How can peach quality be promoted and brown rot prevented through coordinated agricultural practices and storage conditions? : a modeling approach

Enrico-Maria Casagrande

▶ **To cite this version:**

Enrico-Maria Casagrande. How can peach quality be promoted and brown rot prevented through coordinated agricultural practices and storage conditions? : a modeling approach. Other [q-bio.OT]. Université d'Avignon, 2021. English. NNT : 2021AVIG0729 . tel-03456387

HAL Id: tel-03456387

https://theses.hal.science/tel-03456387

Submitted on 30 Nov 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

THÈSE DE DOCTORAT D'AVIGNON UNIVERSITÉ

École Doctorale 536
Agrosciences et sciences

CTIFL – Centre Technique Interprofessionnel des Fruits et Légumes

INRAE - Institut National de Recherche
pour l'Agriculture, l'Alimentation et l'Environnement
(unité PSH - Plantes et Systèmes de culture Horticole)

Présentée par
Enrico-Maria Casagrande

How can peach quality be promoted and brown rot prevented through coordinated agricultural practices and storage conditions? A modeling approach

---

Soutenue publiquement le 14/09/2021 devant le jury composé de :

Sophie BRUNEL-MUGUET, CR	UMR 950 EVA, INRAE-UNICAEN	**Rapportrice**
Didier ANDRIVON, DR	UMR IGEPP, INRAE-AO-UR1	**Rapporteur**
Jean-Noël AUBERTOT, DR	UMR 1248 AGIR, INRAE-INPT	**Examinateur**
Jean-Luc REGNARD, Professeur	L'institut Agro / Montpellier SupAgro	**Président du jury**
Françoise LESCOURRET, DR	UR 1115 PSH, INRAE	**Directrice de thèse**
Sébastien LUROL, Ingénieur	CTIFL St-Rémy-de-Provence	**Co-encadrant de thèse**

French title: Comment favoriser la qualité des pêches et prévenir les pourritures brunes par des pratiques agricoles et des conditions de stockage coordonnées ? Une approche par modélisation

Résumé

Le développement de la qualité des pêches et les maladies fongiques après la récolte sont des questions récurrentes dans la filière fruits. Leur examen bénéficierait d'une approche intégrée qui prendrait en compte les processus impliqués, leurs interactions, et les facteurs qui les gouvernent. Dans ce contexte, les objectifs généraux de la thèse ont été (i) de créer un cadre de modélisation pour simuler le développement de la qualité des pêches et des pourritures brunes, sous différentes conditions pré-récolte (pratiques culturales) et post-récolte (stockage); (ii) et d'utiliser ce modèle pour étudier les moyens d'améliorer la qualité des fruits et de réduire les pertes. Dans cette étude, nous nous sommes concentrés sur le cas de la nectarine (*Prunus persica var. nucipersica*).

Nous avons d'abord défini et calibré, à l'aide de données expérimentales, un modèle mathématique pour simuler l'effet combiné de la croissance du fruit et des conditions de stockage (température et humidité relative) sur les caractéristiques liées à la qualité de la nectarine. Nous avons modélisé l'évolution de la conductance de la surface du fruit à la vapeur d'eau durant la saison de croissance, la perte de masse du fruit pendant le stockage et la dynamique de la concentration en sucres dans la pulpe du fruit. Les données observées ont suggéré que la sucrosité augmentait avec la perte de masse du fruit pendant le stockage, ce qui est également simulé par le modèle. De plus, le modèle suggère que les fruits récoltés tardivement peuvent avoir un taux de sucre plus élevé à

la fin du stockage que les fruits récoltés plus tôt.

Ensuite, nous avons étudié l'incidence de la pourriture brune pendant le stockage. Nous avons vérifié expérimentalement qu'il n'y avait pas d'infections secondaires (sans contact direct entre les fruits) par *Monilinia laxa*. Nous avons utilisé des résultats expérimentaux pour tester l'effet des conditions pré-récolte (y compris des conditions climatiques) et post-récolte sur le délai d'apparition de symptômes liés à la pourriture brune, en utilisant un modèle de survie avec des estimations paramétriques. Plusieurs variables se sont avérées significatives dans l'explication du développement de la maladie, notamment la température moyenne de stockage, la masse individuelle des fruits et la prévalence de la pourriture brune à la récolte, ainsi que la durée moyenne d'humectation dans la semaine précédant la récolte.

Enfin, nous avons intégré les modèles mentionnés ci-dessus à un modèle de culture fruitière qui prend explicitement en compte le rôle des pratiques de pré-récolte sur le développement des caractéristiques des fruits à l'échelle de l'arbre. Nous avons étudié, via une analyse de sensibilité et une exploration du modèle, son comportement en fonction de certaines pratiques au verger (irrigation et charge en fruits) et des conditions de stockage (température et humidité relative). Les simulations du modèle ont correctement reproduit les effets connus des pratiques sur les critères de qualité des fruits, tels que l'augmentation de la masse des fruits dans des conditions de bonne irrigation et de faible charge en fruits, et l'augmentation de la sucrosité en condition de stress hydrique. Le modèle a permis de confirmer que les propriétés des fruits sont contrôlées par les conditions de stockage, notamment que la perte de masse des fruits augmente lorsque la température augmente et que l'humidité relative diminue, et que le développement des pourritures brunes est accéléré par la température d'entreposage. Les simulations ont également montré l'influence des interac-

tions entre les conditions pré et post-récolte sur la prévalence de la pourriture brune et sur le rendement à la fin du stockage. Enfin, nous avons utilisé le cadre de modélisation pour rechercher les combinaisons de conditions pré- et post-récolte qui optimisent un niveau de performance englobant la qualité et la masse totale de fruits par arbre. L'importance relative attribuée aux critères de qualité des fruits a largement influencé le choix des scénarios optimaux. Les résultats ont également mis en évidence un antagonisme entre les critères de qualité, et en particulier la sucrosité, et le rendement en fruits. Ce cadre de modélisation pourrait être utilisé pour stimuler le dialogue entre les acteurs de la filière fruits, en suggérant des scénarios de pratiques de pré-récolte et de conditions de stockage qui répondent à leurs attentes sans préjuger du comportement ultérieur des fruits après stockage.

Abstract

Peach quality development and fungal infections after harvest are issues of concern in the fruit value chain. Their examination would benefit from an integrated approach that considers the processes involved, their interactions, and their drivers. In this context, the general objectives of the thesis were (i) to create a modeling framework to simulate peach quality development and brown rot infections and their control by pre-harvest (cultural practices) and post-harvest (storage) conditions; and (ii) to use this model to investigate ways to improve fruit quality and to reduce losses. In this study, we focused on the nectarine (*Prunus persica var. nucipersica*) case.

We first defined and calibrated, using experimental data, a mathematical model to simulate the combined effect of fruit growth and storage conditions (temperature and relative humidity) on nectarine quality-related traits. We modeled the seasonal course of fruit surface conductance to water vapor, fruit mass loss during storage, and sugar concentration dynamics in fruit pulp. The observed data suggested an increase of sweetness with an increase of fruit mass loss during storage, which was also shown by model simulations. Moreover, the model put forward that fruit from late harvest dates could have higher sweetness at the end of storage than fruit harvested earlier.

Second, we studied the spread of brown rot during storage. We verified experimentally that there were no secondary infections (without direct contact

between fruit) by *Monilinia laxa*. Then, we used experimental results to test the effect of pre-harvest (including meteorology) and post-harvest conditions on the time-to-infection by brown rot, using a survival model with parametric estimates. Several conditions were found to be significant in explaining the disease incidence, notably the mean storage temperature, the fruit mass and the prevalence of brown rot at harvest, and the mean wetness duration in the week before harvest.

Finally, we integrated the above-mentioned models within a fruit crop model that takes explicitly into account the role of pre-harvest practices on the development of fruit characteristics at the tree scale. We studied, via a sensitivity analysis and model exploration, the model behavior in relation to some orchard practices (irrigation and fruit load) and storage conditions (temperature and relative humidity). Model simulations correctly reproduced the well-known effects of practices on fruit quality criteria, such as the increase of fruit size under well-irrigated conditions and low fruit load, and the increase of sweetness under water-stressed regimes. The model was able to support that fruit properties are controlled by storage conditions, notably fruit mass loss increases with increasing temperature and decreasing relative humidity, and the brown rot infections increase with temperature. Simulations also highlighted the influence of interactions between pre- and post-harvest conditions on the brown rot prevalence and the fruit yield at the end of storage. We finally used the modeling framework to search for the combinations of pre- and post-harvest conditions that optimize a performance score encompassing fruit quality and yield. The relative importance assigned to the fruit quality criteria largely affected the choice of the optimal scenarios. The results also pointed out a trade-off between quality criteria, and in particular sweetness, and the fruit yield. The use of this modeling framework could support the dialogue between the actors of the fruit value

chain, by suggesting scenarios of pre-harvest practices and storage conditions that satisfy their expectations, without prejudging the subsequent behavior of the fruit after storage.

Funding

This study was funded by an industrial training agreement through a CIFRE research fellowship (n. 2017/1788) from the CTIFL (Centre Technique Interprofessionnel des Fruits et Légumes) and the ANRT (Association Nationale de la Recherche et de la Technologie) on behalf of the French Ministry of Higher Education and Research. I want to deeply thank both organisations, as well as INRAE (Institut national de recherche pour l'agriculture, l'alimentation et l'environnement) and the Avignon University.

Remerciements

Je voudrais tout d'abord remercier mes encadrants de thèse, pour leur confiance et leur implication dans le travail. Je remercie Françoise, qui a su toujours m'inciter et me soutenir dans les moments de difficultés. Je la remercie pour ses conseils sur l'ouverture vers d'autres domaines et en matière d'écriture scientifique. Je remercie Michel, pour m'avoir donné envie de faire toujours mieux et de chercher plus loin. Merci à Sébastien, pour son soutien incessant et le partage des connaissances. Merci aussi de m'avoir introduit au vaste monde de la filière fruits et légumes. Enfin, je remercie Florence, pour son énergie et positivité, sans lesquelles les expérimentations n'auraient pas pu aboutir. La complémentarité de vos connaissances et les échanges que j'ai eu avec vous m'ont permis de mener à bien ces travaux.

Je voudrais également remercier Sabrina et Maurane, pour leur engagement pendant les expérimentations. Sans elles, ce travail aurait été beaucoup moins qualitatif.

Merci à Daniel et Gilles, pour leur aide en agronomie et pour m'avoir dirigé toujours vers les bonnes ressources. Enfin, je voudrais remercier particulièrement Mohamed et Pierre, pour avoir toujours été là en cas de besoin et pour leur disponibilité presque infinie.

Les remerciements vont ensuite à tous mes collègues d'Avignon car ils ont tou-

jours étés prêts à m'aider: un merci particulier à tous les stagiaires, doctorants et post-docs, avec lesquels j'ai eu l'honneur de partager ces années.
Je remercie énormément aussi mes collègues de Saint-Rémy-de-Provence, qui m'ont toujours accueilli très chaleureusement. Je n'oublie pas les personnels administratifs, sans qui tout aurait été plus compliqué.

Un grand merci également aux membres du jury de thèse, pour leur méticulosité dans la relecture du manuscrit, pour les échanges fructueux lors de la soutenance et pour les améliorations suggérées.
Je remercie enfin les membres de mon comité de thèse : Barbara Gouble, Philippe Debaeke, Alexandre Leca, Davide Martinetti et Vincent Mercier, qui m'ont toujours aidé, encouragé et m'ont apporté beaucoup des conseils pendant ces trois années.

Contents

Introduction **1**

Background 1

Peach supply chain-actors, quality perception and the need for fruit storage after harvest 2

The brown rot disease during pre- and post-harvest 4

Effects of pre-harvest practices and storage conditions on the fruit quality development and the appearance of brown rot disease symptoms in peaches 5

Modeling as a tool to integrate pre-harvest and storage conditions in the simulation of fruit quality development and brown rot loss during storage 11

Objectives and thesis structure 13

1 A process-based model of nectarine quality development during pre- and post-harvest **17**

2 Brown rot disease in nectarine during storage: modeling the joint effects of pre-harvest and storage conditions **33**

2.1 Introduction 36

2.2 Materials and Methods 38

2.2.1 Experimental design to study brown rot secondary infections during storage 38
2.2.2 Assessment of the effects of pre-harvest and storage conditions on brown rot dynamics during storage 40
2.3 Results 45
2.3.1 No brown rot secondary infection symptoms were observed during storage 45
2.3.2 Brown rot incidence during storage under different pre-harvest and storage conditions 46
2.3.3 Modeling the influence of pre- and post-harvest covariates on nectarine time-to-appearance of brown rot symptoms during storage 48
2.4 Discussion 51

3 The synergy between pre-harvest practices and storage conditions to obtain high quality nectarines and to prevent brown rot losses during storage: a modeling framework 57
3.1 Introduction 61
3.2 Modeling framework 64
3.2.1 Modeling the development of fruit quality-related characteristics during the growing season: QualiTree 67
3.2.2 Modeling fruit mass and sugars dynamics during storage 68
3.2.3 Modeling the time-to-appearance of brown rot symptoms on fruit during storage 68
3.3 Materials and Methods 69
3.3.1 Scenarios of pre-harvest practices and storage conditions 69
3.3.2 Model parameters and inputs 71

3.3.3 Performance criteria 73
3.3.4 Sensitivity analysis of performance criteria to pre-harvest practices and storage conditions 74
3.3.5 Search for the combined pre- and post-harvest scenario offering the best compromise in terms of fruit quality and quantity at the end of storage 75
3.4 Results 78
3.4.1 Effects of pre-harvest practices and storage conditions on the performance criteria based on model outputs 78
3.4.2 Storage duration and importance of fruit quality criteria influence the pre- and post-harvest scenarios in terms of the optimal performance score 84
3.5 Discussion 87
3.5.1 The modeling framework satisfactorily integrates the effects of pre-harvest practices and storage conditions on fruit quality development and fruit loss during storage . 87
3.5.2 Factors governing the choice of the optimal pre- and post-harvest scenarios in terms of fruit quality and quantity . 90
3.6 Conclusions 91

General discussion and perspectives **93**

Bibliography **105**

A Supplementary Information - Chapter 1 **135**
A.1 Sugar metabolism represented in sugar dynamics sub-models . . 136
A.2 Sub-model parameter and constant values taken from literature 137
A.3 Measured and simulated fruit cuticular cracks surface area . . . 138

A.4 Simulated part of fruit mass loss due to respiration during storage 139

B Supplementary Information - Chapter 2 **141**

B.1 Results: brown rot secondary infections during storage 142

B.2 Results: cumulative incidence of brown rot disease at the end of storage, under different pre-harvest scenarios and storage conditions (2018-2019) 143

B.3 Survival analysis: model selection 145

C Supplementary Information - Chapter 3 **147**

C.1 Water regime scenarios used in model simulations 148

C.2 Parametrization and initialization of the QualiTree model 149

List of Figures

1 Annual world production of the stone fruit crops during the period 1990-2019 (Source: FAOSTAT). 2

2 Production of peaches during the period 1990-2015 for the four higher European Union producers (Source: FAOSTAT). 3

3 Diagram of the processes and the properties considered in the thesis at the tree and fruit scale, under the influence of pre- and post-harvest conditions. 10

2.1 Experimental set-up for the brown rot secondary infections experiment. The three upper cells contain a central inoculated fruit (I), while the lower are the control groups (C). 40

2.2 Time course of observed incidence of brown rot disease during nectarine storage in 2018 for three different harvest dates. Points are means and bars represent the standard error of the mean. Fruit came from two pre-harvest irrigation treatments: 100% CWR (a) and 50% CWR (b). Fruit were stored at a mean temperature of 20 $^{\circ}C$. 47

2.3 Time course of observed incidence of brown rot disease during nectarine storage in 2019 for different storage temperatures, after a first (a-b, 134 dafb) and a second harvest date (c-d, 141 dafb). Points are means and bars represent the standard error of the mean. Fruit came from two pre-harvest irrigation treatments: 70% CWR (a-c) and 30% CWR (b-d). 47

2.4 Parametric (continuous) and Kaplan-Meier (dotted) estimates of survival probability to brown rot during storage in 2018, for nectarine grown under a 100% CWR (a) and a 50% CWR (b) irrigation treatment, for different harvest dates. 51

2.5 Parametric (continuous) and Kaplan-Meier (dotted) estimates of survival probability to brown rot during storage in 2019, for nectarine harvested at the first (a, 134 dafb) and the second (b, 141 dafb) harvest date, for different storage temperatures. 51

3.1 Diagram of processes and fruit properties considered in the modeling framework to simulate the effect of pre-harvest practices and storage conditions on nectarine quality and brown rot infections during storage. 66

3.2 Utility functions for fruit mass and sweetness used in this study. The red dashed lines represent the value of the fruit quality trait that correspond to a satisfaction of 50%. Points represent the couples of utility values and fruit traits used for parameter calibrations. 77

3.3 Sensitivity index for the performance criteria based on model outputs, according to the five pre- and post-harvest management practices and the prevalence of brown rot at harvest (I_H). The performance criteria are referred to the end of storage and are the fruit mean mass ($Q_{S,mass}$), sweetness index ($Q_{S,sweet}$) and relative mass loss ($L_{S,mass}$), the fruit loss related to the appearance of brown rot symptoms ($L_{S,br}$), and the total (Y_S) and marketable yield (MY_S). The indices reflect the importance of each parameter on the variance of the considered output (main effect) and the strength of interaction with the other parameters (interaction). The red line identifies the threshold of the total effect index (S_T) above which a factor has significant influence on the variance of the considered performance criterion ($S_T > 0.1$). 80

3.4 Simulated effects of pre-harvest practices and storage conditions on the performance criteria based on model outputs. Boxes represent the first and third quantiles (25% and 75%) and the median of 256 simulated replicates of each treatment. The performance criteria are referred to the end of storage and are the fruit mean mass ($Q_{S,mass}$, a), sweetness index ($Q_{S,sweet}$, b), the relative mass loss ($L_{S,mass}$, c), the fruit loss related to the appearance of brown rot symptoms ($L_{S,br}$, d), and the total (Y_S, e) and marketable yield (MY_S, f). The water stress integral values correspond to the irrigation regime scenarios n° 1 (WS_Ψ=0), 11 (WS_Ψ=21), 9 (WS_Ψ=42) and 26 (WS_Ψ=57, Appendix C.1). Colours correspond to the simulated water regimes during the last stage of fruit growth ($p = III$): well-irrigated (blue), mid-stressed (yellow), and high-stressed (red). 83

A.1 Carbon pathways assumed in the pre- and post-harvest sugar dynamics sub-models. Arrows and boxes represent carbon fluxes and carbon components included in the mathematical models, respectively. The ellipses represent carbon input (the tree) and loss by respiration. The proportion of sucrose in the phloem-sourced sugar pool (λ_{ph}) and the parameters sugar transformation are indicated next to each carbon flux to which they relate. In the post-harvest stage, 'sucrose' and 'other compounds' compartment do not participate in the carbon pathways. 136

A.2 Average measured (points) and simulated (lines) values of fruit cuticular cracks surface area over the growing season, under the four experimental pre-harvest conditions of 2018. Bars stand for the standard errors. The time is in days after full bloom (17 March). 138

A.3 Simulated values of the part of fruit mass loss due to respiration, under the six experimental conditions of 2019 (Irrigation x Storage temperature), for two harvest dates (134 and 141 dafb). The time is in days after the beginning of storage. 139

B.1 Spread of brown rot secondary infections on nectarine by contact with dripping juice from infected fruits (a) and from direct contact with infected fruits (b). 142

C.1 Example of tree architecture used as input in QualiTree simulations: 'Nectarlove' tree measured in 2019 after winter pruning at INRAE centre in Avignon (France). 150

C.2 Average observed (continuous) and simulated (dashed) values of fruit and leafy shoot dry mass, and fruit fresh mass. The values refer to different experimental conditions (irrigation regime x fruit load) on nectarine 'Nectarlove' from the 2018 season (Avignon, France). 154

List of Tables

2.1 Covariate values measured for the five different harvest dates during the 2018 and 2019 experiments. In 2019, three different levels of mean storage temperature $T_{mean,s}$ were tested. 49

2.2 Coefficient estimates and associated test statistics for the best model in terms of BIC to explain time-to-infection of nectarine to brown rot during storage. 50

3.1 Irrigation levels in each of the selected nectarine developmental periods and corresponding values of diurnal water potential. . . 70

3.2 Pre-harvest practices and storage conditions considered in the study. 71

3.3 Utility function parameters for the fruit quality-related attributes. 76

3.4 Pre-harvest practices (irrigation regime scenario in terms of water stress integral WS_{Ψ} and the number of fruit left on the tree at thinning N_f) and storage conditions (mean storage temperature $Temp_S$ and relative humidity RH_S) associated with the optimal scenarios in terms of the performance score PS, for different storage durations and relative importance accorded to fruit quality-related criteria (ω_m and ω_s, related to fruit mass and sweetness). For the irrigation regimes, the number of the associated irrigation scenario is also presented between squared brackets. For each optimal scenario, the values of the performance criteria are shown: the fruit mean mass ($Q_{S,mass}$), sweetness index ($Q_{S,sweet}$), the relative mass loss $L_{S,mass}$, the fruit loss related to the appearance of brown rot symptoms $L_{S,br}$, and the total (Y_S) and marketable (MY_S) yield at the end of storage. 86

A.1 Sub-model parameter values taken from literature and used in the models of pre- and post-harvest nectarine quality development 137

B.1 Mean fruit mass (with standard deviation), maximum follow up time and cumulative incidence at the end of storage for brown rot visual assessment during storage in 2018, for each experimental treatment. Harvest dates are referred to full bloom date, which was on 17 March 2018. For fruit mass, comparisons between treatments were realised per harvest date, where means followed by the same letter do not significantly differ from each other (Tukey test with $\alpha = 0.01$). 143

B.2 Mean fruit mass (with standard deviation), maximum follow up time and cumulative incidence at the end of storage for brown rot visual assessment during storage in 2019, for each experimental treatment. Harvest dates are referred to full bloom date, which was on 10 March 2019. For fruit mass, comparisons between treatments were realised per harvest date, where means followed by the same letter do not significantly differ from each other (Tukey test with $\alpha = 0.01$). 144

B.3 Selected variables and number of estimated parameters for the best five Gompertz-shaped survival models in terms of the Bayesian Information Criterion (BIC).The value of the log-likelihood an the Somers' D_{XY} (%) statistic are presented. 145

C.1 Irrigation regime scenarios, identified by the values of the root collar water potential at midday during the fruit growth period p ($\Psi_{min,p}$) and the water stress integral indicator (WS_{Ψ}, MPa days). 148

C.2 Parameter values concerning the carbon economy and water economy in QualiTree for 'Nectarlove' nectarine cultivar grown in France. 153

Introduction

Background

The Food and Agriculture Organisation of the United Nations (FAO) celebrates 2021 as the International Year of Fruits and Vegetables, to stress their health, nutritional and economic importance on everyday life. This importance is also highlighted by the inclusion of these products in eleven of the seventeen Sustainable Development Goals (SDGs), which represent the global goals that United Nations sets to ending poverty and protect the planet in the 2030 horizon (FAO, 2021).

At the world scale, the annual fruit production was estimated at 854.8 Mt (average on 2015-2019 period, data source: FAOSTAT). In the case of stone fruit, which cover the *Prunus* species, production is growing constantly, with a 162% increase during the 1990-2019 period (Figure 1). In this fruit category, peaches (which include nectarines) are the most abundant, with an average of 24.6 Mt produced annually during the 2015-2019 period at the global scale. Production is leaded by China, which accounts for about 60% of the total amount, while European Union accounts for 16%. In the Europe case, Spain and Italy lead the market with a share of about 80% of the total production (average 2015-2019, Figure 2), while France accounts for only 6%, with a production decrease of 59% between 1990 and 2019. This decrease could be partly explained by the increas-

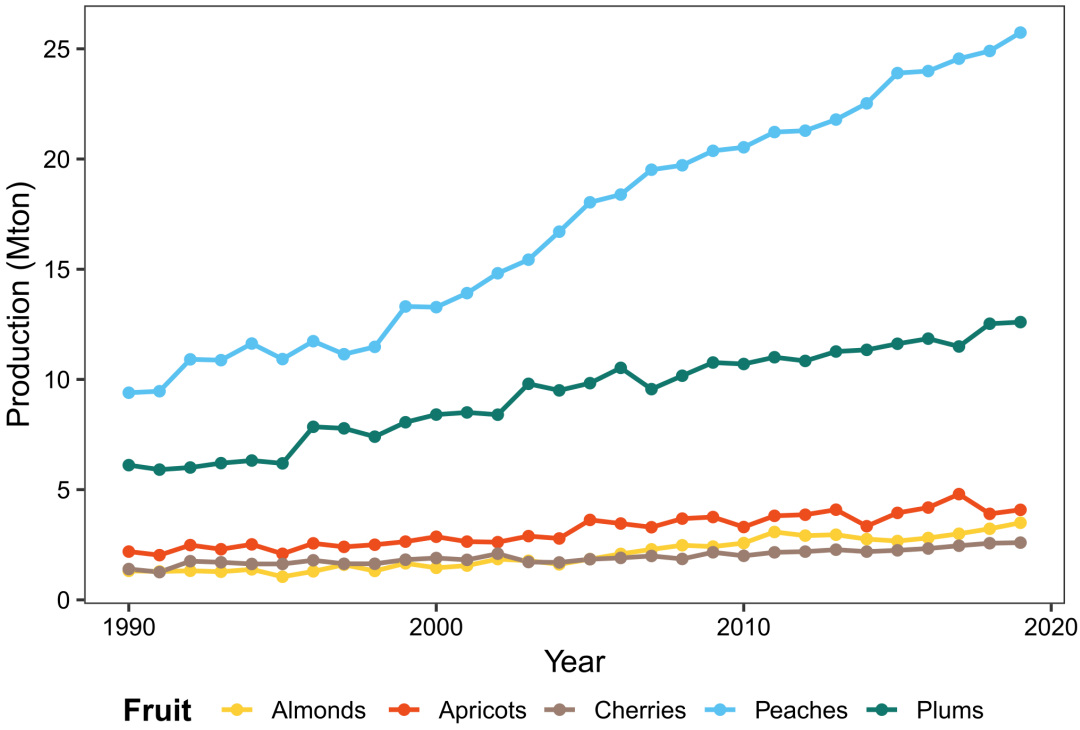

Figure 1 – Annual world production of the stone fruit crops during the period 1990-2019 (Source: FAOSTAT).

ing volume of import from Spain, whose market shows a higher competitiveness and where the pedoclimatic conditions are more favorable than the French ones (Scandella and Roty, 2012).

