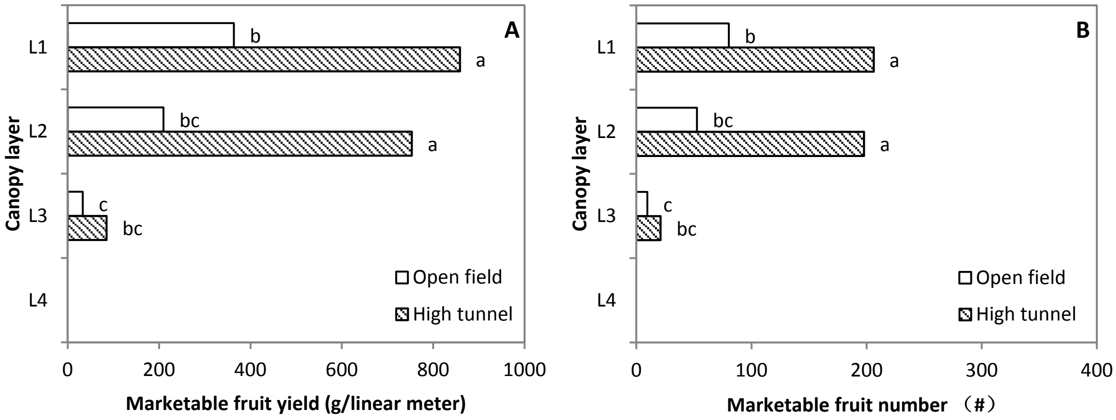

Figure 5.2 Influence of growing conditions (high tunnel and open field) and canopy layers (L1, L2, L3 and L4, from upper to lower) on A) marketable fruit yield and B) fruit number of primocane-fruiting cv. 'Polka'. Horizontal bars followed by different letters are significantly different according to Tukey's multiple range test at 5% level.

5.4.3 Dry biomass accumulation in different canopy layers and whole-canopy

Growing conditions (high tunnel and open field) and layers nested under their growing condition significantly affected canopy layer dry weight in fruiting period (e.g. August 30) (Table 5.1).

During the fruiting period, the uppermost and lowermost layer (L1 and L4) produced similar dry matter, accounting for 20% and 17.6% of whole-canopy dry weight, significantly lower than the 30% and 32.4% measured for the middle layers (L2 and L3) under high tunnel and open field, respectively (Figure 5.3A). Plants grown under high tunnel accumulated approximately 1.4 times more dry weight than in open field during the fruiting period: beginning of harvest (August 8), harvest peak (August 30) and end of harvest (September 22) (Figure 5.3B).

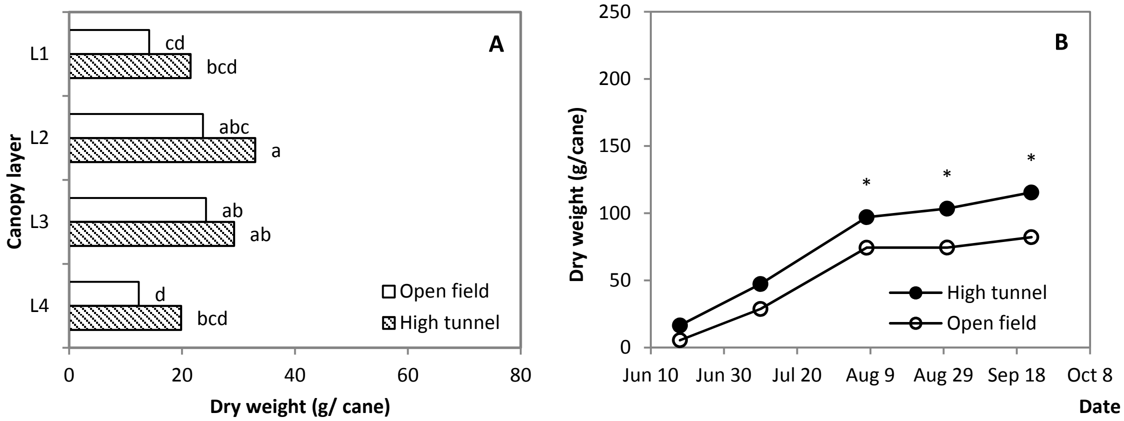

Figure 5.3 Influence of growing conditions (high tunnel and open field) on A) the dry biomass accumulated during the fruiting period in each of the four canopy layers (L1, L2, L3 and L4 from upper to lower layers) and B) the cumulative whole-canopy dry biomass increment over the growing season of primocane-fruiting cv. ‘Polka’. In A), horizontal bars followed by different letters are significantly different according to Tukey’s multiple range test at 5% level, while in B) significant differences in dry weight between high tunnel and open field are indicated by a * sign.

5.4.4 Leaf area accumulation in different canopy layers and whole-canopy

Growing conditions (high tunnel and open field) and layers nested in their growing condition significantly influenced canopy layer leaf area in the fruiting period (e.g. August 30) (Table 5.1).

Under each growing condition, the leaf area of the three upper layers (L1, L2 and L3) was uniformly distributed and was on average 2.4 and 2.7 times larger than in the lowermost layer (L4), where only 12.3% and 10.9% of whole-canopy leaf area were produced under high tunnel and open field, respectively (Figure 5.4A). As for the cumulative whole-canopy leaf area growth over the whole growing season, plants grown under high tunnel cumulated 1.6 times more leaf area than in open field during harvest period (Figure 5.4B).

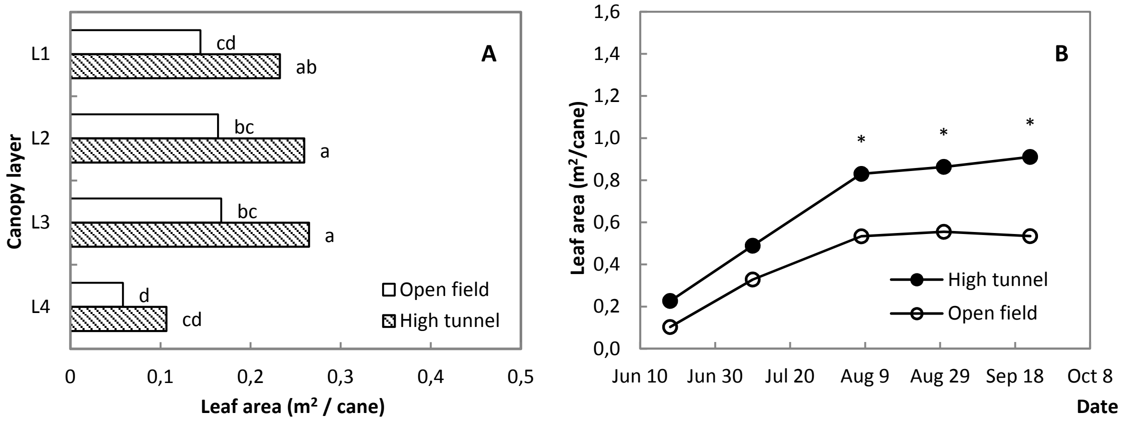

Figure 5.4 Influence of growing conditions (high tunnel and open field) on A) the leaf area accumulated during the fruiting period in each of the four canopy layers (L1, L2, L3 and L4 from upper to lower layers) and B) the cumulative whole-canopy leaf area growth over the growing season of primocane-fruiting cv. 'Polka'. In A), horizontal bars followed by different letters are significantly different according to Tukey's multiple range test at 5% level, while in B) significant differences in canopy leaf area between high tunnel and open field are indicated by a * sign.

5.4.5 Light vertical distribution throughout different canopy layers

Similar to the hedgerow-trained canopy of cv. ‘Jeanne d’Orléans’, the average incident PPFD above and inside the canopy was significantly higher in open field than under high tunnel (Figure 5.5). During the midday (11:00 am to 1:00 pm) in both growing conditions, the PPFD decreased gradually from the top to the bottom layer, while earlier in the morning or later in the afternoon, the PPFD distribution was more uniform throughout the four vertical canopy layers (Figure 5.5).

