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# Estimation of daily carbon demand in sweet cherry (Prunus avium L.) production 

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#### Abstract

Summary In cherry production, the assimilate supply to the fruit is a crucial factor for growth and formation of quality parameters. The assimilate supply per fruit is limited by the relative growth capacity of trees, represented by the leaf area to fruit ratio (LA:F). In the present study, the required leaf area per fruit $\left(\mathrm{LA}_{\text {demand }}\left[\mathrm{cm}^{2}\right.\right.$ fruit $\left.\left.{ }^{-1}\right]\right)$ of two sweet cherry cultivars, 'Bellise' and 'Regina', was estimated in 2018 and 2019, based on measured and interpolated values of fruit growth and fruit respiration rates. $\mathrm{LA}_{\text {demand }}$ changed daily with an overall increase during fruit development, showing average values in stage III in 2018 and 2019 of $139 \mathrm{~cm}^{2}$ and $175 \mathrm{~cm}^{2}$ in 'Bellise', while $199 \mathrm{~cm}^{2}$ and $212 \mathrm{~cm}^{2}$ were found in 'Regina', respectively. Estimated $\mathrm{LA}_{\text {demand }}$ for both cultivars was compared with measurements in cherries grown on girdled branches. In both years, estimated values exceeded measured values. In both years, positive correlation between LA:F and fresh mass, soluble solids content, and coloration was observed. The data obtained can be applied to evaluate the tree's crop load for precise management.


Keywords: carbon balance, dry mass, fruit growth rate, fruit quality, fruit respiration, precision horticulture

## Introduction

Fruit quality of sweet cherry (Prunus avium L.) is frequently described by fruit size, coloration, soluble solids content (SSC), and texture (Kappel et al., 1996). The consumer's acceptance and corresponding market value highly depend on these quality attributes primarily determined by scion-rootstock combination (Gonçalves et al., 2006), management, crop load (Whiting and Lang, 2004), and environmental factors (Blanco et al., 2019). However, the underlying determinant is the fruit growth that enables development of fruit quality parameters, whereas the main variable of quality, the fruit size, even directly depends on the growth of the fruit.
Major driver of fruit growth and accordingly of yield, is the leaf area per fruit ratio (LA:F) (Whiting and Lang, 2004). In sweet cherry, the annual shoot growth is crucial for the development of fruiting branches, because branches usually start to bear fruit from the $3^{\text {rd }}$ year. Heterogeneity in soil properties within an orchard, frequently occurring in soils formed by glacial and post glacial deposits, influences the generative and the vegetative growth of stone fruit trees (KÄthner and Zude-Sasse, 2015; Molina et al., 2016), especially the growth of annual shoots. Therefore, tree size, total leaf area and potential yield per tree vary within orchards heterogeneous in soil properties. Considering that leaves provide the major source of carbohydrate necessary for fruit growth (Kappes and Flore, 1986), the LA:F of trees determines the magnitude of the potential fruit growth and the formation of quality parameters, which is limited by the seasonal environmental conditions at the growing location (Cittadini et al., 2008, Roper and Loescher, 1987; Whiting and Lang, 2004).

[^0]For cherry grown on $P$. avium seedling rootstocks, $16.8 \%$ of the seasonal above-ground dry mass of the whole tree was found in the fruit at harvest (KAPPEL, 1991). However, recent research pointed out that trees grown on dwarfing rootstocks provided larger percentages of carbohydrates to fruit than trees grown on seedling rootstocks (Ayala and LaNG, 2018). Furthermore, different leaf populations supply varying percentage of assimilated carbohydrates to the fruit. The contribution of leaves of current season's extension, non-fruiting spurs, and fruiting spurs of cherry trees grown on a dwarfing rootstock ranged from $17.5 \%$ to $79 \%$ at the different stages of fruit development (Ayala and Lang, 2018). The quantity of spurs usually depends on the number of buds per tree, which is set during pruning. Leaves can start to export assimilates $3 \mathrm{~d}-4 \mathrm{~d}$ after unfolding and current seasons extension shoots from 17 d after bud break (KAPPES and Flore, 1986). Though, it can be assumed that the percentage of carbohydrates supplied by the actual leaf populations on the different branches of the trees varies considerably during the season. Consequently, the leaf number per spur can be described as a function of growing degree day accumulation, but to a different extent for each type of leaf (EISENSMITH et al., 1980). For fruiting trees grown on $P$. avium rootstock at harvest, $45 \%$ of the LA was found on current season's shoots, $34 \%$ on one-year-old shoots, and the rest on older wood. On non-fruiting trees, $54 \%$ of LA grew on current season's shoots, $28 \%$ of the LA on one-year-old shoots and the rest on older wood (KAPPEL, 1991).
The influence of crop load and, particularly, the LA:F on fruit quality parameters was frequently investigated (Overholser and Claypool, 1934; Facteau et al., 1983; Roper and Loescher, 1987; Whiting and Lang, 2004; Cittadini et al., 2008; Usenik et al., 2010) showing positive correlations between LA:F and fresh mass, SSC and coloration of sweet cherry fruit. However, the specific leaf area necessary for high fruit growth and for high fruit quality varies considerably. In the trials of Overholser and Claypool (1934), the highest fruit mass of 7.4 g was achieved at $203 \mathrm{~cm}^{2}$ LA:F, whereas UsENIK et al. (2010) reported a fruit mass of 8.4 g at $99 \mathrm{~cm}^{2}$ LA:F. These differences may result from different cultivar, rootstock and tree size in the experiments as these factors affect yield efficiency, carbon partitioning to the fruit and light interception (GonÇalves et al., 2006). Furthermore, the LA:F in the above studies were all measured at harvest when fruit reached their final size. However, daily fruit growth and respiration rates, and the resulting daily fruit carbon demand of stone fruits underlie seasonal changes (DEJONG and Walton, 1989), as does the percentage of carbon partitioned to the fruit (Ayala and Lang, 2018). Consequently, it can be hypothesized that the leaf area necessary to supply the carbon demand of growing fruit varies during their development. It, additionally, depends on the ambient incident radiation intercepted by the leaves.
Information on the LA:F, necessary to supply the carbon demand of developing fruit, is crucial for precise crop load management. Particularly, the actual status of crop load at different timing during the season needs to be assessed. In some years, excessive crop load can occur, leading to unfavorable LA:F. This, in turn, results in high yield of small fruit (Whiting and LaNG, 2004), not reaching the
commercial quality requirements. The required crop load management should adjust a balanced LA:F. This enables fruit growing to a marketable size, homogeneous fruit calibers and high yield. In commercial sweet cherry production, crop load management can be performed via pruning (LAURI and CLAVERIE, 2005), mechanical flower thinning (Spornberger et al., 2014) or chemical thinning (Stern et al., 2009).
For precise management, information on the leaf area demand of individual trees is needed to assess the tree's actual crop load. In order to develop a method to estimate the seasonal leaf area demand for sweet cherry, the objectives of the present research were (i) to quantify the daily fruit carbon demand during the period of fruit development, (ii) to model the corresponding leaf area demand per fruit with values from the literature, and (iii) to compare the results with fruit grown in the field.

## Material and methods

## Orchard layout and treatment

Trials were carried out in 2018 and 2019 on sweet cherry (Prunus avium L.) trees of the cultivars 'Bellise' and 'Regina', planted in 2009 in the fruit production area of Werder, Germany ( 52.379971 N, 12.866811 E ). Trees were trained in a central leader system on Gisela 5 rootstock with planting distance of $2 \mathrm{~m} \times 4 \mathrm{~m}$. The area covered by the tree canopy, $G_{\text {covered }}\left[\mathrm{m}^{2}\right]$, was $3.2 \mathrm{~m}^{2}$. The management of the orchards was carried out according to the federal regulations of good horticultural practice.
Trees $(\mathrm{n}=30)$ per cultivar were labelled. Full bloom was observed on the 17.04. in 'Bellise' in both years, while in 'Regina' full bloom varied (2018: 25.04., 2019: 23.04.). Gas exchange, dry mass, elemental carbon, and growth of fruit were analyzed weekly for estimating carbon balance and leaf area demand, LA $_{\text {demand }}$. Fruit quality was measured at harvest.
To compare the $\mathrm{LA}_{\text {demand }}$ with LA:F and their effect on fruit quality, an additional trial with adjusted leaf:fruit ratio (L:F) was performed in the same orchard in 2018 and 2019. In both years at 13 d after full bloom (DAFB) three year-old fruiting branches $(\mathrm{n}=18)$ per cultivar, well exposed at the outside of the canopy, in 1.20 m height, forming approximately rectangular angles with the trunk, were girdled and three L:F (1:1, 2:1, 4:1) were adjusted. Initially, tips of the growing shoots and new leaf growth during the season were removed.