Peach supply chain-actors, quality perception and the need for fruit storage after harvest

The fruit supply-chain includes several actors: the producers, the post-harvest supply-chain actors (who perform storage, packaging or processing, distribution and retailing) and the consumers (HLPE, 2017). Depending on their place in the supply chain, these actors have different interests (Soto-Silva et al., 2016). Producers look for high yield, large fruit size, resistance to disease and ease of harvest, while packers, shippers and wholesalers emphasize mechanical properties such as flesh firmness and texture, which simplify fruit shipping, storage and

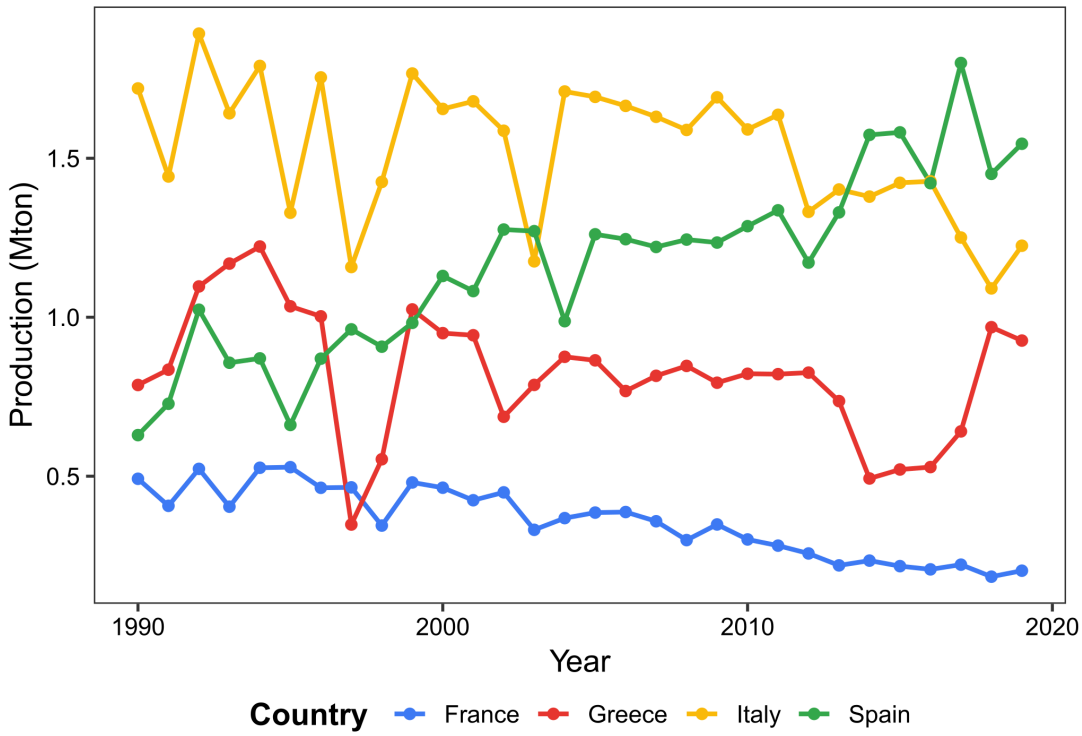

Figure 2 – Production of peaches during the period 1990-2015 for the four higher European Union producers (Source: FAOSTAT).

increase the retail market life potential (Crisosto and Costa, 2008). Consumers, on the other side, focus on fruit quality, demanding less variability in internal and external quality attributes like taste, aroma and appearance (Berna et al., 2005; Hilaire et al., 2013). Consumers have different preferences, so many different consumer profiles exist, which are translated into high efforts by breeders to develop peach cultivar with different maturity times (from june to september, in France) and combination of sensory attributes (from acid to sweet) (Crisosto and Costa, 2008). However, in France, peach quality is often perceived as deceiving by the consumers, who evaluate this fruit as mealy, too firm and not sweet enough (Scandella and Roty, 2012). This is a huge problem for the producers and the post-harvest actors, who have to consider quality and quantity at the same time. In general, quality is assigned to a product by the user (buyer/consumer), who converts the physical, mechanical and chemical properties (e.g. sugar and

acid content) into sensory quality attributes (e.g. sweetness) (Sloof et al., 1996; Crisosto and Costa, 2008).

Consumers do not have access to the fruit just after the harvest, because these products undergo almost always some post-harvest stages. To maintain the quality of fruit during post-harvest, fruit are stored at low temperatures to reduce the speed of metabolic processes associated with fruit ripening. Generally, storage facilities are integrated to packinghouses or directly on-farm (Lopez Camelo, 2004). In the case of peach and nectarines, the ideal storage-room conditions are low temperatures (from -1 °C to 0 °C) and high relative humidity (90-95%), for a storage life that could reach up to 3 weeks (Lill et al., 1989). Unfortunately, low temperatures adversely affect the sensory quality and can cause physiological disorders, such as chilling injury (Lurie and Crisosto, 2005; Yu et al., 2015). In addition, inappropriate storage conditions could also induce fruit shriveling, which causes economic loss due to a decrease in saleable mass (Veraverbeke et al., 2003), and shriveled fruit can be considered as unacceptable by consumers (Nunes and Emond, 2007; Crisosto, 1994).

The brown rot disease during pre- and post-harvest

Another reason of concern for the fruit producers and post-harvest actors is the appearance of several fungal diseases in the orchard and, principally, after the harvest, with product losses that reach, on average, from 30 to 50% during this last stage (Bautista-Baños, 2014). Among these diseases, brown rot is the most important for the stone fruit case, accounting for about 90-95% of losses (source: CTIFL communication).

Brown rot is caused by infections from *Monilinia laxa* (Aderhold & Ruhland) Honey, *Monilinia fructigena* (Aderhold & Ruhland) Honey and *Monilinia fructicola* (Winter) Honey (Byrde and Willetts, 1977). The fungi produce both sexual

(ascospores) and asexual (conidia) spores, the latter being the most commonly present in the orchard (Oliveira Lino et al., 2016). The spores are dispersed in the orchard by wind and rain to susceptible host tissues (leaf, twig, fruit) and germinate under favorable weather conditions such as high humidity, warm temperatures and abundant rainfall (Prusky, 1996), with a production of extensive mycelial growth. The fruit susceptibility to infection increases with increasing ripening (Mari et al., 2003). The conidia produced on infected tissues can thus serve as secondary inoculum for infection of immature and mature fruit. To avoid disease damages, fungicide applications are frequently used during humid periods in the orchard (Abate et al., 2018), with consequent environmental costs and with the emergence of fungicide resistant strains (Obi et al., 2018).

The majority of fruit losses due to brown rot usually occurs during post-harvest stage (principally during storage and transport), with a cumulative incidence that could reach 100% (Larena et al., 2005). In this stage, several control methods have been developed, as alternatives to fungicides: biological control (e.g. bacteria and yeasts), the use of bio-active compounds (e.g. plant extracts) and physicochemical methods (e.g. heat treatment and hot water dipping) (Nunes, 2012; Spadoni et al., 2013).

Effects of pre-harvest practices and storage conditions on the fruit quality development and the appearance of brown rot disease symptoms in peaches

For peaches, the lack of visual defects and the fruit size are among the principal attributes perceived by consumers, along with the peel colour. However, if the

fruit lacks sweetness and aroma, the consumers will unlikely purchase again that product (Crisosto, 2002; Delgado et al., 2013; Cirilli et al., 2016). Consumers are interested in the balance between the sugar and acid concentrations inside fruit pulp (Genard et al., 1999). The former is measured as soluble solid concentration (SSC, %), while the latter is measured by titrable acidity (TA, %) (Crisosto and Day, 2012). Producers, on their side, manage pre-harvest practices, such as the irrigation regime, fertilization, pruning and thinning, to maintain fruit quality attributes at a sufficient level to satisfy consumer expectations and to maximize fruit yield (Minas et al., 2018).

In the orchard, pre-harvest practices and meteorological conditions affect the evolution of fruit quality attributes, by influencing the carbon and water transport inside the tree. The water regime, i.e. the balance between ingoing and outgoing flux of water inside the tree, defines the plant water potential, which influences leaf growth and photosynthesis (Thornley and France, 2007). These processes are responsible for the production of assimilates, which are essential for the fruit growth and the sugar dynamics (Lescourret and Génard, 2005). Fruit mass is generally lowered under water-stressed than under water-comfort regimes, but fruit dry mass can show similar values (Berman and Dejong, 1996). Fruit from water-stressed trees can thus exhibit higher sugar content than those from well-irrigated trees (Alcobendas et al., 2013), but this is influenced by both the intensity and timing during which the water constraint is experienced. Thinning intensity has a strong influence on peach fruit size, maturity time and fruit quality-related properties, by affecting the accumulation of dry mass in the fruit (Grossman and DeJong, 1994; Lescourret et al., 2011).

Fruit growing patterns induced by pre-harvest conditions also influence the development of the fruit cuticle (Gibert et al., 2007), the role of which is to minimize water loss and to protect fruit against physical, biological and chemical

attacks (Lara et al., 2014). Cuticular cracks may appear on the fruit surface during the fruit growth period, as an effect of unbalanced water flux entering or exiting the fruit (Opara et al., 2010). These cuticular failures enhance the fruit surface conductance to water vapour diffusion, which controls the fruit weight loss related to the fruit transpiration (Lescourret et al., 2001), one of the major drivers of fruit quality evolution during storage (Yahia and Carrillo-Lopez, 2018).

Fruit, which are living products, generally undergo one or several post-harvest stages, where fruit properties change. The determination of the harvest date is essential for these changes because the level of maturity affects fruit storage potential: delayed peach harvest improves fruit organoleptic quality at the expense of a shorter shelf-life (Bonghi et al., 1999). In general, fruit quality traits, such as soluble solids concentration (SSC) and titratable acidity (TA) are related to maturation and to the sensory quality of the fruit (Kader, 1999). The harvest date is generally chosen from the farmer's experience, based principally on fruit ground color and fruit size, but indices based on destructive measurements such as the fruit firmness and the balance between SSC and TA (SSC:TA) are also used (Crisosto, 1994). In the recent years, non-destructive indices based on visible/near infrared (vis/NIR) spectroscopy, such as the index of absorbance difference (I_{AD}) (Ziosi et al., 2008; Zhang et al., 2020), have been used to assess fruit maturity and optimal harvest date.

Changes in fruit quality-related characteristics after the harvest are strongly impacted by the temperature and hygrometry of the environment (Yahia and Carrillo-Lopez, 2018; Wills et al., 2016). Transpiration is one of the main processes that impacts product deterioration, by enhancing fruit softening and visual shriveling (Díaz-Pérez, 2019). Changes in sugar metabolism also take place after harvest (Borsani et al., 2009; Lombardo et al., 2011). They depend on

the level of sugars accumulated during the growing season and also on storage conditions (Aubert et al., 2014). However, literature studies usually do not take into account the dynamics of these fruit quality properties during the growing season and the following storage stage.

Another reason of concern for peaches is the fungal infections caused by *Monilinia* spp., which are responsible for brown rot diseases. The fungal spores infect the flowers and the fruit of the peach tree in the orchard. The magnitude of this infection depends on the level of the conidial density in the air (Gell et al., 2008; Villarino et al., 2012) and on the receptivity of the fruit linked to the appearance of micro-cracks during fruit growth (Gibert et al., 2009), the latter being entry sites for fungal conidia. Nevertheless, it is especially during storage that symptoms appear (Hong et al., 1997), as an effect of latent infection (Gell et al., 2008). Storage environmental conditions, namely temperature and humidity, also play a key role in the expression of brown rot disease (Bernat et al., 2017b), which can cause severe losses at these stages (Martini and Mari, 2014).

We have seen that fruit quality development and losses during growing season and storage are interlinked processes that are influenced by both agricultural practices and storage conditions. However, despite the evident link between their biological and physiological processes, pre- and post-harvest worlds are rarely considered as a continuum. The communication between these two worlds is often problematic due to differing viewpoints on the nature of quality and its importance in the supply chain, and also on the trade-off between yield and quality (Tijskens and van Kooten, 2006). This barrier needs to be overcome so that ideas and information can be exchanged. The relationships between the pre- and post-harvest processes presented above and identified as significant for our work should be incorporated into a unitary framework, which allows to evaluate how fruit quality criteria and epidemiological state develop as a function

of the conditions in the two fruit life stages (Figure 3).

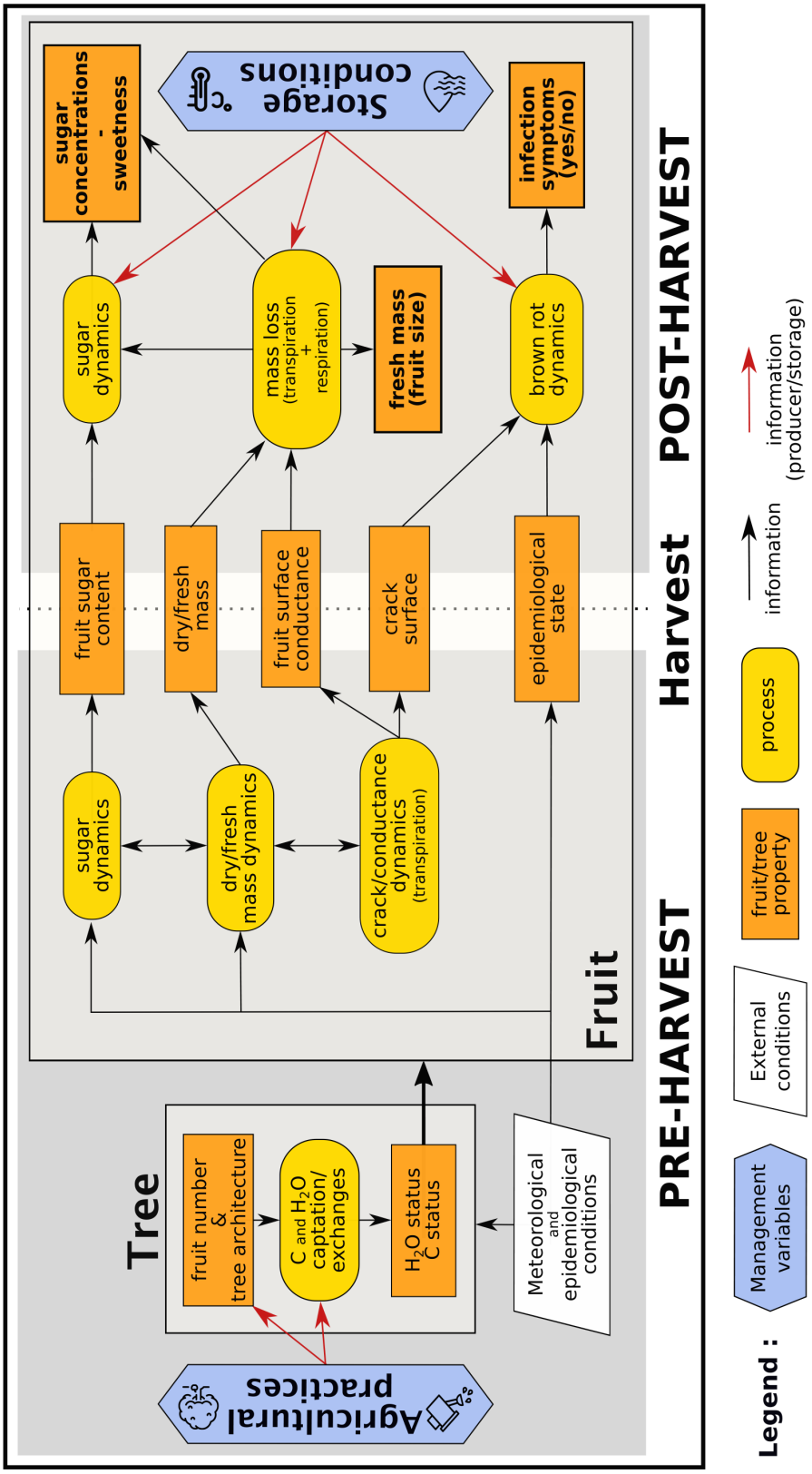

Figure 3 – Diagram of the processes and the properties considered in the thesis at the tree and fruit scale, under the influence of pre- and post-harvest conditions.

Modeling as a tool to integrate pre-harvest and storage conditions in the simulation of fruit quality development and brown rot loss during storage

The improvement of fruit quality and the reduction of fruit loss can be tackled by an integrated approach, in which the effects of pre-harvest practices and storage conditions are both considered. The integration of different parts of a complex system, which is difficult to achieve by experiments alone, could be done with the aid of mathematical modeling and *in-silico* experiments (Thornley and France, 2007). Modeling is the modern version of analyzing and understanding laboratory and practical experiments (Tijskens, 2001), which remain however of fundamental importance.

In modeling the fruit quality-related attributes during pre-harvest, one of the priorities of the last decades has been to consider organ growth in dry weight (Gary et al., 1998; Marcelis and Heuvelink, 2007). Some models have also been proposed to simulate water accumulation in the fruit (Bussières, 1994; Lee, 1990). A fruit growth model integrating both dry matter and water accumulation in the fruit was developed by Fishman and Génard (1998). Although taste is one of the most important attributes for fruit acceptance, fruit composition is still absent from most models. But there are a few exceptions: Génard and Souty (1996) developed a model to predict fruit sugar content and Lescourret and Génard (2005) integrated the dry and fresh mass accumulation with fruit sugar content accumulation during fruit growth. Moreover, Lescourret et al. (2011) proposed a tree model (QualiTree) capable of simulating fruit size, water content, and fruit sugar content under the influence of cultural practices at the

tree scale. The evolution of epidermal micro-cracks throughout fruit growth, involved in *Monilinia* spp. infections and fruit quality via transpiration losses, and its response to cultural factors that modify this growth were also included in a model (Gibert et al., 2005, 2010).

For post-harvest, water exchanges during fruit storage were modeled for several fruits and vegetables (Veraverbeke et al., 2003; Bovi et al., 2016; Xanthopoulos et al., 2017), and the respiration rate was considered in several models (Caleb et al., 2016). The fruit dry mass accumulated during the growing season assures the development of fruit metabolism after harvest (Galindo et al., 2004). The time-course of fruit quality-related attributes evolution during post-harvest has been described for several fruit, in particular regarding fruit firmness and colour (Schouten et al., 2007; Tijskens et al., 2007; Tijskens and Schouten, 2014). However, sugar metabolisms during storage has rarely been modeled, unless in the potato case (Hertog et al., 1997). Moreover, post-harvest dynamics of quality-related attributes with respect to different pre-harvest practices are poorly documented and modeled.

On the epidemiological side, a brown rot SIR (Susceptible-Infected-Removed) model has been proposed by Bevacqua et al. (2018), which predicts the dynamics of the disease during the growing season for peach, based on different cultural factors. For the storage stage, empirical models have been developed that consider the effect of latent infection and the influence of meteorological variables at harvest like temperature and wetness duration (Gell et al., 2008, 2009; Villarino et al., 2012). These empirical models do not take into consideration the fact that *Monilinia* spp. could diffuse in the storage room and the effect of storage conditions. Garcia-Benitez et al. (2020) have recently related the latent infections and the storage conditions to the dynamic incidence of brown rot associated to *Monilinia* spp. during the storage of nectarines, but the model does not take

into account the fruit individual characteristics at harvest, which are influential in the appearance of the disease (Gibert et al., 2009).

Eventually, the state of the art shows two important gaps. First, there is a lack of knowledge on the relationship between pre-harvest and post-harvest dynamics in fruit: the link between fruit growth and storage conditions on the dynamics of fruit quality-related attributes and susceptibility to brown rot during storage remains to be explored. Second, in connection with the previous point, there is a lack of models to evaluate and optimize the integrated functioning of the fruit pre- and post-harvest continuum, with the aim to prevent fruit loss related to fungal disease and to optimize several fruit quality-related attributes.

Objectives and thesis structure

In the context presented in the previous sections, we formulated the following research questions, which also correspond to the three main chapters of the thesis:

- how do peach characteristics that are the major quality-related drivers and criteria, namely the surface conductance to water vapour, the fruit fresh mass and soluble sugar content, evolve during the pre-harvest stage under the influence of growing conditions and then during the post-harvest stage under different storage conditions?

  We will answer to this question in the first chapter by the use of experimentation and mathematical models. We will present the results of field and laboratory experiments, which were used in the design and the calibration of several models of quality-related attributes during pre- and post-harvest stage.

  This chapter was published as a paper in *Postharvest Biology and Technol-*

ogy on 25 January 2021, with the title "*A process-based model of nectarine quality development during pre- and post-harvest*".

- how does the fruit sensitivity to brown rot disease at harvest, controlled by pre-harvest conditions, and the storage conditions influence the incidence of brown rot disease during the storage of peaches?

  We will answer to this question in the second chapter. We will present two experiments which aimed to verify the presence of secondary infections by *Monilinia* spp. during storage and to assess the temporal progress of brown rot disease under the influence of several pre- and post-harvest conditions. The results from these experiments were used to build a mathematical model to estimate the probability of time-to-appearance of brown rot symptoms in peaches during storage.

  The chapter was submitted to *Phytopathology* journal on 13 May 2021.

- is it possible to choose agricultural practices and storage conditions to maximize yield and several quality-related attributes, and, at the same time, to minimize the fruit losses caused by brown rot and excessive water loss?

  We will present our approach to this issue in the third, and last, chapter. We integrated the models presented in the previous chapters in a unique modeling framework to simulate the pre- and post-harvest dynamics of peach quality-related attributes and the brown rot disease during storage. We used this framework to search, using optimisation techniques based on genetic algorithm, for various sets of agricultural practices and storage conditions to optimize the fruit quality criteria, fruit yield and avoid the fruit losses in the pre- and post-harvest continuum.

The models presented in this thesis were designed and calibrated for the nectarine (*Prunus persica var. nucipersica*) case.

The chapters of the thesis will be presented with the structure of research papers.

Chapter 1

A process-based model of nectarine quality development during pre- and post-harvest

Résumé

Nous proposons un nouveau modèle mathématique capable de simuler les effets combinés de la croissance du fruit et des conditions de stockage (température et humidité relative) sur le développement des sucres solubles et de la perte de masse pendant le stockage des nectarines. L'évolution pendant la saison de croissance de la conductance de la surface du fruit à la vapeur d'eau, de la perte de masse du fruit pendant le stockage et des dynamiques de concentration des sucres dans la pulpe du fruit ont été modélisées. Nous avons intégré les trois sous-modèles dans un modèle capable de calculer un indice de sucrosité du fruit et la perte relative d'eau pendant le stockage. Nous avons calibré les paramètres de ces sous-modèles grâce aux résultats d'expériences menées en 2018 et 2019, lors desquelles on a fait varier conjointement certaines des pratiques

en verger (irrigation et charge des fruits) et les conditions de stockage. Le niveau d'irrigation a influencé la conductance de la surface des fruits à la vapeur d'eau lors de la récolte, mais les résultats expérimentaux suggèrent une faible influence de cette variable sur la perte de masse des fruits pendant le stockage, laquelle a été principalement déterminée par l'humidité relative dans la chambre de stockage. L'intensité de l'irrigation a également influencé la dynamique des sucres, tout comme la température de stockage. Les fruits ayant été stockés à la température la plus élevée (25 °C) étaient plus sucrés que ceux stockés à des températures plus basses (2 °C et 15 °C). Ces résultats expérimentaux ont été bien reproduits par les sorties du modèle. Les simulations du modèle pendant le stockage ont révélé une relation positive entre la sucrosité et la perte de poids des fruits, qui augmente avec l'augmentation de la température de stockage et la diminution de l'humidité relative. Le meilleur scénario - celui conduisant à une perte de masse acceptable et à un bon niveau de sucrosité - concernait les fruits d'arbres peu chargés et soumis à un stress hydrique, stockés après récolte à 15 °C avec 70 % d'humidité relative. En outre, les résultats des simulations du modèle ont montré que la durée de stockage augmentait la perte de masse des fruits et, dans une moindre mesure, l'indice de sucrosité, et que les fruits provenant de dates de récolte tardives avaient une sucrosité plus élevée à la fin du stockage. Le modèle pourrait être utilisé pour gérer et optimiser les pratiques pré-récolte et les conditions de stockage, afin de maximiser la sucrosité et de minimiser la perte de masse des fruits, ce qui correspond au respect des normes de qualité des fruits tout au long de la chaîne d'approvisionnement.