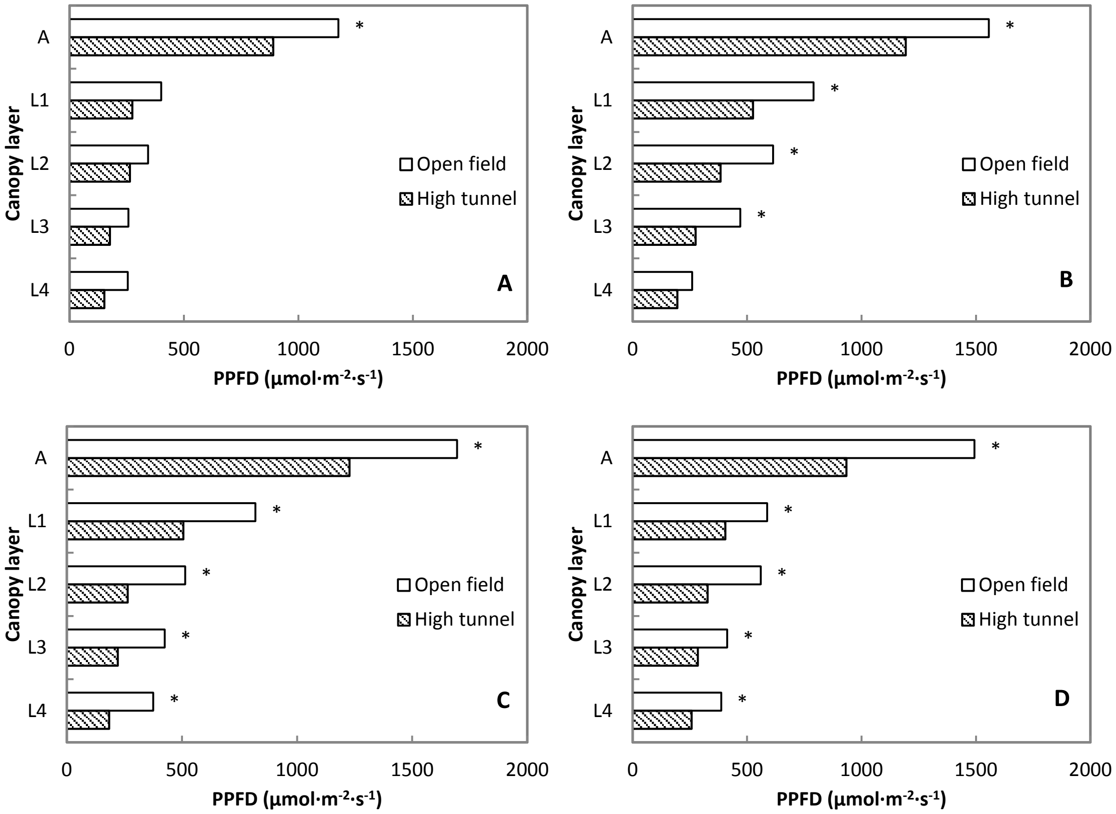

Figure 5.5 Diurnal variations in the vertical distribution of the average incident PPFD among canopy layers (A: above canopy, L1: uppermost, L2: middle, L3: middle and L4: lowermost layer) of primocane-fruiting cv. ‘Polka’ grown under high tunnel and open field on a typical sunny day (August 23 2014) : A) 9:00 am, B) 11:00 am, C) 1:00 pm, D) 3:00 pm Significant differences (P < 0.05) in average PPFD between high tunnel and open field are indicated by a * sign.

The horizontal PPFD distribution was computed automatically from 64 readings recorded by the Sunscan Ceptometer. The PPFD readings on the sunlit side of the canopy were always higher in open field than under high tunnel, whereas on the shaded side the differences were less marked (Appendix, Figure A.5.1). Photosynthetic light response measurements taken concurrently on the same experimental unit demonstrated that the higher available light in open field resulted in higher photosynthetic capacity (P_{max}) (see Appendix, Figure A.5.2).

5.4.6 Photosynthetic accumulation in canopy layers or whole-canopy

Growing conditions (high tunnel and open field) and layers nested in their growing condition significantly affected canopy layer photosynthetic carbon fixation during the fruiting period (Table 5.1).

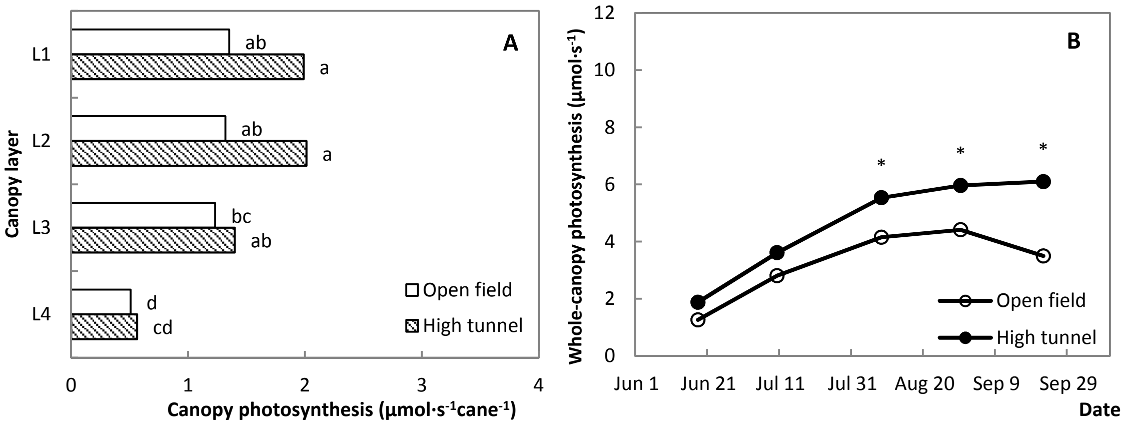

Figure 5.6 Influence of growing conditions (high tunnel and open field) on A) the net photosynthetic gain cumulated during the fruiting period in each of the four canopy layers (L1, L2, L3 and L4 from upper to lower layers) and B) the whole-canopy net photosynthetic gain over the whole growing season of primocane-fruiting cv. 'Polka'. In A), horizontal bars followed by different letters are significantly different according to Tukey's multiple range test at 5% level, while in B) significant differences in whole-canopy photosynthesis between high tunnel and open field are indicated by a * sign.

High tunnel-grown plants presented 1.5 times more photosynthetic accumulation in the two upper canopy layers (L1 and L2, respectively) than those cultivated in open field (Figure 5.6A). The two upper layers (L1 and L2) achieved similar layered-canopy photosynthesis levels under high tunnel; this level was significantly higher by 1.4 and 3.6 times than layer 3 and lowermost layer 4, respectively. Similarly in open field, the three upper layers (L1, L2 and L3) displayed equal canopy photosynthesis, and reached a 2.6 times higher level than lowermost layer 4 (Figure 5.6A). Tunnel-grown plants cumulated approx. 1.4 times more whole-canopy photosynthesis than in open field, with much difference occurring during the fruiting period (Figure 5.6B).

5.5 Discussion

5.5.1 The effects of high tunnel coverings on microclimate

Québec has a pleasant climate with cool air temperature during the summer; temperature is lower than Ontario and less humid than British-Columbia, with same latitude for the three different climate regions. The use of high tunnel creates more desirable microclimate, protects the plants from wind movement, and bad weather damages especially in late autumn, and further positively affects fruit yield or quality of primocane-fruiting red raspberry cv. 'Polka'.

Daytime temperature usually follows the diurnal pattern, with the use of high tunnel, closer to noon, higher temperature under high tunnel than open field. This is indeed what we measured during 2014, and the temperature fluctuation trend was similar to that monitored in 2012 or 2013 (Xu *et al.*, 2013). During the fruiting period, normally from mid-August to early October, temperatures measured from mid-August to early September were still warm for primocane-fruiting cultivar production. These temperatures dropped rapidly after early September. It is therefore necessary to use high tunnel to warm plants in late autumn, since high tunnel created a favorable microclimate for the raspberry growth and production by modifying external climatic conditions.

As mentioned before, PPFD above the canopy was around 15% lower under high tunnel than in open field during the fruiting period of floricane-fruiting cv. ‘Jeanne d’Orléans’ (e.g. July 20). Whereas for primocane-fruiting cv. ‘Polka’, during its fruiting period (e.g. August 23), PPFD was reduced by 25% above canopy under high tunnel as compared with open field, due to the fact that the presence of polyethylene films, and lower solar elevation angle in autumn than summer, caused lower PPFD under high tunnel during the fruiting period of cv. ‘Polka’ than of cv. ‘Jeanne d’Orléans’.

5.5.2 The effects of growing conditions and canopy layers on plant growth

High tunnel-grown plants produced 1.6 times more leaf area and 1.4 times more dry biomass than in open field. Field-grown plants usually had more thigmomorphogenetic response to wind, rain or other natural forces (Latimer, 1991; Jaffe and Forbes, 1993). Apparently, decrease of the plant growth above indicated that this response also occurred in field-grown ‘Polka’ plants.

Under high tunnel and open field conditions, dry matter vertical distribution showed typical ‘bell-shaped’ variation patterns throughout the four canopy layers. While it was not very obvious that leaf area vertical distribution was expressed as the ‘bell-shaped’ variation, for leaf area in the uppermost layer was not significantly lower than the middle layers under high tunnel or open field. In both growing conditions, three upper layers produced approximately 88.4% of whole-plant leaf area. Similarly in another research on peach trees, regardless of training systems (‘central leader’ and ‘Y shape’), on average 80.8% leaf area was distributed in top and middle layers (Caruso *et al.*, 1998).

Even though similar variation trend of leaf area or dry biomass vertical distribution occurred between the both growing conditions, each layered-canopy leaf area and dry biomass under high tunnel was higher than those in corresponding layer in open field, resulting in markedly higher leaf area and dry biomass in whole-canopy level under high tunnel, where plants were protected from any thigmomorphogenetic forces. However, plants grown in open field were strongly touched by wind and rain, and knocked against the trellising system frequently which caused the whole-canopy thigmomorphogenesis.

5.5.3 The effects of growing conditions and canopy layers on marketable fruit yield

As to the contribution of four canopy layers, fruit yield in layer 1 (uppermost), 2 and 3 (middles) accounted for 50.6%, 44.4% and 5.0% under high tunnel and 60.0%, 34.6% and 5.4% of whole-canopy in open field. Most fruits were concentrated in the 2 top layers where more fruiting laterals were found, this growth habit in cv. ‘Polka’ might be caused by attenuation of PPFD vertical distribution which affected the leaf area vertical distribution. In brief, vertical distribution of fruit yield in the four-layer canopy was dependent on plant growth habits and environmental factors especially PPFD distribution.