## Analyses of fruit $\mathrm{CO}_{2}$ gas exchange and fruit growth

In order to analyze the seasonal course of fruit's dark respiration rate, $\mathrm{R}_{\mathrm{dT}}\left[\mathrm{mg} \mathrm{kg}^{-1} \mathrm{~h}^{-1}\right]$, fresh mass, $\mathrm{FM}[\mathrm{g}]$, diameter, D [mm], and elemental carbon content, C [g], was measured in weekly intervals over the entire fruit developmental period in $2018(n=30)$ and $2019(n=40)$ for trees of both cultivars. D and FM were measured immediately after harvesting. Afterwards, respiration of 3 samples á 5 fruit in 2018 and 4 samples á 10 fruit in 2019 were measured in a closed cuvette system at $20^{\circ} \mathrm{C}\left( \pm 1^{\circ} \mathrm{C}\right)$ in 2018 and at $10^{\circ} \mathrm{C}\left( \pm 1^{\circ} \mathrm{C}\right)$ and $20^{\circ} \mathrm{C}$ $\left( \pm 1^{\circ} \mathrm{C}\right)$ in 2019. In 2018, gas samples were taken before closing the cuvettes and after 16 h using a glass syringe. The concentration of $\mathrm{CO}_{2}$ in the internal air $\left[\mu \mathrm{mol} \cdot \mathrm{mol}^{-1}\right]$ was analyzed with a gas chromatograph (GC 17A, Shimadzu Europa GmbH, Duisburg, Germany) at operating temperature of $60^{\circ} \mathrm{C}$. In 2019, fruit were placed in acrylic glass cuvettes equipped with continuously logging NIR- $\mathrm{CO}_{2}$ sensors (FYA600CO2, Ahlborn, Germany). Both systems were calibrated with 0 and $1000 \pm 20 \mathrm{ppm} \mathrm{CO}$ (Linde, Germany). $\mathrm{R}_{\mathrm{dT}}$ was calculated (equ. 1) considering the fruit volume, cuvette volume and actual atmospheric pressure in the system described by Brandes and Zude-Sasse (2019).
(1) $\mathrm{R}_{\mathrm{dT}}\left[\mathrm{mg} \mathrm{kg}^{-1} \mathrm{~h}^{-1}\right]=\Delta \mathrm{CO}_{2} \cdot \mathrm{FM}^{-1} \cdot \Delta \mathrm{t}^{-1}$

Subsequently, at each measuring date, 15 fruit per cultivar were dried at $80^{\circ} \mathrm{C}$ to constant mass. The dry sample was homogenized with a mixer mill (MM400, Retsch Technology, Haan, Germany) at a frequency of 30 Hz for 1 min . C content, $\mathrm{C}_{\text {rel }}[\%]$, of the homogenized dry mass (DM) was analyzed with an elemental analyzer (Vario EL III, Elementar Analysensysteme GmbH, Hanau, Germany) at $1150^{\circ} \mathrm{C}$. In 2018, the measured values of $\mathrm{C}_{\text {rel }}$ were interpolated to obtain daily data over the growing season by means of curve fitting, while reducing the square error (Table Curve 2D Version 5.01, Systat Software Inc., USA) and expressed as function of DAFB (equ. 2, 3). Similarly, equ. 2, 3 were applied in 2019 to estimate the absolute C content of fruit from the DM.
(2) $\mathrm{C}_{\text {rel }}(\mathrm{DAFB})_{\text {Bellise }}=49.9+10.02 \cdot(\exp (-0.5 \cdot((\mathrm{DAFB}-61.2)$. $\left.\left.12.6^{-1}\right)^{2}\right)$ ); $\mathrm{r}^{2}=0.85$
(3) $\mathrm{C}_{\mathrm{rel}}(\mathrm{DAFB})_{\text {Regina }}=\left(49.84-1.947 \cdot \mathrm{DAFB}+0.02686 \cdot \mathrm{DAFB}^{2}\right)$. $\left(1-0.0379 \cdot \text { DAFB }+0.00049 \cdot \text { DAFB }^{2}\right)^{-1} ; \mathrm{r}^{2}=0.87$

## Modelling of fruit growth, daily carbon demand and corresponding leaf area demand

The daily elemental carbon demand per fruit, $\mathrm{C}_{\text {daily }}\left[\mathrm{g} \mathrm{d}^{-1}\right]$, results from fruit growth, changes in storage carbohydrates, and respired carbon. In the present study, fruit growth and changes in storage carbohydrates of the fruit were considered as sum referred to as absolute growth rate, $\mathrm{AGR}_{\mathrm{C}}\left[\mathrm{g} \mathrm{d}^{-1}\right]$, defined as daily change in carbon content per fruit. Absolute growth rates for D, FM and C were calculated for each period (equ. 4-6).
(4) $\mathrm{AGR}_{\mathrm{D}}\left[\mathrm{mm} \mathrm{d}^{-1}\right]=\Delta \mathrm{D} \cdot \Delta \mathrm{t}^{-1}$
(5) $\mathrm{AGR}_{\mathrm{FM}}\left[\mathrm{g} \mathrm{d}^{-1}\right]=\Delta \mathrm{FM} \cdot \Delta \mathrm{t}^{-1}$
(6) $A G R_{C}\left[\mathrm{~g} \mathrm{~d}^{-1}\right]=\Delta \mathrm{C} \cdot \Delta \mathrm{t}^{-1}$

In 2018, measurements started 10 DAFB and 8 DAFB for 'Bellise' and 'Regina', respectively. The daily respired carbon per fruit, $\mathrm{R}_{\text {daily }}$ [g], was calculated from the measured respiration rate of fruit in the field, $R_{\text {field }}\left[\mathrm{mg} \mathrm{kg}^{-1} \mathrm{~h}^{-1}\right]$, and daily values of FM (equ. 7), assuming that no daily course in $\mathrm{R}_{\mathrm{dT}}$ occurred. Additionally, $\mathrm{CO}_{2}$ was converted into C by multiplying with the factor 0.27 representing the fraction of atomic mass of $\mathrm{C}\left(12.01 \mathrm{~g} \mathrm{~mol}^{-1}\right)$ of the molecular mass of $\mathrm{CO}_{2}$ ( $44.01 \mathrm{~g} \mathrm{~mol}^{-1}$ ).
(7) $\mathrm{R}_{\text {daily }}\left[\mathrm{g} \mathrm{d}^{-1}\right]=\mathrm{R}_{\text {field }} \cdot \mathrm{FM} \cdot 24 \cdot 0.27 \cdot 10^{-3}$
$\mathrm{R}_{\text {field }}$ was calculated from equ. 8, where $\mathrm{T}_{\text {mean }}$ is the average daily temperature $\left[{ }^{\circ} \mathrm{C}\right]$ in 2 m height recorded with temperature sensor (PT100 1/3 Class B, iMetos ${ }^{\circledR} 3.3$, Pessl Instruments GmbH, Austria) in the neighboring orchard $(52.453684 \mathrm{~N}, 12.824633 \mathrm{E})$.
(8) $\mathrm{R}_{\text {field }}\left[\mathrm{mg} \mathrm{kg}^{-1} \mathrm{~h}^{-1}\right]=$

$$
\begin{array}{ll}
\mathrm{R}_{\mathrm{d} 10^{\circ} \mathrm{C}}+\left(\mathrm{T}_{\text {mean }}-10\right) \cdot\left(\mathrm{R}_{\mathrm{d} 20^{\circ} \mathrm{C}}-\mathrm{R}_{\mathrm{d} 10^{\circ} \mathrm{C}}\right) \cdot 10^{-1} & \text { if } \mathrm{T}_{\text {mean }}<20^{\circ} \mathrm{C} \\
\mathrm{R}_{\mathrm{d} 20^{\circ} \mathrm{C}}+\left(\mathrm{T}_{\text {mean }}-20\right) \cdot\left(\mathrm{R}_{\mathrm{d} 20^{\circ} \mathrm{C}}-\mathrm{R}_{\mathrm{d} 10^{\circ} \mathrm{C}}\right) \cdot 10^{-1} & \text { if } \mathrm{T}_{\text {mean }}>20^{\circ} \mathrm{C}
\end{array}
$$

$\mathrm{Q}_{10-20}$ values were calculated at each measurement date (equ. 9). The $\mathrm{Q}_{10-20}$ values were applied in 2019 for temperature correction considering the same cultivar. Additionally, to estimate $\mathrm{R}_{\mathrm{d} 10^{\circ} \mathrm{C}}$ in 2018, $\mathrm{Q}_{10-20}$ of 2019 at the different measurement dates were applied in 2018 considering cherries at the same fruit size.
(9) $\mathrm{Q}_{10-20}=\mathrm{R}_{\mathrm{d} 20^{\circ} \mathrm{C}} \cdot \mathrm{R}_{\mathrm{d} 10^{\circ} \mathrm{C}}{ }^{-1}$
$\mathrm{C}_{\text {daily }}$ was quantified by the sum of $\mathrm{AGR}_{\mathrm{C}}$ and $\mathrm{R}_{\text {daily }}$ (equ. 10).
(10) $\mathrm{C}_{\text {daily }}\left[\mathrm{g} \mathrm{d}^{-1}\right]=\mathrm{AGR}_{\mathrm{C}}+\mathrm{R}_{\text {daily }}$