Postharvest Biology and Technology 175 (2021) 111458

Contents lists available at ScienceDirect

Postharvest Biology and Technology

journal homepage: www.elsevier.com/locate/postharvbio

A process-based model of nectarine quality development during pre- and post-harvest

Enrico Casagrande [a,b,*], Michel Génard [b], Sébastien Lurol [a], Florence Charles [c], Daniel Plénet [b], Françoise Lescourret [b]

[a] Centre Technique Interprofessionnel des Fruits et Légumes, 13210 Saint-Rémy-de-Provence, France
[b] UR 1115 Plantes et Systèmes de Culture Horticoles, INRAE, Avignon Cedex, France
[c] Qualisud, Avignon Université, CIRAD, Université de Montpellier, Montpellier SupAgro, Université de la Réunion, 84000 Avignon, France

ARTICLE INFO

Keywords:
Fruit quality
Mathematical modeling
Pre-post-harvest
Sugars
Mass loss
Nectarine

ABSTRACT

A new mathematical modeling framework able to simulate the combined effect of fruit growth and post-harvest storage conditions (temperature and relative humidity) on nectarine quality is here proposed. The seasonal course of fruit surface conductance to water vapor, fruit mass loss during storage, and sugar concentration dynamics in fruit pulp were modeled. The three sub-models were integrated into a model capable of calculating a fruit sweetness index and relative water loss during storage, which were selected as nectarine quality criteria. Sub-models parameters were calibrated through results from experiments carried on during 2018 and 2019, where horticultural practices (irrigation and fruit load) and storage conditions were jointly varied.

Irrigation level influenced fruit surface conductance to water vapor at harvest, but experimental results point out that this variable may have little influence on fruit mass loss during storage, which was mainly driven by relative humidity in the storage chamber. Irrigation intensity was also influential on sugar dynamics, along with storage temperature, with fruit stored at the higher temperature (25 °C) being sweeter than those stored at lower ones (2 and 15 °C). These experimental results were well replicated by the sub-model outputs.

Model simulations during storage revealed a trade-off between the two selected quality criteria, which increased with increasing storage temperature and decreasing relative humidity. The best scenario in terms of acceptable fruit mass loss and sweetness index was for fruit from water-stressed and low crop-loaded trees, 15 °C and 70% relative humidity. Moreover, storage duration was shown to increase fruit mass loss and, to a lesser extent, the sweetness index, while fruit from late harvest dates had higher sweetness at the end of storage. The model can potentially be used to manage and optimize pre-harvest and storage practices that will maximize sweetness and minimize mass loss to meet fruit quality standards along supply chains.

1. Introduction

Fruit quality is generally defined as a set of fruit properties (mechanical, sensory and nutritional) measured in different ways by different stakeholders along the supply chain, such as producers, retailers and consumers (Sloof et al., 1996). In this context, two of the most important quality attributes for peach and nectarine are fruit size and sugar concentration (Byrne et al., 2019; Cirilli et al., 2016), which are valued by all parties (Crisosto, 2002).

The development of fruit quality begins in the orchard, where horticultural practices (like thinning and irrigation) as well as climatic conditions, influence fruit physiology during the growing season (Minas et al., 2018). Among these practices, thinning influences carbon source-sink relationships and consequently fruit growth by increasing or decreasing competition for resources (Grossman and DeJong, 1994; Inglese et al., 2002), while influencing the sugar dynamics inside the fruit mesocarp (Génard and Souty, 1996). Irrigation affects plant–water relationships and thus fruit water supply and fruit size at harvest (Lopez, Hossein Behboudian et al., 2012). Another important effect related to water stress is the increase in sugar and soluble solid concentrations, which generally occurs during the last stage of the growing season (Ripoll et al., 2014). Irrigation also influences the appearance of cuticular surface microcracks, which are among the main determinants of fruit conductance to water vapor diffusion (Knoche et al., 2002). Water

* Corresponding author at: Centre Technique Interprofessionnel des Fruits et Légumes, 13210 Saint-Rémy-de-Provence, France.
E-mail address: enrico-maria.casagrande@ctifl.fr (E. Casagrande).

https://doi.org/10.1016/j.postharvbio.2020.111458
Received 7 August 2020; Received in revised form 24 December 2020; Accepted 28 December 2020
Available online 25 January 2021
0925-5214/© 2020 Elsevier B.V. All rights reserved.

diffusion regulates the degree of fruit transpiration (Lescourret et al., 2001), which is one of the major determinants of fruit quality. In this regard, a higher fruit surface conductance also occurs when agronomic practices lead to the production of larger fruit on trees (Gibert et al., 2007).

Stone fruit quality and physiological maturity at harvest greatly influence subsequent post-harvest performance and quality changes (Crisosto, 2002). During storage, transpiration is among the most important factors which determine the deterioration of fruit (Kader, 2002). This water loss induces water stress in fruit tissues, enhancing or accelerating their senescence because of an increased rate of cellular membrane disintegration and leakage of solutes. From the retailer's and consumer's point of view, mass loss resulting in fruit shriveling significantly reduces visual quality and marketability (Ben-Yehoshua and Rodov, 2002). Peach and nectarine consumer acceptance decreases when more than 11% mass loss takes place during storage (Nunes and Emond, 2007). However, growers or retailers may experience economic loss when as little as 8% of the fruit fresh mass is lost (Crisosto et al., 1994). This process is influenced by fruit surface area and storage conditions such as temperature and relative humidity (Díaz-Pérez, 2019). Moreover, during post-harvest storage sugar metabolism is modified and the fruit use sugars as an energy source for respiration (Yahia et al., 2019). Processes that affect the seasonal course of fruit quality from the pre-harvest stage to the end of storage are thus strongly interlinked. In this situation, process-based models can help to understand and simulate the effects of combined growing and storage conditions on the development of fruit quality characteristics (Martre et al., 2011). Several pre-harvest models have been developed to simulate the temporal change of fruit surface conductance to water vapor (Knoche et al., 2002; Gibert et al., 2005). Moreover, mathematical models able to simulate the primary metabolism kinetics inside fruit pulp have been designed for fruit such as peach (Génard and Souty, 1996), mango (Léchaudel et al., 2013) and tomato (Beauvoit et al., 2014). On the post-harvest side, models have been developed to simulate fruit transpiration and mass loss as a function of storage conditions (Veraverbeke et al., 2003; Bovi et al., 2016; Xanthopoulos et al., 2017). For sugar metabolism dynamics during post-harvest, a simulation model was developed for the potato by Hertog et al. (1997). However, to our knowledge, the integration of pre- and post-harvest simulation models of fruit quality in a combined model has never been done.

To fill this gap, a new process-based modeling framework to simulate the combined effect of horticultural practices and storage conditions on nectarine quality characteristics was here proposed.

The pre- and post-harvest dynamics of surface conductance to water vapor, mass loss and sugar concentration in the pulp were modeled under the influence of horticultural and storage conditions. These sub-models were then grouped in a single model, aimed at simulating fruit fresh mass loss and the concentration of different sugars in the fruit fresh pulp during storage, as a result of both horticultural practices and storage conditions. Finally, model behavior was studied through a parameter sensitivity analysis as well as the simulation of different irrigation and fruit load conditions combined with temperature and humidity storage scenarios.

2. Materials and methods

2.1. Description of the model

The model is composed of three sub-models, as presented in Fig. 1.

Fruit dry and fresh mass dynamics during the growing season, which depend on horticultural practices, are the inputs of the pre-harvest models that deal with the seasonal course of fruit surface conductance and the accumulation of different sugars inside the fruit mesocarp throughout the growing season. At harvest, the fruit has observed dry and fresh mass, and modeled fruit surface conductance and sugar concentrations. These fruit characteristics are, in turn, the initial conditions for the two post-harvest quality sub-models, which are governed by storage conditions. The first one deals with fruit mass loss during storage, namely through the processes of transpiration and respiration, while the second focuses on sugar dynamics. The final outputs of the model are the fruit fresh mass at the end of storage and the concentration of each sugar inside the fruit pulp. These outputs allow to calculate several fruit quality indicators such as the relative mass loss during storage with reference to the mass at harvest (as a result of fruit shriveling) and a sweetness index. The latter was calculated as a linear combination of individual sugar concentrations based on the sweetness rating for each sugar relative to that of sucrose (Génard and Souty, 1996; Kulp et al., 1991).

2.1.1. Fruit surface water vapor conductance and cuticular crack development

The seasonal course of fruit surface conductance to water vapor diffusion has been described and modeled for peach and nectarine by Gibert et al. (2010). In the model, the total fruit surface conductance to

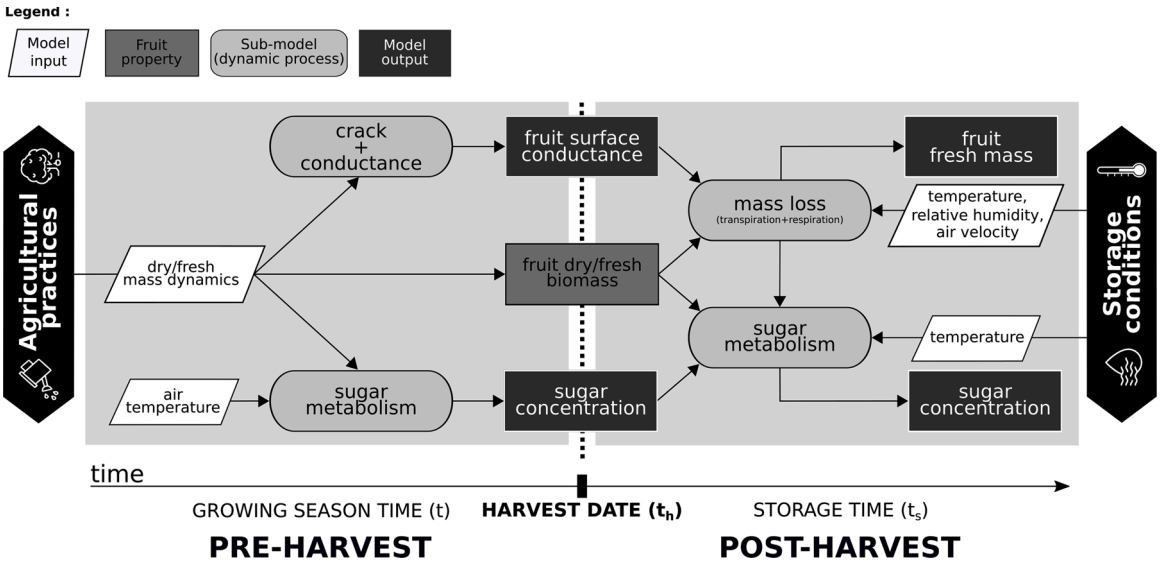

Fig. 1. Diagram of processes and fruit properties considered in the mathematical model of nectarine quality dynamics under pre- and post-harvest conditions. The arrows represent flows of information.

water vapor g_f (mol m^{-2} s^{-1}) was calculated daily and expressed as:

$$g_f(t) = g_{\text{sto}}(t) + g_{\text{cut}}(t) + g_{\text{cra}}(t) \quad (1)$$

where t is the time in days after full bloom and the components related to stomata (g_{sto}), cuticle (g_{cut}) and cracks (g_{cra}) are distinguished. The importance of each component varies during the growing season and depends on the percentage of the component area with respect to the total fruit surface area. The stomatal component was described by:

$$g_{\text{sto}}(t) = \frac{g'_{\text{sto}} \cdot n_{\text{sto}}}{A_f(t)} \quad (2)$$

where g'_{sto} (mol m^{-2} s^{-1} at a stomatal density of 1 cm^{-2}) is the stomatal specific conductance, n_{sto} (dimensionless) is the stomata number at the onset of anthesis, and A_f (cm^2) is the fruit surface area. The special feature of the model of Gibert et al. (2010) is that it explicitly calculates the development of cuticular crack surface area, which is done by considering that new cracks are generated when the expansion rate of fruit surface area is bigger than that of cuticle surface area A_{cut} (cm^2). The relative growth rate of the latter depends on the relative growth rate of fruit surface area and fruit mass during the growing season W (g) as follows:

$$\frac{\text{dA}_{\text{cut}}}{A_{\text{cut}}(t) \cdot \text{dt}} = (-\text{cut}_1 \cdot W(t) + \text{cut}_2) \cdot \frac{\text{dA}_f}{A_f(t) \cdot \text{dt}} \quad (3)$$

where cut_1 (g^{-1}) and cut_2 (dimensionless) are two empirical parameters. Moreover, the generated cuticular crack surface can also heal, with a healing ratio per wounded surface area δ (dimensionless) that decreases with fruit maturation:

$$\delta(t) = \text{dh}_1 \cdot exp[-dh_2 \cdot RI(t)] \quad (4)$$

where dh_1 (cm^2 cm^{-2}) and dh_2 (dimensionless) are two empirical parameters, and RI (dimensionless) is the fruit ripening index, described as:

$$\text{RI} = \frac{t}{t_{\text{CM}}} \quad (5)$$

where t_{CM} is the harvest date at commercial maturity (in days after bloom). With respect to the original model, in order to take account of the fact that cuticle deposition ceases prior to the onset of the ripening process (Lara et al., 2015), the cuticle component g_{cut} was assumed to decreases with time, while depending on the ratio between the cuticle surface area and the fruit surface area as well:

$$g_{\text{cut}}(t) = g'_{\text{cut}}(t) \cdot \frac{A_{\text{cut}}(t)}{A_f(t)} = g_{\text{cut1}} \cdot exp[-t \cdot g_{cut2}] \cdot \frac{A_{\text{cut}}(t)}{A_f(t)} \quad (6)$$

where g'_{cut} is the specific cuticular conductance (mol m^{-2} s^{-1}) and g_{cut1} (mol m^{-2} s^{-1}) and g_{cut2} (s^{-1}) are two empirical coefficients.

2.1.2. Fruit mass loss during storage: transpiration and respiration

The model considers the daily fruit mass loss related to transpiration and respiration during storage. For transpiration, we used Fick's law of diffusion, to which we added the effect of storage conditions on the boundary layer. In the absence of clear trends in the literature (see the review of Lara et al. (2019)), fruit surface conductance during storage g_{tot_s} (mol m^{-2} d^{-1}) was considered as not being influenced by post-harvest water loss, as in tomato (Romero and Rose, 2019). This fruit conductance was assumed to result from the boundary layer conductance g_{bl} (mol m^{-2} d^{-1}) and from the fruit surface conductance at harvest g_{f_h} (mol m^{-2} d^{-1}), which act in series. In this case:

$$g_{\text{tot}_s}(t_s) = \frac{g_{\text{bl}}(t_s) \cdot g_{f_h}}{g_{\text{bl}}(t_s) + g_{f_h}} \quad (7)$$

where t_s is the time after the beginning of storage, measured in days. In the previous equation, g_{bl} depends on the ratio between the binary diffusion coefficient for water vapor in air at normal pressure D_w (m^2 d^{-1}; Eq. (8)) and the boundary layer thickness d_x (m; Eq. (9)), along with storage room temperature and atmospheric pressure. The diffusion coefficient equation was obtained by interpolating the values presented in Bolz and Tuve (1973):

$$D_w(t_s) = 1.944 \cdot (T(t_s)/273.15)^{1.8} \quad (8)$$

where T (K) is the mean daily temperature in the storage room. The boundary layer thickness is calculated assuming that the nectarine is a sphere:

$$d_x(t_s) = \frac{2.8\sqrt{\frac{D}{v(t_s)}} + \frac{0.25}{v(t_s)}}{1000} \quad (9)$$

where D (m) is the fruit diameter and v (m s^{-1}) is the average daily air speed next to the fruit surface. Based on these assumptions, fruit mass loss due to transpiration at day t_s of storage Tr_s (g d^{-1}) is driven by the vapor pressure deficit VPD (bar) between the fruit surface and the atmosphere, and was calculated as:

$$\text{Tr}_s(t_s) = \frac{A_f(t_s) \cdot g_{\text{tot}_s}(t_s) \cdot M_w \cdot \text{VPD}(t_s)}{P_{\text{atm}}} \quad (10)$$

where M_w is the water molecular mass (18 g mol^{-1}) and P_{atm} is the atmospheric pressure (assumed to be 1.01325 bar). The $VPD(t_s)$ was calculated as $P^*(t_s)[1 - (RH(t_s) \setminus 100)]$, where P^* is the saturation water vapor pressure (bar), calculated through the Goff–Gratch equation, and RH is the daily average relative humidity (%) in the storage room, assuming that the value of fruit water activity remains constant during storage (≈1).

The fruit mass loss related to respiration during storage Re_s (g d^{-1}) was then calculated using an Arrhenius-type equation with respect to temperature:

$$\text{Re}_s(t_s) = q_{m,\text{post}} \cdot W_s(t_s) \cdot exp\left[\frac{E_{a,resp}}{R}\left(\frac{1}{T_{ref}} - \frac{1}{T(t_s)}\right)\right] \quad (11)$$

where $q_{m,post}$ is the maintenance respiration coefficient at the reference temperature (d^{-1}), W_s is the fruit fresh mass during storage (g), R (8.314 J mol^{-1} K^{-1}) is the ideal gas constant, $E_{a,resp}$ is the activation energy for the respiratory process (J mol^{-1}), T is the daily average temperature in the storage room (K) and T_{ref} (293.15 K) is the reference temperature.

Finally, fruit mass at the t_sth day of storage W_s (g) was calculated as:

$$W_s(t_s) = W_s(0) - \int_0^{t_s} [\text{Re}_s(t) + \text{Tr}_s(t)]\, \text{dt} \quad (12)$$

2.1.3. Pre- and post-harvest sugar sub-model

Seasonal dynamics of carbon present in fruit pulp in each form of sugar during the pre-harvest stage were described by the metabolic model initially developed by Génard et al. (2003). In this model, the carbon partitioning pathways Supplementary Information A were represented in a simplified way by the following system of equations:

$$\frac{\text{dM}_{\text{su}}}{\text{dt}} = \lambda_{\text{ph}} \frac{\text{dM}_{\text{ph}}}{\text{dt}} - k_1(t) \cdot M_{\text{su}} \quad (13a)$$

$$\frac{\text{dM}_{\text{so}}}{\text{dt}} = (1 - \lambda_{\text{ph}}) \frac{\text{dM}_{\text{ph}}}{\text{dt}} - [k_2(t) + k_3(t)] \cdot M_{\text{so}} \quad (13b)$$

$$\frac{\text{dM}_{\text{gl}}}{\text{dt}} = \frac{k_1(t)}{2} M_{\text{su}} + k_2(t) \cdot M_{\text{so}} - k_4(t) \cdot M_{\text{gl}} - \frac{M_{\text{gl}}}{M_{\text{gl}} + M_{\text{fr}}} \frac{\text{dM}_{\text{re}}}{\text{dt}} \quad (13c)$$

$$\frac{\text{dM}_{\text{fr}}}{\text{dt}} = \frac{k_1(t)}{2} M_{\text{su}} + k_3(t) \cdot M_{\text{so}} - k_4(t) \cdot M_{\text{fr}} - \frac{M_{\text{fr}}}{M_{\text{gl}} + M_{\text{fr}}} \frac{\text{dM}_{\text{re}}}{\text{dt}} \quad (13d)$$

where M_{su}, M_{so}, M_{gl} and M_{fr} are the carbon amounts in terms of sucrose, sorbitol, glucose and fructose (g), respectively, λ_{ph} is the proportion of sucrose in the phloem-sourced sugar pool resulting from plant metabolism, assumed to be constant during the growing season, and $\frac{dM_{re}}{dt}$ (g d^{-1}) is the amount of carbon used for respiration. k_1, k_2, k_3 and k_4 (d^{-1}) are the functions describing the sucrose transformation into glucose and fructose, the sorbitol transformation into glucose, the sorbitol transformation into fructose, and the glucose and fructose consumption for synthesis of compounds other than sugars (i.e., acids, lignin, cellulose, etc.), respectively. These functions may depend on fruit physiology and environmental conditions, which change over time. In this version of the fruit sugar accumulation sub-model, the equation of k_1 was modified to include the effect of thermal time accumulation during the growing season and the decrease in sucrose invertase (which is implied in k_1) during the last stage of fruit growth (Lo Bianco et al., 1999). For these reasons, k_1 depends on the growing degree-days *GDD* (°C) since full bloom day, calculated with the single sine, horizontal cutoff method (critical temperatures: 7 and 35 °C). This relationship was expressed as:

$$k_1(t) = \frac{k_{11}}{1 + exp[-k_{12}\cdot(\mathrm{GDD}(t) - k_{13})]} \tag{14}$$

Parameter k_4 was also modified assuming a lineat dependence on the relative growth rate of fruit pulp fresh mass:

$$k_4(t) = k_{41}\frac{dW_p}{dt}\frac{1}{W_p(t)} \tag{15}$$

where W_p is the pulp fresh mass (g), given as an input to the model. Additionally, as sorbitol oxidase and dehydrogenase enzymatic activities are influenced by post-harvest temperature (Aubert et al., 2014), it was tested whether the rate (or degree) of pre-harvest sorbitol conversion to fructose and glucose (expressed by the functions k_2 and k_3) were also temperature dependent. Model parameters were then estimated under different hypotheses of temperature dependence for k_2 and k_3, following the Van't Hoff-Arrhenius law, and then selected the best model in terms of AIC (Akaike Information Criterion) performance.

The input of the model is the pulp dry mass $W_{p,dry}$ (g), which was used in the calculation of the phloem carbon flux in the fruit $\frac{dM_{ph}}{dt}$ (g d^{-1}):

$$\frac{dM_{ph}}{dt} = \sigma_{fl}\frac{W_{p,dry}}{dt} + \frac{dM_{re}}{dt} \tag{16}$$

where σ_{fl} is the carbon content of fruit dry pulp (g g^{-1}). The concentrations of individual sugars in fruit pulp were then calculated by dividing the amount of carbon of each sugar by the fruit pulp mass and the respective sugar carbon content (values presented in Supplementary Information B).

For the post-harvest sugar dynamics, several assumptions were introduced with respect to pre-harvest stage (Supplementary Information A) to deal with the physiological and metabolic differences between the pre- and post-harvest stages (Lombardo et al., 2011). First of all, the phloem sugar flux was set to zero due to the fact that the fruit is no longer linked to the plant ($\frac{dC_{ph}}{dt_s} = 0$). Sorbitol degradation depends on temperature during storage (Aubert et al., 2014), so do $k_{2,s}$ and $k_{3,s}$ according to the Van't Hoff-Arrhenius law, as:

$$k_{i,s}(t_s) = k_{i1,s}\cdot exp\left[\frac{E_{ai,s}}{R}\left(\frac{1}{T_{ref}} - \frac{1}{T(t_s)}\right)\right] \tag{17}$$

where $k_{i1,s}$ (d^{-1}) is the rate constant at the reference temperature and $E_{ai,s}$ (J mol^{-1}) is the activation energy (with i={2,3}). Based on the literature, sucrose dynamics during storage can either be significant or negligible (Aubert et al., 2014; Borsani et al., 2009), and the consumption and synthesis rates can be considered equal. For the sake of simplicity, the net sucrose change during storage was assumed equal to zero ($\frac{dM_{su}}{dt} = 0$). At this stage there is no creation of new cell walls and acids; hence glucose and fructose are not consumed in this pathway ($k_4 = 0$), while the release of carbon related to the respiratory process $\frac{dM_{re,s}}{dt_s}$ (g d^{-1}) is due to the maintenance component $Re_s(t_s)$ alone:

$$\frac{dM_{re,s}}{dt_s} = \sigma_C\cdot \mathrm{Re}_s(t_s) \tag{18}$$

where $\sigma_C = 0.27$ is the carbon content of carbon dioxide. A share of the respiratory demand k_{re} (dimensionless) is satisfied by glucose and fructose, with the remaining part contributed by the other compounds, specifically acids (Lombardo et al., 2011). Taking these assumptions into consideration, the post-harvest sugar dynamic sub-model was written as:

$$\frac{dM_{su}}{dt_s} = 0 \tag{19a}$$

$$\frac{dM_{so}}{dt_s} = -\left[k_{2,s}(t_s) + k_{3,s}(t_s)\right]\cdot M_{so} \tag{19b}$$

$$\frac{dM_{gl}}{dt_s} = k_{2,s}(t_s)\cdot M_{so} - k_{re}\frac{M_{gl}}{M_{gl} + M_{fr}}\frac{dM_{re,s}}{dt_s} \tag{19c}$$

$$\frac{dM_{fr}}{dt_s} = k_{3,s}(t_s)\cdot M_{so} - k_{re}\frac{M_{fr}}{M_{gl} + M_{fr}}\frac{dM_{re,s}}{dt_s} \tag{19d}$$

where the sugar mass is expressed in terms of carbon (g), as for the pre-harvest sub-model.

2.2. Experimental data

Data from several pre- and post-harvest experiments during the years 2018 and 2019 were used to calibrate the parameters of the sub-models presented in Section 2.1. Fruit were taken from 24 trees of *Prunus persica var. nucipersica*, cultivar 'Nectarlove', planted in 2013 at the INRAE station in Avignon (southern France, 43°60 N, 4°49 E) on a GF677 rootstock (3.5 m between each tree).

During the pre-harvest stage, routine horticultural care and uniform pruning for commercial fruit production were ensured for all trees during the 2018 and 2019 growing seasons. The crop water requirement (CWR), calculated as the difference between the potential evapotranspiration and the rainfall over the irrigation period (Allen et al., 1998), i.e., the requirement for irrigation water, was an indicator used to manage irrigation. In 2018, two levels of water supply were tested: a well-irrigated (100% CWR) and a water-stressed one (50% CWR). Two crop loads were also applied by hand-thinning in combination with the irrigation regimes, namely a low load (200 fruit per tree) and a high load (400 fruit per tree), for a total of four pre-harvest horticultural treatments. Full bloom occurred on March 17, and the trees were thinned on May 22 (66 dafb; dafb being days after full bloom). Measurements were taken at different time intervals (fortnightly and weekly), from the thinning date to the date when fruits were harvested at commercial maturity.