In other fruit trees such as citrus, a greater percentage of fruit was found in the upper parts of the tree canopy at closer spacing (in the hedgerow) (Whitney and Wheaton, 1984). Similar results were obtained in olive orchards, most fruits were produced at 2 upper layers (1.0-2.0 m height) in the hedgerow-trained trees (Gómez-del-Campo *et al.* 2009). In southern Spain, olive fruit distribution was investigated in a high-density orchard to facilitate development of mechanical harvest, the results demonstrated that more than 60% of total fruits was distributed in the middle-outer and upper canopy (Castillo-Ruiz *et al.*, 2015).

However, for other training forms such as delayed vase- and perpendicular Y-shaped, other than hedgerow type, applied in fruit trees like peach trees, regardless of training types, fruit yield per layer were highest in the central part of the canopy (Farina *et al.*, 2005). As for red raspberry, to our knowledge, it was the first time in our study to report vertical fruit distribution through whole canopy supported by hedgerow trellising system under high tunnel *vs.* open field.

5.5.4 The relationship between canopy photosynthesis and plant growth and fruit yield

In section 4.5.4 (see Chapter 4), the relationship between canopy photosynthesis and fruit yield was discussed. Canopy-level photosynthesis, preferably time-integrated, rather than average instantaneous leaf-level photosynthesis, should be used as a correlate to crop yield. Similar to floricane-fruiting cv. 'Jeanne d'Orléans', the cv. 'Polka' results also indicated that during the fruiting period there was a strong positive correlation between canopy photosynthesis and total/marketable fruit yield under high tunnel (r = 0.992/0.987, P = 0.0787/0.1025) and in open field (r = 0.990/0.978, P = 0.0879/0.1350) (Figure 5.7).

In our case, canopy photosynthesis was computed by scaling-up the average individual leaf photosynthetic light response of a given canopy layer to the whole-layer leaf area using the PPFD distribution across that layer, then summing up over all canopy layers. Since ultimately all plant biomass accumulation is created by canopy photosynthesis, the relationship between canopy photosynthesis and plant biomass or total leaf area can only be a positive one (see Appendix Figure A.5.3). It is not surprising then that in our study the raspberry crop fruit yield correlated positively with canopy photosynthesis under both high tunnel and open field conditions (Figure 5.7).

Contrary to what was observed with cv. 'Jeanne d'Orléans' in Chapter 4, the photosynthetic crop efficiency of the high tunnel-grown cv. 'Polka' at its lower range fell below that of open field-grown plants, showing greater loss of reproductive capacity in lower canopy layers of high tunnel-grown cv. 'Polka' comparatively to cv. 'Jeanne d'Orléans' (compare see Figure 5.7 with Figure 4.8). The difference in total photosynthetic crop efficiency between high tunnel and open field is greater for cv.

‘Polka’ than that of ‘Jeanne d’Orléans’, because of the greater beneficial effect of tunnel warming in the fall compared to summer (Figures 5.8 and 5.9).

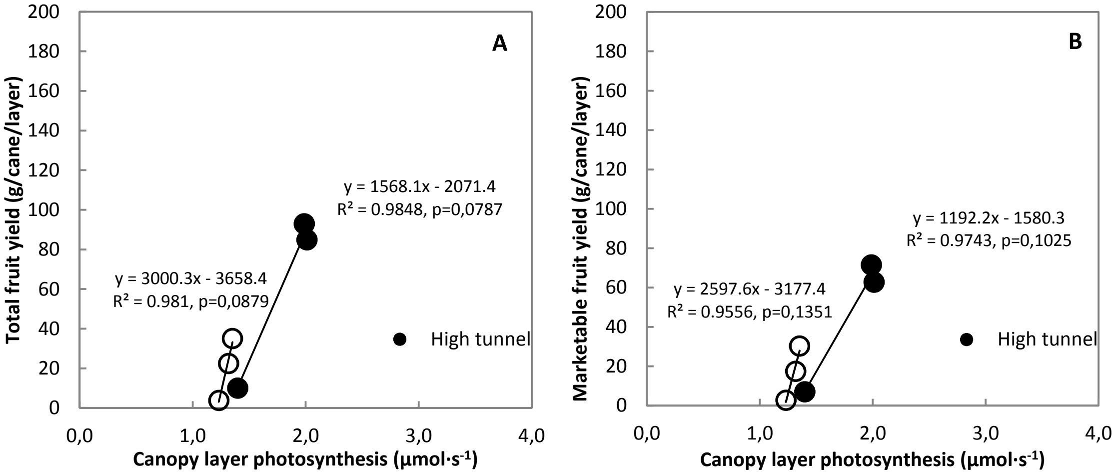

Figure 5.7 The relationship between canopy photosynthesis and (A) total or (B) marketable fruit yield for primocane-fruiting cv. ‘Polka’ grown under high tunnel and open field.

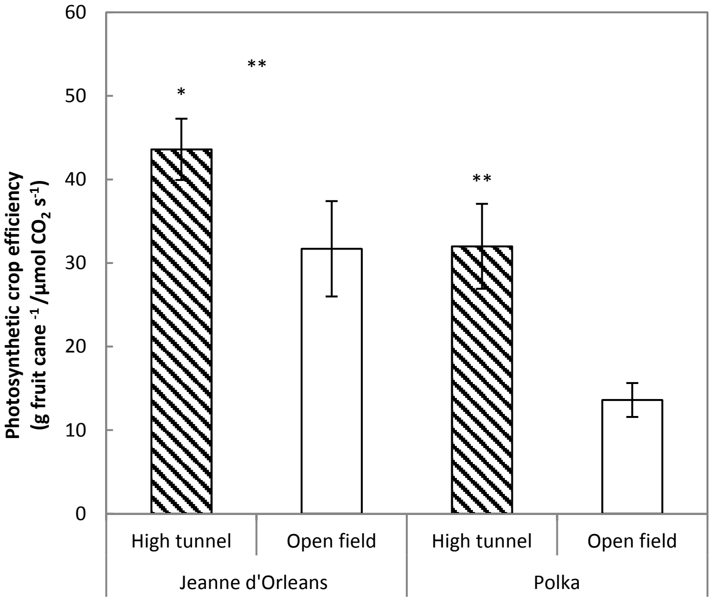

Figure 5.8 The photosynthetic crop efficiency of floricane-fruiting cv. ‘Jeanne d’Orléans’ and primocane-fruiting cv. ‘Polka’ cultivated under high tunnel and open field. The * and ** symbols represent the significance level at $P < 0.05$ and $P < 0.01$, respectively.

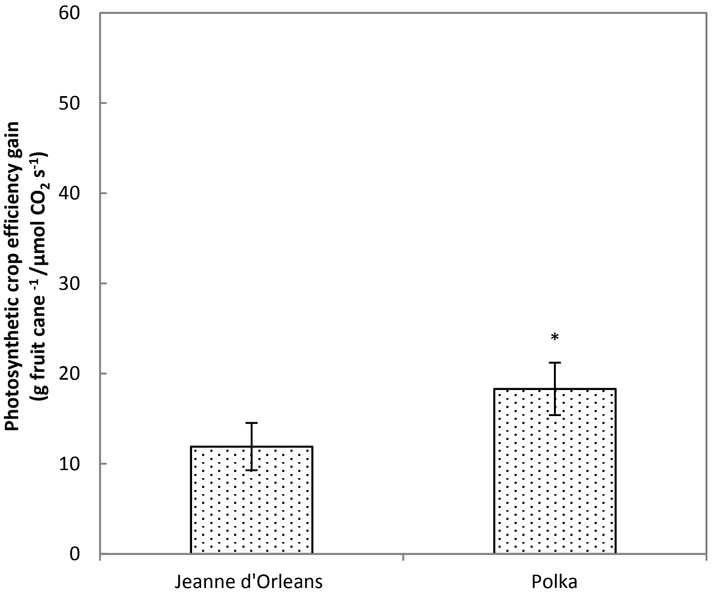

Figure 5.9 The gain in photosynthetic crop efficiency of tunnel-grown plants compared to open field-grown plants for floricane-fruiting cv. 'Jeanne d'Orléans' and primocane-fruiting cv. 'Polka'. The * represents the significance level at $P < 0.05$.

5.5.5 Comparisons of the fruit yield gain between tunnel-grown floricane- and primocane-fruiting red raspberry

More and more producers use high tunnel to extend the growing season of primocane-fruiting red raspberries in late autumn, whereas for floricane-fruiting cultivars production high tunnels are scarcely adopted due to their fruiting period being in the summer. It is generally believed that high midday tunnel temperatures stress plants and decrease their fruit yield potential. Indeed, the optimal growing temperature of raspberry is considered to be around 21-23°C (Carew *et al.*, 2003; Sønsteby and Heide, 2009).

However, according to our results, the fruit yield gains of tunnel-grown summer-fruiting cv. 'Jeanne d'Orléans' were very similar to those of autumn-fruiting cv. 'Polka', showing in both cases a gain of nearly 2.9 times marketable fruit yield as compared to field-grown plants. Although the cultivars used in this study ('Jeanne d'Orléans' and 'Polka') are not widely used in commercial red raspberry cultivation in Canada, if other commercial floricane-fruiting varieties are found to respond similarly to cv. ‘Jeanne d’Orléans’ to high tunnel cultivation, significant fruit yield gains are to be expected in these cultivars as well.