To estimate the leaf area demand, $\mathrm{LA}_{\text {demand }}\left[\mathrm{cm}^{2}\right]$, necessary to assimilate $\mathrm{C}_{\text {daily }}$, the $\mathrm{C}_{\text {daily }}$ was related to the daily assimilated C per tree, $\mathrm{P}_{\text {daily }}\left[\mathrm{g} \mathrm{d}^{-1}\right], \mathrm{G}_{\text {covered }}$ and the leaf area index of the tree, LAI $\left[\mathrm{m}^{2} \mathrm{~m}^{-2}\right]$, assuming that the fraction of the assimilated carbohydrates partitioned to fruit, $\mathrm{C}_{\text {part }}[0-1]$, was 0.5 (equ. 11). $\mathrm{P}_{\text {daily }}$ was calculated by use of equ. 12 , modified from the equation of the canopy daily net photosynthesis integral of Charles-Edwards (1982), analogue to the canopy photosynthesis model for apple developed by LAKSO and Johnson (1990).
(11) $\mathrm{LA}_{\text {demand }}\left[\mathrm{cm}^{2}\right]=\mathrm{C}_{\text {daily }} \cdot\left(\mathrm{P}_{\text {daily }} \cdot \mathrm{G}_{\text {covered }}{ }^{-1} \cdot \mathrm{LAI}^{-1} \cdot 10^{-4} \cdot \mathrm{C}_{\text {part }}\right)^{-1}$
(12) $\mathrm{P}_{\text {daily }}\left[\mathrm{g} \mathrm{d}^{-1}\right]=\left(\alpha \cdot \mathrm{S} \cdot \mathrm{h} \cdot{ }^{\max } \mathrm{J}_{\mathrm{CO} 2} \cdot\left(1-\exp \cdot\left(-\mathrm{k} \cdot \mathrm{LAI} \cdot \mathrm{F}_{\max }{ }^{-1}\right)\right)\right) \cdot$ $\left(\alpha \cdot \mathrm{k} \cdot \mathrm{S}+\mathrm{h} \cdot{ }^{\max } \mathrm{J}_{\mathrm{CO} 2}\right)^{-1} \cdot \mathrm{P}_{\mathrm{T}} \cdot \mathrm{G}_{\text {covered }} \cdot 0.27$

The leaf photochemical efficiency, $\alpha\left[\mu \mathrm{g} \mathrm{J}^{-1}\right]$, and rate of light saturated photosynthesis, ${ }^{\max } \mathrm{J}_{\mathrm{CO} 2}\left[\mathrm{~g} \mathrm{~m}^{-2} \mathrm{~s}^{-1}\right]$, were set 5.027 and 0.000788 , transformed from Flore (1994) under the assumption that the fraction of photosynthetic active radiation ( $400-700 \mathrm{~nm}$ ), PAR, from the solar radiation is 0.5 and the conversion factor from $\mu \mathrm{mol} \mathrm{s}^{-1} \mathrm{~m}^{-1}$ (PAR) to $\mathrm{W} \mathrm{m}{ }^{2}$ (PAR) is 0.2188 (McCree, 1972). The daily integral of solar radiation, $\mathrm{S}\left[\mathrm{MJ} \mathrm{m}^{-2} \mathrm{~d}^{-1}\right]$, was recorded by a pyranometer (CMP 3, Kipp \& Zonen, The Netherlands) in the spectral range of 300-2800 nm. The day length, $\mathrm{h}[\mathrm{s}]$, resulted from the daily hours where solar radiation ( $>0 \mathrm{~W} \mathrm{~m}^{-2} \mathrm{~h}^{-1}$ ) was abundant multiplied with $3600 \mathrm{~s} \mathrm{~h}^{-1}$. The canopy light extinction coefficient, k , was set 0.6 (Cittadini et al., 2008), the maximum daily light interception, $\mathrm{F}_{\max }, 0.7$. The LAI was assumed to increase with time from 0.5 at full bloom to a final value of 3.2 at 98 DAFB, when extension shoot growth was completed, in a sigmoid course (equ. 13). The curve was fitted with Table Curve 2D, using the data of Steiner et al. (2015), Нвотко (personal communication) and final LAI of 3.2 , measured on neighboring trees ( $n=6$; data not shown) when the canopy was fully developed.
(13) $\mathrm{LAI}(\mathrm{DAFB})=0.5+2.8010247 \cdot(1-\exp (-0.033901796 \cdot \mathrm{DAFB}))$

The temperature dependence of $\mathrm{P}_{\text {daily }}$ was considered by applying the normalized equation, $\mathrm{P}_{\mathrm{T}}[0-1]$, from Higgins et al., 1992 (equ. 14) for the average temperature in the hours when solar radiation was abundant, $\mathrm{T}_{\text {day }}\left[{ }^{\circ} \mathrm{C}\right]$.
(14) $\mathrm{P}_{\mathrm{T}}[0-1]=\left(11.985+3.846 \cdot \mathrm{~T}_{\text {day }}-0.20867 \cdot \mathrm{~T}_{\text {day }}{ }^{2}+0.0053294 \cdot\right.$ $\left.\mathrm{T}_{\text {day }}{ }^{3}-0.0000535728 \cdot \mathrm{~T}_{\text {day }}{ }^{4}\right) \cdot 16.1694^{-1}$

## Fruit quality and leaf area analyses

D of all fruit was measured weekly. At harvest, FM, SSC [\%Brix], hue angle, and apparent modulus of elasticity, E [kPA], were quantified for all fruit using a caliper, a refractometer (DR-301-95, Krüss, Germany), a texture analyzer (TA.XT, Stable Micro Systems Ltd., UK ) with a spherical steel body (diameter $\mathrm{D}=6.35 \mathrm{~mm}$ ) and a colorimeter (CM-2600d, Minolta Co. Ltd., Japan), respectively. E was calculated from the deformation, $\mathrm{L}[\mathrm{mm}]$ at a force, F , of 0.5 N (equ. 15; Mohsenin, 1986), where $\mu$ is the Poisson's ratio, which was assumed 0.5 . $\mathrm{R}_{1}$ and $\mathrm{R}_{2}$ are the radii of the individual cherry measured crosswise.
(15) $\mathrm{E}[\mathrm{MPa}]=\left(0.531 \cdot \mathrm{~F} \cdot\left(1-\mu^{2}\right)\right) \cdot \mathrm{L}^{1.5} \cdot\left(1 \cdot \mathrm{R}_{1}{ }^{-1}+1 \cdot \mathrm{R}_{2}{ }^{-1}+4 \cdot \mathrm{D}^{-1}\right)^{-0.5}$

Additionally, all branches were defoliated after harvest and individual leaf area were measured with a leaf area meter (CI-203, CID Bio-Science, Camas, WA USA). In 2019, strong winds caused branch breakage on 'Regina' trees one week prior to harvest. Therefore, data of 9 branches could not be recorded on the last date. Analysis of vari-
ance of D considering the different LA:F treatments on each measurement date at $5 \%$ confidence level was carried out with software R (Version 3.4.1, R Core Team, 2018) using the package 'userfriendlyscience' (PETERS, 2018). Regression equation of LA:F and quality attributes were calculated with the program Table Curve 2D (Version 5.01, AISN, Systat Software, CA, USA).

## Results

## Fruit development

In 2018 and 2019, trees of the early cultivar 'Bellise' flowered 8 d and 6 d earlier than those of 'Regina'. Fruit of 'Bellise' trees achieved the final size in a shorter period of time than those of 'Regina' in both years (2018: 10 d, 2019: 7 d). In 2018, FM of 'Regina' fruit exceeded that of 'Bellise', but fruit of both cultivars were similar in D (Fig. 1). In 2019, 'Bellise' fruit exceeded D and FM of 'Regina' fruit. Fruit of 'Bellise' grew to a final FM of $9.1 \pm 1.4 \mathrm{~g}$ and $8.7 \pm 1 \mathrm{~g}$ in 2018 and 2019, respectively, while those of 'Regina' reached $10.0 \pm 0.5 \mathrm{~g}$ and $8.4 \pm 1.2 \mathrm{~g}$, respectively. The dry mass content, $\mathrm{DM}_{\mathrm{rel}}[\% \mathrm{FM}]$, of 'Bellise' fruit varied between $11 \%-26 \%$ and $13 \%-21 \%$, while those of 'Regina' showed a variation of $10 \%-17 \%$ and $13 \%-22 \%$ during fruit development in 2018 and 2019, respectively. Flowers had an average $\mathrm{DM}_{\text {rel }}$ of $14 \%$, mature fruit of $17 \%$ and $20 \%$ for 'Bellise' and 'Regina', respectively.