For the estimation of cuticular crack surface area, analyses were carried out on five fruits per treatment per measurement date during the 2018 growing season, using the methods presented in Gibert et al. (2007). Six zones were considered on each fruit to calculate the proportion of fruit epidermal surface covered by cracks. The proportion of crack surface area over the total fruit surface area was then calculated by averaging the values found in the six zones. The images were analyzed using the ImageJ software (version 1.8; U.S. National Institutes of Health, Bethesda, MD, USA). On the same dates, the fruit surface conductance was estimated on 10 fruit per treatment by measuring fruit transpiration over 7 h. Peduncles were sealed with sealant joint and fruits were placed in a ventilated controlled room. Hourly fruit surface conductance was then calculated as in Gibert et al. (2005).

During the 2019 experimental season, two irrigation regimes in the

growing season and three storage temperatures after harvest were tested, for a total of six experimental treatments that covered both pre- and post-harvest. Full bloom occurred on March 10, and a commercial thinning procedure was used for all trees, ensuring from 400 to 500 fruit per tree. A well-irrigated (70% CWR) and a water-stressed regime (30% CWR) were applied in the orchard. Fruit from two harvest dates (22 and 29 July) were initially stored at 2 °C for the first two days. After that, fruit were placed at different temperatures in separated storage chambers, namely at 2, 15 and 25 °C until 10 days after harvest. During storage, 10 fruit per experimental treatment were randomly selected on three dates (4, 7 and 10 days of storage) and weighed, in order to calculate mass loss since the beginning of storage. During storage, relative humidity was measured hourly but not controlled. The biochemical measurements were made on five sampling dates during the pre-harvest stage in 2018 and 2019. Four replicates of five fruits (20 fruits per treatment) were sampled per date to measure pulp and stone fresh mass, and flesh dry mass concentration (oven dried at 80 °C for 72 h). The sucrose, glucose, fructose, and sorbitol concentrations in the fruit pulp were determined by the HPLC protocol of Gomez et al. (2002).

For the post-harvest biochemical dynamics assessment for the 2019 experiments, only fruit from the first harvest date (July 22, 134 dafb) were measured. Four replicates of five fruits per treatment were randomly selected at harvest and at 4, 7 and 10 days after the beginning of storage. Pulp dry and fresh mass were measured as for pre-harvest. The sucrose, glucose, fructose and sorbitol concentrations in fruit pulp were measured by HPLC, as described by Aubert et al. (2014).

2.3. Input data and numerical integration

The sub-model of the seasonal course of conductance to water vapor (Section 2.1.1) required the time series of fruit fresh mass and surface area pattern during the growing season. Moreover, stomata number at fruit anthesis was needed to calculate the fruit surface conductance related to stomata: this parameter was assumed to be the average number of stomata on the peach surface observed in Gibert et al. (2007) ($n_{sto} = 70\,592$). Fruit geometry measurements (cheek and suture diameter, and fruit height) were also used to express the relationship between fruit fresh mass and fruit surface area, according to the formula:

$$A_f(t) = a \cdot W(t)^b \tag{20}$$

where $a = 5.125$ and $b = 0.645$.

For the post-harvest mass loss sub-models, conductance was assumed not to vary during storage and be defined at harvest by the growing conditions (Gibert et al., 2007). For this reason, the value of fruit conductance g_{f_h} (introduced in Eq. (7)) at the beginning of storage was assumed to be the average value of the measured fruit surface conductance at harvest (expressed at daily scale) for each 2019 pre-harvest irrigation treatment level (30% CWR and 70% CWR). The other inputs were the daily measured values of temperature, relative humidity, and air velocity inside the storage room under the different experimental conditions.

The model equations and simulations were implemented in the R programming language (version 3.5.1). The systems of equations of the pre- and post-harvest sugar model were numerically solved using R's *ode45* solver for ordinary differential equations (from the *ode* R package, Soetaert et al. (2010)), which implements a Runge-Kutta method with a variable time step. For the sugar pre-harvest model, the dynamics of pulp fresh mass (W_p) and dry mass ($W_{p,dry}$) were needed, as well as the time series of growing degree days. The fruit mass series (fresh and dry) were reconstructed for each experimental treatment by interpolating fruit fresh and dry mass measurements from the 2018 and 2019 growing seasons, using a LOESS (locally estimated scatterplot smoothing) algorithm (Cleveland et al., 1992). For the pre-harvest stage, the simulations started at 66 dafb in 2018 and at 81 dafb in 2019, and ended at the first commercial harvest, at 117 dafb in 2018 and 128 dafb in 2019. The average observed sugar mass for each experimental treatment on the first measurement date was used as an initial value, expressed in grams of carbon. For simulation of sugar concentration dynamics during storage, the initial sugar values in terms of carbon were assumed to be the average of values observed at harvest (134 dafb).

2.4. Sub-model parameterization

Sub-model parameters valid for nectarine were either retrieved from the literature (Supplementary Information B) or calibrated by means of an optimization strategy. A total of 20 parameters were calibrated for the previously presented fruit quality sub-models, plus the average air velocity inside the storage room (in Eq. (9)), which could not be measured (too low for instrument precision). The latter variable was considered as a constant in the study. Each sub-model was separately calibrated with specific experimental data, to avoid compensation errors between the considered processes. Parameters for all the sub-models were estimated by minimizing the sum of squared deviations between the observed and simulated values, using a genetic optimization algorithm (*ga* function, from the GA package, Scrucca (2013)) and then of a derivative-free optimization algorithm based on the Nelder-Mead algorithm (*optim* function in R, with the "L-BFGS-B" method), in order to refine the best solution found by the genetic algorithm.

For the pre-harvest sugar metabolic processes, pooled data from the 2018 and 2019 experimental campaigns were used, while for the post-harvest sugar dynamics, we used the data from the 2019 experiment. Model parameters were calibrated by minimizing the errors between simulated and observed sugar concentrations in fruit pulp dry mass. The goodness-of-fit criteria were the root mean squared error (RMSE) and the relative RMSE (RRMSE), which are commonly used to quantify the mean distance between simulations and measurements.

2.5. Model sensitivity analysis and use

After parameterization, the different sub-models were linked together to obtain the pre- and post-harvest quality model. The inputs of this model are the daily temporal series of fruit fresh mass, and fresh and dry pulp mass for the pre-harvest stage. For the storage phase, the inputs are the average daily temperature, the relative humidity, and the air velocity next to the fruit surface in the storage room.

A sensitivity analysis was performed on the parameters by using the extended FAST methodology to calculate variance-based sensitivity indices (Saltelli et al., 1999), implemented in R with the *fast99* function, from *sensitivity* package (Iooss et al., 2020). The Sobol index is related to the proportion of output variance that can be explained by each parameter variation (main effect), as well as the interaction between the other parameters (interaction). The outputs of interest were the relative fruit mass loss (%) from the beginning of storage and, the fruit sweetness index (g kg^{-1}, on a pulp fresh mass basis) at the end of storage. The analyses were carried out for the 27 model parameters. Parameter boundaries were established by considering a 20% variation above and below the values that were found during parameter calibration and in the literature.

The model was also used to simulate the combined effects of horticultural practices, namely the irrigation and fruit load before harvest, and relative humidity and temperature during storage. For the pre-harvest stage, the irrigation and fruit load levels of the 2018 pre-harvest experiment presented in Section 2.2 were considered. Accordingly, the fresh and dry mass growth curves from this experiment were used. For the scenarios of the post-harvest stage, three temperatures (2, 15 and 25 °C) and three relative humidity (RH) levels (namely 70%, 80% and 90%) were considered. Average relative fruit mass loss and sweetness index were thus evaluated over 36 hypothetical scenarios, considering the growing stage until commercial maturity (117 dafb in 2018) and 10 days of storage.

Finally, the effects of harvest date and storage duration were

Table 1
Parameter acronyms, estimated values, confidence intervals at 95% confidence level (C.I.), units and references to the equations presented in Section 2.1 for nectarine, cultivar 'Nectarlove'.

Parameter	Value	C.I.	Unit	Equation
Pre-harvest conductance				
dh_1	0.612	0.574–0.651	–	Eq. (4)
dh_2	0.825	0.803–0.848	–	Eq. (4)
cut_1	0.160×10^{-1}	0.149–0.164 × 10^{-1}	g	Eq. (3)
cut_2	2.56	2.48–2.64	–	Eq. (3)
g'_{sto}	3.14×10^{-6}	3.02–3.27 × 10^{-6}	mol m^{-2} s^{-1}	Eq. (2)
g'_{cra}	0.09	0.089–0.091	mol m^{-2} s^{-1}	Eq. (2)
g_{cut1}	1.824	1.824–1.825	mol m^{-2} s^{-1}	Eq. (6)
g_{cut2}	0.0493	0.0493–0.0495	s^{-1}	Eq. (6)
Pre-harvest sugar				
λ_{ph}	0.254	0.251–0.258	–	Eq. (13)
k_{11}	0.137	0.132–0.143	d^{-1}	Eq. (14)
k_{12}	0.011	0.010–0.012	$°C^{-1}$	Eq. (14)
k_{13}	930	919–942	°C	Eq. (14)
k_2	0.87	0.865–0.876	d^{-1}	Eq. (13)
k_3	0.80	0.791–0.809	d^{-1}	Eq. (13)
k_{41}	4.69	4.67–4.72	–	Eq. (15)
Post-harvest sugar				
k_{21}	1.09×10^{-2}	0.95–1.27 × 10^{-2}	d^{-1}	Eq. (17)
k_{31}	7.39×10^{-2}	7.11–7.67 × 10^{-2}	d^{-1}	Eq. (17)
$E_{a2,s}$	54 615	52 176–57 053	J mol^{-1}	Eq. (17)
$E_{a3,s}$	74 056	70 103–78 001	J mol^{-1}	Eq. (17)
k_{re}	0.451	0.436–0.468	–	Eq. (19)

evaluated on the quality index simulated by the model. To do this, the non-limiting growth conditions of the 2018 experiment presented in Section 2.2 (100% CWR and 200 fruit per tree) were chosen, with 15 °C and 80% RH as storage conditions. The model outputs were then evaluated as a function of a change in harvest date of plus or minus seven days (with respect to the 2018 commercial one; Section 2.2) and storage duration (from 0 to 15 days).

3. Results

The calibrated and fixed parameters for the nectarine cultivar 'Nectarlove' are presented in Table 1 and Supplementary Information B, respectively.

3.1. Fruit surface conductance and post-harvest mass loss sub-models

For this sub-model, the values of eight parameters were estimated (Table 1). The measurements of the cuticular crack surface area during the 2018 experiment and the simulated values can be found in Supplementary Information C. No cuticular cracks were detected on fruit from high-loaded trees (400 fruit per tree) before 108 dafb, whereas they appeared earlier on fruit from low-loaded trees (200 fruit per tree), at 95 dafb. At harvest date (117 dafb), the cuticular crack surface area was significantly larger for the well-irrigated (100% CWR) than for the water-stressed treatment (50% CWR) and for the lower rather than the higher fruit load.

The surface conductance to water vapor decreased in the first stage after thinning, when fruit had no cuticular cracks on the skin, and then increased during the days before harvest (Fig. 2). The fruit conductance from well-irrigated treatments at harvest was significantly higher than that of fruit from the water-stressed treatment, with an average of 0.031 and 0.017 mol m^2 s^{-1}, respectively. Fruit load had no significant effect on fruit surface conductance. The model reproduced these patterns with an average RMSE of 0.0036 mol m^2 s^{-1} and a RRMSE of 0.18.

For the sub-model of fruit mass loss during storage, the estimated value of average daily air speed inside the storage room was very low ($v = 0.004$ m s^{-1}). Relative mass loss (Fig. 3) was highest at 25 °C (10% on average on the last day of storage) and lowest at 15 and 2 °C (2.14% and 2.17%, respectively). Despite the higher temperature, the transpiration at 15 °C was comparable to that at 2 °C because relative humidity, which was not controlled during the experiment, was higher in the 15 °C chamber (87% on average over the whole experiment) than in the 2 °C (82%) and 25 °C (74%) storage chambers.

The model error was larger for the 25 °C storage (RMSE = 1.8%) than for the 15 °C (RMSE = 0.45%) and the 2 °C storage (RMSE = 0.6%). Based on the model simulations, the part of mass loss due to respiration was highest in the 15 °C case, with 33% on average after the first harvest and 21% after the second one; this component was lowest in the 25 °C storage (11% and 10%, after the first and second harvest, respectively, Supplementary Information D).

3.2. Pre- and post-harvest sugar dynamics sub-model

According to the AIC results, the most parsimonious sugar pre-harvest sub-model was the one with constant $k_2(t) = k_2$ and $k_3(t) = k_3$ throughout the growing season. In total, seven parameters were estimated for this sub-model (Table 1). The experimental data (Figs. 4 and 5) confirmed the fact that sucrose is the most abundant sugar in the nectarine mesocarp and accumulates during stage 4 of fruit physiological development, even if, according to the model, the percentage of carbon that enters through the phloem to the fruit pulp as sucrose (λ_{ph}) is low (~26%). Glucose and sucrose were nearly equivalent, while sorbitol was always present in small amounts. The seasonal pattern of sucrose concentration, which is the most abundant sugar (Figs. 4 and 5), was well described by the model for both 2018 and 2019 growing seasons. In

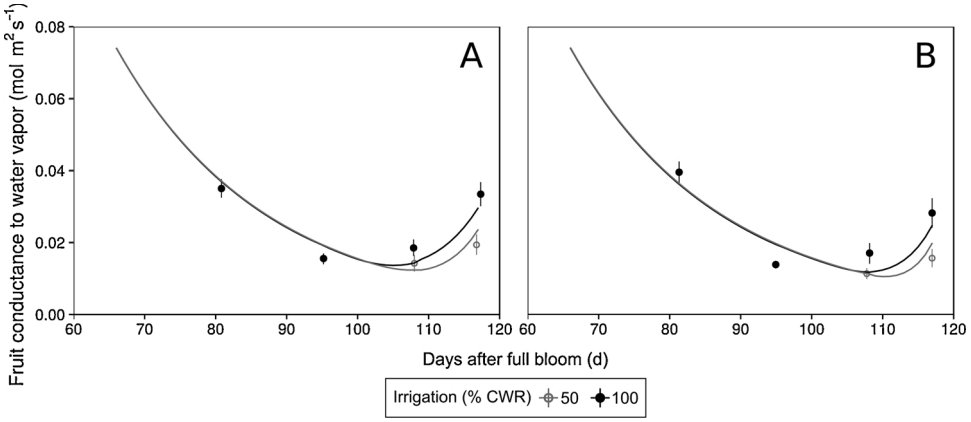

Fig. 2. Average fruit surface conductance to water vapor values measured during fruit growth in 2018 (points) and simulated (lines), under two fruit loads (A, 200 fruit per tree and B, 400 fruit per tree) and irrigation treatments; % CWR is the percentage of crop water requirement satisfied by irrigation. Bars represent the standard error of the mean.

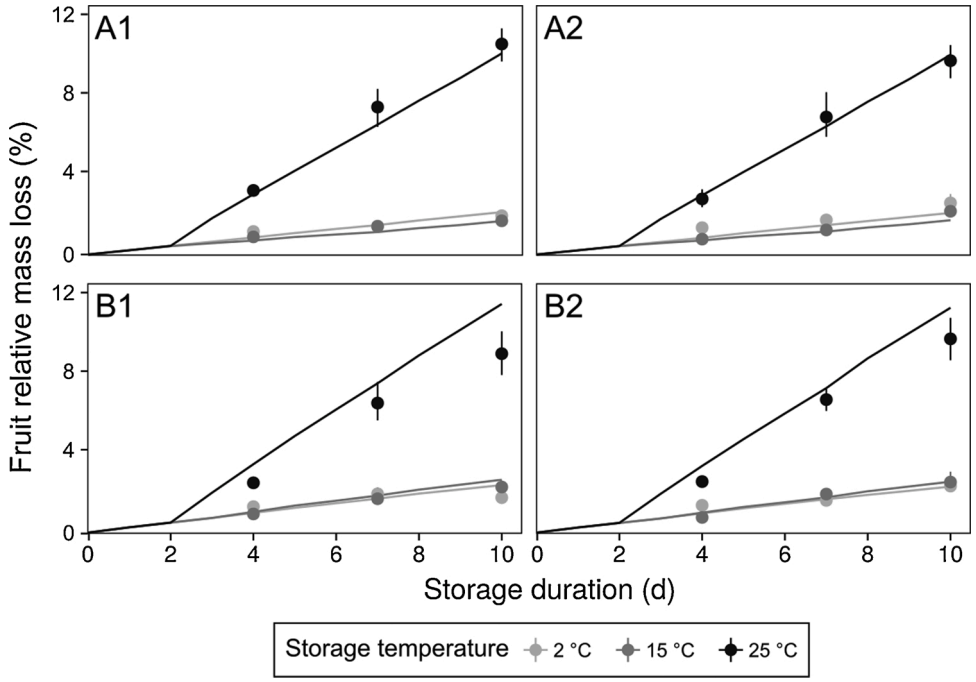

Fig. 3. Average relative fruit mass loss measured during storage in 2019 (points) and simulated (lines), at first (A1-A2, 134 dafb) and second harvest date (B1-B2, 141 dafb). Fruit came from two pre-harvest irrigation treatments: 30% CWR (A1-B1) and 70% CWR (A2-B2); % CWR is the percentage of crop water requirement satisfied by irrigation. Bars represent the standard error of the mean.

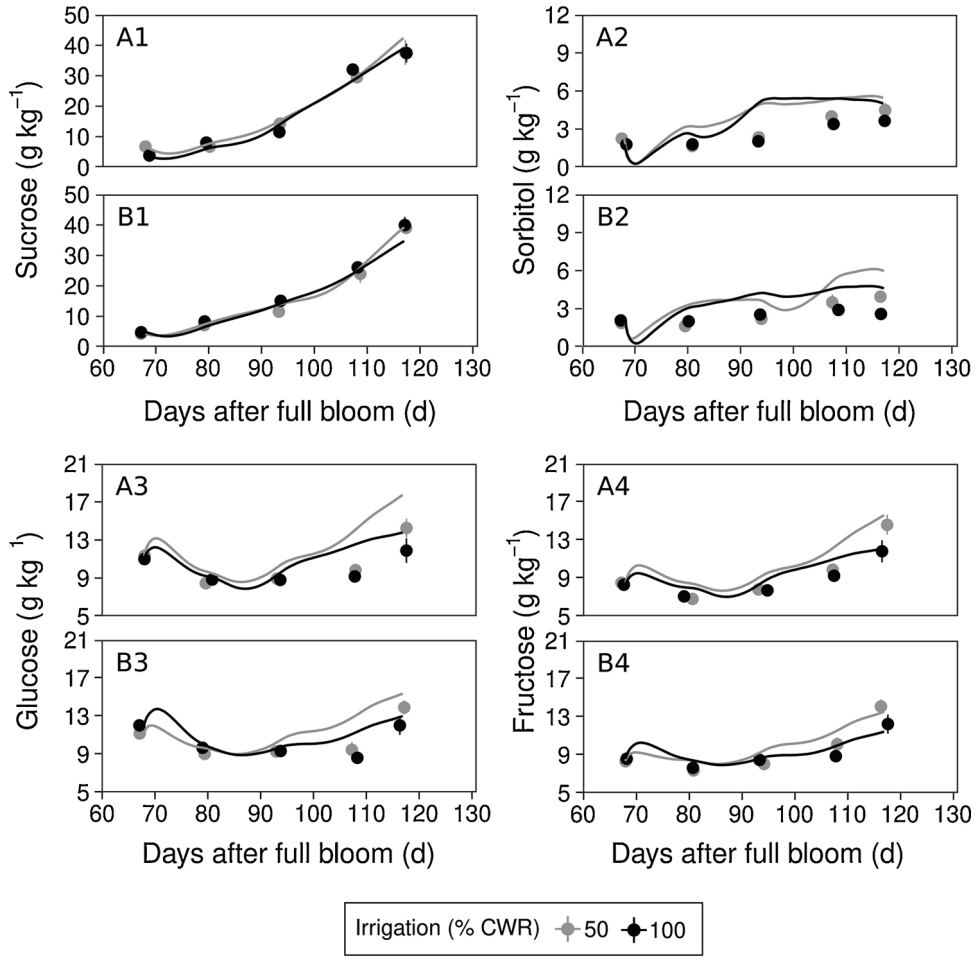

Fig. 4. Average sucrose, sorbitol, glucose and fructose concentration measured during fruit growth in 2018 (points) and simulated (lines), under a low (A1-A4, 200 fruit per tree) and high tree-crop load (B1-B4, 400 fruit per tree). Fruit also came from trees under two different irrigation treatments; % CWR is the percentage of crop water requirement satisfied by irrigation. Bars represent the standard error of the mean.

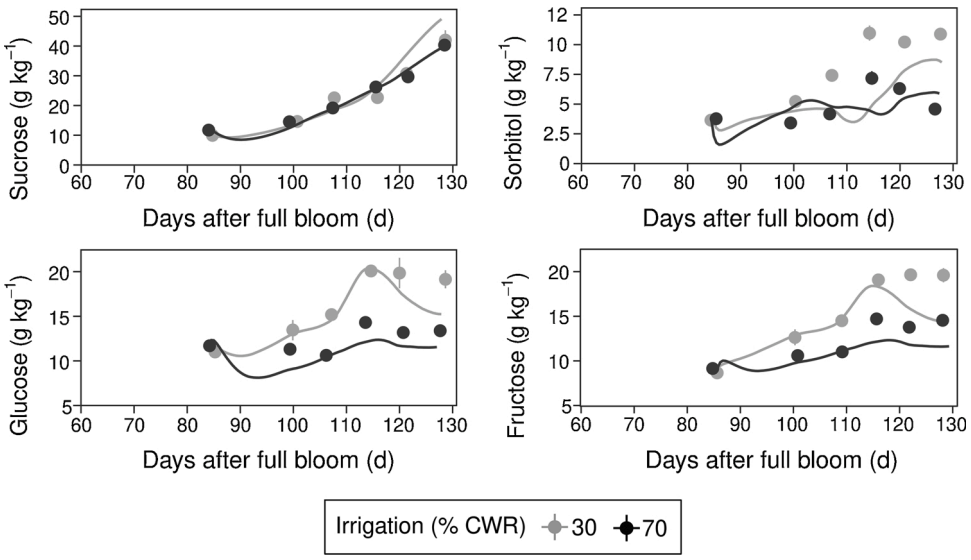

Fig. 5. Average sucrose, sorbitol, glucose and fructose concentration inside fruit pulp measured during fruit growth in 2019 (points) and simulated (lines), under two irrigation treatments; % CWR is the percentage of crop water requirement satisfied by irrigation. Bars represent the standard error of the mean.

2019, the fruit had a higher value of reducing sugars (glucose and fructose) and sorbitol. Regarding the latter, the concentration in fruit pulp fresh mass was markedly higher during the 2019 season, averaging 6.4 g kg^{-1}, compared to an average of 2.8 g kg^{-1} in 2018. Moreover, in the 2019 growing season, fruit from the water-stressed treatment (30% CWR) showed a pronounced increase in sorbitol concentration (11.3 g kg^{-1} at the commercial harvest date) with respect to the one in fruit from the well-irrigated treatment (70% CWR) trees (4 g kg^{-1}).

On average, the sub-model showed a RMSE = 5.50 g kg^{-1} (RRMSE = 0.097) for the sweetness index throughout the growing seasons, (Fig. 6). The sweetness index followed the pattern of sucrose, which accounted for 54% of its value at harvest in 2018 and 48% in 2019.

For the post-harvest sugar sub-model, five parameters were estimated (Table 1). The dynamics of fruit fresh mass during storage for this model was calculated using the fruit mass loss sub-model presented in Section 2.1.2, with measured data of daily storage conditions at the different storage temperatures (Section 2.2). The temporal pattern of sucrose concentration showed an increase for the 15 and 25 °C storage compared to 2 °C, which, however, was not statistically significant (Fig. 7). Sorbitol significantly decreased during storage at 15 and 25 °C, as it was consumed for glucose and fructose metabolism. The fructose concentration in the fruit fresh pulp was higher (18.8 g kg^{-1} average during storage) than that of glucose (13.7 g kg^{-1}), and the parameter calibration suggested that the part of sorbitol that is consumed for fructose metabolism ($k_{31} = 7.55 \times 10^{-3}$ d^{-1}) is higher than that of

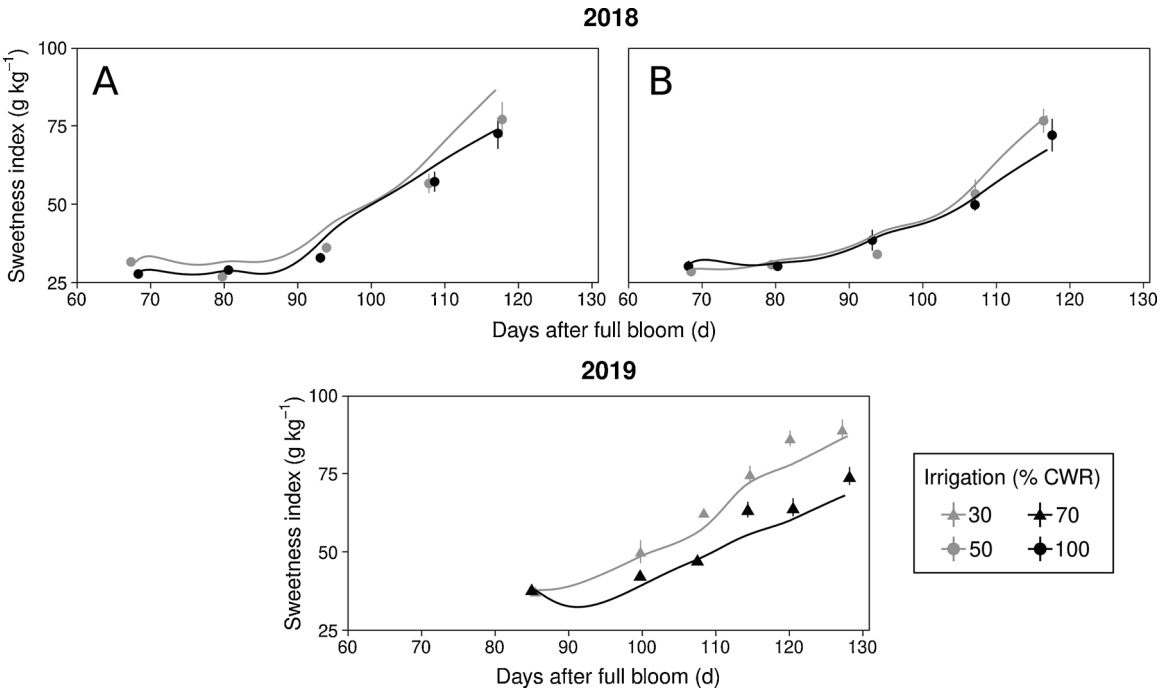

Fig. 6. Average sweetness index inside fruit pulp measured during fruit growth in 2018 and 2019 (points), and simulated (lines) under different pre-harvest conditions (irrigation and fruit load). In 2018, fruit were submitted to a low (A, 200 fruit per tree) and high tree-crop load (B, 400 fruit per tree); % CWR is the percentage of crop water requirement satisfied by irrigation. Bars represent the standard error of the mean.

