Leaf removal effects on light absorption in virtual Riesling canopies (*Vitis vinifera* L.)

Christopher Bahr*, Dominik Schmidt¹, Matthias Friedel² and Katrin Kahlen¹

¹Department of Modeling and Systems Analysis, Hochschule Geisenheim University, 65366 Geisenheim, Germany

²Department of General and Organic Viticulture, Hochschule Geisenheim University, 65366 Geisenheim, Germany

* Corresponding author’s e-mail address: christopher.bahr@hs-gm.de

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Abstract

Leaf removal is a standard vineyard management technique to influence grape composition or to reduce disease pressure, however the timing and intensity of leaf removal is a widely discussed issue. The interplay of different goals and effects over time does not make experimental studies any easier. To gain insight into positive and negative consequences of leaf removal on grapevine development, a first step can be to study how leaf removal affects the canopy’s light absorption using a dynamic model approach. Functional-structural plant models combine canopy architecture with physiological processes and allow analyzing canopy interaction with the environment with great topological detail. The functional-structural plant model Virtual Riesling simulates Riesling vines in a vineyard setup depending on temperature and plant management. We implemented leaf removal and applied this method in or above the bunch zone to compare the light absorption in canopies. Leaf removal in the bunch zone led to greater loss of absorbed light, but canopies of both scenarios could compensate for most of the loss during the simulation time frame. Compensation was mainly driven by lateral leaves closing the gaps induced by leaf removal and by leaves in the proximity of the leaf removal zones, re-exposed to light. Results showed similar effects as observed in in vivo studies, hence, we suggest extending these simulations to investigate other effects linked to light distribution such as berry sunburn. Simple modifications of implemented leaf removal techniques also allow for testing different application scopes and their impact on canopy light absorption.

Keywords: leaf removal, bunch zone, grapevine, climate change, functional-structural plant modeling, light model
1 Introduction

Grapevines (Vitis vinifera L.) are subject to different management practices over the course of a year to control yield and fruit quality (e.g., Diago et al., 2010; Palliotti et al., 2011; Poni et al., 2018). Management decisions influence the growth of vines strongly and can even have an effect across seasons (Diago et al., 2010; Toth, 2020; Wang et al., 2020). Many practices, such as shoot positioning, pruning or leaf removal, affect the canopy architecture, whilst the canopy plays an important role in the interaction of grapevines with the environment and affects the microclimate (Friedel et al., 2015; Poni et al., 2018; Verdenal et al., 2019). Leaf size, shape, position and orientation influence sunlight and wind penetration as well as temperature and humidity inside the canopy (Deloire, 2012; Reynolds and Heuvel, 2009; Schmidt and Kahlen, 2018; Smart, 1985; Zoecklein et al., 1998). These conditions affect the risks of diseases and physiological disorders, such as fungus or berry sunburn. If management practices alter the canopy architecture, conditions within the canopy and thus risks of diseases can change abruptly (Gambetta et al., 2021). One such practice with a sudden impact is leaf removal.

Leaf removal is a technique in viticulture to influence and protect grape development. It is traditionally applied to improve grape composition and to reduce disease pressure by changing the microclimate around the bunches (Poni et al., 2018; Verdenal et al., 2019). Leaf removal can also be applied to control yield and to delay berry ripening (Palliotti et al., 2011; Poni et al., 2013; Stoll et al., 2013; VanderWeide et al., 2020; Verdenal et al., 2019). Details of leaf removal techniques, like timing, severity (number of removed leaves) and location in the canopy, differ substantially between studies. Leaf removal is applied between fruit set and véraison (onset of berry ripening) to improve light penetration and air circulation in the bunch zone (Diago et al., 2010; Poni et al., 2018) and at prebloom to control yield as well as bunch rot disease (e.g., Diago et al., 2010; Komm and Moyer, 2015; Poni et al., 2018; VanderWeide et al., 2021). For details on developmental stages of grapevine we refer to e.g., Dry and Coombe (2004). In most of the above mentioned studies, basal leaves in the bunch zone were removed, reducing the main sources for assimilates to decrease fruit set. In contrast, leaf removal above the bunch zone after flowering aims at delaying maturation (Poni et al., 2013; Stoll et al., 2013) and leaf removal in apical zone or bunch zone after véraison may improve grape composition (Poni et al., 2018). The number of removed leaves ranges from three basal leaves (e.g., VanderWeide et al., 2020; Verdenal et al., 2019) up to all leaves around the bunches (e.g., Gambetta et al., 2019). In certain cases, only east side or sun-exposed leaves were removed (Gambetta et al., 2019; Kurtural et al., 2013; Schüttler et al., 2015; Wang et al., 2020; Yu et al., 2016). Some authors suggested to reduce leaf area proportional to canopy size depending on the respective management (Poni et al., 2018; Stoll et al., 2013). Although excessive leaf removal may pose a risk to grapevine quality, practical recommendations regarding the scope of leaf removal are sparse.