Fig. 1: Time course fresh mass, diameter and carbon content of developing 'Bellise' (closed symbol, solid line) and 'Regina' (open symbol, dotted line) sweet cherry fruit during two growing seasons. Error bars show the standard deviation
$\mathrm{C}_{\text {rel }}$ of 'Bellise' and 'Regina' fruit was $49 \%$ and $50 \%$, respectively, at the beginning of the 2018 season. Values of fruit of both cultivars were similar until 39 DAFB and 28 DAFB for 'Bellise' and 'Regina', respectively, when $\mathrm{DM}_{\text {rel }}$ increased to $61 \%$ and $62 \%$, respectively, at harvest. Seasonal course of $\mathrm{C}_{\text {rel }}$ of fruit of both cultivars was interpolated using smoothing average and described as function of DAFB (equ. 2, 3).
The seasonal course of fruit diameter, D, followed a double sigmoid curve in both years (Fig. 1), indicating the stone hardening stage with reduced fruit growth from 20-27 DAFB in 'Bellise' and 19-27 DAFB in 'Regina' in 2018, while in 2019 the stone hardening periods were extended between 19-33 DAFB and 20-41 DAFB, respectively. In comparison, the C contents steadily increased in both years and in fruit of both cultivars until 2 and 3 weeks prior to harvest. During the last weeks of fruit development, the increase in C content of all fruit was pronouncedly accelerated. The derived growth rates


Fig. 2: Time course of absolute growth rates in fresh mass $\left(\mathrm{AGR}_{\mathrm{FM}}\right)$, diameter $\left(\mathrm{AGR}_{\mathrm{D}}\right)$, and elemental carbon $\left(\mathrm{AGR}_{\mathrm{C}}\right)$ of developing 'Bellise' (closed symbol, solid line) and 'Regina' (open symbol, dotted line) sweet cherry fruit in two years.
(Fig. 2) show similar patterns for both cultivars. In 2018, all growth rates peaked in 'Bellise' fruit at 20 DAFB, where AGR $_{D}$ achieved the highest values during fruit development. The first growth peak before stone hardening was less pronounced in 'Regina'. Growth rates showed unexpected minima in 2018, which were not found in 2019. The typical minimum during the stone hardening stages were measured for fruit of both cultivars in 2019. The decrease of fruit growth rates indicated the optimum harvest date. Only 'Regina' fruit in 2018 didn't reach the optimum harvest date, since the experiment was ended at the commercial harvest appearing earlier. The integral of growth rates of 'Bellise' fruit were enhanced in comparison to that of 'Regina'.
During fruit development, $\mathrm{R}_{\mathrm{d} 20}$ decreased from full bloom until harvest in a course typical for non-climacteric fruit (Fig. 3). Seasonal changes in $\mathrm{R}_{\mathrm{d} 20}$ in the two years were similar for fruit of both cultivars, though the average values during the last two weeks of fruit development were enhanced in 2019 compared to 2018. Maximum $\mathrm{R}_{\mathrm{d} 20}$ of $908 \mathrm{mg} \mathrm{kg}^{-1} \mathrm{~h}^{-1}, 702 \mathrm{mg} \mathrm{kg}{ }^{-1} \mathrm{~h}^{-1}$ in fruit of 'Bellise' and of 'Regina', respectively, were measured at the beginning of fruit development, while $\mathrm{R}_{\mathrm{d} 20}$ were minimal ( $45 \mathrm{mg} \mathrm{kg}^{-1} \mathrm{~h}^{-1}, 38 \mathrm{mg} \mathrm{kg}^{-1} \mathrm{~h}^{-1}$ ) at harvest and the week before in 2018. In 2019, $\mathrm{R}_{\mathrm{d} 20}$ were higher during this time $\left(76 \mathrm{mg} \mathrm{kg}^{-1} \mathrm{~h}^{-1}, 82 \mathrm{mg} \mathrm{kg}^{-1} \mathrm{~h}^{1}\right)$. In 2019, values of $\mathrm{R}_{\mathrm{d} 20}$ were 1.7-3.5 and 2.2-3.4 fold higher than $\mathrm{R}_{\mathrm{d} 10}$ for all fruit (Fig. 3, 4). $\mathrm{Q}_{10-20}$ varied during the season (Fig. 4).

## Carbon demand

In fruit of both cultivars, the temperature-corrected fruit respiration rate, $\mathrm{R}_{\text {field }}$, was highest after full bloom and declined afterwards (Fig. 5). During the initial 10 d of fruit development, average air temperature was, below $21^{\circ} \mathrm{C}$. In $2018, \mathrm{R}_{\text {field }}$ was lowest during the last days of fruit development in fruit of both cultivars, while in 2019 the lowest $\mathrm{R}_{\text {field }}$ were measured on May 15 due to prevailing low temperature of $7.6^{\circ} \mathrm{C}$ for samples of both cultivars. At 25 DAFB and 43 DAFB , elevated $\mathrm{R}_{\text {field }}$ were recorded for 'Regina' cherries as a response to elevated temperature of $17.2{ }^{\circ} \mathrm{C}$ and $24.1^{\circ} \mathrm{C}$, respectively. At these days, 'Bellise' fruit was less responsive to the high temperature.
The amount of carbon respired per day per fruit, $\mathrm{R}_{\text {daily }}$, increased during fruit development from bloom until the final fruit size was achieved (Fig. 5). Highest annual value of $\mathrm{R}_{\text {daily }}$ of 'Bellise' fruit was $0.0040 \mathrm{~g} \mathrm{~d}^{-1}(42 \mathrm{DAFB}, 2018)$ and $0.0059 \mathrm{~g} \mathrm{~d}^{-1}(49 \mathrm{DAFB}, 2019)$; that


Fig. 3: Time course of fruit dark respiration rate at $10{ }^{\circ} \mathrm{C}\left(\mathrm{R}_{\mathrm{d} 10}\right.$; dotted and dash-dotted line) and $20^{\circ} \mathrm{C}\left(\mathrm{R}_{\mathrm{d} 20}\right.$; solid and dashed line) of developing 'Bellise' (closed symbol) and 'Regina' (open symbol) sweet cherry fruit in two years. Error bars show the standard deviation.


Fig. 4: $\mathrm{Q}_{10-20}$ values for fruit respiration between $10^{\circ} \mathrm{C}$ and $20^{\circ} \mathrm{C}$ of 'Bellise' (closed symbol) and 'Regina' (open symbol) cherries during fruit development in 2019. Error bars show the standard deviation.
of 'Regina' cherries were $0.0040 \mathrm{~g} \mathrm{~d}^{-1}$ (36 DAFB, 2018) and 0.0069 $\mathrm{g} \mathrm{d}^{-1}$ (53 DAFB, 2019). Integration of $\mathrm{R}_{\text {daily }}$ over the entire fruit development yielded 0.12 g C respired per fruit ( $56 \mathrm{~d}, 2019$ ) in 'Bellise' whereas 'Regina' totally respired $0.17 \mathrm{~g} \mathrm{C} \mathrm{(63} \mathrm{d}, \mathrm{2019)} .\mathrm{Dark} \mathrm{respira-}$ tion accounted for $10 \%$ and $13 \%$ of the total C demand of developing 'Bellise' fruit in 2018 and 2019, respectively, with daily variation of $2 \%-44 \%$ and $5 \%-37 \%$. For fruit of 'Regina', the average percentage of dark respiration of the total C demand was $9 \%$ and $15 \%$, with daily variation of $3 \%-27 \%$ and $3 \%-41 \%$ in 2018 and 2019 , respectively. The daily carbon consumption per fruit, $\mathrm{C}_{\text {daily }}$ considering fruit respiration and fruit growth were lowest at full bloom in 2019 ('Bellise': $0.004 \mathrm{~g} \mathrm{~d}^{-1}$; 'Regina': $0.002 \mathrm{~g} \mathrm{~d}^{-1}$ ) and highest at harvest in 2018 ('Bellise': $0.09 \mathrm{~g} \mathrm{~d}^{-1}$, 'Regina': $0.06 \mathrm{~g} \mathrm{~d}^{-1}$ ) (Fig. 6). Starting at 40 DAFB and 47 DAFB (2018) as well as at 39 DAFB and 40 DAFB