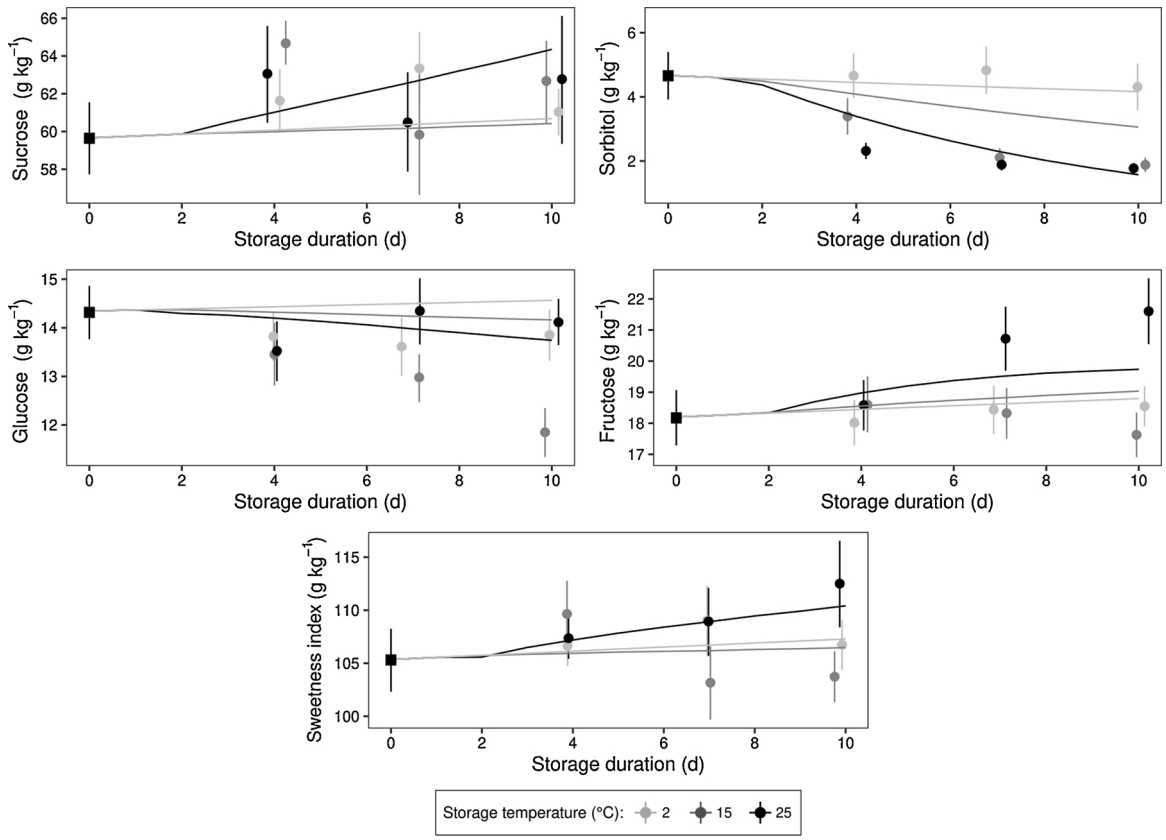

Fig. 7. Average sucrose, sorbitol, glucose and fructose concentrations inside fruit pulp, and sweetness index dynamics measured during storage in 2019 (points) and simulated (lines), under three storage temperatures (2, 15 and 25 °C); squared points represent the average measured value of each variable at harvest. Bars stand for the standard error of the mean.

glucose ($k_{21} = 2.46 \times 10^{-3}\,d^{-1}$). Glucose metabolism at 15 °C was not well described by the model. However, the model captured the observed sweetness index pattern during storage with accuracy (RMSE = 2.8 g kg^{-1}, RRMSE = 0.027), although not with the same precision over time. The index presented a significant increase only at 25 °C at the end of storage, which was well captured by model simulations.

3.3. Sensitivity analysis and model exploration

With respect to relative mass loss, the most influential parameters were those related to the seasonal course of cuticular formation and conductance during the growing season (cut_1, cut_2 and g_{cut2}), with crack

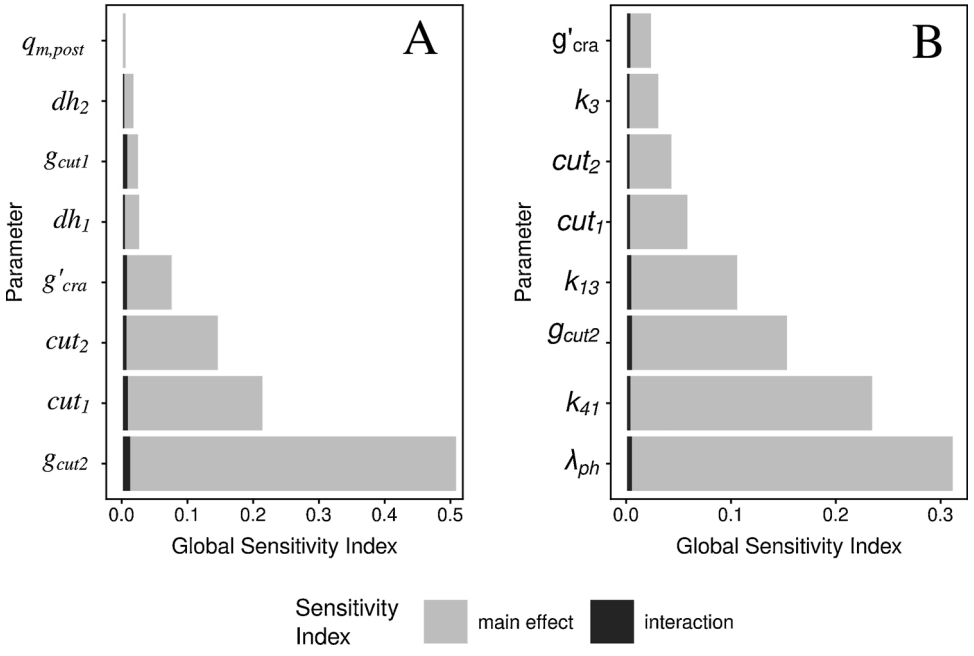

Fig. 8. Global sensitivity index (Sobol index) for the eight most influential parameters resulted from model sensitivity analysis related to simulated fruit relative mass loss (A) and sweetness index (B) at the end of storage. Parameters were varied by a ±20% from their original values (Table 1 and Supplementary Information B). The index expresses the importance of each parameter on the variance of the considered output (main effect) and the strength of interaction with the other parameters (interaction).

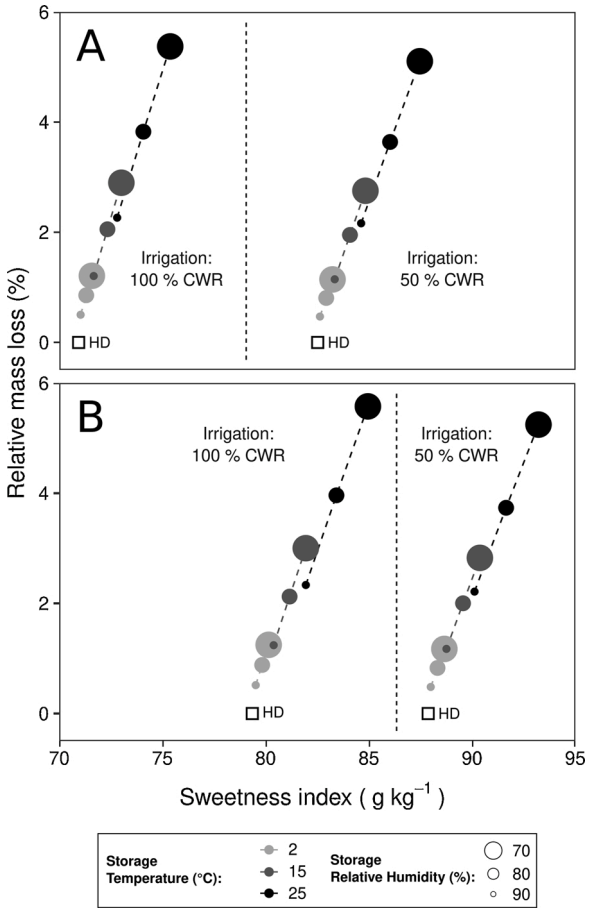

Fig. 9. Impact of horticultural practices and storage conditions (temperature and relative humidity) scenarios on fruit sweetness index and relative mass loss after 10 days of storage, according to model simulations. Scenarios of low (A, 400 fruit per tree) and high-crop load level (B, 200 fruit per tree) were tested, along with two irrigation levels. Dotted lines link scenarios with the same storage temperature. The value of the sweetness index at harvest date (HD) under each combination of horticultural practices is presented as an open square; % CWR is the percentage of crop water requirement satisfied by irrigation.

specific conductance g'_{cra} as well (Fig. 8).

These parameters accounted for more than 85% of the output variance. In the case of the sweetness index, the most influential parameters were as follows: the proportion of carbon phloem flux that is imported as sucrose (λ_{ph}); the parameter that regulates the transformation of glucose and fructose into other compounds during the growing season (k_{41}); the parameters related to cuticular formation and conductance development; and the one related to sucrose degradation to glucose and fructose (k_{13}). No parameter of the post-harvest sugar dynamics sub-model was found among the most influential parameters on the sweetness index at the end of storage. For both outputs, the interaction effects can be considered as negligible.

The effects of various pre- and post- harvest hypothetical scenarios on model outputs are shown in Fig. 9. An air velocity of 0.004 m s^{-1} was used in all simulations as determined via model parameterization. The simulation based on a scenario where fruit were grown at 50% CWR, under low fruit load, and then stored at 25 °C and 70% relative humidity, yielded the highest sweetness index (102.9 g kg^{-1}) after storage for 10 days, with a predicted high relative mass loss of 15.2%. In comparison, the scenario with high fruit loading at 50% CWR, where fruit were stored at 2 °C and 90% relative humidity, resulted in the lowest relative mass loss of 1.5% and a sweetness index estimated at 82.8 g kg^{-1}. In general, increases in storage temperature and decreases in relative humidity increased the trade-off between fruit mass loss and sweetness index. The sweetness index was maximized (94.8 g kg^{-1}) and relative mass loss minimized (8.4%), where fruit were grown at 50% CWR, under low fruit load, and then stored at 15 °C and 70% relative humidity. Under these growing and storage conditions the relative water loss remained under the maximum acceptable threshold of 11% (Nunes and Emond, 2007).

Finally, varying the harvest date and storage duration showed that the harvest date had a positive influence on the sweetness index, but not on the relative fruit mass loss during storage (Fig. 10). Compared to fruit harvested at commercial maturity, fruit harvested one week later were sweeter on average by 17%, whereas fruit harvested one week earlier were less sweet by 14%. As expected, storage length increased fruit mass loss and, to a lesser extent, sweetness. For this reason, length of storage could also have an effect on the best compromise scenarios between fruit sweetness and relative mass loss. As an example (simulation not shown here), when the storage duration was shortened to 5 days (instead of 10 days), the best compromise scenario was the one with water-stressed (50% CWR) and low-load (200) conditions, but with fruit stored at the highest temperature (25 °C) and low relative humidity (70%).

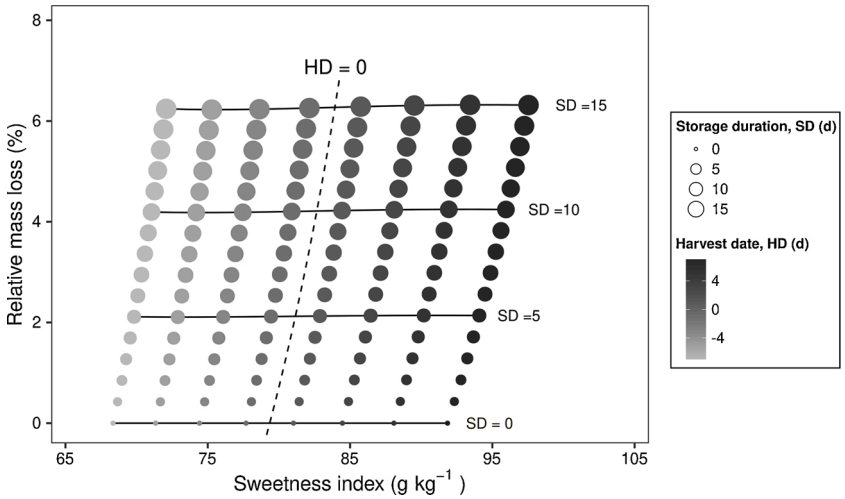

Fig. 10. Impact of harvest date (HD, d) and storage duration (SD, d) on fruit sweetness index and relative mass loss at the end of storage, according to model simulations (15 °C and 80% RH storage conditions). Harvest dates relate to the 2018 date of commercial maturity (HD = 0, 117 dafb). Dotted line represents the storage patterns of fruit quality criteria under the commercial harvest scenario (HD = 0), whilst continuous lines connect scenarios with the same storage duration.

4. Discussion

4.1. Simulations of sweetness and mass loss dynamics during fruit development and storage

The experimental results showed that fruit from well-irrigated and low-loaded trees showed a higher conductance to water vapor, mainly through the occurrence of cuticular cracks during the last stage of fruit growth (Gibert et al., 2007). The cuticular and crack components of the conductance were thus larger than the stomatal one. The sub-model of fruit surface conductance development during fruit growth was able to reproduce the observed patterns. It was thus possible to take account of the value of this fruit property at harvest when modeling the loss of fruit mass during storage, which has not generally been done explicitly in these types of models according to Bovi et al. (2018). The effect of mass loss related to respiration during storage was also included in the model, because neglecting it can lead to errors as demonstrated by Xanthopoulos et al. (2017) in pears and Lufu et al. (2019) in pomegranates. The sub-model was able to correctly simulate the mass loss during storage by taking account of both intrinsic factors (such as fruit size and morphology) and extrinsic ones (storage room temperature, relative humidity and air velocity) that have been cited as influential in this process (Díaz-Pérez, 2019). The temperature and the relative humidity of the storage room during post-harvest were influential factors in our experimental conditions (even if the relative humidity was not controlled) and these observations were well captured by the fruit mass loss sub-model. Moreover, air velocity near the fruit surface is a factor to consider in the calculation of fruit mass loss during storage, due to its effect on the boundary layer (Whitelock et al., 1994), despite the difficulties in measuring it. In our case, the calibrated value of air velocity was very low, suggesting that boundary layer conductance prevails over fruit surface conductance to water vapor under our storage conditions. Moreover, model simulations showed no influence of harvest date on fruit mass loss during storage, in disagreement with Guerra and Casquero (2008) on plum, probably because the low air velocity and boundary layer conductance hid the effects of the increase of fruit surface conductance with harvest date.

Regarding the pattern of the sweetness index inside fruit pulp during the growing season, fruit from trees in less-irrigated treatments (especially the 30% CRW in 2019) showed a higher sweetness during the growing season due to a dehydration and concentration effect, which is in line with the observations of Thakur and Singh (2012) on peach soluble solid concentrations. In addition, low fruit load increased fruit sweetness in fruit pulp during the 2018 experiment, as reported also by Kumar et al. (2010). This could be related to the increase in the availability of carbohydrate resources that depend on the number of fruit on the tree (Lopresti et al., 2014) and because of a higher dry mass accumulation with respect to the fruit water intake. The sugar sub-model was able to reproduce the observed pre-harvest patterns, even if glucose concentrations were overestimated in 2018 and underestimated in 2019, which could be related to the fact that sucrose hydrolysis (here linked to k_1 parameter) and sorbitol dehydrogenase and invertase (linked to k_2 and k_3) can depend on the level of plant water stress due to active osmotic adjustment, as suggested for peach by Lo Bianco et al. (2000), and for citrus fruit by Yakushiji et al. (1998). This was not considered in the present study. Moreover, the parameter λ_{ph} can also be influenced by drought stress (Lo Bianco et al., 2000). However, its value was estimated at 0.254, which is in the range of values found in the literature (Moing et al., 1992; Escobar-Gutiérrez et al., 1998). More research should therefore be undertaken to integrate these mechanisms into mathematical models. The sweetness index was nevertheless well captured by the sugar sub-model for all the experimental conditions because it was mainly influenced by sucrose concentrations, which were especially well simulated.

During post-harvest storage, sorbitol decreased with increasing temperature and it was rapidly transformed into reducing sugars (glucose and fructose), as observed in peach (Aubert et al., 2014) and pear (Itai et al., 2015). According to the sub-model, the glucose concentration did not significantly change with storage temperature. However, our data showed a decrease in glucose concentration at 15 °C. This could be ascribed to the fact that the metabolic responses of fruits can be different at intermediate temperatures due to different levels of ethylene production and ripening (Villalobos-Acu na and Mitcham, 2008). Nevertheless, the model was able to correctly reproduce the quantitative evolution of sugar concentration for two of the three temperatures studied (2 and 25 °C) and that of the sweetness index for the duration of storage. However, more data are necessary to understand better the physiological and biochemical processes that underlie fruit sugar dynamics under different storage conditions, as expressed by Brizzolara et al. (2020). These advancements could then be useful for improving the presented model.

4.2. Multiple sources of variation and compromises characterize fruit quality at the end of storage

The sensitivity analysis showed that parameters related to cuticular surface and conductance pattern predominantly affected relative fruit mass loss during storage, in line with the evidence that cuticle formation and cracking are important in the development of quality in horticultural crops (Lara et al., 2019) and, in particular, for the mass loss process during storage (Díaz-Pérez et al., 2007). With respect to the sweetness index, the most influential parameters were related to sucrose input (λ_{ph}) and metabolism (k_{13}), which confirms the importance of capturing the dynamics of this sugar to describe this index during post-harvest. In addition, the parameters related to cuticular surface and conductance pattern were influential in the variance of the sweetness index at the end of storage since they influenced post-harvest moisture loss (through transpiration), enhancing the process of sugar concentration inside the fruit pulp. Since physiological and biochemical characteristics of peach/nectarine are cultivar-dependent (Minas et al., 2018), the variation of all these influential parameters is probably cultivar-dependent. Fruit surface conductance to water vapor at harvest has been shown to vary from about 0.02 to 0.09 mol m^{-2} s^{-1} according to the cultivar (Lescourret et al., 2001; Gibert et al., 2005, 2010). In a modeling study, Wu et al. (2012) found that sugar model parameters related to fructose and sucrose metabolism were different between peach cultivars, while Escobar-Gutierrez and Gaudillere (1994) found that the sorbitol:sucrose ratio in peach leaves can change with genotype. Moreover, data in Wu et al. (2003) showed that sucrose concentration in peach pulp under different cultivars at fruit maturity could vary from about 6 to 157 g kg^{-1}, while glucose and fructose concentrations ranged from 1 to 39 g kg^{-1}. This suggests that cultivar dependence should be carefully considered when using the present model.

The model simulations under different pre-harvest and storage scenarios pointed out the importance of horticultural practices on fruit quality at harvest, as reported for peach by Minas et al. (2018), and their influence on post-harvest evolution. This agrees with the observations of Crisosto et al. (1994) on 'O'Henry' peaches submitted to different water-deficit regimes. A combination of high relative humidity and low-temperature storage was shown to be more effective in extending product marketability and in avoiding fruit shriveling than low temperature storage alone, as suggested by Díaz-Pérez (2019). The first factor helps to reduce the fruit water loss from transpiration, while the second slows down the respiratory loss by the fruit. The simulations revealed a trade-off between the two quality criteria since higher temperatures and lower relative humidity during storage increased both fruit sweetness (expected to be high) and mass loss (expected to be low). They also demonstrated the capacity of the model to explore the storage factors (temperature x relative humidity) to manage this trade-off. The model simulations showed that the choice of the harvest date, which determines the level of maturity at the beginning of storage, is important for obtaining a high sweetness index at the end of storage, as in mango

(Joas et al., 2009) and plum (Guerra and Casquero, 2008). The metabolic processes that underlie these changes are greatly influenced by fruit maturity and ethylene production because nectarines are climacteric fruit. However, these processes were not taken into consideration in the present model. In the future, they could be included by considering the modeling framework proposed by Génard and Gouble (2005) for ethylene emission. Storage duration impacts fruit mass loss during storage, suggesting the importance of finding an optimal value for this variable as well as storage conditions to maximize fruit sweetness while keeping fruit mass loss under an acceptable threshold.

4.3. Model improvements and possibilities

The use of mathematical modeling techniques allowed us to analyze the effect of different irrigation and fruit load conditions, combined with storage temperature and humidity scenarios, on two quality criteria for nectarine. The model may now be used to reveal interactions and trade-offs between pre- and post-harvest stages, which are often treated separately. However, more data are required to refine the calibration and to validate the sub-models.

The use of the model is currently limited since in its present form it did not explicitly consider the effects of irrigation and fruit thinning on fruit tree status. Instead, it used experimental fruit growth curves from different horticultural practices as inputs. To overcome this limitation, this model could be coupled with a generic fruit tree model such as QualiTree (Rahmati et al., 2018), which is capable of describing changes in the water and carbon status of the plant according to pre-harvest practices (irrigation, thinning and pruning, etc.). This type of model also considers fruit yield, which is an important criterion for producers. In this way, it would be possible to look for joint horticultural and storage strategies that optimize the choices of producers, retailers, and consumers.

Authors' contribution

Enrico Casagrande: conceptualization, methodology, investigation, software, formal analysis, data curation, writing – original draft, visualization. Michel Génard: conceptualization, methodology, writing – review & editing. Sébastien Lurol and Florence Charles: investigation, resources, writing – review & editing. Daniel Plénet: resources, writing – review & editing. Françoise Lescourret: supervision, conceptualization, methodology, writing – review & editing.

Declaration of Competing Interest

The authors report no declarations of interest.

Acknowledgments

This study was funded by an industrial training agreement through a CIFRE research fellowship from the CTIFL (Centre Technique Interprofessionnel des Fruits et Légumes) and the ANRT (Association Nationale de la Recherche et de la Technologie) on behalf of the French Ministry of Higher Education and Research.

We gratefully acknowledge all of our colleagues for their assistance during the field experiments, C. Aubert and G. Chalot from CTIFL, and E. Rubio, L. Gomez and P. Laugier from INRAE for their assistance in sugar analyses. We want to specially thank S. Azehaf and M. Damoiseaux for their commitment during the experimental seasons, and H. Sallanon for the patient discussions around fruit physiology.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.postharvbio.2020.111458.

References

Allen, R.G., Pereira, L.S., Raes, D., Smith, M., 1998. Crop Evapotranspiration – Guidelines for Computing Crop Water Requirements – FAO Irrigation and Drainage Paper 56. https://doi.org/10.1016/j.eja.2010.12.001.

Aubert, C., Bony, P., Chalot, G., Landry, P., Lurol, S., 2014. Effects of storage temperature, storage duration, and subsequent ripening on the physicochemical characteristics, volatile compounds, and phytochemicals of western red nectarine (*Prunus persica* L. Batsch). J. Agric. Food Chem. 62, 4707–4724. https://doi.org/10.1021/jf4057555.

Beauvoit, B.P., Colombié, S., Monier, A., Andrieu, M.H., Biais, B., Bénard, C., Chéniclet, C., Dieuaide-Noubhani, M., Nazaret, C., Mazat, J.P., Gibon, Y., 2014. Model-assisted analysis of sugar metabolism throughout tomato fruit development reveals enzyme and carrier properties in relation to vacuole expansion. Plant Cell 26, 3224–3242. https://doi.org/10.1105/tpc.114.127761.

Ben-Yehoshua, S., Rodov, V., 2002. Transpiration and water stress. Postharvest Physiology and Pathology of Vegetables. Marcel Dekker, New York, NY, USA, pp. 111–159. https://doi.org/10.1201/9780203910092.ch5.

Bolz, R.E., Tuve, G.L., 1973. CRC Handbook of Tables for Applied Engineering Science. CRC Press. https://doi.org/10.1201/9781315214092.

Borsani, J., Budde, C.O., Porrini, L., Lauxmann, M.A., Lombardo, V.A., Murray, R., Andreo, C.S., Drincovich, M.F., Lara, M.V., 2009. Carbon metabolism of peach fruit after harvest: changes in enzymes involved in organic acid and sugar level modifications. J. Exp. Bot. 60, 1823–1837. https://doi.org/10.1093/jxb/erp055.

Bovi, G.G., Caleb, O.J., Herppich, W.B., Mahajan, P.V., 2018. Mechanisms and modeling of water loss in horticultural products. Reference Module in Food Science. https://doi.org/10.1016/b978-0-08-100596-5.21897-0.