The more leaves are removed on the sun-exposed side of the bunch zone, the more berries might get sun-burned, since berry sunburn is directly related to sudden sun-exposure (Gambetta et al., 2021). Leaf removal can also lead to adverse source limitation, an effect which can have consequences across seasons (Verdenal et al., 2019; Wang et al., 2020). Such threats are expected to increase due to climate change and adjustments of leaf removal techniques might become more important in the future (e.g., Santos et al., 2020). One such adjustment relates to the timing of leaf removal. Early leaf removal in the bunch zone can allow berries to better adapt to sunlight and, thereby, reduce their susceptibility to sunburn (Gambetta et al., 2021). An adjustment can also be achieved by changing the location of leaf removal. For example, Hayman et al. (2012) explicitly suggest removing only basal leaves instead of leaves in the bunch zone to protect berries from exposure to sunlight and sunburn. Overall, these findings indicate that characteristics of leaf removal applications, such as timing, number of removed leaves and location in the canopy, may have negative effects on grapevine performance as well.

To better understand the positive and negative consequences of leaf removal over time, a first step can be to systematically analyze the effect of leaf removal on light
distribution within the canopy by the help of a dynamic computer model. Since canopy architecture and its topology is important, functional-structural plant models seem useful to investigate such a complex system (Guo, 2006).

Functional-structural plant models combine the three-dimensional architecture of a plant with physiological processes on the basis of plant organs and their topology (Vos et al., 2009). They allow addressing each single simulated plant organ during run time, e.g. for modulating organs depending on their physiological or topological (i.e. location) state. Schmidt et al. (2019) developed the dynamic functional-structural plant model Virtual Riesling, which simulates the growth of grapevines of cultivar Riesling based on descriptive growth functions, management techniques and temperature conditions. The model can be used to simulate daily canopy growth at the experiment site of model parameterization (Geisenheim University, Germany) taking into account i.a. growth variability and management such as vertical shoot positioning (VSP trellis system). Recently, Virtual Riesling has been coupled with a light model (cf. Evers and Bastiaans (2016) and Evers et al. (2010)) to simulate diffuse and direct light interacting (absorption, reflection, transmission) by the virtual grapevine canopy (Bahr et al., 2020), but not affecting growth. The current version of the model Virtual Riesling can now simulate a vineyard, measure light interception and manipulate plant organs on a daily basis, such as primary and lateral leaves, i.e. leaves grown at primary and lateral shoots, on a daily basis. Therefore, the model is suitable to be extended for leaf removal applications in virtual vineyards.

The aim of this study was to examine the effect of leaf removal on light distribution using the model Virtual Riesling. First, the model was extended by a method for leaf removal that resembles practical application techniques in vineyards. Then, we simulated grapevine growth within a virtual vineyard applying leaf removal scenarios that differed in application height. The effect of leaf removal on light distribution was evaluated by the temporal development of absorbed photosynthetic radiation over a period of three weeks after leaf removal by considering different canopy zones and differentiating between primary and lateral leaves.

2 Materials and Methods

2.1 Virtual Riesling

The functional-structural plant model Virtual Riesling simulates the dynamic growth of Riesling grapevines from bud burst on the cane to end of flowering in daily time steps (Schmidt et al., 2019). Currently considered plant organs include the cane, the primary and lateral shoots and the leaves at both shoot levels. The architecture is influenced by the growth behavior of the vine, environmental conditions and management practices. The model includes various stochastic components, i.e. bud burst or shoot orientation in space, to mimic natural variability in the model. It is based on digitized data of vines grown at the experiment site of the VineyardFACE-project at Geisenheim University, Germany (Schmidt et al., 2019; Wohlfahrt et al., 2018). The code is written in the programming language XL and the interactive modeling platform GroIMP (v.1.5) was used for model development (www.grogra.de/software/groimp) (Kniemeier and Kurch, 2008).