Fig. 5: Time course of average daily air temperature, measured at 2 m height, $\mathrm{T}_{\text {mean }}$, fruit respiration rate calculated for $\mathrm{T}_{\text {mean }}, \mathrm{R}_{\text {field }}$, and daily respired carbon per fruit, $\mathrm{R}_{\text {daily }}$, of developing 'Bellise' (closed symbol, solid line) and 'Regina' (open symbol, dashed line) sweet cherries during the growing seasons 2018 and 2019.
(2019) in 'Bellise' and 'Regina' fruit, respectively, $\mathrm{C}_{\text {daily }}$ increased until harvest with reduced rate around harvest. From 16 DAFB till harvest 'Bellise' cherries consumed 0.93 g C and 0.92 g C in 2018 and 2019, respectively, whereas 'Regina' cherries consumed 1.18 g C and 1.09 g C in 2018 and 2019, respectively. Values of both years point out an enhanced total C demand of 'Regina' fruit compared to 'Bellise' fruit.
The daily assimilated C per tree, $\mathrm{P}_{\text {daily }}$, was lowest at full bloom in 2018 ('Bellise': $10 \mathrm{~g} \mathrm{~d}^{-1}$; 'Regina': $7 \mathrm{~g} \mathrm{~d}^{-1}$ ) and early in the season in 2019 ('Bellise': 17 DAFB; 'Regina': 11 DAFB) and increased over the season with fluctuations (Fig. 6). Highest values ( $37 \mathrm{~g} \mathrm{~d}^{-1}, 2018$ ) were observed at harvest for 'Bellise' cherries at the same time when LAI reached the maximum of 2.8 considering the period of fruit development. Maximum value of $P_{\text {daily }}\left(37 \mathrm{~g} \mathrm{~d}^{-1}\right)$ of 'Regina' fruit was observed at 43 DAFB, when solar radiation, $S$, achieved its seasonal maximum ( 28 MJ). In 2019, $\mathrm{P}_{\text {daily }}$ of 'Bellise' cherries was maximal $\left(35 \mathrm{~g} \mathrm{~d}^{-1}\right)$ at 49 DAFB, when S peaked. 'Regina' trees showed maximum $\mathrm{P}_{\text {daily }}\left(36 \mathrm{~g} \mathrm{~d}^{-1}\right)$ at harvest when LAI was 3.0 . The magnitude of $\mathrm{P}_{\text {daily }}$ coincided with that of S , a major determinant of $\mathrm{P}_{\text {daily. }}$. The integral of $\mathrm{P}_{\text {daily }}$ of 'Bellise' was 1347 g C and 1205 g C in the 2018 ( $52 \mathrm{d)} \mathrm{and} 2019$ ( $56 \mathrm{d)}, \mathrm{respectively} .\mathrm{During} \mathrm{fruit} \mathrm{development}$, $\mathrm{P}_{\text {daily }}$ of 'Regina' trees was 1664 g C in 2018 ( 62 d ) and 1484 g C in 2019 ( 63 d ). The seasonal course of $\mathrm{LA}_{\text {demand }}$ derived from $\mathrm{C}_{\text {daily }}$ varied considerably over both seasons (Fig. 6).
Resulting, the seasonal course of $\mathrm{LA}_{\text {demand }}$ was inverse to that of S . Minima in $S$ coincided with peaks in $\mathrm{LA}_{\text {demand }}$, e.g. at 29 DAFB,

35 DAFB, 41 DAFB, and 50 DAFB for 'Bellise' cherries in 2019 (Fig. 6). A maximum of $643 \mathrm{~cm}^{2}$ was estimated for the $\mathrm{LA}_{\text {demand }}$ at 60 DAFB in 2018 of 'Regina' cherries when $\mathrm{T}_{\text {field }}$ was $13{ }^{\circ} \mathrm{C}$ and S was minimal ( 8 MJ ). In 'Bellise' cherries, $\mathrm{LA}_{\text {demand }}$ was highest ( $504 \mathrm{~cm}^{2}$ ) at 49 DAFB in 2018 as a result of $\mathrm{C}_{\text {daily }}$ being maximal despite relatively high S and $\mathrm{T}_{\text {field. }}$. During fruit development $\mathrm{LA}_{\text {demand }}$ increased. However, temporary reduction in $\mathrm{LA}_{\text {demand }}$ appeared corresponding to the stages of fruit growth (Fig. 6, Tab. 1). In the last days of fruit development after stone hardening, $\mathrm{LA}_{\text {demand }}$ varied between cultivars and years due to differences in $\mathrm{C}_{\text {daily }}$ and $\mathrm{P}_{\text {daily }}$. 'Regina' fruit had a total higher $\mathrm{LA}_{\text {demand }}$ in 2018 and 'Bellise' appeared more demanding in 2019.

## Results considering adjusted $\mathrm{L}: \mathrm{F}$

The average individual leaf area from the trial was $23 \mathrm{~cm}^{2}, 26 \mathrm{~cm}^{2}$ for 'Bellise' and $28 \mathrm{~cm}^{2}, 28 \mathrm{~cm}^{2}$ for 'Regina' in 2018 and 2019, respectively. Results from the trial on untreated trees and adjusted L:F on girdled branches were compared considering the LA and number of fruits measured in the laboratory (Tab. 2).
In 2018, 'Bellise' fruit grown with $115 \mathrm{~cm}^{2}$ LA:F reached enhanced size from 20 DAFB until harvest compared to fruit D of treatments with LA:F of $19 \mathrm{~cm}^{2}$ and $50 \mathrm{~cm}^{2}$, while treatments with $19 \mathrm{~cm}^{2}$ and $50 \mathrm{~cm}^{2}$ showed no difference (Fig. 7). In 2018, in the real world experiment with no thinning treatment (control) and resulting unknown LA:F of 'Bellise' fruit, $\mathrm{LA}_{\text {demand }}$ was higher than the actual LA:F


Fig. 6: Time course of changes in total carbon demand per fruit, $\mathrm{C}_{\text {daily }}$, solar radiation, S , estimated carbon assimilation, $\mathrm{P}_{\text {daily }}$, and daily leaf area demand per fruit, $\mathrm{LA}_{\text {demand }}$, of developing 'Bellise' (solid line) and 'Regina' (dashed line) sweet cherries in the growing season 2018 and 2019 under the assumption that $50 \%$ of the assimilated carbon is partitioned to fruit.

Tab. 1: Leaf area demand [ $\mathrm{cm}^{2}$ ] of sweet cherry fruit considering the 8 day interval in two years. Values in parenthesis are mean values with local maxima excluded, compare Fig. 6.

| Cultivar/Year | Average $\mathrm{LA}_{\text {demand }}$ fruit ${ }^{-1}\left[\mathrm{~cm}^{2}\right]$ |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 1-8 DAFB | 9-16 DAFB | 17-24 DAFB | 25-32 DAFB | 33-40 DAFB | 41-48 DAFB | 49 DAFB-harvest |
| 'Bellise' |  |  |  |  |  |  |  |
| 2018 | - | - | 101 | 112 (101) | 70 | 164 (124) | 464 |
| 2019 | 16 | 48 | 89 | 106 (84) | 90 (56) | 209 (188) | 328 |
| 'Regina' |  |  |  |  |  |  |  |
| 2018 | - | 27 | 47 | 75 | 152 | 98 | 330 (307) |
| 2019 | 10 | 30 | 99 (75) | 56 | 89 | 157 | 249 |

Tab. 2: Diameter of cherries (D) grown at adjusted leaf to fruit ratios (L:F) on girdled branches $(\mathrm{n}=18)$ and corresponding leaf area to fruit ratio (LA:F) measured in the laboratory; and leaf area demand per fruit $\left(\mathrm{LA}_{\text {demand }}\right)$, estimated for crop found in untreated trees (control, $n=30$ ), see Fig. 6.

| Cultivar | Year | L:F | $\begin{aligned} & \text { LA:F } \\ & {\left[\mathrm{cm}^{2}\right]} \end{aligned}$ | $\begin{gathered} \mathrm{LA}_{\text {demand }} \\ {\left[\mathrm{cm}^{2}\right]^{*}} \end{gathered}$ | $\begin{gathered} \mathrm{D} \\ {[\mathrm{~mm}]} \end{gathered}$ |
| :---: | :---: | :---: | :---: | :---: | :---: |
| 'Bellise' | 2018 | 1 | 19 | - | $22.9 \pm 1.6^{\text {a }}$ |
|  |  | 2 | 50 | - | $23.4 \pm 1.5^{\text {a }}$ |
|  |  | 4 | 115 | - | $26.5 \pm 1.4{ }^{\text {b }}$ |
|  |  | Control | - | 226 (202) | $27.2 \pm 1.2^{\text {b }}$ |
|  | 2019 | 1 | 25 | - | $21.0 \pm 1.8^{\text {a }}$ |
|  |  | 2 | 59 | - | $25.0 \pm 2.0^{\text {b }}$ |
|  |  | 4 | 110 | - | $27.1 \pm 1.7^{\text {c }}$ |
|  |  | Control | - | 260 | $26.7 \pm 1.2^{\text {c }}$ |
| 'Regina' | 2018 | 1 | 32 | - | $22.4 \pm 1.2^{\text {a }}$ |
|  |  | 2 | 63 | - | $25.0 \pm 1.6^{\text {b }}$ |
|  |  | 4 | 132 | - | $25.4 \pm 1.6^{\text {b }}$ |
|  |  | Control | - | 237 (208) | $27.0 \pm 0.8^{\text {c }}$ |
|  | 2019 | 1 | 23 | - | $20.9 \pm 1.5^{\text {a }}$ |
|  |  | 2 | 68 | - | $23.4 \pm 2 .{ }^{\text {b }}$ |
|  |  | 4 | 132 | - | $25.6 \pm 1.6^{\text {c }}$ |
|  |  | Control | - | 214 | $25.2 \pm 1.5^{\text {c }}$ |