5.6 Conclusion

This experiment was aimed to determine the effects of growing season conditions (high tunnel *vs.* open field) and the contribution of different canopy layers on plant growth, PPFD distribution, canopy photosynthesis, and fruit yield in primocane-fruiting red raspberry ‘Polka’.

High tunnel effects

High tunnel increased ambient air temperature by 3.2/6.8°C (mean/max.) relative to open field during the 2014 growing season. Compared to open field-grown plants, ‘Polka’ plants grown under high tunnels produced 1.4 times more dry biomass, 1.6 times more leaf area, 1.5 times more whole-canopy photosynthesis, which taken together translated into 2.8 times more fruit yield.

Canopy layer effects

During the fruiting period, approximately 82% of the dry weight, 88% of the leaf area, 90% of the canopy photosynthesis, and 100% of the fruit yield were distributed in the three upper layers under each growing condition (high tunnel or open field). In addition, dry biomass vertical distribution followed a ‘bell-shaped’ pattern variation over the four-layer canopy. No fruits were found in the lowermost layer in cv. ‘Polka’.

Seasonal effects

Under high tunnel and open field, leaf area, dry weight, and canopy photosynthesis all increased linearly during the vegetative growth phase, reached their respective maximum and then remained essentially constant during fruiting period, the only exception being that canopy photosynthesis in open field decreased slightly at the end of harvest, probably due to low temperature-induced leaf senescence in late autumn.

Relationship between canopy photosynthesis and plant growth or fruit yield

Canopy photosynthesis was positively correlated with dry biomass, leaf area and fruit yield under both growing conditions. Despite consistently lower photosynthesis rates at the leaf level, the overall whole-canopy photosynthetic production of high tunnel-grown plants exceeded that of open field-grown plants by 46%, due to the fact that plants grown under high tunnel produced on average 1.6 times more leaf area than those grown in open field. Crop yield as a function of accumulated biomass was higher under high tunnel, due to the significant increase in whole-canopy leaf area that overcompensated for the leaf-level photosynthetic depression either caused by lower leaf PPFD.

5.7 Acknowledgements

The author wishes to ackonowledge Agriculture and Agri-Food Canada (AAFC), The Conseil Canadien de l'Horticulture (CCH), Natural Sciences and Engineering Research Council of Canada (NSERC), Les Fraises de l'Île d'Orléans Inc., Fafard et Frères ltd. and Pépinière Luc Lareault inc. for the technical and financial support.

Chapter 6: General conclusion and further perspectives

6.1 Conclusion

In summary, the experiments conducted on red raspberry (*Rubus idaeus* L.) from 2012 to 2014 in Québec, Canada were aimed to 1) determine the influence of a) growing environments (high tunnel and Voen shelter *vs.* open field), b) presence of white reflective ground cover, and c) plant managements practices (like summer pruning for floricane-fruiting cultivars and cane density optimization for primocane-fruiting cultivars) on marketable fruit yield; 2) further explain the main effects of growing conditions on fruit yield by making leaf-level microclimate *vs.* photosynthesis measurements; and 3) investigate in more details the differences between tunnel- and field-grown plants in terms of canopy growth, PPFD distribution and canopy-level photosynthesis and fruit yield throughout the four vertical canopy layers.

6.1.1 Objective 1

The first objective was to determine the influence of a) growing conditions (high tunnel and Voen shelter *vs.* open field), b) addition of white reflective ground cover, and c) summer pruning (for floricane-fruiting cv. 'Jeanne d'Orleans') or cane density (for primocane-fruiting cv. 'Polka') on the marketable fruit yield of both fruiting types of red raspberry cultivated under Quebec climatic condition (71°01′W, 46°52′N), and thereby to identify the optimum cropping system for each fruiting type.

For both floricane-fruiting cv. 'Jeanne d'Orléans' and primocane-fruiting cv. 'Polka', plants grown under high tunnel had the highest marketable fruit yield, followed by those grown under Voen shelter, in comparison to plants growing in open field, which produced significantly less fruit yield. The use of white reflective ground cover significantly improved marketable fruit yield.

More specifically, for cv. 'Jeanne d'Orléans', high tunnel significantly increased fruit yield by 2.1-fold in 2012 and 2.4-fold in 2013 compared to open field respectively.

Plants grown under Voen shelter comparatively produced 1.6 and 2.3 times more fruits than in open field over the two respective years. White reflective mulch significantly improved fruit yield by 13.9% and 10.3% during 2012 and 2013, respectively. Plants grown with their current-year shoots pruned tended to produce significantly more fruits than unpruned plants in 2012 and in 2013. Pruning of new current-year shoots in biennial floricane-fruiting raspberry culture increased fruit yield only slightly in the first year, but significantly more so in the following year.

For primocane-fruiting cv. ‘Polka’, compared to Voen shelter high tunnel significantly increased marketable fruit yield 1.3-fold in 2012 and 1.6-fold in 2013, whereas compared to open field the increases were 1.8-fold and 3.4-fold over the two respective years. White reflective mulch significantly improved fruit yield by 18.3% and 15.8% during 2012 and 2013, respectively. Additionally, increasing cane density from 2 to 4 to 6 canes per pot (giving 6 to 12 to 18 canes per linear meter) decreased the marketable fruit size and fruit yield per cane, but this inter-cane competition effect was not important enough to prevent the fruit yield per pot to significantly increase proportionally to cane density.

In summary, for floricane-fruiting cv. ‘Jeanne d’Orléans’, the best cropping system was to use high tunnel, white reflective ground cover, and pruning the flushes. For primocane-fruiting cv. ‘Polka’, the use of high tunnel, reflective mulch and a density of 4 stems per pot constituted the optimal cultivation system.

6.1.2 Objective 2

The second objective consisted of determining the effects of growing conditions (high tunnel and Voen shelter *vs.* open field) and white reflective ground mulch or canopy positions (lower *vs.* upper canopy) on the leaf microclimate prevailing around the peripheral fruiting region of the row crop and the corresponding average photosynthesis rate per unit leaf area of both floricane-fruiting (cv. ‘Jeanne d’Orleans’) and primocane-fruiting (cv. ‘Polka’) red raspberries grown under Quebec cool climatic condition (2013).

Firstly, with respect to reflective mulch effects, during the fruiting period of cv. ‘Jeanne d’Orléans’, reflective ground cover presented a significant positive effect on PPFD reflected from the ground to the lower canopy under high tunnel and open field. No such effect was found under Voen shelter, which likely due to the significantly greater proportion of diffuse light produced by the special Voen coverings. During the fruiting season of ‘Polka’, a significant positive effect of white mulch on reflected PPFD in the lower canopy was only observed in open field. In all cases, ground cover type had no significant effect on the total leaf PPFD. Reflective mulch increased the total leaf PPFD in the fruiting canopy region by only about 10% for cv. ‘Jeanne d’Orléans’ and 5% for cv. ‘Polka’.

As a result, under each growing condition, the reflective mulch hardly benefited photosynthesis accumulation, at least over the short experimental time scale used in this study (i.e. around the fruiting period). In contrast, the effect of the reflective white ground cover on marketable fruit yield was significantly positive (see Chapter 2). That is possibly because fruit yield production is a long-term process wherein greater light reflection from the ground may have benefited vegetative growth and flower production, and most likely cumulative photosynthesis as well, during the earlier stages of cultivation.

Secondly, concerning canopy position effects, for cv. ‘Jeanne d’Orléans’ the leaf PPFD increased by 30% from lower to upper canopy in open field, but no differences were found under protected structures. In contrast, for cv. ‘Polka’ leaf PPFD increased by a similar 31.5% from lower to upper canopy under both protected structures, with concomitant photosynthetic increases of 25.7% and 20.9% under high tunnel and Voen shelter, respectively. This inter-varietal performance difference was likely due to the fact that cv. ‘Polka’ developed appreciably larger leaf canopies (with a higher density, 4 canes per pot) than cv. ‘Jeanne d’Orléans’ (2 canes per pot), resulting in significantly different vertical light gradient patterns between the two cultivars.

Thirdly, concerning growing condition effects, for cv. ‘Jeanne d’Orléans’, the leaf PPFD was attenuated by approximately 46% under the both type of protective coverings compared to open field. Corresponding leaf photosynthesis was on average reduced by 43% under high tunnel and by 17% under Voen shelter. Cultivar ‘Polka’ plants shared similar growing condition effects on leaf PPFD and photosynthesis. The consistently lower leaf photosynthesis rates observed under high tunnel were most likely caused by the significantly higher air temperature under this growth environment. Further analysis of pooled leaf photosynthesis *vs.* temperature data under the three different growing conditions confirmed that the net leaf photosynthetic rates of both cv. ‘Jeanne d’Orléans’ and ‘Polka’ fell steeply when leaf temperatures exceeded 25°C and 20°C, respectively.

In summary, compared with open field-grown plants, higher-yielding cultures were obtained under protected structures, yet with consistently lower photosynthesis per unit leaf area. To better explain this, for objective 3 we set up to scale individual leaf photosynthesis measurements up to the total leaf area of the canopy for the two most contrasting growing conditions: high tunnel *vs.* open field.