The following features of Virtual Riesling are based on grapevine and trellis setup in the VineyardFACE-project. The cane-supporting wires are set between posts 0.70 m above ground. Eight winter buds are placed on the cane in slightly varying positions to mimic an alternate-distichous phyllotaxis including natural variability. Shoot positioning is applied four times with two wires, each being attached on one side of the posts. The

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**Figure 1:** A virtual vineyard (5 × 5 plants) simulated with the model **Virtual Riesling** for temperature data of Geisenheim, Germany, 2018 on day of the year 172. In this virtual vineyard, the distance between plants is 0.9 m and row distance equals 1.3 m.

Canopy development follows a thermal time approach with a base temperature of 10 °C (Schmidt et al., 2019). Bud break at the cane is modeled with a variability of 12 °C d. Phytomeres then appear approximately every 22 °C d on both primary and lateral shoots and grow with thermal time depending on their rank. Lateral shoot bud break is modeled with a probability, depending on the phytomere rank, with a maximum asymptotic probability of 98% approximately reached at rank 13. A breaking lateral shoot starts to grow with a thermal time lag following its bud appearance and depending on its rank, but not before 67 °C d are reached and with a stochastic component (standard deviation of 28 °C d). Using Geisenheim temperature data for the 2018 season lateral bud break in the simulations is peaking at approximately day of the year 155 to 160 (Schmidt et al., 2019, Fig. 13). A shoot-related alternate-distichous phyllotaxis controls petiole orientation. Initial petiole angle to the parent shoot is approximately 45° before they are rotated to match observed angles to the horizontal plane of approx. 40° and 36°, respectively. Petioles on primary shoots grow almost perpendicular to the row, with a variation induced by initial shoot orientation, obstacle avoidance and shoot positioning. The leaf’s midrib follows the petiole orientation, but the horizontal angle of the leaf is altered to match observations. For leaves at primary shoots the horizontal angle is related to leaf size and rank with a trend of smaller leaves being more horizontal than larger leaves. For leaves at lateral shoots the horizontal angle is fixed to approximately 25°, i.e. slightly downward facing. For more details we refer to eqs. 3-17 from Schmidt et al. (2019).

During one virtual day different model steps for plant development are applied in a specific order. A simulation starts with the appearance of new plant organs and growth depending on temperature conditions. Subsequently, vertical shoot positioning is applied when shoots are long enough for defined heights.

Virtual Riesling allows setting up vines in multiple rows with defined row and plant distance to simulate a vineyard. An example of a virtual vineyard simulated using Virtual Riesling is given in Figure 1. In this setup rows were aligned along a
north-south axis and the cane was always bend towards the south of the trunk, resembling the vineyard in the Geisenheim VineyardFACE project.

Recently, *Virtual Riesling* has been coupled with a light model (cf. Evers and Bastiaans, 2016) to simulate diffuse and direct light interacting within the virtual grapevine canopy, but not affecting growth (Bahr et al., 2020). A dome of 72 light sources for diffuse light and 24 light sources representing the daily course of sun are placed around the center of the virtual crop (see Supporting Information Figure S3, Table S1 and Table S2 for details on an exemplary configuration on day 153). In correspondence to the VineyardFACE location the latitude is set to 50°. Other parameters describing the incoming light are taken from the studies of Evers and Bastiaans (2016); Evers et al., (2010). Ray- tracing simulations run using 20 million rays as a compromise between computational time and accuracy (see also Henke and Buck-Sorlin, 2017). The interaction of rays with leaves of the canopy includes optical properties for grapevine leaves derived from literature (Cabello-Pasini and Macías-Carranza, 2011). Leaf surface reflectance and transmittance to photosynthetic active radiation (PAR, 400-700 nm) are set to 0.14 and 0.15, respectively. During a simulation daily absorbed photosynthetic active radiation (PARabs, µmol s⁻¹) is estimated at leaf scale (m²), where PAR is derived from simulated incoming global radiation according to the approach from Evers and Bastiaans (2016). The conversion originates at the light sources where emitted daily incoming global radiation (GR, MJ m⁻²) is translated into photo- synthetically active photon flux density (PPFD, µmol m⁻²s⁻¹) following Eq. (1), considering the current daylength (s) (Spitters et al., 1986, eq. 17), conversion factors for the units and the assumed PAR fraction (0.35).

\[
\text{PPFD} = \frac{1600 \cdot 0.55 \cdot 4.55 \cdot \text{GR}}{\text{daylength}} \text{ in } \mu\text{mol m}^{-2}\text{s}^{-1} \tag{1}
\]