*from 41 DAFB - harvest, values in parenthesis are mean values with local maxima excluded
between 41 DAFB and harvest. D of fruit grown at $115 \mathrm{~cm}^{2}$ LA:F was 26.5 mm , which is 0.7 mm less than D of the untreated fruit from the untreated trees. In 2019 at 20 DAFB, D of 'Bellise' fruit grown on low ( $25 \mathrm{~cm}^{2}$ ) LA:F was significantly ( $\mathrm{p}<0.005$ ) lower than that of fruit grown on medium ( $59 \mathrm{~cm}^{2}$ ) or high ( $110 \mathrm{~cm}^{2}$ ) LA:F (Tab. 2). From 26 DAFB until harvest, differences between D of fruit of all treatments were significant ( 26 DAFB: $\mathrm{p}<0.001,33$ DAFB - harvest: $\mathrm{p}<0.0001$ ). Fruit grown at $110 \mathrm{~cm}^{2}$ LA:F achieved higher D than that of untreated fruit with an average estimated $\mathrm{LA}_{\text {demand }}$ of $260 \mathrm{~cm}^{2}$. In 2018, D of 'Regina' fruit grown on low LA:F was lower than that of fruit grown at $63 \mathrm{~cm}^{2}, 132 \mathrm{~cm}^{2}$ from 27 DAFB to harvest (Fig. 7). Fruit grown at high LA:F had lower D then untreated fruit from the


Fig. 7: Time course of changes in fruit diameter of sweet cherry cultivars 'Bellise' (a: 2018, c: 2019) and 'Regina' (b: 2018, d: 2019) developing at different leaf:fruit ratio (star: 1:1, open triangle: $2: 1$, closed triangle: 4:1). Error bars show the standard deviation.
control tress, and LA:F was also lower LA demand of untreated fruit. In 2019, 'Regina' fruit grown at $23 \mathrm{~cm}^{2}$ LA:F and $68 \mathrm{~cm}^{2}$ LA:F showed no differences in D until 56 DAFB when D of fruit grown at $68 \mathrm{~cm}^{2}$ LA:F exceeded D of fruit grown at $23 \mathrm{~cm}^{2}$ LA:F to harvest. Fruit grown at LA:F of $132 \mathrm{~cm}^{2}$ exceeded D of fruit from the other treatments from 34 DAFB to harvest. At harvest, D of fruit grown at $132 \mathrm{~cm}^{2}$ LA was higher than D of untreated fruit with $\mathrm{LA}_{\text {demand }}$ of $208 \mathrm{~cm}^{2}$ (when peaks were excluded). In addition, fruit maturity was delayed in every trial on trees of the lowest LA:F treatment in comparison to those of untreated trees.
The leaf area to fruit ratio (LA:F) affected FM, coloration and SSC, while no effect on E was found considering fruit of both cultivars in two years (Fig. 8, Tab. 3). In 2018, fresh mass of 'Bellise' fruit pronouncedly increased with LA:F in the range of $11 \mathrm{~cm}^{2}$ to $126 \mathrm{~cm}^{2}$. In 2019 lowest FM of 'Bellise' fruit of 3.7 g was observed when grown at $14 \mathrm{~cm}^{2}$ LA:F and highest FM of 10.9 g at $136 \mathrm{~cm}^{2}$ LA:F. FM of








Fig. 8: Means of fresh mass (FM), hue angle (), SSC () and modulus of elasticity (E; of sweet cherries of 'Bellise' (closed symbol, solid line) and of 'Regina' (open symbol, dotted line) grown with different leaf area to fruit ratio (LA:F) in 2018 and 2019. Error bars show the standard deviation.

Tab. 3: Equations relating fruit quality attributes, $y$, and leaf area to fruit ratio (LA:F), $x$, and corresponding coefficient of determination, $R^{2}$, of 'Bellise' and 'Regina' sweet cherry fruits in two years.

| Cultivar | Attribute | Year | Regression equation | $\mathrm{R}^{2}$ |
| :---: | :---: | :---: | :---: | :---: |
| 'Bellise' | FM [g] | 2018 | $y=-132.041 \cdot \exp (-0.0002536 \cdot x)+136.7$ | 0.58 |
|  |  | 2019 | $y=-9.146 \cdot \exp (-0.017219 \cdot x)+11.05$ | 0.65 |
|  | hue angle [ ${ }^{\circ}$ ] | 2018 | $y=1.15+24.824 \cdot(1+0.009796 \cdot x)^{-0.5}$ | 0.78 |
|  |  | 2019 | $y=14.87+11.274 \cdot \exp (-0.010588 \cdot x)$ | 0.61 |
|  | SSC [\%Brix] | 2018 | $y=-247.343 \cdot \exp (-0.00028148 \cdot x)+256.02$ | 0.47 |
|  |  | 2019 | $y=-338.642 \cdot \exp (-0.00026261 \cdot x)+347.13$ | 0.55 |
| 'Regina' | FM [g] | 2018 | $y=-8.5609 \cdot \exp (-0.023849 \cdot x)+10.02$ | 0.40 |
|  |  | 2019 | $y=-10.2947 \cdot \exp (-0.01468 \cdot x)+11.2$ | 0.28 |
|  | hue angle [ ${ }^{\circ}$ ] | 2018 | $y=9.32+27.877 \cdot(1+0.305193 \cdot x)^{-0.5}$ | 0.56 |
|  |  | 2019 | $y=15.69+10.82519 \cdot \exp (-0.020641686 \cdot x)$ | 0.69 |
|  | SSC [\%Brix] | 2018 | $y=-17.7442 \cdot \exp (-0.00987962 \cdot x)+24.25$ | 0.52 |
|  |  | 2019 | $\mathrm{y}=-11.118 \cdot \exp (-0.0067048 \cdot \mathrm{x})+24.01$ | 0.41 |

'Regina' cherries increased similarly with LA:F (Tab. 2). Hue angle of 'Bellise' fruit decreased with increasing LA:F in both years, while results of 'Regina' fruit showed no clear trend. SSC was in expected ranges, showing an influence of LA:F on SSC. In 'Regina' fruit, SSC increased with LA:F from 10 \%Brix to 21 \%Brix in 2018 and $16 \%$ Brix to 22 \%Brix in 2019. In contrast, LA:F and E showed no correlation.

## Discussion

## Fruit development

Fruit of both cultivars showed typical growth patterns for sweet cherry (Lilleland and Newsome, 1934) reaching similar fruit sizes. In the present study, time course of the development of fresh mass and diameter did not differ between fruit of both cultivars in 2018. In 2019, however, FM and D development of 'Regina' fruit was slower than those of 'Bellise'. Furthermore, in 'Regina' cherries, overall fruit development from full bloom to harvest was generally retarded in both years. The generally higher standard deviation of data observed in 2018 but not in 2019 may be due to the dry and hot weather in former year. The findings that absolute growth rates in both fresh mass $\left(\mathrm{AGR}_{\mathrm{FM}}\right)$ and diameter $\left(\mathrm{AGR}_{\mathrm{D}}\right)$, but not in total carbon content $\left(\mathrm{AGR}_{\mathrm{C}}\right)$, decreased during mid growing period (35 DAFB 41 DAFB) irrespective of year and cultivar was also described earlier (Lilleland and Newsome, 1934). This effect was explained by independent growth of flesh, endocarp and kernel in stone fruit as well as by changes in fruit composition during fruit development.
The assumed enhanced growth rate of early mature 'Bellise' in comparison to 'Regina' fruit was confirmed for $\mathrm{AGR}_{\mathrm{FM}}$ and $\mathrm{AGR}_{\mathrm{D}}$. In sweet cherry (BRÜGGENWIRTH et al., 2016) and peach (DeJong et al., 1987), dry mass-based absolute growth rates peaked shortly before final fruit size was reached. In contrast, the dry mass-based carbon content, $\mathrm{AGR}_{\mathrm{C}}$, increased further. Consequently, considering fruit quality, harvest should be as late as possible because AGR $_{C}$ and SSC continue to increase even after the end of fruit size growth (Proebsting and Mills, 1981). As present dry mass-based data clearly indicate, the increase in SSC did not only result from a concentrating effect due to the reduction of fruit water content.
The seasonal changes in fruit $\mathrm{DM}_{\text {rel }}$ observed for both cultivars and seasons are common in cherries and occur due to water potential gradient-induced vascular water flow (BRÜGgENwIRTH et al., 2016). Generally, $\mathrm{DM}_{\mathrm{rel}}$ of mature fruit at harvest are expected to increase with leaf area per fruit (Overholser and Claypool, 1934). Consistently, SSC and LA:F were positively correlated in the present study. $\mathrm{C}_{\text {rel }}$, measured during early season well reflected former results, though values gathered at the end of the season exceeded data
reported for sweet cherry pits (53.9\%, Petrov et al., 1999), whole peaches ( $47.5 \%$, DeJong and Walton, 1989) and mature apples (44.5\%, Lakso and Denning, 1996).