6.1.3 Objective 3

The third objective was to combine measurements of light distribution over the canopy leaf area and leaf level photosynthetic light-response curves to model the whole-canopy photosynthesis of floricane- and primocane-fruiting cultivars under high tunnel *vs.* in open field, and to characterize the photosynthetic contribution of different horizontal canopy layers to plant growth and fruit yield.

Firstly, with respect to high tunnel effects, high tunnel created ambient air temperatures 3.2/6.8°C (mean/max.) above that of open field during the 2014 growing season. Compared to open field-grown plants, high tunnel-grown ‘Jeanne d’Orléans’ and ‘Polka’ plants produced 1.6 and 1.4 times more dry biomass, 1.9 and 1.6 times more leaf area, and 1.5 and 1.5 times more whole-canopy photosynthesis, which taken together translated into 3.0 and 2.8 times more fruit yield, respectively.

Secondly, for the canopy layer effects, for cv. ‘Jeanne d’Orléans’ grown under high tunnel approximately 85% of the whole-canopy dry biomass, leaf area, canopy photosynthesis, and fruit yield were distributed in the three upper layers, while in open field the vertical distribution of dry biomass, leaf area, and canopy layer photosynthesis followed a ‘bell-shaped’ variation. As for fruit yield in the open field, all four canopy layers contributed equally. For cv. ‘Polka’, approximately 82% of the dry weight, 88% of the leaf area, 90% of the canopy photosynthesis, and 100% of the fruit yield was distributed in the three upper layers under each growing condition. In addition, dry biomass vertical distribution followed a ‘bell-shaped’ pattern variation over the four-layer canopy. No marketable fruits were found in the lowermost layer.

Thirdly, concerning seasonal effects, for cv. ‘Jeanne d’Orléans’ grown under high tunnel leaf area and dry weight increased linearly during the vegetative growth period and curvilinearly at a much lesser rate during the fruiting period. In open field, plants ceased their vegetative growth earlier at the beginning of fruiting period. Canopy photosynthesis increased until the harvest peak under high tunnel, whereas in open field it reached its maximum at the beginning of harvest, then decreased slightly until the end of harvest. For cv. ‘Polka’, under both growing conditions leaf area, dry weight, and canopy photosynthesis increased linearly during the vegetative growth phase and reached their respective maximum then remained constant during the fruiting period. The only exception was for canopy photosynthesis in open field, which decreased towards the end of harvest. This likely was caused by the occurrence of lower temperatures in autumn resulting in leaf senescence.

Lastly, regarding the relationship between canopy photosynthesis and plant growth or fruit yield, for both fruiting type cultivars whole-canopy photosynthesis was positively correlated with dry biomass, leaf area and fruit yield under both growing conditions. Despite consistently lower photosynthesis rates at the leaf level, the overall whole-canopy photosynthetic production of high tunnel-grown plants exceeded that of open field-grown plants by 51% and 46% for cv. ‘Jeanne d’Orléans’ and ‘Polka’, respectively, due to the fact that plants grown under high tunnel produced on average 1.9 and 1.6 times more leaf area than those grown in open field. Crop yield as a function of accumulated biomass was therefore higher under high tunnel, due to the significant increase in whole-canopy leaf area that overcompensated for the leaf-level photosynthetic depression either caused by lower leaf PPFD or high leaf temperatures.

6.2 Confirmation of the working hypotheses

Red raspberry cultivation under protected structures (high tunnel or Voen shelter) requires different cultural practices depending on cultivar fruiting type. For biennial floricane-fruiting cultivars, canopies can become very dense because both fruit-bearing floricanes and vegetative primocanes coexist and shade each other. In order to increase light availability in such dense canopies, two cultural practices, namely summer pruning of new vegetative shoots and laying down a white reflective mulch as ground cover were tested in our experiments. For annual primocane-fruiting cultivars, we tested cutting down the canes to the ground each consecutive year after fruit harvest to then try to optimize cane density in the following year to improve the harvest efficiency and keep higher fruit yielding.

Accordingly, in comparing the growth and fruit yield of both fruiting types of red raspberry grown in open field conditions *vs.* under high tunnel or Voen shelter, it was hypothesized that 1) summer pruning of new vegetative shoots and the presence of white reflective ground cover would stimulate the plant growth, fruit yield and leaf photosynthesis of floricane-fruiting red raspberry (‘Jeanne d’Orleans’) more so when grown under protected structures than in open field; and 2) optimization of cane density in the presence of reflective mulch would be more effective in improving the plant growth and fruit yield of primocane-fruiting red raspberry (‘Polka’) when grown under protective structures than in open field.

For both fruiting type cultivars, plants grown under high tunnel produced the highest marketable fruit yield during 2012 and 2013, followed by those grown under Voen shelter. On average, plants grown in open field produced 49.5% lower fruit yield than under protected structures. Using white reflective ground cover significantly improved marketable fruit yield in both open field (approx. 22.7%) and protected cultivation (13.0% on average), but contrary to our hypothesis, the effect was greater in open field due to the greater prevalence of ground reflected direct beam solar radiation. For cv. ‘Jeanne d’Orléans’, plants treated with pruning of new shoots produced on average 23.5% and 6.7% more fruit yield under protective structures and open field, respectively, than unpruned plants. For cv. ‘Polka’, as cane density increasing from 6 to 12 or 18 canes per linear meter, fruit yield increased by 56.9% or 86.1% under protective structures, and by 47.4% or 85.2% in open field. Consequently, fruit yield gain from summer pruning (cv. ‘Jeanne d’Orléans’) and high cane densities (cv. ‘Polka’) were higher under protective structures than in open field, thereby confirming our original hypotheses.

Despite consistently lower measured individual leaf photosynthetic rates, fruit yield was greater under protected structures than in open field. To better address the question of why field-grown raspberry plants gave the lowest fruit yield but highest leaf photosynthetic rates, we set to model the whole-canopy photosynthesis by integrating individual leaf-level photosynthetic light response measurements over the entire canopy leaf area to verify our hypothesis that the lesser leaf area of open field-grown raspberry plants (both fruiting type cultivars) would generate less total canopy photosynthesis despite greater leaf-level PPFD and photosynthesis than for plants grown under protective structures.

Experiments on floricane- or primocane-fruiting cultivar were conducted in 2014 under high tunnel *vs.* open field condition to estimate the whole-canopy photosynthesis. Plants were divided in four canopy layers and the light distribution in each layer was determined to integrate the leaf photosynthesis over the whole layer leaf area. Once scaled-up to the whole canopy, photosynthetic production under high tunnel was 51% higher for the floricane-fruiting cv. 'Jeanne d'Orléans' and 46% higher for the primocane-fruiting cv. 'Polka' due to the occurrence of almost two times more leaf area compensating the depression of leaf photosynthesis per unit area under high tunnel, hence confirming our hypothesis.

In summary, this study reported that cultivation under high tunnel effectively tripled the fruit yield of both floricane- and primocane-fruiting red raspberries grown in open field. This was largely due to the suppression of thigmomorphogenetic pressure onto the plant leaf area development, which resulted in significant increases in whole-canopy leaf area (1.9-fold for cv. 'Jeanne d'Orléans' and 1.6-fold for cv. 'Polka') that overcompensated for the leaf-level photosynthetic depression either caused by lower light or high leaf temperature under high tunnel.

6.3 Further perspectives

The experiments described herein contrasted field production *vs.* protected cultivation (high tunnel and Voen shelter) for two different fruiting types of red raspberry: floricane-fruiting cv. 'Jeanne d'Orléans', a local variety issued by Agriculture and Agri-food Canada (AAFC) that is now being popularized in Quebec, and primocane-fruiting cv. 'Polka', a popular variety originated from Poland known for its good yield performance.

In our studies, high tunnel and Voen shelter combined with other cultural practices like reflective ground cover, summer pruning and cane density optimization were used successfully for commercial production of both floricane- and primocane-fruiting red raspberries grown under northern Canadian climate. The superior yielding of plants grown under high tunnel could be explained by their greater biomass cumulating a bigger photosynthetic output even if the latter was shown to be reduced compared to the other two growing environments when evaluated on a per leaf area basis. A somewhat surprising finding was to note that both fruiting type cultivars used in our studies were highly sensitive to temperature above 20-25˚C, which explained the lower photosynthetic performance of leaves located in the hotter high tunnel. Further studies on the physiology of carbohydrate production and allocation in relation to temperature and/or vapour pressure deficit (VPD) stress would be required to better understand the cause of the aforementioned temperature-induced photosynthetic depression.

Because we worked with potted raspberry cultures with substantial leaf area receiving two to three irrigation pulses per day, there is a possibility that mild to moderate short-term water deficits may have regularly developed in between the irrigation events. Under field conditions, red raspberry have showed moderate tolerance to short-term water deficit (Crandall, 1995; Percival *et al.*, 1998; Privé and Janes, 2003; Morales *et al.*, 2013). However, little is known about the physiological responses to recurrent water deficits for potted raspberry plants grown under high tunnel. The significantly larger leaf area of these plants, coupled with the greater evaporative demand of the warmer tunnel environment (i.e. higher VPD), potentially makes them more vulnerable to temporary water deficits, and may require a tighter irrigation control. Moreover, multi-year cultivation of such perennial plants in pots eventually creates significant root restriction, which has often been associated with elevated abscisic acid levels in plant tissues and ensuing reduction of stomatal conductance and leaf photosynthesis (e.g. Shi *et al.*, 2008; Zaharah & Razi, 2009). More research would be required to find out if the above factors were involved in the photosynthetic depression we observed for high tunnel-grown raspberry plants, and if further optimization of the irrigation regime would help prevent the latter.