The simulated course of incoming radiation is given in Supporting Information Figure S2, covering a range of approx. 14 MJ m⁻² d⁻¹ to 19 MJ m⁻² d⁻¹ during the time frame of the simulations (also see Supporting Information Table S3). At each leaf PARabs is then calculated from absorbed PPFDabs by multiplication with the respective leaf area (Aleaf m²; Eq. (2)):

\[
\text{PARabs} = \text{PPFDabs} \cdot A_{\text{leaf}} \text{ in } \mu\text{mol s}^{-1} \tag{2}
\]

For the results we converted PARabs to the unit MJ d⁻¹ reverting the calculation from Eq. (1) by replacing PPFD with PARabs (µmol s⁻¹) from Eq. (2).

### 2.2 Modeling Leaf Removal

The goal of this study was to simulate early leaf removal in a vineyard on the east side of canopies, i.e. the morning side, within or above the bunch zone and to evaluate the impact on light absorption.

Therefore, we needed to develop a model that allows removing virtual leaves related to the east side of the canopy at different heights. Realizing leaf removal at different heights for zones in the canopy was straightforward. Using the leaf base position as a reference point for leaf location, leaves within a certain height can be selected and removed from the scene. In order to mimic the local expert opinion on removing leaves only from the east side, we wanted our model to consider, whether a leaf might contribute to the east side canopy. It should not only remove leaves located at the east side of the canopy, also leaves facing east and potentially extending to the east side should be removed. We decided to keep leaves which expand from east to the west side and to remove leaves which expand from the west side to the east, but only if origins of such leaves were not located further away than 5 cm from the center of the row. Due to the dimensions of leaves in the model this local restriction assures that at least parts of such leaves cross the center of the row. This part of the leaf removal model assigning leaves to either the east or the west side of the canopy can be summed up in a mathematical expression as follows:

\[
\text{LR(loc,dir)} = \begin{cases} 
\text{east} & \text{if } \left(\text{dir}=\text{east} \land D_{\text{east}}(\text{loc, row.center}) < 0.05m\right) \\
\text{west} & \text{else}
\end{cases}
\tag{3}
\]

considering the location (loc) and cardinal direction (dir) of the leaf and the signed distance from the leaf’s location to the row center plane, where the sign is based on the distance to the opposite side of the leaf removal target side, in this study the distance to the west side (D_{west}(loc, row.center), m). This function is combined with a defined height range, so that only east side leaves whose base is located within that range, are subjected to a leaf removal event. Furthermore, we also used Eq. (3) in the results to assign leaves to the east and west side of the canopy, rather than just using their location in relation to the row center.

### 2.3 Virtual Leaf Removal Scenarios

Based on information by local experts and their experiences in the field, possible target zones for leaf removal in the canopy were defined. The general aim was to remove leaves either within or above the bunch zone. This aim required an estimation about where bunches are located in the canopy of vines growing on the VineyardFACE site in Geisenheim. The bottom and top height of the bunch zone were estimated to be at 0.7 m (height of cane) and 1.1 m and these values were taken to define the zone for the first leaf removal scenario (S1). To remove leaves above the bunch zone, scenario two (S2), application heights were set to the range between 1.1 m and 1.4 m (Fig. 2). The control scenario was defined as a case without applying leaf removal (control).

Depending on plant growth the number of leaves within these heights changed over time. Therefore, the amount of light which could be absorbed in between these heights changed over time as well. In order to make meaningful comparisons between light absorption of the two leaf removal scenarios, the application day was selected based on the amount of absorbed light in these zones in canopies where no leaves were removed (Fig. 3). On day 153 of the year 2018 the light absorption was nearly the same in both zones and chosen to be the application day. This day was the 2nd of June 2018, one day before the estimated growth stage full bloom (BBCH 65) and five days before end of blooming in Geisenheim (https://rebschutz.hs-geisenheim.de/rebentwicklung/repbaenologie.php).

In summary, the developed leaf removal method and the described scenarios remove specific leaves in the virtual canopy derived from practical application techniques in vineyards at Geisenheim University.