The seasonal courses of $\mathrm{R}_{\mathrm{dT}}$ and $\mathrm{R}_{\text {daily }}$ were found to be similar for fruit of both cultivars in the present study. In addition, very similar $\mathrm{R}_{\mathrm{dT}}$ was measured earlier in sweet cherries at the end of the fruit development (Sekse, 1988). In the present study, higher $\mathrm{Q}_{10-20}$ values were measured than $\mathrm{Q}_{10}$ values published for sour cherry ranging from 1.5-2 (Flore and Layne, 1999) and fruit developmentaveraged $\mathrm{Q}_{20-30}$ values of 1.9 for peach (DeJong et al., 1987). However, $\mathrm{Q}_{12-20}$ reported for pear in shelf life was higher (Brandes and Zude-Sasse, 2019), while $\mathrm{Q}_{20-30}$ of peach (DeJong et al., 1987) fluctuated during the season with no visible trend. In the literature, average percentages of dark respiration on total carbon demand were estimated as $13 \%-23 \%$ for sweet cherry (Loescher et al., 1986), $30.9 \%$ for sour cherry (Flore and Layne, 1999), and 16.3\%, 20.5\% for peach considering two cultivars (DeJong and Walton, 1989). The latter results were in the daily range of the values found in the present study.
In contrast, the total percentage of dark respiration was lower than values reported earlier. Although fruit photosynthesis reduces net $\mathrm{CO}_{2}$ losses by refixation of respirational $\mathrm{CO}_{2}$ (PAVEl and DeJong, 1993), fruit photosynthesis was not considered in the presented estimations, nor in the previous analyses. In sour cherry, fruit photosynthesis contributed $11.2 \%$ of the fruit's carbon balance and this rose up to $29.7 \%$ in stage II, when expressed on a daily basis, especially for fruit grown in exposed positions (Kappes and Flore, 1986). In the present investigation, the difference in $\mathrm{C}_{\text {daily }}$ for both cultivars originated mostly from $\mathrm{AGR}_{\mathrm{C}}$, because respiration had a much lower contribution to $\mathrm{C}_{\text {daily }}$ than $\mathrm{AGR}_{\mathrm{C}}$.

## Leaf area to fruit ratio

Daily carbon demand per fruit, $\mathrm{C}_{\text {demand }}$, increased during fruit development, resulting in an increased $\mathrm{LA}_{\text {demand }}$. Furthermore, peaks of $\mathrm{C}_{\text {demand }}$ and $\mathrm{LA}_{\text {demand }}$ appeared, potentially exceeding the available leaf area, which highly depends on solar radiation. Additionally, when $\mathrm{LA}_{\text {demand }}$ was elevated on days with low photosynthesis, fruit growth could have been maintained by consumption of malate, which is available in fruit, and of other stored reserves previously partitioned to the fruit. Previous research on apple demonstrated shaded fruit had reduced growth rates after 30 hours of $90 \%$ shade (Zibordi et al., 2009). In the present study, on none of the days solar radiation was below $10 \%$ of the average, and periods of low light lasted no longer than one day. Therefore peaks of $\mathrm{LA}_{\text {demand }}$ were ex-
cluded, when they appeared for less than 2 d . Carbon partitioning to the fruit is influenced by various factors such as weather, source-sink relations, developmental stage, sink-strength or position of the fruit. In the present study, the estimation was obviously simplified.
Ayala and Lang (2018) reported that the percentage of assimilated carbon available to fruit varied between $17.5 \%$ and $79 \%$ depending on leaf population and time. Leaves on fruiting spurs provided the highest percentage of assimilates to the fruit, while leaves on current seasons extension shoots contributed lowest to the fruit carbon yield. Moreover, in the late season, when daily $\mathrm{C}_{\text {demand }}$ of developing fruit was highest, $\mathrm{C}_{\text {part }}$ of every leaf population increased. Speculating that $\mathrm{C}_{\text {demand }}$ in the present study was reduced by $10 \%$ due to fruit photosynthesis and $\mathrm{C}_{\text {part }}$ during the final 10 days before harvest was $65 \%$ (average $\mathrm{C}_{\text {part }}$ at 56 DAFB from Ayala and Lang, 2018), the $\mathrm{LA}_{\text {demand }}$ in the period 41 DAFB till harvest was $135 \mathrm{~cm}^{2}$ and $166 \mathrm{~cm}^{2}$ for 'Bellise' fruit, $149 \mathrm{~cm}^{2}$ and $147 \mathrm{~cm}^{2}$ for 'Regina' fruit in 2018 and 2019 , respectively. Such weighing of the type of leaves resulted in estimations closer to the actual values of the LA:F confirmed in the trial with girdled branches. Though, comparison between the estimated $\mathrm{LA}_{\text {demand }}$ and measured LA:F in the experiment with girdled branches and adjusted L:F has limited validity as the leaf population of the girdled branches consisted of fruiting spur leaves close to the fruit with high $\mathrm{C}_{\text {part }}$. Whereas, observations on random fruiting branches of 'Regina' showed that the percentage of fruiting spur leaves per total leaf numbers varied from $17 \%-58 \%$ (data not shown). This indicates a generally higher leaf area demand of fruit on whole trees in comparison to the adjusted branches, due to the abundance of leaves from non-fruiting shoots and current season's extension shoots with lower $\mathrm{C}_{\text {part }}$. Furthermore, girdling interrupted vascular connections of the branches to other sink organs within the tree and removal of the shoots tips reduced the sink organs of the branches to mainly fruit. As a result of the absence of other strong sink organs and its competition for assimilates, $\mathrm{C}_{\text {part }}$ of the girdled branches can be assumed to be elevated. In general, there is lack of data (not necessarily practical knowledge) on the temporal composition of the different leaf populations in the varying training systems. Flore and Layne (1999) reported that leaf emergence on sour cherries of spurs and long shoots occurred at 30 d and 60 d after bud break, respectively, demonstrating seasonal variation. LOESCHER et al. (1986) found that the growth of current season's long shoots was completed at 114 d after bud break in 'Bing' sweet cherry. The seasonal course of the percentage of different leaf populations on the total leaf area per tree, the exposure of leaf to solar radiation (EISENSMITH et al., 1980), and carbon partitioning to the fruit need to be further investigated in sweet cherry to increase the accuracy of carbon balance estimation. Also, estimation models for the final leaf area of sweet cherry, early in the season need to be further developed, to enable prediction of each tree's potential maximum yield and, together with the carbon demand of targeted fruit size, the fruit bearing capacity (FBC) of the tree. FBC is defined as the crop load of a specific tree, which enables fruit growth to a certain size. Knowledge of the tree-specific FBC would improve current methods to evaluate the tree's current crop load status at any time during the season for precision management. Nevertheless, the strong daily variation in $\mathrm{LA}_{\text {demand }}$ was figured out for fruit of both cultivars in all fruit growth stages. Also, it was demonstrated that differences in $\mathrm{LA}_{\text {demand }}$ between two cultivars yielding early and later mature fruit occurred, but with varying results, not clearly stating if one cultivar has a different $\mathrm{LA}_{\text {demand }}$ when comparing both years. Such varying cultivar-dependent responses to the seasonal occurring growth factors are well known in practice.
The estimated leaf area demand in the experiment on girdled branches provide the explanation for lower size fruit grown at a LA of $19 \mathrm{~cm}^{2}-32 \mathrm{~cm}^{2}$ and $50 \mathrm{~cm}^{2}-68 \mathrm{~cm}^{2}$ compared to fruit grown at $110 \mathrm{~cm}^{2}-132 \mathrm{~cm}^{2}$ LA:F. The growth in every treatment was source
limited by carbon availability. In the two treatments with the lowest L:F, the leaf area was sufficient to fulfil $\mathrm{LA}_{\text {demand }}$ of the fruit in the first stages of fruit development, while $\mathrm{LA}_{\text {demand }}$ exceeded the adjusted LA:F in the period from 20 DAFB - 40 DAFB and afterwards. The treatment with $110 \mathrm{~cm}^{2}-132 \mathrm{~cm}^{2}$ LA:F allowed similar fruit size as the untreated real world fruit. $\mathrm{LA}_{\text {demand }}$ of the untreated fruit was lower than the $110 \mathrm{~cm}^{2}-132 \mathrm{~cm}^{2}$ LA:F until 20 DAFB, whereas it was similar until 40 DAFB. In 2019, LA $_{\text {demand }}$ of untreated fruit exceeded LA:F of $110 \mathrm{~cm}^{2}-132 \mathrm{~cm}^{2}$ LA.