High tunnel structure is semi-closed system with rather limited microclimate control via the opening and closing of side walls or end doors, whereas Voen shelter is a more open protective cultivation system with better air ventilation. As was pointed out before, high tunnel increased the plant leaf area obtained in open field by almost two times. We think the larger leaf area of tunnel-grown plants was caused by the quasi-absence of wind-induced thigmomorphogenetic pressure (Chehab *et al.*, 2009). Raspberry fruits are not only susceptible to rainwater or sunburn, both essentially prevented by protective structure coverings, but also potentially affected by strong wind occurrence, which was frequent during our research on Île d'Orléans, Quebec.

Thus, it would be interesting to investigate more specifically the extent of the influence of wind speed on raspberry plant growth, carbohydrate allocation, and fruit yield, and on fruit quality such as fruit size and firmness. Experiments could be conducted in glasshouses at University Laval where the microclimate, including turbulent air mixing, can be better controlled than in field tunnels. These researches would provide necessarily theory support (better explain the yield loss in open field *vs.* under protective coverings) and more complete recommendations for commercial production of potted red raspberries cultures under protective cover.

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Appendix

Chapter 2

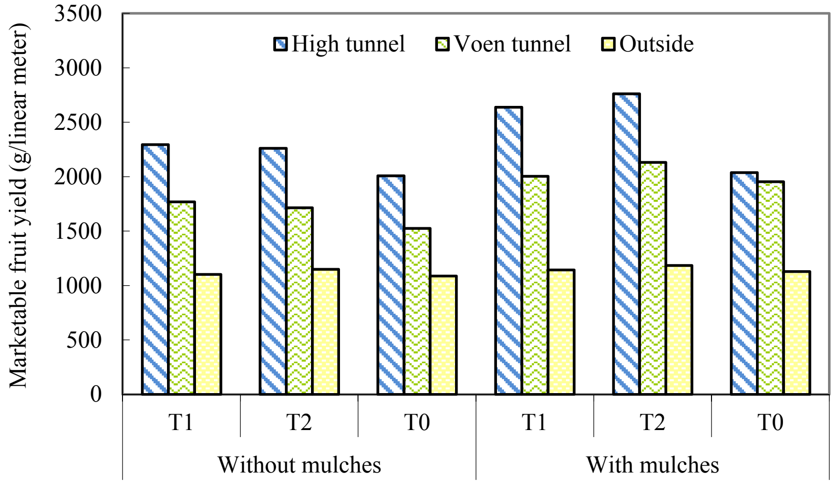

Figure A.2.1 The marketable fruit yield in each plot of floricane-fruiting cv. 'Jeanne d'Orléans' treated with or without reflective mulches and pruning (T0, unpruned; T1, pruned at 1st flush (June 5); T2, pruned at 2nd flush (July 5)) under high tunnel, Voen shelter and open field (2012).

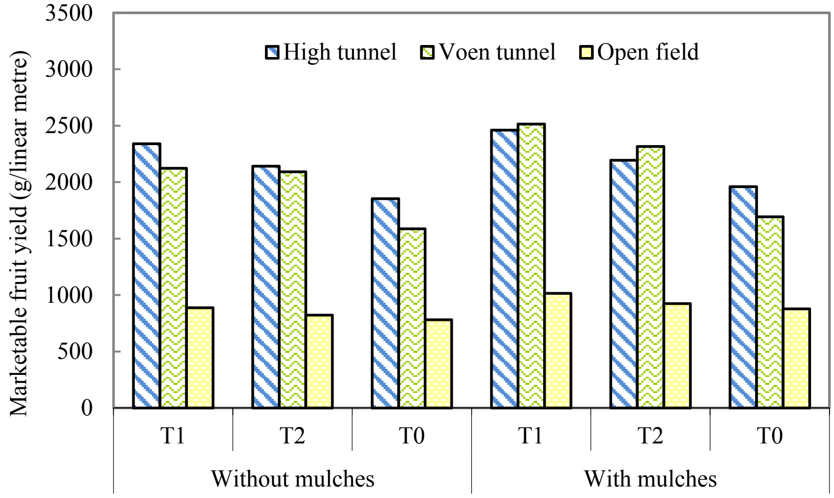

Figure A.2.2 The marketable fruit yield of floricane-fruiting cv. 'Jeanne d'Orléans' treated with or without reflective mulches and pruning (T0, unpruned; T1, pruned at 1st flush (June 5); T2, pruned at 2nd flush (July 5)) under high tunnel, Voen shelter and open field (2013).

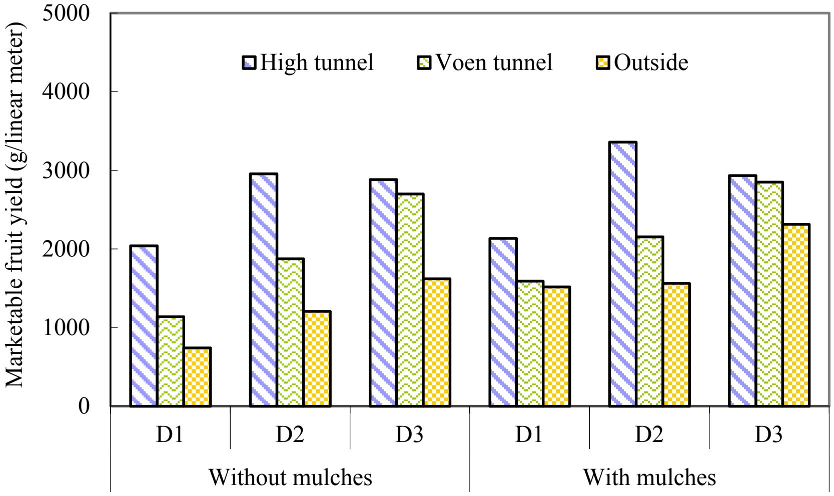

Figure A.2.3 The marketable fruit yield of primocane-fruiting cv. 'Polka' treated with or without reflective mulches and densities (D1, 2 canes per pot; D2, 4 canes per pot; D3, 6 canes per pot) under high tunnel, Voen shelter and open field (2012).

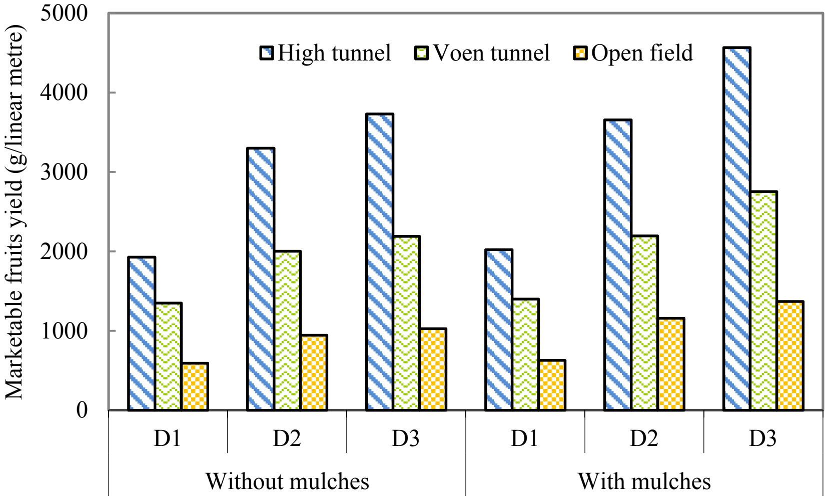

Figure A.2.4 The marketable fruit yield of primocane-fruiting cv. 'Polka' treated with or without reflective mulches and densities (D1, 2 canes per pot; D2, 4 canes per pot; D3, 6 canes per pot) under high tunnel, Voen shelter and open field (2013).

Chapter 3

Table A.3.1 ANOVA of photosynthesis of floricane-fruiting cv. ‘Jeanne d’Orléaans’ and primocane-fruiting cv. ‘Polka’: effect of reflective ground cover

Effect	**Photosynthesis** (µmol $CO_2 \cdot m^{-2} \cdot s^{-1}$)	**Leaf temperature** (°C)	**Total leaf PPFD** (µmol photons$\cdot m^{-2} \cdot s^{-1}$)	**Reflected PPFD** (µmol photons$\cdot m^{-2} \cdot s^{-1}$)
‘Jeanne d’Orléans’				
Lower canopy				
Protected cultivation (PC)	___<.0001*___	___0.0002*___	___0.0005*___	___<.0001*___
Mulch (M)	0.9546	0.5825	0.6422	___<.0001*___
PC*M	0.9743	0.5560	0.9417	___0.0167*___
Upper canopy				
PC	___<.0001*___	___<.0001*___	___<.0001*___	___<.0001*___
M	0.4189	0.5253	0.3234	___0.0002*___
PC*M	0.5175	0.8658	0.2344	___0.0017*___
‘Polka’				
Lower canopy				
PC	___0.0038*___	___0.0050*___	___<.0001*___	___<.0001*___
M	0.7936	0.8214	0.2751	___0.0148*___
PC*M	0.8133	0.4557	0.6501	0.1953
Upper canopy				
PC	___0.0082*___	___0.0025*___	___<.0001*___	___0.0022*___
M	0.3729	0.3632	0.4433	0.2784
PC*M	0.3368	0.6505	0.7469	0.6563

The * represents the significane level at $P < 0.05$.