Bovi, G.G., Caleb, O.J., Linke, M., Rauh, C., Mahajan, P.V., 2016. Transpiration and moisture evolution in packaged fresh horticultural produce and the role of integrated mathematical models: a review. Biosyst. Eng. 150, 24–39. https://doi.org/10.1016/j.biosystemseng.2016.07.013.

Brizzolara, S., Manganaris, G.A., Fotopoulos, V., Watkins, C.B., Tonutti, P., 2020. Primary metabolism in fresh fruits during storage. Front. Plant Sci. 11, 80. https://doi.org/10.3389/fpls.2020.00080.

Byrne, D.H., Nikolic, A.N., Burns, E.E., 2019. Variability in sugars, acids, firmness, and color characteristics of 12 peach genotypes. J. Am. Soc. Horticult. Sci. 116, 1004–1006. https://doi.org/10.21273/jashs.116.6.1004.

Cirilli, M., Bassi, D., Ciacciulli, A., 2016. Sugars in peach fruit: a breeding perspective. Horticult. Res. 3, 15067. https://doi.org/10.1038/hortres.2015.67.

Cleveland, W.S., Grosse, E., Shyu, W.M., 1992. Local regression models. Statistical Models in S. Routledge 309–376. https://doi.org/10.1201/9780203738535-8.

Crisosto, C.H., 2002. How do we increase peach consumption? Acta Horticulturae 601–605. https://doi.org/10.17660/ActaHortic.2002.592.82.

Crisosto, C.H., Johnson, R.S., Luza, J.G., Crisosto, G.M., 1994. Irrigation regimes affect fruit soluble solids concentration and rate of water loss of 'O'Henry' peaches. HortScience 29, 1169–1171. https://doi.org/10.21273/hortsci.29.10.1169.

Díaz-Pérez, J.C., 2019. Transpiration. Postharvest Physiology and Biochemistry of Fruits and Vegetables 157–173. https://doi.org/10.1016/b978-0-12-813278-4.00008-7.

Díaz-Pérez, J.C., Muy-Rangel, M.D., Mascorro, A.G., 2007. Fruit size and stage of ripeness affect postharvest water loss in bell pepper fruit (*Capsicum annuum* L.). J. Sci. Food Agric. 68–73. https://doi.org/10.1002/jsfa.2672.

Escobar-Gutierrez, A.J., Gaudillere, J.P., 1994. Variability in sorbitol: Sucrose ratios in mature leaves of different peach cultivars. J. Am. Soc. Horticult. Sci. 119, 321–324. https://doi.org/10.21273/jashs.119.2.321.

Escobar-Gutiérrez, A.J., Moing, A., Gaudillère, J.P., 1998. Time course of carbohydrates concentration in mature leaves of peach seedlings [*Prunus persica* (L.) Batsch] during the night. Acta Horticulturae 465, 337–344. https://doi.org/10.17660/ActaHortic.1998.465.42.

Génard, M., Gouble, B., 2005. ETHY. A theory of fruit climacteric ethylene emission. Plant Physiol. 139, 531–545. https://doi.org/10.1104/pp.105.063339.

Génard, M., Lescourret, F., Gomez, L., Habib, R., 2003. Changes in fruit sugar concentrations in response to assimilate supply, metabolism and dilution: a modeling approach applied to peach fruit (*Prunus persica*). Tree Physiol. 23, 373–385. https://doi.org/10.1093/treephys/23.6.373.

Génard, M., Souty, M., 1996. Modeling the peach sugar contents in relation to fruit growth. J. Am. Soc. Horticult. Sci. 121, 1122–1131. https://doi.org/10.21273/jashs.121.6.1122.

Gibert, C., Chadœuf, J., Vercambre, G., Génard, M., Lescourret, F., 2007. Cuticular cracking on nectarine fruit surface: spatial distribution and development in relation to irrigation and thinning. J. Am. Soc. Horticult. Sci. 132, 583–591. https://doi.org/10.21273/JASHS.132.5.583.

Gibert, C., Génard, M., Vercambre, G., Lescourret, F., 2010. Quantification and modelling of the stomatal, cuticular and crack components of peach fruit surface conductance. Funct. Plant Biol. 37, 264–274. https://doi.org/10.1071/FP09118.

Gibert, C., Lescourret, F., Génard, M., Vercambre, G., Pérez Pastor, A., 2005. Modelling the effect of fruit growth on surface conductance to water vapour diffusion. Ann. Bot. 95, 673–683. https://doi.org/10.1093/aob/mci067.

Gomez, L., Rubio, E., Augé, M., 2002. A new procedure for extraction and measurement of soluble sugars in ligneous plants. J. Sci. Food Agric. 82, 360–369. https://doi.org/10.1002/jsfa.1046.

Grossman, Y.L., DeJong, T.M., 1994. Peach: a simulation-model of reproductive and vegetative growth in peach trees. Tree Physiol. 14, 329–345. https://doi.org/10.1093/treephys/14.4.329.

Guerra, M., Casquero, P.A., 2008. Effect of harvest date on cold storage and postharvest quality of plum cv. Green Gage. Postharvest Biol. Technol. 47, 325–332. https://doi.org/10.1016/j.postharvbio.2007.07.009.

Hertog, M.L., Tijskens, L.M., Hak, P.S., 1997. The effects of temperature and senescence on the accumulation of reducing sugars during storage of potato (*Solanum tuberosum* L.) tubers: a mathematical model. Postharvest Biol. Technol. 10, 67–79. https://doi.org/10.1016/S0925-5214(97)87276-6.

Inglese, P., Caruso, T., Gugliuzza, G., 2002. Crop load and rootstock influence on dry matter partitioning in trees of early and late ripening peach cultivars. J. Am. Soc. Horticult. Sci. 127, 825–830. https://doi.org/10.21273/jashs.127.5.825.

Iooss, B., Janon, A., Pujol, G., Broto, B.T., Boumhaout, K., Da Veiga, S., Delage, T., Fruth, J., Gilquin, L.R., Guillaume, J., Le Gratiet, L., Lemaitre, P., Marrel, A., Mey-Naoui, A., Nelson, B.L., Monari, F.I., Oomen, R., Rakovec, O., Ramos, B., Roustant, O., Song, E.H., Staum, J., Sueur, R., Touati, T., Weber, F., 2020. Package 'Sensitivity': Global Sensitivity Analysis of Model Outputs. Technical Report.

Itai, A., Hatanaka, R., Irie, H., Murayama, H., 2015. Effects of storage temperature on fruit quality and expression of sucrose phosphate synthase and acid invertase genes in Japanese pear. Horticult. J. 84, 227–232. https://doi.org/10.2503/hortj.MI-047.

Joas, J., Caro, Y., Lechaudel, M., 2009. Comparison of postharvest changes in mango (cv Cogshall) using a Ripening class index (Rci) for different carbon supplies and harvest dates. Postharvest Biol. Technol. 54, 25–31. https://doi.org/10.1016/j.postharvbio.2009.04.008.

Kader, A.A., 2002. Postharvest biology and technology: an overview. In: Postharvest Technology of Horticultural Crops. 3rd ed. University of California, Agriculture and Natural Resources, USA, pp. 39–48.

Knoche, M., Peschel, S., Hinz, M., 2002. Studies on water transport through the sweet cherry fruit surface: III. Conductance of the cuticle in relation to fruit size. Physiol. Plant. 114, 414–421. https://doi.org/10.1034/j. 1399-3054.2002.1140311.x.

Kulp, K., Lorenz, K., Stone, M., 1991. Functionality of carbohydrate ingredients in bakery products. Food Technol. 136–142.

Kumar, M., Rawat, V., Rawat, J.M., Tomar, Y.K., 2010. Effect of pruning intensity on peach yield and fruit quality. Sci. Horticult. 125, 218–221. https://doi.org/10.1016/j.scienta.2010.03.027.

Lara, I., Belge, B., Goulao, L.F., 2015. A focus on the biosynthesis and composition of cuticle in fruits. J. Agric. Food Chem. 63, 4005–4019. https://doi.org/10.1021/acs.jafc.5b00013.

Lara, I., Heredia, A., Domínguez, E., 2019. Shelf life potential and the fruit cuticle: the unexpected player. Front. Plant Sci. 10, 770. https://doi.org/10.3389/fpls.2019.00770.

Léchaudel, M., Lopez-Lauri, F., Vidal, V., Sallanon, H., Joas, J., 2013. Response of the physiological parameters of mango fruit (transpiration, water relations and antioxidant system) to its light and temperature environment. J. Plant Physiol. 170, 567–576. https://doi.org/10.1016/j.jplph.2012.11.009.

Lescourret, F., Génard, M., Habib, R., Fishman, S., 2001. Variation in surface conductance to water vapor diffusion in peach fruit and its effects on fruit growth assessed by a simulation model. Tree Physiol. 21, 735–741. https://doi.org/10.1093/treephys/21.11.735.

Lo Bianco, R., Rieger, M., Sung, S.J.S., 1999. Carbohydrate metabolism of vegetative and reproductive sinks in the late-maturing peach cultivar 'Encore'. Tree Physiol. 19, 103–109. https://doi.org/10.1093/treephys/19.2.103.

Lo Bianco, R., Rieger, M., Sung, S.J.S., 2000. Effect of drought on sorbitol and sucrose metabolism in sinks and sources of peach. Physiol. Plant. 108, 71–78. https://doi.org/10.1034/j. 1399-3054.2000.108001071.x.

Lombardo, V.A., Osorio, S., Borsani, J., Lauxmann, M.A., Bustamante, C.A., Budde, C.O., Andreo, C.S., Lara, M.V., Fernie, A.R., Drincovich, M.F., 2011. Metabolic profiling during peach fruit development and ripening reveals the metabolic networks that underpin each developmental stage. Plant Physiol. 157, 1696–1710. https://doi.org/10.1104/pp.111.186064.

Lopez, G., Hossein Behboudian, M., Girona, J., Marsal, J., 2012. Drought in deciduous fruit trees: implications for yield and fruit quality. In: Plant Responses to Drought Stress: From Morphological to Molecular Features. Springer-Verlag Berlin Heidelberg, pp. 441–459.

Lopresti, J., Goodwin, I., McGlasson, B., Holford, P., Golding, J., 2014. Variability in Size and Soluble Solids Concentration in Peaches and Nectarines. Horticultural Reviews: Vol. 42 253–312. https://doi.org/10.1002/9781118916827.ch05.

Lufu, R., Ambaw, A., Opara, U.L., 2019. The contribution of transpiration and respiration processes in the mass loss of pomegranate fruit (cv. Wonderful). Postharvest Biol. Technol. 157, 110982. https://doi.org/10.1016/j.postharvbio.2019.110982.

Martre, P., Bertin, N., Salon, C., Génard, M., 2011. Modelling the size and composition of fruit, grain and seed by process-based simulation models. New Phytol. 191, 601–618. https://doi.org/10.1111/j. 1469-8137.2011.03747.x.

Minas, I.S., Tanou, G., Molassiotis, A., 2018. Environmental and orchard bases of peach fruit quality. Sci. Horticult. 235, 307–322. https://doi.org/10.1016/j.scienta.2018.01.028.

Moing, A., Carbonne, F., Rashad, M.H., Gaudillère, J.P., 1992. Carbon fluxes in mature peach leaves. Plant Physiol. 100, 1878–1884. https://doi.org/10.1104/pp.100.4.1878.

Nunes, C.N., Emond, J.P., 2007. Relationship between weight loss and visual quality of fruits and vegetables. Proc. Fla. State Hort. Soc. 120, 235–245. https://doi.org/10.1017/CBO9781107415324.004.

Rahmati, M., Mirás-Avalos, J.M., Valsesia, P., Lescourret, F., Génard, M., Davarynejad, G. H., Bannayan, M., Azizi, M., Vercambre, G., 2018. Disentangling the effects of water stress on carbon acquisition, vegetative growth, and fruit quality of peach trees by means of the qualitree model. Front. Plant Sci. 9, 3. https://doi.org/10.3389/fpls.2018.00003.

Ripoll, J., Urban, L., Staudt, M., Lopez-Lauri, F., Bidel, L.P., Bertin, N., 2014. Water shortage and quality of fleshy fruits-making the most of the unavoidable. J. Exp. Bot. 65, 4097–4117. https://doi.org/10.1093/jxb/eru197.

Romero, P., Rose, J.K., 2019. A relationship between tomato fruit softening, cuticle properties and water availability. Food Chem. 295, 300–310. https://doi.org/10.1016/j.foodchem.2019.05.118.

Saltelli, A., Tarantola, S., Chan, K.P., 1999. A quantitative model-independent method for global sensitivity analysis of model output. Technometrics 41, 39–56. https://doi.org/10.1080/00401706.1999.10485594.

Scrucca, L., 2013. GA: a package for genetic algorithms in R. J. Stat. Softw. 53, 1–37. https://doi.org/10.18637/jss.v053.i04.

Sloof, M., Tijskens, L.M., Wilkinson, E.C., 1996. Concepts for modelling the quality of perishable products. Trends Food Sci. Technol. 7, 165–171. https://doi.org/10.1016/0924-2244(96)81257-X.

Soetaert, K., Petzoldt, T., Setzer, R.W., 2010. Solving differential equa tions in R: Package deSolve. J. Stat. Softw. 33, 1–25. https://doi.org/10.18637/jss.v033.i09.

Thakur, A., Singh, Z., 2012. Responses of 'Spring Bright' and 'Summer Bright' nectarines to deficit irrigation: fruit growth and concentration of sugars and organic acids. Sci. Horticult. 135, 112–119. https://doi.org/10.1016/j.scienta.2011.12.013.

Veraverbeke, E.A., Verboven, P., Van Oostveldt, P., Nicolaï, B.M., 2003. Prediction of moisture loss across the cuticle of apple (*Malus sylvestris* subsp. *mitis* (Wallr.)) during storage. Part 1. Model development and determination of diffusion coefficients. Postharvest Biol. Technol. 30, 75–88. https://doi.org/10.1016/S0925-5214(03)00083-8.

Villalobos-Acu na, M., Mitcham, E.J., 2008. Ripening of European pears: the chilling dilemma. Postharvest Biol. Technol. 49, 187–200. https://doi.org/10.1016/j.postharvbio.2008.03.003.

Whitelock, D.P., Brusewitz, G.H., Smith, M.W., Zhang Xihai, 1994. Humidity and airflow during storage affect peach quality. HortScience 29, 798–801. https://doi.org/10.21273/hortsci.29.7.798.

Wu, B., Quilot, B., Kervella, J., Génard, M., Li, S., 2003. Analysis of genotypic variation of sugar and acid contents in peaches and nectarines through the principle component analysis. Euphytica 132, 375–384. https://doi.org/10.1023/A:1025089809421.

Wu, B.H., Quilot, B., Génard, M., Li, S.H., Zhao, J.B., Yang, J., Wang, Y.Q., 2012. Application of a SUGAR model to analyse sugar accumulation in peach cultivars that differ in glucose-fructose ratio. J. Agric. Sci. 150, 53–63. https://doi.org/10.1017/S0021859611000438.

Xanthopoulos, G.T., Templalexis, C.G., Aleiferis, N.P., Lentzou, D.I., 2017. The contribution of transpiration and respiration in water loss of perishable agricultural products: the case of pears. Biosyst. Eng. 158, 76–85. https://doi.org/10.1016/j.biosystemseng.2017.03.011.

Yahia, E.M., Carrillo-López, A., Bello-Perez, L.A., 2019. Carbohydrates. Postharvest Physiology and Biochemistry of Fruits and Vegetables 175–205. https://doi.org/10.1016/B978-0-12-813278-4.00009-9.

Yakushiji, H., Morinaga, K., Nonami, H., 1998. Sugar accumulation and partitioning in Satsuma mandarin tree tissues and fruit in response to drought stress. J. Am. Soc. Horticult. Sci. 123, 719–726. https://doi.org/10.21273/jashs.123.4.719.

In the Discussion section, we've found a possible error that we pointed out to the journal editor.

The sentences below were indeed not supported by evident experimental results: "In addition, low fruit load increased fruit sweetness in fruit pulp during the 2018 experiment, as reported also by Kumar et al. (2010). This could be related to the increase in the availability of carbohydrate resources that depend on the number of fruit on the tree (Lopresti et al., 2014) and because of a higher dry mass accumulation with respect to the fruit water intake.".

We would like to modify it to: "Low fruit load did not increase the fruit sweetness during the 2018 experiment, in contrast with the evidences that an increase in thinning intensity could increase the availability of carbohydrate resources and the sugar content in peach (Kumar et al., 2010; Lopresti et al., 2014).".

Supplementary Information

- **A.1** Sugar metabolism represented in sugar dynamics sub-models
- **A.2** Sub-model parameters and constant values taken from literature
- **A.3** Measured and simulated fruit cuticular cracks surface area (2018)
- **A.4** Simulated part of fruit mass loss due to respiration during storage

Chapter 2

Brown rot disease in nectarine during storage: modeling the joint effects of pre-harvest and storage conditions

Authors

Enrico Casagrande[1,2], Michel Génard[2], Sébastien Lurol[1], Florence Charles[3], Daniele Bevacqua[2], Davide Martinetti[4], Françoise Lescourret[2]

[1] Centre Technique Interprofessionnel des Fruits et Légumes, 13210 Saint-Rémy-de-Provence, France.

[2] UR 1115 Plantes et Systèmes de Culture Horticoles, INRAE, 84914 Avignon Cedex, France.

[3] Avignon Université, UMR Qualisud, 84916 Avignon, France. Qualisud, Université de Montpellier, Avignon Université, CIRAD, Institut Agro, Université

de La Réunion, Montpellier, France.

[4] UR 546 Biostatistique et Processus Spatiaux, INRAE, 84914 Avignon Cedex, France.

Résumé

La maladie de la pourriture brune causée par *Monilinia* spp. est responsable de fortes pertes de fruits à noyau au stade post-récolte. La sensibilité des fruits à cette maladie pendant le stockage est liée à des facteurs pré et post-récolte, mais leurs effets conjoints ont rarement été étudiés. De plus, des infections secondaires non liées à des contacts directs pourraient avoir lieu pendant le stockage, mais cette hypothèse n'a jamais été testée. Pour répondre à ces questions, nous avons mis en place deux expériences sur des nectarines (cv. 'Nectarlove') : la première a eu pour objectif de vérifier si les fruits infectés étaient capables de propager l'infection aux fruits environnants pendant le stockage, tandis que la seconde a permis de suivre l'apparition des pourritures pendant le stockage en 2018 et 2019, sous l'influence de plusieurs conditions pré- et post-récolte. Aucun symptôme secondaire n'a été observé au cours de la première expérience. Les résultats de la deuxième expérience en 2018 ont montré que l'incidence de la maladie augmentait avec la masse individuelle des fruits, influencée par les pratiques agricoles, et avec la date de récolte. Les résultats de l'expérience de 2019 ont montré que l'incidence de la pourriture brune augmentait aussi avec la température de stockage. Ces résultats ont permis d'identifier des variables candidates liées aux caractéristiques épidémiologiques et physiques des fruits à la récolte, et aux conditions de stockage, que nous avons utilisées pour construire un modèle mathématique permettant d'estimer la probabilité de la date d'apparition de la pourriture brune chez les nectarines pendant le stockage. Une

procédure de sélection du modèle a montré que la masse individuelle des fruits, la prévalence de la pourriture brune à la récolte, la durée moyenne d'humectation journalière dans la semaine précédant la récolte et la température pendant le stockage étaient les variables les plus influentes. La qualité d'ajustement du modèle aux données expérimentales a été satisfaisante. Ce modèle, qui montre la nécessité d'accorder plus d'attention à l'interaction entre les conditions de pré-récolte et de stockage, pourrait être utilisé pour évaluer des stratégies de gestion visant à réduire l'impact de la pourriture brune pendant le stockage des nectarines.

Abstract

Brown rot disease caused by *Monilinia* spp. is responsible for several losses in the postharvest stage of stone fruit. The fruit sensitivity to this disease during storage could be related to pre- and post-harvest factors, but their joint effects have rarely been studied in the literature. Moreover, secondary infections could take place during storage, but this process has never been tested when fruit are not in direct contact. To investigate these issues, two experiments on nectarine (cv. 'Nectarlove') were set up: the first one aimed to verify if infected fruit could be able to spread the infection to surrounding fruit during storage, while the second one concerned the visual assessment of brown rot disease dynamics during storage in 2018 and 2019, under the influence of several pre- and post-harvest conditions. No visual symptoms from secondary infections were observed during the first experiment. The results from the second experiment in 2018 showed that the incidence of the disease increased with an increase in fruit mass, influenced by orchard practices, and with a later harvest date. Those from 2019 experiment suggested that brown rot incidence increases with an increase

in storage temperature. These findings allowed the identification of candidate variables related to the fruit epidemiological and physical characteristics at harvest, and to storage conditions, which were used to build a mathematical model to estimate the probability of time-to-appearance of brown rot symptoms in nectarine during storage. A model selection procedure identified the individual fruit mass, the prevalence of brown rot at harvest, the mean wetness duration during the week before harvest and the temperature during storage as the most influential variables. The model well fitted experimental data, stressing out the need to pay more attention to the interaction between pre-harvest and storage conditions. This model could be used to evaluate management strategies to reduce the impact of the brown rot disease during storage of nectarine.

2.1 Introduction

Stone fruit infections by *Monilinia (M.)* spp. (especially *M. fructicola* and *M. laxa*) are challenging for both farmers and retailers, since they can occur in the orchard and during storage, with economic losses that can reach 1.7 M$ per year at the global scale (Martini and Mari, 2014). In the orchard, the probability of infection depends both on fruit susceptibility, which is influenced by fruit growth rate and maturity stage (Xu et al., 2007), and exposure to the pathogen, which depends on the concentration of fungal spores in the air (Madden et al., 2017). However, it is after harvest that most of the disease-related losses occur (Hong et al., 1997). Quiescent infections could develop when fruit are still on the tree, which then express after harvest under favourable storage conditions (Emery et al., 2000; Gell et al., 2008). Moreover, the level of inoculum present on fruit surface at harvest could triggers new infections during storage, with the following development of brown rot during storage (Tian and Bertolini, 1999).

During refrigerated storage, abiotic conditions such as temperature and relative humidity are important factors for the disease development, influencing the infection and colonization rate (Xu et al., 2001; Casals et al., 2009; Bernat et al., 2017b). Moreover, secondary infections during storage and handling operations (Michailides and Manganaris, 2009; Bernat et al., 2017a) could be of considerable epidemiological importance. Tian and Bertolini (1999) and Bernat et al. (2017b) observed that fruit infected by *M. laxa* could be able to sporulate (generating conidia) during storage and suggested that they can infect the surrounding fruit. However, to our knowledge, there are no published studies on brown rot secondary infections during storage.

Furthermore, environmental conditions before harvest, such as air temperature and wetness duration, were shown to influence the onset of post-harvest infections, when they enhance spore dispersion in the orchard and latent infection (Gell et al., 2008; Holb, 2008; Bannon et al., 2009). In addition, cultural practices such as thinning and irrigation can play an important role by promoting the appearance of cuticle micro-cracks (Gibert et al., 2007; Bellingeri et al., 2018), which act as entry sites for brown rot spores (Gibert et al., 2009). It could therefore be useful to understand which combination of pre- and post-harvest conditions are responsible for observed variations in fruit rotting dynamics during storage.

To describe and simulate brown rot infections dynamics, several mathematical models were used or developed, both in the orchard (e.g. Bevacqua et al., 2018) and after harvest. In the latter stage, attention has been focused on the effect of latent infection and on the influence of meteorological variables before and at harvest, like temperature and wetness duration (Gell et al., 2009; Villarino et al., 2012), and on handling practices (Garcia-Benitez et al., 2020). Attention has also been paid to the influence of temperature and relative humidity on the

development of brown rot *in vitro* and directly on fruit (Bernat et al., 2017b, 2018). However, the effects of fruit individual characteristics at harvest, which are influenced by pre-harvest practices, of orchard epidemiological indicators and of storage conditions on brown rot spread during storage have not been considered together in the literature.

The objective of this study was thus to evaluate if fruit infected by *M. laxa* could lead to a secondary spread of the disease and how pre-harvest and storage conditions influence the brown rot disease development during storage. To answer these questions, we set up two experiments: the first aimed to verify if infected fruit could be able to spread the infection to surrounding fruit during storage, while the second monitored brown rot development during storage, under the influence of several pre- and post-harvest conditions. Finally, based on the experimental results, we proposed a mathematical model to estimate the probability of visual appearance of brown rot symptoms during storage in nectarine, based on both pre- and post-harvest conditions.

2.2 Materials and Methods

2.2.1 Experimental design to study brown rot secondary infections during storage

The observation protocol was based on the experience presented in Baggio et al. (2017) on black rot. The experiment involved two nectarine mid-season cultivars, 'Honey Fire' and 'Magique'. 'Honey Fire' fruit were retrieved from a commercial producer situated in the south of France, while 'Magique' were harvested at INRAE station in Avignon (France). A culture of *M. laxa* was grown on PDA medium before the start of the experiment at 25 °C for 3 days, in or-

der to artificially inoculate the fruit. The *M. laxa* dry spores (FlAbBerga2014) were provided by the Microbiology Laboratory of the University of Montpellier (France).