### 2.4 Virtual Leaf Removal Simulations

Simulations to study the effect of leaf removal on light absorption were limited to the year 2018, using temperature data from a weather station in Geisenheim located at the experimental site. A simulation started with bud burst on the cane and stopped at an average height of 2.3 m, just before first pruning would have
been applied (cf. Schmidt et al., 2019), approximately covering a period from doy 103 to doy 172. Leaf removal in the model Virtual Riesling, if activated, is applied after the appearance and growth of plant organs and after shoot positioning, but before simulating light rays for that simulation day. Simulations of the vineyard (Fig. 1) were performed 112 times for each variant, i.e. the control and the two leaf removal application scenarios, to analyze light absorption of the resulting 1008 inner plants. It is 1008 inner plants per scenario, as each virtual vineyard leads to \(3 \times 3 = 9\) inner plants and this multiplied by 112 (number of repetitions per scenario) is 1008. This number was selected to assure robust estimates of the average light absorption for stochastic simulations (Byrne, 2013; Schmidt et al., 2019). Light absorption data in combination with topological leaf data was analyzed with R (v.3.6.3) (R Core Team, 2020) and visualized using the ggplot2-package (v.3.3.3.9000) (Wickham, 2016). To capture the variability within the simulation results we estimated the arithmetic mean and the 50% highest density interval (HDI) (R-package HDInterval, v.0.2.2) in our statistical analysis. For robustness, both estimates are based on 1008 single plants per scenario. We provide the mean as a point estimate for a best guess given the data. The 50% HDI represents the narrowest interval containing the most probable, i.e. frequent, values. Overlaps of 50% HDI indicate that there is a likely chance of similar observations between scenarios. The FSP-model output includes data for all individual leaves of a plant (size, location, parent shoot, etc.). This data allowed us to calculate summary statistics on leaf areas (mean and standard deviation) and number of leaves removed.

### 3Results and Discussion

First, we take a closer look at the effects of the two different leaf removal scenarios on the canopy itself. The second part focuses on how leaf removal affects the leaf light absorption of a grapevine plant.

#### 3.1 Leaf Removal Intensities

We conducted simulations to study two leaf removal scenarios, where leaves are removed on the selected day of leaf removal (doy 153) from the east side of the canopy only. To compare expected leaf removal intensities, i.e. number of removed leaves and respective leaf area, we used data from the control scenario where no leaves were removed at doy 153. For S1 we estimated an average removal of 3.59 ± 0.94 (mean ± sd) leaves per shoot, while in S2 on average 1.91 ± 0.77 were removed. The average leaf area of removed leaves in S1 and S2 was 97.53 ± 46.59 cm² and 116.81 ± 59.9 cm², respectively. Projecting this to the entire canopy of a single plant, from a total leaf area of 1.06 ± 0.03 m² S1 takes out 0.28 ± 0.03 m² and S2 0.18 ± 0.02 m². This approximately equals 26% of the total leaf area for S1 and 17% for S2. Such values are not uncommon for practical leaf removal applications, for instance, Komm and Moyer (2015) compared pre-bloom, bloom, and four weeks post-bloom leaf removal applications on Riesling shoots with total leaf areas removed in the range of 22.4% to 59.6%, while removing leaves from both sides of the canopy. In the study of Diago et al. (2012) leaf areas of Tempranillo were reduced by ca. 30% at pre-bloom.

![Figure 2](https://academic.oup.com/insilicoplants/advance-article-doi/10.1093/insilicoplants/diab027/6354732)

**Figure 2:** Leaf removal zones between 0.7 m and 1.1 m (bunch zone, east) above ground in scenario one (S1) and between 1.1 m and 1.4 m above ground in scenario two (S2): leaf removal zones are illustrated as grey areas on a digitized plant (without leaves) (A); three exemplary plants show canopies before (B) and after leaf removal for S1 (C) and S2 (D) with a view of the east side and with a view along the row.
3.2 Absorption of PAR

To evaluate the effect of leaf removal on light absorption in Riesling canopies, we now compare data from the control and the two leaf removal scenario simulations over the covered time period. In Figure 4 light absorption curves of the control and the two scenarios are separated into east and west side of a row. Light absorption in the control increases continuously over the full period of the simulation. This can be explained by steadily increasing canopy height, leaf area and incoming radiation (Fig. 5 and Supporting Information Figure S2). As expected, light absorption in canopies with leaves removed either in or above the bunch zone decreases on the east side on application day. On the west side light absorption slightly increases for both scenarios. Canopies of S1 absorbed less light on both sides of the row compared to S2 over the period of simulation. This can be explained by the decrease of S1 on the east side being higher than in S2, while at the same time the increase on the west side of S1 is lower than in S2. On the day after application a plant of the control simulation absorbed on average \( \text{PAR}_{\text{abs}} = 3.12 \text{ MJ d}^{-1} \) with a 50% highest density interval (HDI) of [2.85, 3.20] MJ d\(^{-1}\) on the east side of the canopy and 3.14 [2.97, 3.30] MJ d\(^{-1}\) on the west side. The average drop on the east side of the S1-canopies is 1.21 MJ d\(^{-1}\), while on the east side of the S2-canopies a plant only absorbs on average approx. 0.85 MJ d\(^{-1}\) less than the control on day 153. The aforementioned increases in \( \text{PAR}_{\text{abs}} \) on the west sides of S1 and S2 scenarios immediately after leaf removal application were on average at 0.12 MJ d\(^{-1}\) and 0.20 MJ d\(^{-1}\), respectively (Fig. 4).