Table A.3.2 ANOVA of photosynthesis of floricane-fruiting cv. ‘Jeanne d’Orléans’ and primocane-fruiting cv. ‘Polka’: effect of canopy positions

Effect	**Photosynthesis** (µmol$CO_2 \cdot m^{-2} \cdot s^{-1}$)	**Leaf temperature** (°C)	**Total leaf PPFD** (µmol photons$\cdot m^{-2} \cdot s^{-1}$)
‘Jeanne d’Orléans’			
Protected cultivation (PC)	___0.0017*___	___<.0001*___	___<.0001*___
Position (P)	0.2079	0.2132	___0.0165*___
PC*P	0.7017	0.9579	___0.0088*___
‘Polkas’			
PC	___0.0099*___	___0.0029*___	___<.0001*___
P	___0.0127*___	0.2102	___<.0001*___
PC*P	___0.0445*___	0.1945	0.2494

The * represents the significance level at $P < 0.05$.

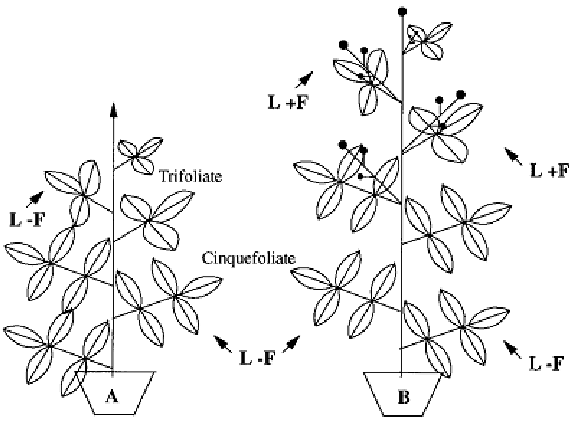

Figure A.3.1 Primocane-fruiting raspberry plant leaves in the absence (L –F) or presence (L +F) of a flowering or fruiting cane for A) a young vegetative, and B) a mature flowering or fruiting cane (Privé *et al.*, 1997).

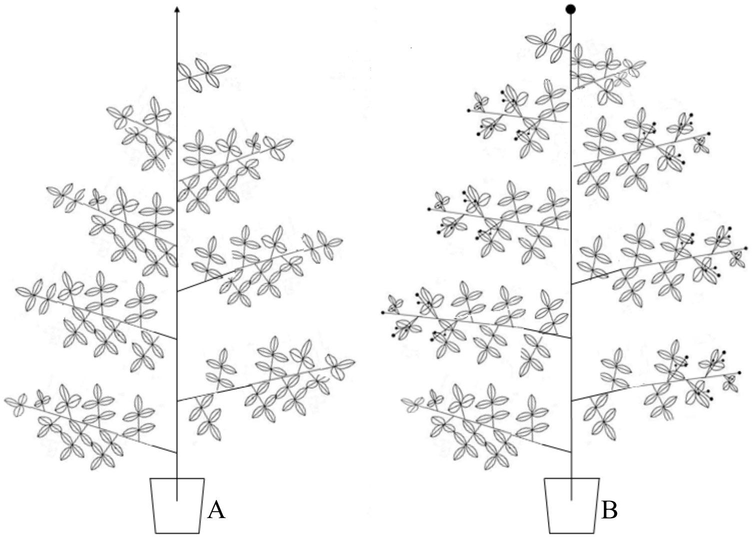

Figure A.3.2 Floricane-fruiting raspberry plant schematic diagram of leaves in the absence (L –F) or presence (L +F) of a flowering or fruiting lateral shoot for A) a young vegetative, and B) a mature flowering or fruiting lateral shoot. Trifoliate and pentafoliate leaves are also indicated.

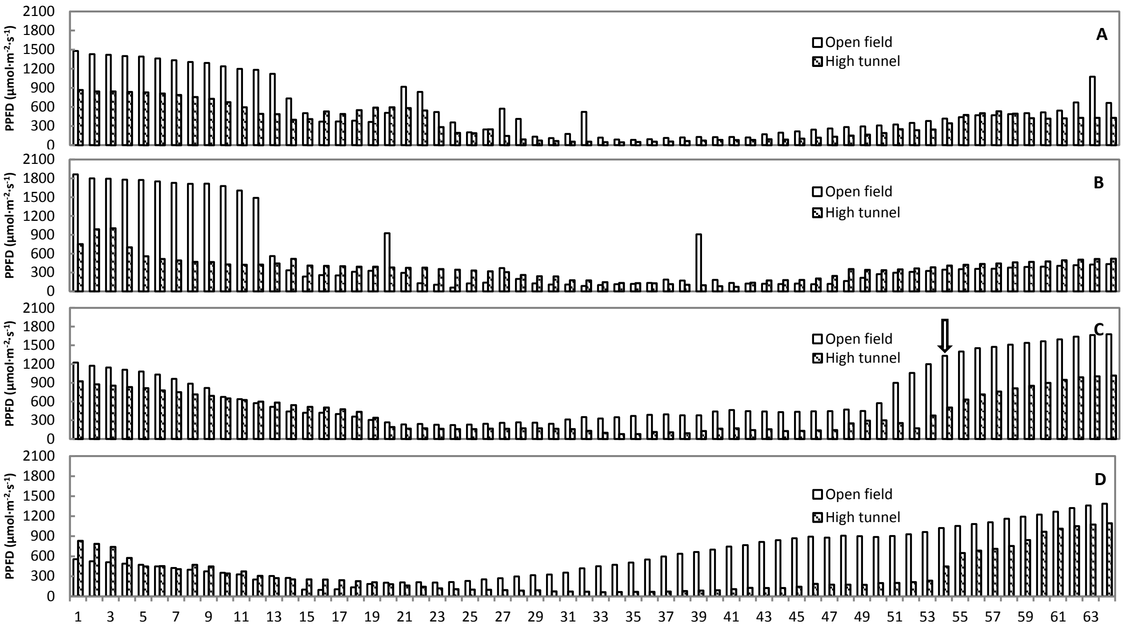

Figure A.4.1 Diurnal variations in horizontal PPFD distribution across canopy layer L3 of floricane-fruiting cv. 'Jeanne d'Orléans' grown under high tunnel and open field on July 20 2014: A) 9:00 am, B) 11:00 am, C) 1:00 pm and D) 3:00 pm. The arrow mark at panel C indicates one pared values of 64 diode readings (tunnel, 504 *vs.* field, 1332 μmol photons·m^{-2}·s^{-1}), thus resulting in the difference in leaf photosynthesis (see Figure A 4.2).

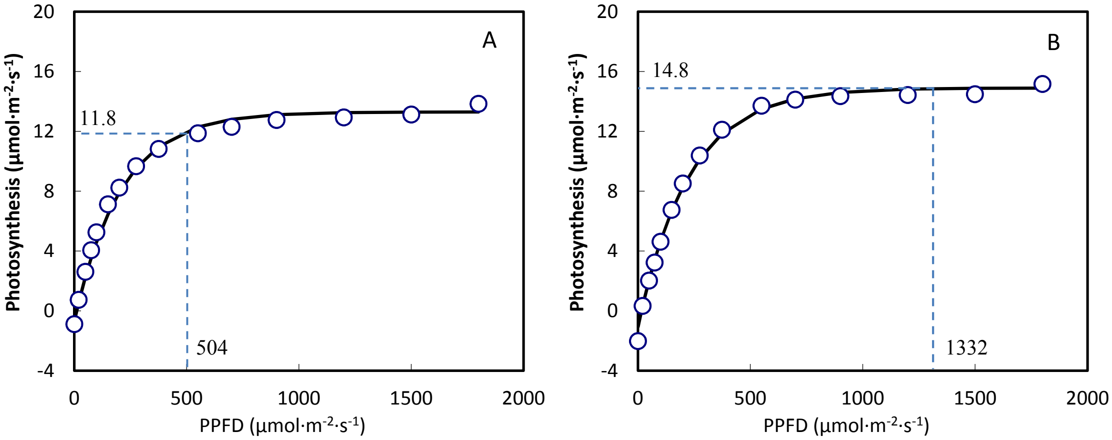

Figure A.4.2 Representative photosynthetic light response (A-Q) curves of floricane-fruiting cv. 'Jeanne d'Orléans' grown under A) high tunnel or B) open field. Shown here are measurements taken at 01:00 pm on canopy **Layer 3** on July 20, 2014 (cf. Fig. 4.6C). Values indicated beside the dotted lines represent the incident PPFD and net photosynthetic rate of each leaf under current ambient conditions prior to initiating the A-Q curve.