## Fruit quality

Minimum quality requirement for sweet cherry on the fresh market is in general $\mathrm{D} \geq 26 \mathrm{~mm}$, although individual retailers also accept $\mathrm{D} \geq 24 \mathrm{~mm}$. However, the enhanced fruit size is strongly desired. 'Bellise' cherries with D of 26 mm showed a FM of 8 g , 'Regina' fruit of 26 mm had a FM of 8.8 g . On the basis of the regression equations as shown in Tab. 2, 'Bellise' required $101 \mathrm{~cm}^{2}$ LA:F and $64 \mathrm{~cm}^{2}$ LA: F to achieve FM of 8 g in 2018 and 2019, respectively. 'Regina' required $83 \mathrm{~cm}^{2}$ LA:F and $99 \mathrm{~cm}^{2}$ LA:F in 2018 and 2019, respectively, to achieve FM of 8.8 g . The corresponding SSC at this LA:F was $16 \%$ Brix for fruit of both cultivars in 2018 and $14 \%$ Brix and $18 \%$ Brix in 2019 for 'Bellise' and 'Regina', respectively. In terms of taste, fruit should have $18 \%$ Brix (Proebsting and Mills, 1981). Considering the relationship of fruit quality attributes and LA:F (Tab. 2), e.g. LA:F of $137 \mathrm{~cm}^{2}, 109 \mathrm{~cm}^{2}$ for 'Bellise' cherries in 2018, 2019, respectively, were necessary to produce a cherry of 18 \%Brix. Data demonstrate that the leaf area demand to produce a high-quality fruit based on FM was higher in 'Bellise' cherry in comparison to 'Regina' in 2018, but lower than 'Regina' in 2019. When the optimum LA:F was based on SSC, 'Bellise' fruit production required a higher LA to produce fruit of $18 \%$ Brix in both years compared to 'Regina' fruit production. Therefore, no conclusive statement can be made, which cultivar has a higher leaf area demand to produce fruit of a marketable quality. Additionally, the high temperature in both years had strong influence on the results. June 2019 was one of the hottest months recorded in Germany within the last 70 years. In 2019 during fruit growth 105 h with average temperature above $30^{\circ} \mathrm{C}$ were measured, spread over 11 d with maximum temperature of $37{ }^{\circ} \mathrm{C}$. In 2018 during fruit development 52 h with average temperature $>30^{\circ} \mathrm{C}$ were measured, spread over 11 d . The maximum air temperature in 2018 from full bloom to harvest was $32{ }^{\circ} \mathrm{C}$. In general the effect of extreme weather events need to be further investigated on fruit growth and FBC of cherries.
However, the obtained results confirm findings of former studies showing that D, FM, SSC and coloration can be expressed as function of LA:F, while no relation between texture and LA:F existed (Cittadini et al., 2008). The positive correlation between LA:F and D, FM, SSC, and coloration originates from an increasing carbohydrate supply when LA:F is increasing during source limited fruit growth. When the carbon supply from the tree exceeds the carbohydrate demand of the growing fruit, the fruit growth will be sink limited (Warren Wilson, 1967). Therefore, the functions to describe the relation between LA:F and FM or SSC should be a saturation curve, in which the asymptote indicates sink limited growth. A linear relationship between LA:F and FM (FACTEAU et al., 1983; Roper and Loescher, 1987; Cittadini et al., 2008) may be due to measuring in the range of LA:F where growth is still source limited. Fruit firmness and E are supposed to be influenced by the water relations within the tree. Positive correlations between LA:F and to SSC, D, FM, and coloration (Tab. 4) was expected and reported earlier. UsENIK et al. (2010) reported for 'Lapins'/Gisela 5 that FM of 8.4 g was achieved at $93 \mathrm{~cm}^{2}$ LA:F, which confirmed FACTEAU et al. (1983) reporting L:F of 3.4 to achieve FM of 8.4 g of 'Bing' and 'Lambert' cherries, which equals $99 \mathrm{~cm}^{2}$ LA:F, when average LA is assumed

Tab. 4: Summary of studies on the relation between leaf area (LA)/ leaf number (L) per fruit (F) on soluble solids content (SSC), diameter (D), fresh mass (FM) and coloration of sweet cherry

| Source | Cultivar | Rootstock | Region | LA:F ( $\mathrm{cm}^{2}$ ) | L:F | Relation to LA:F |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  |  |  | SSC | D/FM | Color |
| Overholser and Claypool, 1934 | Napoleon | - | Wash. State | 20-203 | 0.5-8 | + | + | + |
| Facteau et al., 1983 | Bing, Lambert | - | Canada | - | 0.9-9 | + | + | n.i. |
| ROPER and LOESCHER, 1987 | Bing | - | Wash. State | 5-110 | - | + | + | + |
| Whiting and Lang, 2004 | Bing | Gisela 5 | Wash. State | 50-600 | - | + | + | n.i. |
| Cittadini et al., 2008 | Bing | P. mahaleb | Argentina | 125-500 | - | + | + | n.i. |
| UsENIK et al., 2010 | Lapins | Gisela 5 | Slovenia | 21; 65; 93 | 0.7; 2; 3 | + | + | + |

${ }^{+)}$Trait is positively related or correlated to LA:F/ L:F
${ }^{n . i .)}$ Relation was not investigated
$30 \mathrm{~cm}^{2}$. In contrast for 'Bing'/Gisela 5, regression between LA:F and FM showed that LA:F of $175 \mathrm{~cm}^{2}$ were necessary to produce a fruit of 8.4 g (Whiting and Lang, 2004), whereas 'Bing'/P. mahaleb required LA:F of $216 \mathrm{~cm}^{2}$ to grow to a final mass of 8.4 g (Cittadini et al., 2008). In other studies (Overholser and Claypool, 1934; ROPER and LOESCHER, 1987) fruit did not achieve a final fruit mass of 8.4 g at the highest LA:F. Additionally, Cittadini et al., 2008 found that there is no correlation between LA:F and firmness. Despite the positive correlations between LA:F and main quality attributes, the actual leaf area demand to produce a certain fruit quality varies in the literature, as the trials were conducted with different scion-rootstock combinations in different growing regions.
Two studies (Facteau et al., 1983; Usenik et al., 2010) describe LA:F around $100 \mathrm{~cm}^{2}$ as sufficient to achieve a $F M$ of 8.4 g , which is considered marketable. Other studies reported LA $>170 \mathrm{~cm}^{2}$ to produce a cherry of 26 mm , representing a FM of 8.4 g . In the present study, $\mathrm{LA}_{\text {demand }}$ was lower in early fruit developmental stage, but $>200 \mathrm{~cm}^{2}$ in the last weeks of fruit development, where $\mathrm{C}_{\text {demand }}$ is highest considering the entire fruit development. Results from the girdled branches trial with adjusted LA:F demonstrated that the production of fruit of marketable size and taste requires $99 \mathrm{~cm}^{2}-$ $137 \mathrm{~cm}^{2}$ LA:F capturing leaves from fruiting spurs. For a concluding result more trials are necessary, but as a recommendation the LA:F in the first 20 DAFB may be below $100 \mathrm{~cm}^{2}$. Afterwards it should be maintained $>100 \mathrm{~cm}^{2}$ and in stage III exceed $170 \mathrm{~cm}^{2}$ or $200 \mathrm{~cm}^{2}$ depending on cultivar and target fruit size.

## Conclusion

To produce a high fruit quality in terms of size, coloration and SSC, a high LA:F over $170 \mathrm{~cm}^{2}$ LA:F should be maintained during the whole season, but are of enhanced importance in the third developmental stage of the fruit as the carbon demand in this period is the highest of the whole season. In the first stage the LA:F can be lower, which is usually the case due to maturation of leaves during the same period. Estimations of the leaf area demand based on the tree carbon balance enables to calculate an individual tree's fruit bearing capacity (FBC) from the total LA of the tree in different growing systems, however, the leaf area demand was maybe slightly overestimated in the present study. The requested daily carbon demand and derived leaf area demand per fruit determines the optimum crop load and can be used to evaluate tree's current crop load at any time during the season.

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## Conflict of interest statement

The authors declare no conflict of interest.

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