![Figure 3: Light absorption of east-side leaves from the control simulation (no leaf removal) for the two different scenario zones given as absorbed PAR (\( \text{PAR}_{\text{abs}} \)) per vine and the 50% highest density interval (HDI) of 1008 simulated plants. Scenario one (S1) corresponds to 0.7 m-1.1 m, scenario two (S2) to 1.1 m-1.4 m. On the selected day of leaf removal both zones approximately absorb the same amount of \( \text{PAR}_{\text{abs}} \).](https://academic.oup.com/insilicoplants/advance-article/doi/10.1093/insilicoplants/diab027/6354732)

![Figure 4: Absorbed PAR (\( \text{PAR}_{\text{abs}} \)) per vine and the 50% highest density interval (HDI) of 1008 simulated plants for two scenarios and the control, separated into east and west side of canopies (leaf removal applied on east side only). Absorption curves are plotted for the control (no leaf removal); scenario one (S1) with leaves removed in the bunch zone and scenario two (S2) with leaves removed above the bunch zone. The dotted line indicates the day of leaf removal application for S1 and S2. In addition, the difference in \( \text{PAR}_{\text{abs}} \) between the control and both leaf removal scenarios for both sides is given as \( \Delta \text{PAR}_{\text{abs}} \).](https://academic.oup.com/insilicoplants/advance-article/doi/10.1093/insilicoplants/diab027/6354732)
The effect of compensation over time is clearly evident. At day 172, the average difference per plant of S1 to the control decreases to approximately 0.33 MJ d\(^{-1}\) on the east side and in S2 to approximately 0.16 MJ d\(^{-1}\), which is half the difference of S1 on the east side of the canopy. Differences on the west side are close to zero on day 172. Brandt et al. (2019) measured mean daily solar radiation in the range of 3.88 \(\text{MJ m}^{-2}\) to 5.10 \(\text{MJ m}^{-2}\) between the 4th-7th July in 2017 (day 185-188) using horizontally placed light sensitive films (20 mm 35 mm) in bunch zones of Riesling vineyards at a height of 1.1 m. Assuming a leaf absorption of 71\% and an approximate leaf declination angle between 20° to 25° (Schmidt et al., 2019) this approximately equals 2.5 \(\text{MJ m}^{-2} \text{d}^{-1}\) to 3.4 \(\text{MJ m}^{-2} \text{d}^{-1}\). These values are higher, but still in the order of values estimated at the end of our simulation timeframe, where the average light absorption at day 172 for leaves in the bunch zone, i.e., between 0.7 m and 1.1 m, of the control simulation was found to be 1.2 - 1.0 \(\text{MJ m}^{-2} \text{d}^{-1}\). Sources of uncertainty in this comparison include the different year and time points, as well as comparing a point-wise measurement in the field with a zonal average from the simulations.

To sum this up, light absorption data over time revealed clear differences between the two leaf removal scenarios, representing bunch zone and above bunch zone leaf removal practice, however, differences to the control were almost compensated in less than 20 days after leaf removal.

3.2.1 East Side Compensation of Light Absorption due to Lateral Growth

Observations in the 3D-views of the model Virtual Riesling indicated why compensation of the loss of light absorption was possible. Gaps in the grapevine canopy caused by leaf removal diminished over time and were negligible at the end of the simulation period. This process was particularly related to lateral leaf growth as illustrated in an example with three vines in Figure 5, where lateral leaves are marked to highlight their contribution to canopy closure.

These visual observations are supported by light absorption...
data of primary and lateral leaves from the control (Fig. 6). Light absorption of lateral leaves gained momentum approxim- ately at leaf removal and steadily increased thereafter, whereas light absorption of primary leaves peaked one week after leaf removal followed by a slight decrease. The increase for lateral leaves was ca. four times larger than the remaining positive bal- ance for primary leaves. This indicates that lateral leaf growth could be predominantly responsible for light compensation in our simulation scenarios.