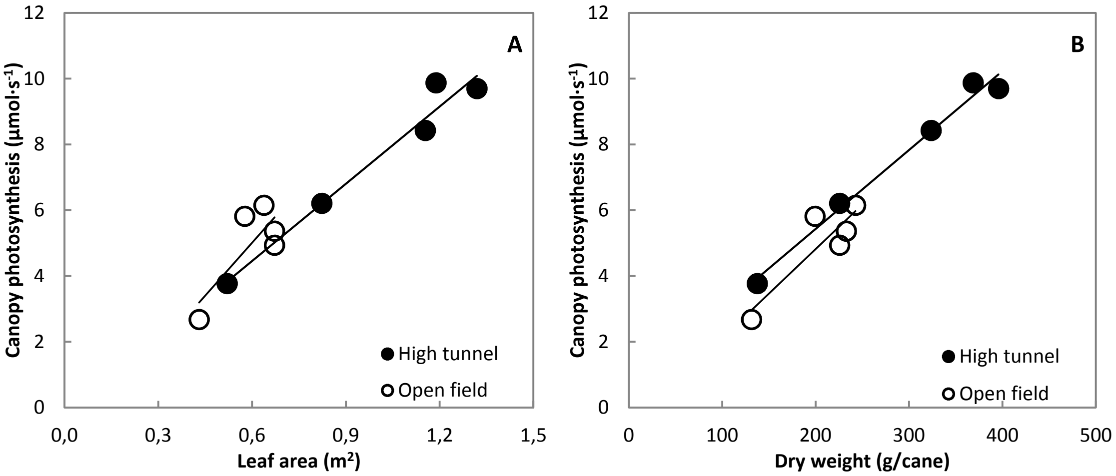

Figure A.4.3 The relationship between canopy photosynthesis and plant growth (A, leaf area and B, Dry weight) for floricane-fruiting cv. 'Jeanne d'Orléans' grown under high tunnel *vs.* open field during the 2014 growing season. Equations for the linear regression lines in A) were y = 7.83x - 0.24 ($R^2 = 0.96$, $P = 0.0029$) and y = 10.75x - 1.44 ($R^2 = 0.63$, $P = 0.11$) for high tunnel and open field, respectively, and in B) were correspondingly y = 0.02x + 0.63 ($R^2 = 0.98$, $P = 0.0008$) and y = 0.03x - 0.60 ($R^2 = 0.79$, $P = 0.0445$).

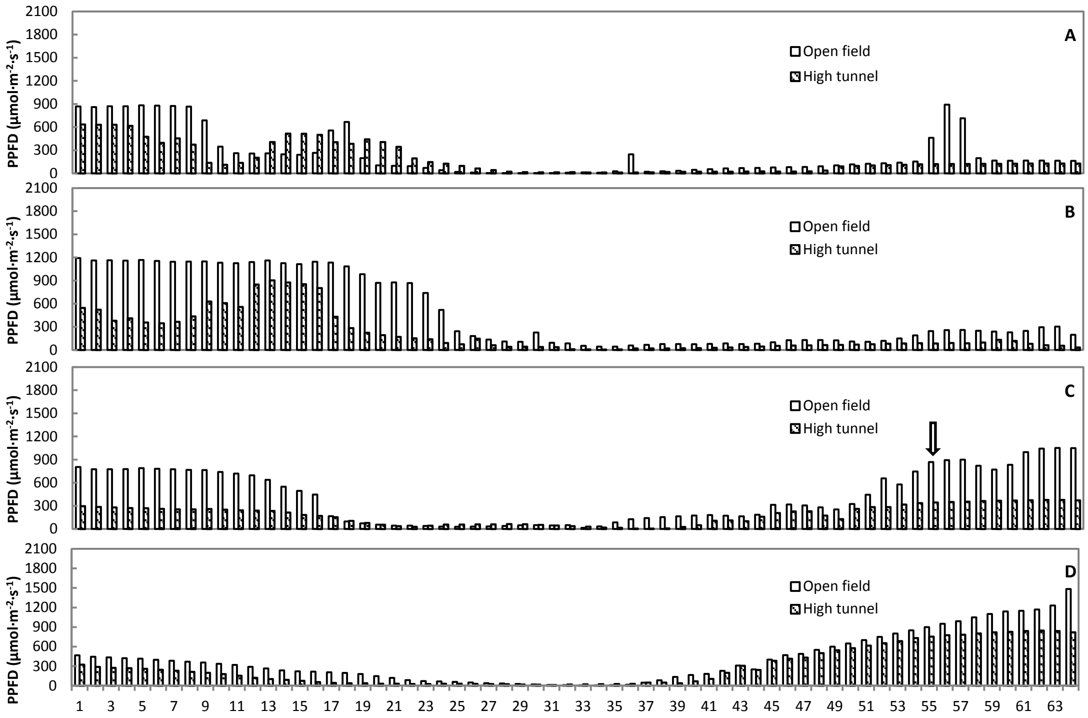

Figure A.5.1 Diurnal variations in horizontal PPFD distribution across canopy layer L3 of primocane-fruiting cv. 'Polka' grown under high tunnel and open field on August 23, 2014: A) 9:00 am, B) 11:00 am, C) 1:00 pm, D) 3:00 pm. The arrow mark at panel C indicates one pared values of 64 diode readings (tunnel, 344 *vs.* field, 868 µmol photons·m^{-2}·s^{-1}), thus resulting in the difference in leaf photosynthesis (see Figure A 5.2).

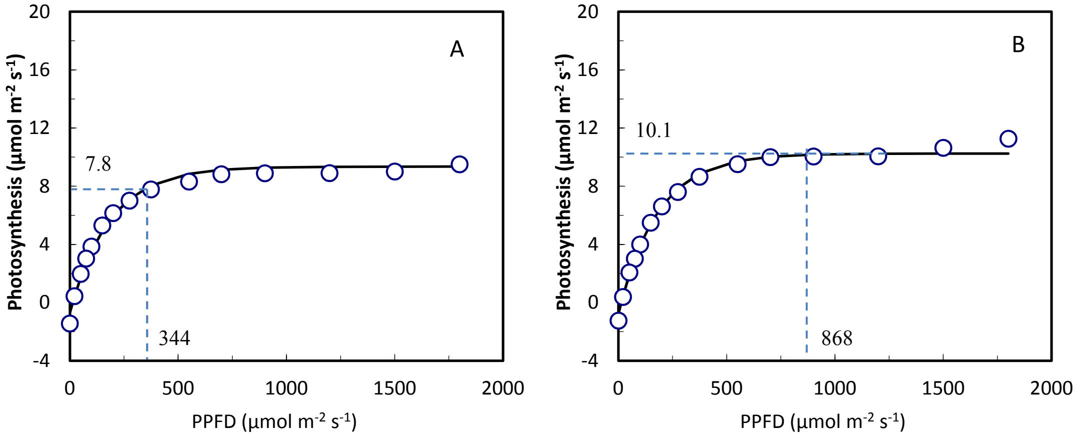

Figure A.5.2 Representative photosynthetic light response (A-Q) curves of primocane-fruiting cv. 'Polka' grown under A) high tunnel or B) open field. Shown here are measurements taken at 01:00 pm on canopy Layer 3 on August 23, 2014 (cf. Figure 5.5C). Values indicated beside the dotted lines represent the incident PPFD and net photosynthetic rate of each leaf under current ambient conditions prior to initiating the A-Q curve.

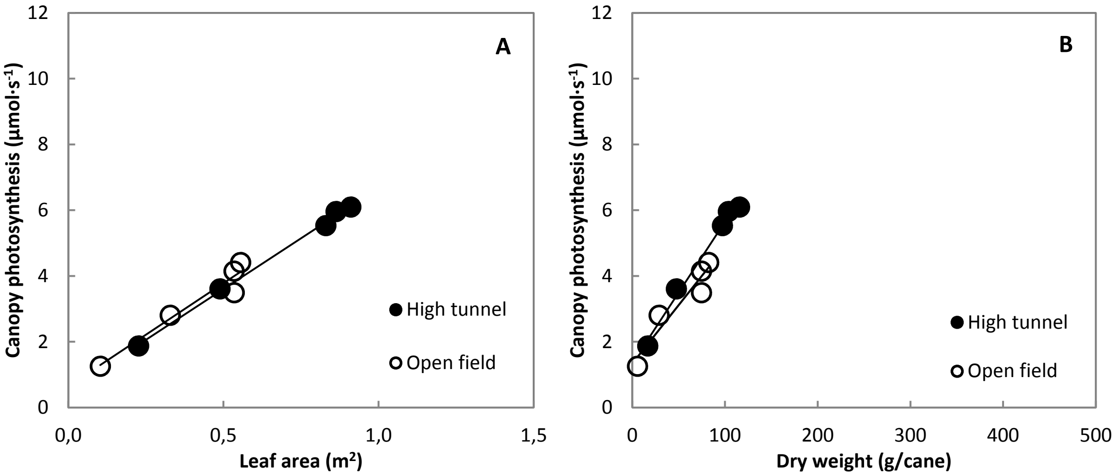

Figure A.5.3 The relationship between canopy photosynthesis and plant growth (A, leaf area and B, dry weight) for primocane-fruiting cv. 'Polka' grown under high tunnel *vs.* open field during the 2014 growing season. Equations for the linear regression lines in A) were $y = 6.17x + 0.52$ ($R^2 = 0.99$, $P = 0.00006$) and $y = 6.27x + 0.65$ ($R^2 = 0.94$, $P = 0.006$) for high tunnel and open field, respectively, and in B) were correspondingly $y = 0.043x + 1.34$ ($R^2 = 0.99$, $P = 0.0006$) and $y = 0.036x + 1.34$ ($R^2 = 0.91$, $P = 0.01$).