For each cultivar, 150 fruit of uniform caliber were collected at commercial maturity. First, three fruit were randomly selected, disinfected using a 0.5% chlorine solution for 3 minutes and inoculated: one cheek from each fruit was wounded with a sterile box cutter (1 cm in length 0.5 cm in depth), and a plug of agar (1 cm of diameter) with visible mycelial growth of the fungus was collected from the PDA medium and was placed against the wounded cuticle of the fruit. A water-soaked cotton pad was taped to the fruit, which were then placed in a plastic box incubated at 22 °C and 100% RH (relative humidity) during three days. Then, the other nectarines were disinfected by soaking in a 0.5% chlorine solution for 3 minutes and placed on paper towels to dry at room temperature. Two experimental groups were then set up: a control group (C), without a central inoculated fruit, and a treatment group with a central inoculated fruit (I). In the control group, 25 fruit were arranged in transparent cells on Plexiglas plates to form 5x5 squares, taking care to separate all fruit by a uniform distance of 1 cm. In the treatment group, 24 healthy fruit were placed as in the previous configuration, with one inoculated (and germinated) fruit in the middle of the square. Three replications of the experiment were carried out. In order to simulate the turbulence inside the storage room, two low-power fans were placed in each cell that in turn were placed in a chamber at 25 °C. A small plastic container filled with water was placed in each cell to maintain high humidity conditions (∼95% RH). A light cycle 12 h day/12 h night corresponding to the preferential cycle of *M. laxa* was set up Byrde and Willetts (1977). The fruit were observed daily for seven days, in order to track the infection progress. Infection could be visually monitored without manipulating the fruit by using

the device illustrated in Fig. 2.1.

Figure 2.1 – Experimental set-up for the brown rot secondary infections experiment. The three upper cells contain a central inoculated fruit (I), while the lower are the control groups (C).

2.2.2 Assessment of the effects of pre-harvest and storage conditions on brown rot dynamics during storage

Experimental design to study the brown rot temporal pattern during storage

A monitoring of brown rot disease during storage was carried out in 2018 and 2019 on nectarine (*Prunus persica var. nucipersica*, cultivar Nectarsweet© 'Nectarlove'). The experiments aim was to test the effect of several covariates on the nectarine time-to-infection by brown rot during storage. Fruit came from trees planted in 2013 at the INRAE station in Avignon. Trees were submitted each year to a single fungicide treatment four weeks before the first predicted

harvest date, in order to avoid an early diffusion of the brown rot disease in the orchard. Routine horticultural care and uniform pruning for commercial fruit production were ensured for the trees in both growing seasons. Daily measurements of meteorological variables (atmospheric temperature, wetness duration and rainfall) were retrieved from the INRAE 'CLIMATIK' platform (https://intranet.inrae.fr/climatik/) for the entire growing season. Moreover, at each harvest date (three in 2018 and two in 2019), we measured the value of the prevalence of the brown rot at harvest (ratio of the number of infected fruit on the total number of fruit on the trees).

Several combinations of horticultural and storage conditions were tested. In 2018, full bloom occurred on March 17, while the trees were thinned on May 22 (66 dafb, days after full bloom). Two levels of water supply were tested: a well-irrigated (100% CWR, crop water requirement) and a water-stressed one (50% CWR). CWR was calculated as the difference between the potential evapotranspiration and the rainfall over the irrigation period (Allen et al., 1998), and it was used as an indicator to manage irrigation. Two crop loads were also applied by hand-thinning in combination with the irrigation regimes, namely a low load, with 200 fruit per tree (200 FL, fruit load) and a high load (400 fruit per tree, 400 FL), for a total of four pre-harvest horticultural treatments. 60 fruit per treatment (4 boxes of 15 fruit) were harvested randomly at three different dates (from 12 July to 27 July) and weighted separately. Fruit were then stored in a cold storage chamber, following a 'standard' storage: 48h at 2 °C and then at 20 °C. Brown rot spread was followed by visual inspection at different time intervals, during 14 days of storage: fruit were assessed individually and considered as infected (and thus unmarketable) when brown rot infection appeared on fruit surface. Infected fruit were removed from the tray, in order to avoid further infections.

In 2019, two irrigation regimes in the growing season and three storage temperatures after harvest were tested. Full bloom occurred on March 10, and a commercial thinning procedure was used for all the trees, ensuring from 400 to 500 fruit per tree. A well-irrigated (70% CWR) and a water-stressed regime (30% CWR) were applied in the orchard. 240 fruit were randomly harvested at two dates (22 and 29 July 2019). After harvest, fruit were first stored at 2 °C during 2 days and then at 2, 15 and 25 °C separately (80 fruit per treatment, (4 boxes of 20 fruit). During storage, relative humidity was measured, but not controlled. The appearance of the brown rot disease during storage was followed as in the 2018 experiment, until three weeks after harvest.

Survival analysis of fruit time-to-appearance of brown rot symptoms by *Monilinia* spp. during storage

To assess the influence of several variables on the time-to-appearance of brown rot symptoms on nectarine during storage, we used a survival analysis technique. This ensemble of modeling techniques has been used in plant pathology (Scherm and Ojiambo, 2004; Pethybridge et al., 2010; Humplík et al., 2020), while very few applications to fruit epidemiology can be found in the literature, as for example in the case of citrus black rot (Frare et al., 2019). Survival analysis supports the use of censored observations (i.e. individuals for whom the event of interest does not occur before the end of the study) and repeated measurements on the epidemiological state of the same individual, while considering the effects of several covariates (Muenchow, 1986; Bradburn et al., 2003). For each individual fruit i, we considered the time when infection was visually detected t_i (in days), or when the follow-up period finished. Fruit that were not yet infected at the end of each experiment were thus considered as 'censored', and so a censoring indicator c_i was introduced. Moreover, each fruit i was associated

to a vector of p covariates $\boldsymbol{x}_i = (1, x_{i,1}, ..., x_{i,p})$. The individual time of brown rot visual infection during storage (in days) was used as the response random variable. The probability that a fruit i shows visual symptoms of brown rot infection before time t was expressed by a cumulative density function $F_i(t)$. To consider the positive effect of fruit ripening and senescence on the probability of fruit infection (Flaishman and Kolattukudy, 1994; Díaz Ricci et al., 2020; Xu et al., 2007), we used a Gompertz functional shape for survival time probability distribution (Ricklefs and Scheuerlein, 2002). The individual infection probability was described as :

$$F_i(t) = 1 - exp(\,-\frac{b_i}{a}(e^{a \cdot t} - 1)\,) \tag{2.1}$$

where b_i is an individual rate parameter (controlling the magnitude of the hazard), which depends on the individual covariates vector, and a is a shape parameter (controlling the time-evolution of the hazard, which increases over time if $a > 0$), which is instead constant among fruit. The dependence of the rate parameter on covariates was described as:

$$log(b_i) = \boldsymbol{x}_i^T \cdot \boldsymbol{\beta} \tag{2.2}$$

where the log-link is used to ensure the parameter to be positive and $\boldsymbol{\beta} = (\beta_0, \beta_1, ..., \beta_p)$ is the vector of the corresponding regression coefficients.

In proportional-hazard models, for a given covariate, the exponential of the coefficient estimate is the hazard ratio, which is the ratio of the hazard between two observations having a different value of this covariate. In the case of continuous variables, for a unitary increase of a covariate the hazard of the event (in our case study, being infected by brown rot) is multiplied by the value of the hazard ratio. The cohort of covariates was selected on the basis of a literature survey

and included a total of 9 variables, 8 related to the pre-harvest stage and 1 to the post-harvest one:

- fruit mass w (g). We assumed that this variable is a proxy of fruit cuticular crack surface, which is directly related to the infection probability (Gibert et al., 2009). This variable is principally influenced by agricultural practices in the orchard (Minas et al., 2018);

- growing degree-days at the harvest date GDD_h (°C). They are the cumulated degree-days along the growing season, which is an indicator of plant development. The plant developmental stage can influence the epidemiological state (Lovell et al., 2004), and, more precisely, fruit maturity enhances brown rot infections (Luo and Michailides, 2001). The indicator was calculated with the single sine, horizontal cutoff method (critical temperatures: 7 and 35°C), as in DeJong and Goudriaan (1989);

- prevalence of brown rot at harvest I_h (%). It can be correlated to the development of brown rot during storage (Emery et al., 2000; Luo and Michailides, 2003). It was calculated at each harvest for the entire fruit population, as the ratio of visually infected fruit on the total harvested fruit;

- indicators related to the meteorological variables in the week before harvest: the minimum $T_{min,h}$, maximum $T_{max,h}$ and mean $T_{mean,h}$ value of atmospheric temperature (°C), the mean wetness duration $wd_{mean,h}$ (h) and the cumulated rainfall $R_{sum,h}$ (mm). These variables affect the latent infection by *Monilinia* spp. (Gell et al., 2008; Luo and Michailides, 2003; Emery et al., 2000);

- the mean temperature during storage $T_{mean,s}$ (°C), because of its impor-

tance in rot developmental rate (Bernat et al., 2017b; Tamm and Fluckiger, 1993).

All the covariate combinations were tested, for a total of 511 alternative model formulations, using a maximum likelihood estimation in R through the *flexsurvreg* package. The best model was selected on the basis of the Bayesian Information Criterion (BIC) (Burnham and Anderson, 2004). Moreover, we also checked for the best model in terms of predictive quality trough a k-fold cross-validation procedure (k=6), where we used the mean value of Somers' D_{XY} statistic for censored data across the k considered folds (Chen et al., 2012; Newson, 2006), calculated with the *rcorr.cens* function (from the R's *Hmisc* package). The last statistic is a measure of association between two ordinal variables, which in this case are the mean predicted and the observed brown rot infection appearance. It can vary from -1, for a perfect disagreement, to 1, for a perfect agreement (Newson, 2006). We finally compared the model estimates to the observed data, by the mean of non-parametric Kaplan-Meier curves. This last technique allows to calculate the observed survival probability (which is the probability that a nectarine does not show visual symptoms of brown rot disease) from the observed survival times and censoring times (Clark et al., 2003).

2.3 Results

2.3.1 No brown rot secondary infection symptoms were observed during storage

For both 'Honey Fire' and 'Magique' cultivar, no infection was observed in control cells without inoculum (C). In the cells containing a central fruit inoculated (I), nectarine showed no symptoms of secondary infection by *M. laxa* when non-

inoculated fruit did not touch the central infected fruit. However, when juice from central fruit came in contact with the other fruit, it induced brown rot secondary infections. During the experiment, fruit that accidentally came into contact with the infected fruit were also infected by *M. laxa* spores. The spores were thus able to be transmitted through the dripping juice and by direct contact between touching fruit, with a consequent spread of infection (see Appendix B.1). Finally, when *Rhizopus* spp. infection was observed, this fungus quickly infected other fruit.

2.3.2 Brown rot incidence during storage under different pre-harvest and storage conditions

In 2018, the cumulative incidence of brown rot disease increased with the harvest date, from an average of 10.4% at the end of storage after the first harvest, to 52.5% after the third harvest (Figure 2.2). The disease progress curves were steeper after the third harvest than after the other ones. The fruit from trees submitted to well-irrigated treatment (100% CWR) were the most affected by the disease, with an average of 70% cumulated loss at the end of storage, compared to 35% for fruit grown under the water-stressed treatment (50% CWR). In all the experimental treatments, fruit from the well-irrigated trees showed higher brown rot incidence during storage than those from water-stressed ones, while fruit load did not seem to play a marked effect on disease progress (data not shown). Fruit loss was the most severe after the third harvest and from the well-irrigated and low-load treatment, i.e. 83.3 %, whereas only 3.3 % of fruit collected after the first harvest from water-stressed and high-load treatment trees showed symptoms at the end of the storage period.

In 2019, the cumulative incidence curves similarly increased with the harvest

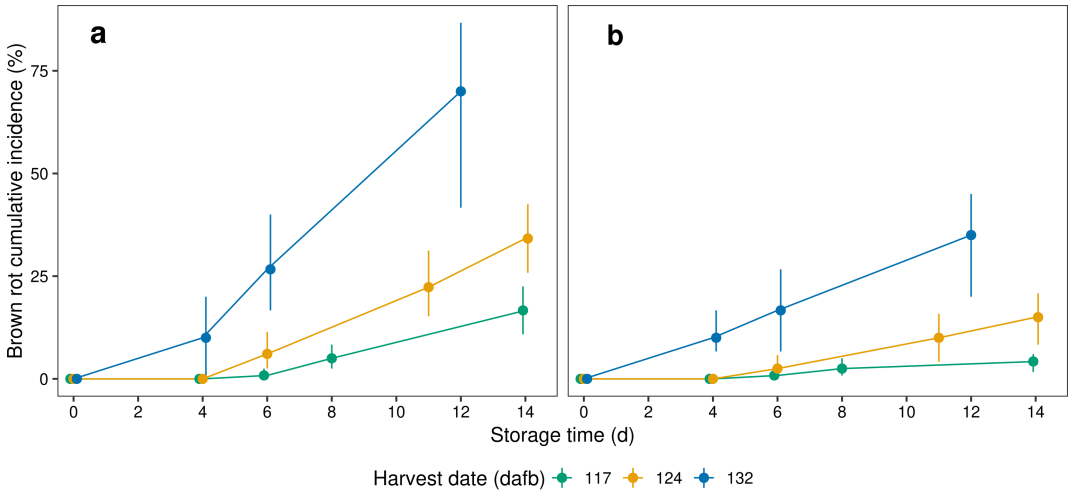

Figure 2.2 – Time course of observed incidence of brown rot disease during nectarine storage in 2018 for three different harvest dates. Points are means and bars represent the standard error of the mean. Fruit came from two pre-harvest irrigation treatments: 100% CWR (a) and 50% CWR (b). Fruit were stored at a mean temperature of 20 $°C$.

date, but also with storage temperature (Figure 2.3).

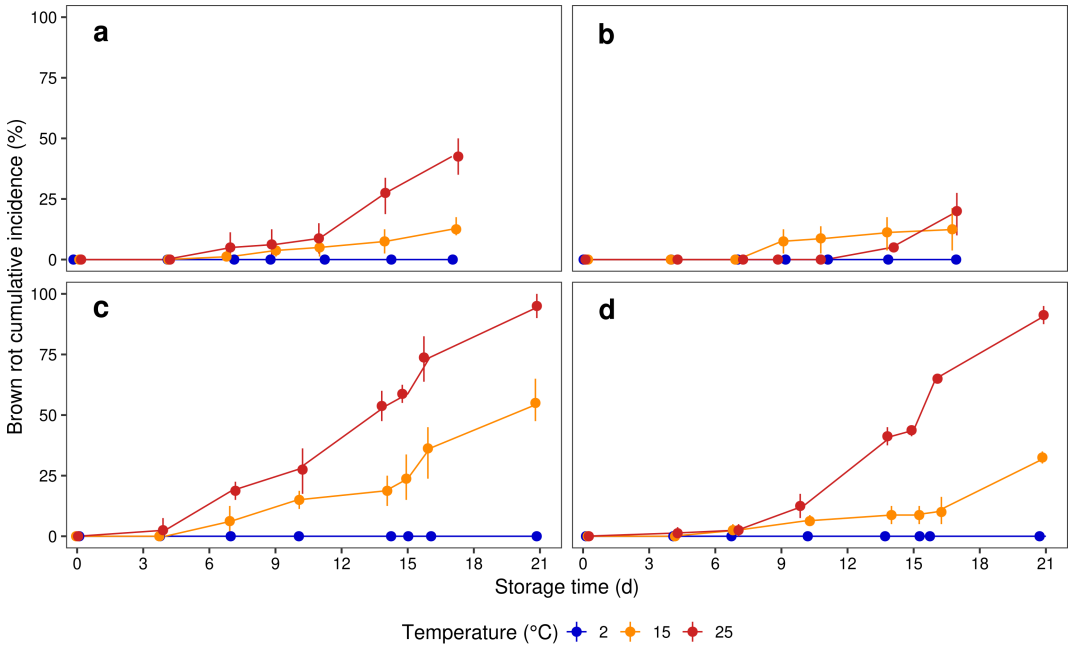

Figure 2.3 – Time course of observed incidence of brown rot disease during nectarine storage in 2019 for different storage temperatures, after a first (a-b, 134 dafb) and a second harvest date (c-d, 141 dafb). Points are means and bars represent the standard error of the mean. Fruit came from two pre-harvest irrigation treatments: 70% CWR (a-c) and 30% CWR (b-d).

The irrigation level also impacted the disease development, but not in a

uniform way across storage temperatures and harvest dates. fruit stored at 2 °C showed no sign of infection during storage (both for the first and second harvest dates), while increasing incidence was observed at 15 °C (28%, on average at the end of the storage) and 25 °C (62%). The maximal loss at the end of storage was observed after the second harvest, for fruit from 70% CWR irrigation level and stored at 25 °C (95%).

2.3.3 Modeling the influence of pre- and post-harvest covariates on nectarine time-to-appearance of brown rot symptoms during storage

The considered horticultural practices did not act directly on the disease during storage, but on the host susceptibility during the pre-harvest stage, namely the level of cuticular cracking, accounted by the fruit mass as a proxy. Both irrigation and fruit load levels significantly influenced the fruit mass at harvest, but the differences between mass were larger between irrigation levels than between fruit load levels (data presented in Appendix B.2). In the same way, the harvest date had no direct influence on brown rot during storage, but it acted through meteorological, physiological and epidemiological variables, which were considered as covariates in the survival analysis (Table 2.1).

Covariate (name and symbol)		**Value**				
Year			2018		2019	
Harvest date (dafb)		117	124	132	134	141
Pre-harvest conditions at harvest						
fruit mass[a] (g)	w	181±33	162±33	180±38	161±27	136±25
growing degree-days (°C)	GDD_h	1357	1495	1652	1548	1685
brown rot prevalence (%)	I_h	0.16	0.65	2.41	0.77	1.18
Meteorological conditions (statistics over a week before harvest)						
minimum temperature (°C)	$T_{min,h}$	19.8	15.6	17.8	16.5	18
maximum temperature (°C)	$T_{max,h}$	33.6	35.4	36.8	35	37.5
mean temperature (°C)	$T_{mean,h}$	26.7	26	26	26.2	27.8
mean wetness duration (h)	$wd_{mean,h}$	0.56	3.26	3.09	0.13	2.04
cumulated rainfall (mm)	$R_{sum,h}$	0	0	0	0	9.5
Storage condition						
mean temperature (°C)	$T_{mean,s}$	20	20	20	2/15/25	2/15/25

[a] mean value ± standard deviation

Table 2.1 – Covariate values measured for the five different harvest dates during the 2018 and 2019 experiments. In 2019, three different levels of mean storage temperature $T_{mean,s}$ were tested.

During 2018 and 2019, on the 1560 fruit observed for brown rot disease during storage, 433 were infected at the end of the experiments (72% right-censoring). The best five models in terms of BIC are presented in the Appendix B.3. The model selection procedure retained the following covariates for the best model in terms of BIC:

$$\boldsymbol{x} = \{1,\, w,\, I_h,\, wd_{mean,h},\, T_{mean,s}\} \tag{2.3}$$

The model showed a good average predictive quality over the 6-folds cross-validation procedure ($D_{XY} = 0.68$). The fitting of the most parsimonious model resulted in 6 parameters (Table 2.2), which were all significative ($P \leq 0.05$). The hazard ratios were larger than one for all selected variables. Thus, an increase in storage temperature, fruit mass, brown rot prevalence at harvest and mean wetness duration in the week before the harvest increased the risk of brown rot during storage. The model suggested that for an increase in temperature from

2 to 25 °C, the hazard of infection increases by more than 60 times, while for a fruit of 200 g compared to a fruit of 150g the hazard increases nearly three times.

Parameter	Coef. estimate	95% C.I.	$P > \chi^2$	exp(Coef.)
shape, a	0.295	[0.272,0.318]	< 0.0001	
rate, b				
intercept, β_0	-15.482	[-16.38,-14.57]	< 0.0001	$1.89 \cdot 10^{-7}$
w (g)	0.021	[0.019,0.024]	< 0.0001	1.02
I_h (%)	0.637	[0.456,0.818]	< 0.0001	1.58
$wd_{mean,h}$ (h)	0.446	[0.342,0.551]	< 0.0001	1.41
$T_{mean,s}$ (°C)	0.172	[0.151,0.193]	< 0.0001	1.19

Table 2.2 – Coefficient estimates and associated test statistics for the best model in terms of BIC to explain time-to-infection of nectarine to brown rot during storage.

To calculate the survival probability with the calibrated model, we used the mean fruit mass (w) and the values of other selected covariates (I_h, $wd_{mean,h}$, $T_{mean,s}$) at each harvest date and storage temperature (Table 2.1). In 2018, the model estimates of the probability of survival to brown rot were satisfactory for the different irrigation treatments and harvest dates, even if there was an overestimation for nectarine harvested at the third harvest date (Figure 2.4). In 2019, the model well captured the fact that decrease in observed survival probability was steeper after the second harvest that after the first one (Figure 2.5). Moreover, also the temperature effect was well described by the model, especially for the minimum (2 °C) and maximum (25 °C) temperature.

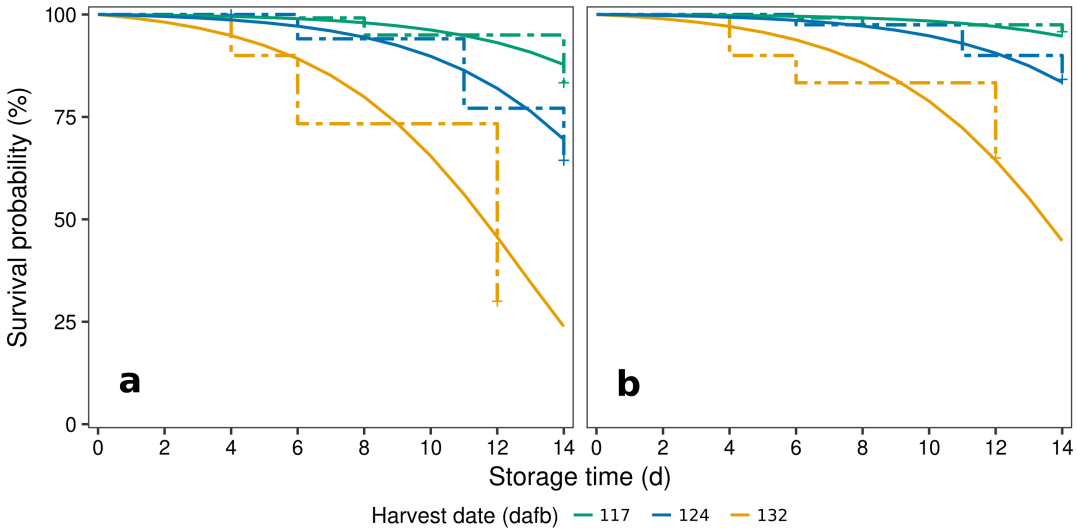

Figure 2.4 – Parametric (continuous) and Kaplan-Meier (dotted) estimates of survival probability to brown rot during storage in 2018, for nectarine grown under a 100% CWR (a) and a 50% CWR (b) irrigation treatment, for different harvest dates.

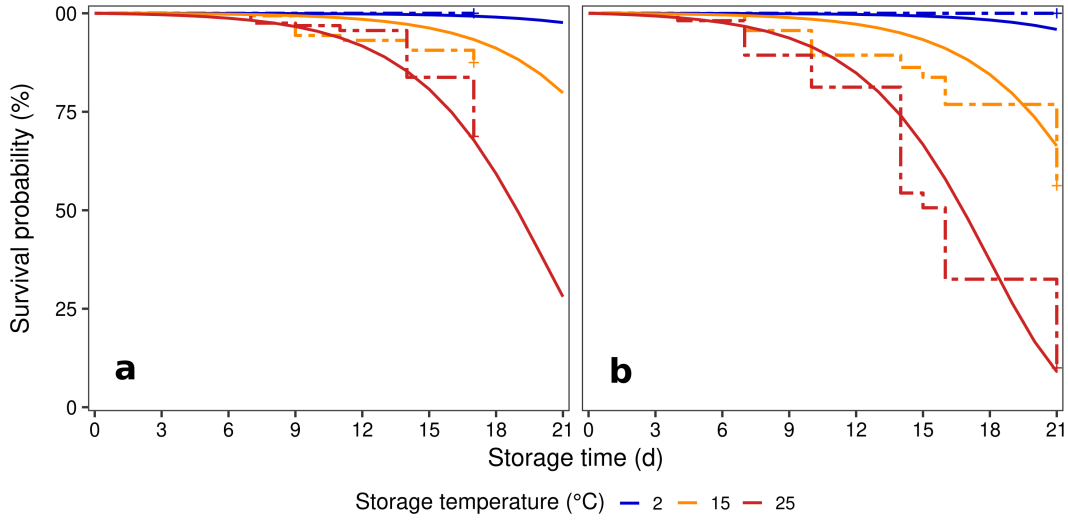

Figure 2.5 – Parametric (continuous) and Kaplan-Meier (dotted) estimates of survival probability to brown rot during storage in 2019, for nectarine harvested at the first (a, 134 dafb) and the second (b, 141 dafb) harvest date, for different storage temperatures.

2.4 Discussion

During storage, the development of brown rot disease on stone fruit could be related to two causes: primary inoculation from orchard or post-harvest fruit

manipulations, or rotten fruit that spread the disease to neighbouring fruit (Dutot et al., 2013). Secondary infections during storage were observed for fungal species such as black rot (*Rhizopus stolonifer*) in peach by Baggio et al. (2017), but the fruit were into contact. To date, no specific experiment on brown rot secondary spread without fruit direct contact was reported on stone fruit for *Monilinia* spp., which was thus tested in this study. The results suggested that the only source of brown rot infections during storage was from primary inoculation sources. This could suggest that the appearance of visual symptoms related to brown rot during storage for nectarine derived from the germination of fungal spores being already present on fruit surface at the start of the storage or coming from latent infections in the orchard (Xu et al., 2007; Gell et al., 2008; Gibert et al., 2009). The finding is in contrast with those of Tian and Bertolini (1999), who speculated that conidia by *Monilinia* spp. produced during storage could be important in the spread of secondary infections, through the turbulent movement of air. Also Bernat et al. (2017b) indicated that secondary infection in storage room of fruit should be possible for *M. laxa*, but not for *M. fructicola*. These authors also suggested that conidia could remain viable on storage room surfaces, which we did not test in our experiments. We also did not test whether airborne spores were present on the fruit surrounding the central infected one. More specific experiments and trials in different storage conditions and for longer observation periods are thus necessary to confirm the observed results. However, stone fruit are generally not stored for long periods (Lopez Camelo, 2004). In the current state of knowledge, attention must been paid to the control of spore dispersion on harvested fruit by fruit handling practices at harvest and during storage (Amorim et al., 2008), such as calibration and use of separated crates. In addition, practices able to reduce the primary inoculum on harvested fruit, such as water immersions (Karabulut et al., 2010), are of

interest.