![Figure 6: Absorbed PAR (PAR_{ave}) of primary and lateral leaves per vine and the 50% highest density interval (HDI) from 1008 simulated plants in control canopies without leaf removal. The dotted line indicates the day of leaf removal application for S1 and S2.](image)

To assess the role of lateral leaves in light absorption com- pensation after leaf removal, especially of leaves newly emerging in the zone of leaf removal, we subtracted the contribution of these lateral leaves growing in the leaf removal zone from the simulated east side absorption (Supporting Information Figure S1A,B). The resulting absorption curves show that newly emer- ging lateral leaves were able to absorb light in the leaf removal zones for the first time on day 154. If lateral leaves in the zones of S1 and S2 are excluded from the data, the trend of canopies to compensate for lost light absorption after leaf removal became very weak in S1 or even vanished in S2 when comparing absolute values (Supporting Information Figure S1A,B). The difference between absorbed light data in S2 without the absorption of lateral leaves in the leaf removal zone (no absorption of lateral leaves; n.A.o.L.L.) compared to the control increased from day 154 to 172 from on average 0.84 MJ d^{-1} to 0.91 MJ d^{-1}. In scenario one, with leaf removal in the bunch zone, compensation on the east side of the canopy was still present, but reduced when the contribution of laterals in the leaf removal zone is excluded in the comparison to the control. The decrease in the difference from day 154 to 172 ranges from on average 1.18 MJ d^{-1} to 0.78 MJ d^{-1}. This compensation is less than half as strong as when including lateral leaves (1.19 MJ d^{-1} to 0.33 MJ d^{-1}, see above).

When estimating this data as percentages (Figs. 7A, B) of deviation to the average of the control we see S2 gaining absorption of up to approximately 95 % of the control by day 172 and S2 of up to 98 %. When not considering lateral leaves only 88 % and 87 % of the control are reached by S1 and S2, respectively.

This reveals a strong contribution to total light absorption of lateral leaves, growing in the zones of leaf removal after applica- tion day. These leaves were responsible for the ability of canopies in regaining light absorption capacity in both scenarios. The increasing difference between scenario two (n.A.o.L.L.) and the control shows that light absorption of lateral leaves was even more important than in scenario one for the compensation. This can be explained with decreasing light absorption in lower parts of the canopies. To analyze the vertical light distribution we split the east side canopy of the control simulation into three zones: Zone 1 (Z1: \( h = 1 \) m) includes the bunch zone and all leaves below the cane; zone 2 (Z2: \( h \leq 1.4 \) m) similar to the S2 leaf removal zone and zone 3 (Z3) includes all leaves above \( h > 1.4 \) m. The leaves of the control in the zone equal to the leaf removal zone of scenario two (Z2) absorbed more light than those in the bunch zone and below the cane together (Z1) at the end of the simulations on day 172 (Fig. 7C). During the simulation period of Virtual Riesling the height of canopies increases due to the implemented upward growth (cf. Fig. 5). Hence, lower leaves were more and more suspected to shading and more light was absorbed in upper parts of the simulated canopies over time, reflecting an observed linear decrease in light in the bunch zone (Kurturali et al., 2013).

Canopies, where leaves were removed either in or above the bunch zone, were able to partially compensate for the loss of light absorption over time. The simulation data revealed, that lateral leaves were responsible for this effect that we observed.

![Image](https://academic.oup.com/insilicoplants/advance-article/doi/10.1093/insilicoplants/diab027/6354732)

3.2.2 Compensation of Light Absorption due to Re-exposure

The analyzed data showed that light absorption, even immedi- ately after leaf removal, was different between S1 and S2 on both sides of the canopies although we aimed to remove leaves with similar absorption potential (cf. Fig. 3). This can be explained by leaves no longer covered in the canopy that got re-exposed to light after leaf removal. On the east side this effect was limited to leaves, which absorbed light below zones of leaf removal. Hence, in S1, where leaf removal started at the height of the cane (0.7 m), only a few leaves (0.02 m² per plant, approximately 2 % of the total leaf area at day 154) were located below the cane because shoots tended to grow upwards and were stabilized with wires. These leaves were from shoots that started growing from the bottom or the side of the cane. Below the zone of scenario two (9.1 m) there were all the leaves of the bunch zone plus those growing below the cane. When leaf removal is applied, light rays, which would have been intercepted by leaves growing in the leaf removal zones, were now reaching lower parts of the canopy. Hence, in scenario one some rays got intercepted by leaves growing below the cane. In scenario two many more light rays got intercepted by leaves in the bunch zone and below the cane, simply because there were a lot more leaves in their way. This effect is clearly visible in Figure 8 showing light absorption of the control and both scenarios, but limited to heights of the leaf zone removal.

The impact of S2 was expected, because leaves lower than leaf removal zone (S2 1.1 m) suddenly absorbed a lot more light than the control (approx. \(+0.52 \) MJ d^{-1}; \(+20 \) %). In contrast, in scenario one the difference of light absorption below the leaf...
removal zone (S1 0.7 m) to the control was negligible. This effect applied to both sides of the canopies, that is why light absorption increased on the west side and even more in scenario two. As already seen in Figure 4, this effect was not limited to heights below the leaf removal zones, because light absorption on the west side increased after leaf removal also at heights corresponding to the respective zone of leaf removal. Overall, canopies, where leaves were removed in the bunch zone, did not benefit from this compensation-by-re-exposure effect as much as canopies with leaf removal applied above the bunch zone. Similar effects of leaves, re-exposed to light, partially compensating the impact of leaf removal on light absorption has also been observed in previous studies on real vines (Poni et al., 2018).

4Conclusion

To study effects of leaf removal on grapevine canopy light absorption in silico, we implemented a new method for simulating leaf removal techniques into the functional-structural plant model Virtual Riesling. We compared two scenarios, where leaf removal was applied in and above the bunch zone of canopies in virtual vineyards using the extended Virtual Riesling model. Applying leaf removal on the same day in different heights in canopies led to evident differences in light absorption between both scenarios. Furthermore, the model allowed us to study the impact of leaf removal on light absorption over the entire simulation period. Thereby, simulation results were consistent with findings of previous studies of vines that were able to regain a large proportion of light absorption capacity after leaf removal, similar to levels without leaf removal. Investigating the role of leaf growth revealed that in the simulations lateral leaves were mainly responsible for compensating for lost light absorption within 20 days after leaf removal. Such data sets created by the model Virtual Riesling will be used in future studies to model and estimate other impacts on vines, especially the risk of berry sunburn, which is closely related to local light intensities. Implementing a
Figure 8: Absorbed PAR (PAR$_{abs}$) per vine and the 50% highest density interval (HDI) from 1008 simulated plants below leaf removal zones ($\leq 0.7$ m, $\leq 1.1$ m) including both sides of the canopy for: canopies without leaf removal (control) compared to the canopies from the respective leaf removal scenarios (S1: $\leq 0.7$ m, S2: $\leq 1.1$ m).

Responsiveness of growth on local light conditions might further enhance the models predictive potential of microclimatic effects. Since plant management can be adjusted in simulations, the model is also a promising tool to systematically analyze different management techniques and their impact on plant architecture and light distribution in canopies 

available from the Germany’s National Meteorological Service (the Deutscher Wetterdienst (DWD)) local weather station as daily mean, minimum and maximum temperatures (2 m above ground). Daylength (h) is calculated using the local latitude of Geisenheim (50°) following Spitters et al. (1986, eq. 17)

Author Contributions
conceptualization, C.B., D.S., M.F. and K.K.; methodology, C.B., D.S., M.F. and K.K.; software, C.B., D.S.; validation, D.S., C.B. and K.K.; formal analysis, D.S.; investigation, C.B., D.S. and K.K.; resources, D.S. and K.K.; data curation, C.B. and D.S.; writing—original draft preparation, C.B., D.S., M.F. and K.K.; writing—review and editing, C.B., D.S., M.F. and K.K.; visualization, C.B. and D.S.; supervision, K.K.; project administration, D.S. and K.K.

Model and Data Availability
Processed and raw data, as well as the model code, are available from the authors upon request.

Sources of Funding
We acknowledge support by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) - project numbers 449374897 and 432888308 and the Open Access Publishing Fund of Geisenheim University. Funds for running the VineyardFACE were provided by the Hessisches Landesamt für Naturschutz, Umwelt und Geologie (HNLUG, Hessian Agency for Nature Conservation, Environment and Geology).

Conflict of Interest
None declared.
Acknowledgements

We thank the Department of General and Organic Viticulture for sharing expertise on viticulture and plant management in VineyardFACE, Claudia Kammann and her team for supporting and maintaining the VineyardFACE-facility and Michael Henke for his support with the modeling platform GroIMP.

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