The results of the secondary infection experiment justified the choice of survival analysis, a model at the individual level, to explain the pattern of observed brown rot during storage. A high censoring rate was observed, which may indicate that experiments ended too soon. The model could indeed be improved by adding data from new and longer experiments in a broader range of conditions. The model selection retained variables related to the fruit susceptibility to the disease, which were influenced by pre-harvest conditions, and to the storage conditions. The first ones were physiological (fruit mass), epidemiological (brown rot prevalence at harvest) and meteorological (mean daily wetness duration in the week before the harvest).

The fruit mass was a proxy for fruit cuticular crack surface (Gibert et al., 2007; Borve et al., 2000), which act as entry sites for spores (Borve et al., 2000). However, cuticular development during growing season depends on fruit cultivar (Lara et al., 2014), so that cuticular crack size and fruit mass can be related by different relationships. It could be thus of interest, in the future, to relate directly fruit cuticular crack size to brown rot during storage. Fruit mass is also an indicator of the fruit physiological state (Kader, 1999), which is important in the setting of brown rot infections. With increasing maturation and ripening, biochemical and structural changes happen in fruit cuticle, promoting the germination and sporulation by the fungal spores (Oliveira Lino et al., 2016). The fruit mass is influenced by horticultural practices, such as irrigation and fruit thinning, and this points out the importance of these conditions in influencing the development of the disease after harvest.

Regarding the meteorological variables, only the mean wetness duration in the week before harvest was selected as explaining variable for the brown rot observed dynamics during storage. It was already considered as an influential

variable in the penetration and infection stage by *Monilinia* spp. in stone fruit (Koball et al., 1997; Luo and Michailides, 2003; Gell et al., 2008). However, meteorological variables such as rainfall and environmental temperature before harvest were selected in other studies as important variables for spore germination and for the installation of latent infection in the orchard (Biggs and Northover, 1988; Tamm and Fluckiger, 1993). These processes can prepare the *Monilinia* spp. infections, which then express during storage. Probably, a larger variability of meteorological variables (see for example the values of the cumulated rainfall during 2018 and 2019, Table 2.1) could help to better select the influential covariates.

The last variable related to pre-harvest conditions to be selected as significative by the survival model was the prevalence of brown rot at harvest. The incidence of fruit rot during post-harvest stage was also found to be positively correlated to this variable in different climatic and crop conditions (Emery et al., 2000; Luo and Michailides, 2003; Xu et al., 2007; Gell et al., 2009; Villarino et al., 2012). Horticultural practices may also have direct effects on *Monilinia* spp. infection in the orchard, by modifying the distance between the fruit, which can favours spore dispersion (Bellingeri et al., 2018), and by creating a micro-climate favourable to *Monilinia* spp. sporulation (Mercier et al., 2008). However, the prevalence of brown rot at harvest was found to be positively related to the density of conidia on fruit surface (Gell et al., 2008; Holb, 2008). Gibert et al. (2009) also found a significant positive relationship between the incidence of brown rot infections after harvest and the numbers of conidia of *Monilinia* spp. on the fruit surface. This last variable (or a proxy as the density of airborne conidia at harvest) should then be further considered in nectarine survival analysis to brown rot disease after harvest as a more direct covariate.

The temperature during storage was also identified by the survival analysis

model selection as an important factor of occurrence of brown rot symptoms during storage. Its effect increased in the 0-25 °C range, as already observed by Bernat et al. (2017b) on peach, and Tamm and Fluckiger (1993) and Xu et al. (2001) in Petri dish. At 2 °C no visual symptoms of brown rot infection were observed during storage, but others studies showed an exponential phase of brown rot infections after longer storage period at almost this temperature (Bernat et al., 2017b; Garcia-Benitez et al., 2020). It could be interesting to consider in the survival model the introduction of storage temperature as a time-changing covariates (Petersen, 1986), in order to test the effect of a change in temperature during different post-harvest stages on the appearance of brown rot symptoms (Garcia-Benitez et al., 2020). The relative humidity during storage was not considered in this analysis, since the measurement of this variable was carried out only during 2019 experiments. Gibert et al. (2009) observed no influence of relative humidity on nectarine infection by brown rot during storage. In contrast, Bernat et al. (2018) found that a high relative humidity associated to a low temperature could extend the conidia viability during storage. Several studies pointed out the importance of this variable in spore germination, but they were in vitro and their results were significative only at near saturation conditions ($\geq$ 97%) (Byrde and Willetts, 1977; Tamm et al., 1995; Xu et al., 2001). The effect of relative humidity on brown rot infections during storage needs to be tested in further experiments.

Finally, the model showed a satisfactory explanatory and predictive quality, tested through model cross-validation. The covariates chosen by the model technique were thus able to highlight that fruit with higher caliber are more susceptible to the apparition of brown rot symptoms after storage (Gibert et al., 2009), suggesting that these fruit require a storage at low temperature or a short consumption delay. Moreover, the survival analysis also suggested that

if favourable epidemiological and meteorological conditions favourable to brown rot development during storage occur at harvest, a low temperature storage should be envisaged to avoid massive fruit loss during storage. Eventually, the model could be used to calculate the expected time-to-appearance of visual symptoms of brown rot disease during storage for individual fruit (Collett, 2015), in order to assess the expected percentage of fruit loss due to brown rot disease for a defined storage length.

Supplementary Information

- **B.1** Results: brown rot secondary infections during storage
- **B.2** Results: cumulative incidence of brown rot disease at the end of storage, under different pre-harvest scenarios and storage conditions (2018-2019)
- **B.3** Survival analysis: model selection

Chapter 3

The synergy between pre-harvest practices and storage conditions to obtain high quality nectarines and to prevent brown rot losses during storage: a modeling framework

Authors

Enrico Casagrande[1,2], Michel Génard[2], Sébastien Lurol[1], Florence Charles[3], Pierre Valsesia[2], Mohamed-Mahmoud Memah[2], Françoise Lescourret[2]

[1] Centre Technique Interprofessionnel des Fruits et Légumes, 13210 Saint-Rémy-de-Provence, France.

[2] UR 1115 Plantes et Systèmes de Culture Horticoles, INRAE, 84914 Avignon Cedex, France.

[3] Avignon Université, UMR Qualisud, 84916 Avignon, France. Qualisud, Université de Montpellier, Avignon Université, CIRAD, Institut Agro, Université de La Réunion, Montpellier, France.

Résumé

Les domaines pré et le post-récolte sont rarement considérés ensemble dans les études sur la qualité des fruits et le développement des maladies, malgré les liens évidents entre ces deux stades de la vie des fruits. Afin de combler cette lacune, nous introduisons ici un nouveau cadre de modélisation pour simuler les effets de certaines des pratiques pré-récolte (régime d'irrigation et éclaircissage des fruits) et des conditions de stockage (température et humidité relative) sur le développement des caractéristiques de qualité des fruits pendant la saison de croissance et le stockage, le rendement et l'apparition de pourritures brunes pendant le stockage. Nous avons d'abord calculé un ensemble de critères de performance basés sur les sorties du modèle, afin de résumer le comportement du modèle en termes de qualité des fruits (taille du fruit et sucrosité), de rendement et de perte de fruits pendant le stockage (causée par une perte de masse excessive ou par des pourritures brunes). Nous avons ensuite effectué une analyse de sensibilité et réalisé des simulations de modèles pour étudier les relations entre les critères de performance et les pratiques pré-récolte ou les conditions de stockage. Les résultats ont montré que le régime d'irrigation et l'intensité de l'éclaircissage pesaient de façon significative sur la qualité des fruits, tandis que les conditions de stockage influençaient la perte de fruits pendant le stockage. Les interactions

entre les conditions de pré-récolte et de post-récolte se sont également avérées importantes pour les pertes liées aux pourriture brunes et le rendement en fruits à la fin du stockage. Nous avons finalement utilisé le modèle en combinaison avec un algorithme d'optimisation, afin de trouver les scénarios de pré- et post-récolte qui maximisaient la qualité et la quantité des fruits, agrégés en une valeur de performance unique, pour différentes durées de stockage et différentes séries d'importances relatives (poids) attribuées aux critères de qualité des fruits. L'importance accordée aux critères de qualité a largement influencé les résultats de l'optimisation. Les résultats ont également montré un antagonisme entre les critères de qualité, et en particulier la sucrosité, et le rendement des fruits. Le cadre de modélisation proposé a mis en évidence que les conditions pré- et post-récolte doivent être considérées ensemble car elles peuvent influencer à la fois la qualité et la quantité des fruits, y compris la perte de fruits. Par conséquent, le modèle pourrait être utilisé pour stimuler le dialogue entre les acteurs de la chaîne d'approvisionnement des fruits, et pour l'élaboration de scénarios de pratiques de pré-récolte et de conditions de stockage qui répondent à leurs attentes concernant l'état des fruits à la fin du stockage (avant les étapes d'emballage, d'expédition et de distribution).

Abstract

The pre- and post-harvest stages are rarely considered together in the studies of fruit quality and disease development, despite the evident connections between these two fruit life stages in terms of the underlying processes. In order to fill this gap, we introduce here a new modeling framework to simulate the effects of pre-harvest practices (irrigation regime and fruit thinning intensity) and storage conditions (temperature and relative humidity) on the development of fruit

quality traits during the growing season and storage, the fruit yield, and the appearance of brown rot infections during storage. The model was built and calibrated for the nectarine (*Prunus persica var. nucipersica*) case.

First, we developed a set of performance criteria based on model outputs, to summarize the model behaviour in terms of fruit quality (fruit size and sweetness), yield and fruit loss during storage (caused by excessive mass loss or brown rot infections). We then carried out a sensitivity analysis and performed model simulations to study the relationships between the performance criteria and pre-harvest practices and storage conditions. The results pointed out that irrigation regime and thinning intensity were significant in defining fruit quality traits, while storage conditions influenced the fruit loss during storage. The interactions between pre- and post-harvest conditions were also found to be important when considering the fruit loss related to the brown rot infections and the fruit yield at the end of storage.

We finally used the model in combination with an optimization algorithm, in order to retrieve the pre- and post-harvest scenarios that maximised fruit quality and quantity, aggregated into a unique performance score, calculated for different storage durations and relative importances assigned to fruit quality criteria. The importance assigned to quality criteria largely affected the optimization outcomes. The results also pointed out a trade-off between quality criteria, and in particular sweetness, and the fruit yield.

The proposed modeling framework highlighted that the pre- and post-harvest conditions should be considered together because they can influence both fruit quality and quantity, including also fruit loss. Therefore, it could be used as a supporting tool for the dialogue between the fruit supply-chain actors, and for the building of scenarios of pre-harvest practices and storage conditions that satisfy their expectations relative to the fruit state at the end of storage (before

packing, shipping, and distribution stages).

3.1 Introduction

In the fruit market, consumers have become increasingly aware of fruit quality (Fearne et al., 2006), paying particular attention to the fruit appearance and internal quality (Berna et al., 2005). Fruit producers are trying to follow consumer preferences, which could be in conflict with their own interests: i.e. there is a trade-off between harvested quantity and fruit quality (Bevacqua et al., 2019). In addition, different satisfaction criteria are considered by different actors in the food system, but these criteria have rarely been included in a unified framework (Sloof et al., 1996; Tijskens and van Kooten, 2006).

In the case of peach, two of the most important quality attributes are fruit size and sugar concentration (Byrne et al., 2019; Cirilli et al., 2016). These attributes are built during fruit growth and are strongly influenced by agricultural practices (Minas et al., 2018). On the one hand, the irrigation regime during the growing season is the major driver of tree and fruit water status (Fishman and Génard, 1998; Qian and Mahdi, 2020). It also impacts the dynamics of fruit sugars, the concentrations of which generally increase during the last stage before harvest (Ripoll et al., 2014). On the other hand, fruit thinning influences the carbon status and transport inside the plant, increasing or decreasing the competition for resources between growing fruit and other plant organs (Grossman and DeJong, 1995; Lopresti et al., 2014). Thinning intensity is positively correlated to peach fruit size (Inglese et al., 2002) and soluble solids accumulation (i.e. fruit dry mass) in the fruit pulp (Intrigliolo and Castel, 2010).

However, consumers rarely have direct access to the product soon after the harvest, and producers or wholesalers are forced to store fruit for a certain amount of

time (Parajuli et al., 2019). During this post-harvest stage, fruit quality-related attributes change under the influence of storage conditions: transpiration and respiration enhance fruit mass loss, mainly under the effect of storage temperature and relative humidity (Ben-Yehoshua and Rodov, 2002; Bovi et al., 2018), while sugar concentrations continue to evolve into fruit pulp (Casagrande et al., 2021).

The problem of fruit waste and loss during storage adds another degree of complexity to this frame (Porat et al., 2018). Consumers can judge excessive fruit shrinkage or softening during post-harvest stage as unacceptable, and this makes fruit unmarketable and generates food waste (Nunes and Emond, 2007; Crisosto, 1994). Indeed, fruit remain acceptable after harvest only for a certain period of time (shelf life) depending on many limiting criteria (e.g. colour, firmness, etc.). The length of this period depends on storage conditions (Sousa Gallagher and Mahajan, 2011; Tijskens and Polderdijk, 1996). Fungal infections such as those caused by *Monilinia* spp. in stone fruit (Martini and Mari, 2014) hit fruit in the pre-harvest stage but they occur particularly in the post- harvest stage, with a notable incidence for the post-harvest actors (Bautista-Baños, 2014). The infection probability depends both upon fruit characteristics at harvest (Gibert et al., 2009) and storage conditions (Garcia-Benitez et al., 2020; Bernat et al., 2017a).

In this context, knowledge must be integrated in a framework which bridges the fruit pre- and post-harvest stages (Tijskens and Schouten, 2014). Mathematical modeling can be helpful for this purpose. It could allow to explore how fruit quality-related attributes and fruit losses due to fungal disease infections are impacted by the pre-harvest practices and the storage conditions. In addition, models allow to formulate and simulate different quality criteria for different fruit supply chain actors, as well as the yield for the producers. Few models

have been built that take into account the effect of pre-harvest practices (i.e. the agricultural practices) such as irrigation and thinning on the development of individual fruit quality attributes during the growing season. In the case of peach, the L-PEACH model developed by Allen et al. (2005) simulates the plant functioning and growth of individual organs, but the model does not account for sugar development. The QualiTree model (Lescourret et al., 2011) allows the simulation of important attributes such as sugar concentrations and also fruit surface conductance to water vapour, which influence fruit water loss during storage (Maguire et al., 1999). Furthermore, QualiTree explicitly considers the effect of horticultural practices and seasonal meteorology on the development of individual fruit characteristics during the growing season at the tree scale. On the other side, different models have been developed for the simulation of post-harvest evolution of fruit quality-related attributes under different fruit initial and storage conditions (Hertog, 2002; Tijskens and Schouten, 2014; Schouten et al., 2004). However, to our knowledge, there is no available model considering at the same time the effects of pre-harvest practices and storage conditions. Regarding the brown rot disease in peach, models predicting the appearance of brown rot symptoms at different storage conditions exist (Garcia-Benitez et al., 2020; Bernat et al., 2017a; Gell et al., 2008), but only the model described in Chapter 2 is able to integrate the effects of pre-harvest factors and storage conditions on this process.

The objective of the study was to build and use a modeling framework integrating the effects of both pre-harvest practices and storage conditions on the development of peach quality attributes and brown rot infections during storage. The model was built for nectarine (*Prunus persica var. nucipersica*), and it was calibrated in the case of a mid-season cultivar (i.e. 'Nectarlove'). The framework was then used to search for the scenarios of pre-harvest practices and

storage conditions that result in the best profile of fruit quality characteristics and yield.

To attain these objectives, we first integrated a pre-harvest model, QualiTree, and two post-harvest models, presented in the Chapter 1 and Chapter 2 of the thesis. The first post-harvest model is able to simulate the fruit mass loss and sugar dynamics under different storage conditions. The second post-harvest model allows to predict the expected time of appearance of brown rot symptoms during storage, based on the value of several pre- and post-harvest covariates. Second, we tested the sensitivity of the model outputs to the pre-harvest practices and the storage conditions. We finally searched for the combinations of pre- and post-harvest management variables that result in the optimal value of an aggregated objective, which includes the fruit quality profile, the fruit yield and the aptitude to storage.

3.2 Modeling framework

The proposed modeling framework (Figure 3.1) combines process-based and statistical approaches. The entire model runs at a daily scale after full bloom date, until the end of the post-harvest fruit storage. The framework includes a pre-harvest stage, with the simulation of the fruit characteristics under the influence of horticultural practices during the growing season, and a post-harvest storage stage, where fruit are submitted to various storage conditions. The framework simulates the progress of brown rot disease incidence during storage, by estimating the mean time-to-appearance of brown rot symptoms during storage.

The QualiTree model simulates, at the tree scale, the seasonal dynamics of mass, sugar concentrations and surface conductance to water vapour for fruit of each fruiting unit (Lescourret et al., 2011; Mirás-Avalos et al., 2011), by explicitly

considering the effects of horticultural practices (irrigation regime, fruit thinning and pruning) and meteorological conditions (See Section 3.2.1).

At harvest, the simulated values of the fruit properties are used in turn as inputs of two post-harvest models. The first post-harvest model simulates the fruit mass loss (through the processes of transpiration and respiration) and sugar dynamics during storage (Casagrande et al., 2021). More details on this model are given in Section 3.2.2. The second post-harvest model evaluates the expected time-to-appearance of brown rot symptoms of nectarine during storage under the influence of pre-harvest conditions and storage temperature (See Section 3.2.3 for more details). The outputs of these two post-harvest models are the fruit fresh mass, the mass loss during storage, the concentration of each sugar inside the fruit pulp, and the expected time of appearance of brown rot symptoms during storage.

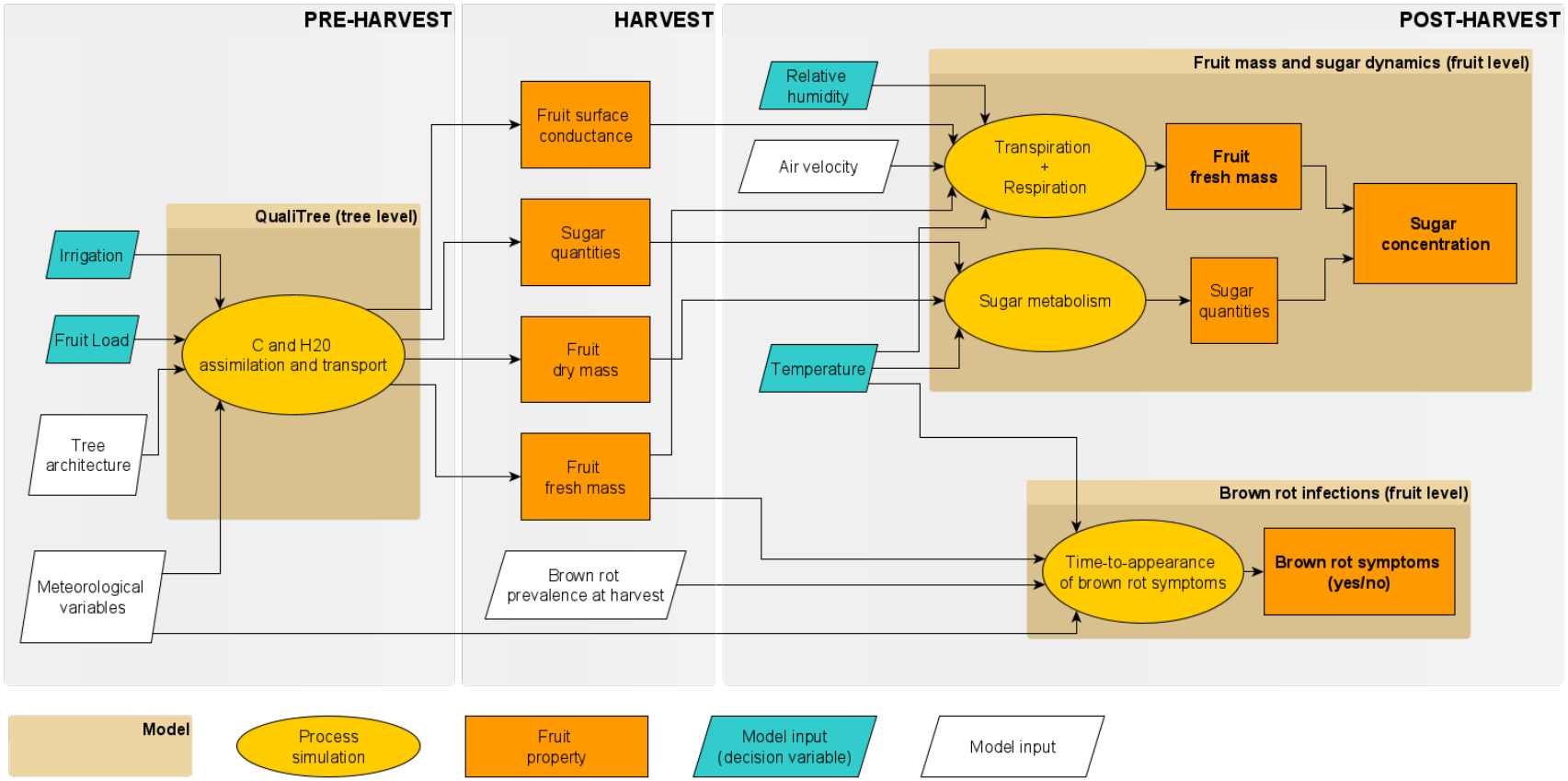

Figure 3.1 – Diagram of processes and fruit properties considered in the modeling framework to simulate the effect of pre-harvest practices and storage conditions on nectarine quality and brown rot infections during storage.

3.2.1 Modeling the development of fruit quality-related characteristics during the growing season: QualiTree

The QualiTree model runs on a daily basis, from bloom until the end of the fruit growing season. The model describes the tree as a set of interacting objects: fruiting units (composed of fruit, leafy shoots and stem wood), old wood (trunk and branches), coarse roots, and fine roots. All these objects are represented in a 3D tree architecture, which is a model input. The model uses a source-sink approach to simulate the growth of the tree parts in terms of dry masses. This includes carbon assimilation (photosynthesis), growth demands, allocation rules and exchanges within the tree. The effects of water stress on photosynthesis and leafy shoots growth and the accumulation of water into the fruit are also simulated by the model. QualiTree calculates the water status and water flow in the plant, which are important for the above-mentioned processes (Fishman and Génard, 1998; Rahmati et al., 2018). The boundary conditions for plant water status are fixed at the root collar through the hourly water potential $\Psi_{r,hourly}$. The hourly water potential is given as model input, reflecting the combined effect of rainfall and irrigation regimes during the growing season.

QualiTree simulates, at the fruiting unit level and during the growing season, the time course of several fruit quality-related traits, such as fruit size, dry mass proportion in fruit flesh, sugars concentrations and fruit surface conductance. Individual sugar concentrations were aggregated into a sweetness index for each fruit, as a linear combination of sugar concentrations based on the sweetness rating for each sugar relative to that of sucrose (Génard and Souty, 1996; Kulp et al., 1991). The simulated fruit masses were also used to calculate the caliber grade for each singular fruit, based on the international standards by the OECD

(2010). The classification of fruit into size classes allows to select at harvest which fruit are of marketable size or not, discarding too small or too big fruit (Plénet et al., 2009).

3.2.2 Modeling fruit mass and sugars dynamics during storage

This model is originally composed of two sub-models, which represent the process of fruit mass loss, due to transpiration and respiration, and the dynamics of sugar concentrations in the fruit fresh pulp during storage, respectively, as presented in Casagrande et al. (2021) (Chapter 1). The model is deterministic and runs at a daily scale. It can easily be connected with the pre-harvest model i.e. it can accept as inputs some outputs of the QualiTree model.
The storage temperature is a driving force of these two sub-models. Transpiration is also highly dependent on relative humidity and on air velocity next to fruit surface, which are considered in the fruit mass loss sub-model. The daily values of these storage conditions are given as inputs to the model.

3.2.3 Modeling the time-to-appearance of brown rot symptoms on fruit during storage

This model was introduced in the Chapter 2 of the thesis. It made use of the survival analysis, which is a statistical technique, to predict the fruit individual survival probability $Surv_i(t_S)$. This is the probability that individual fruit i does not show visual symptoms of brown rot infection by *Monilinia* spp. during the time elapsed since the beginning of storage (t_S, in days). $Surv_i(t_S)$ is calculated as a function of fruit individual characteristics at harvest (individual fruit mass), of epidemiological (prevalence of brown rot in the orchard at harvest)

and meteorological (mean wetness duration in the week before harvest) conditions, and average of the storage temperature. The individual expected time of appearance of brown rot infection symptoms during storage (μ_i, days) could be calculated as the integral of the survival function:

$$\mu_i = \int_0^{\infty} Surv_i(t_S)\, dt_S \tag{3.1}$$

3.3 Materials and Methods

3.3.1 Scenarios of pre-harvest practices and storage conditions

For the pre-harvest period, we considered several virtual irrigation regimes and fruit load scenarios. Irrigation scenarios were set-up by dividing the simulation period, i.e. the fruit growing season, into three periods p=$\{I, II, III\}$ corresponding to the last part of pit hardening stage (I, 66–80 days after full bloom, dafb), the initial (II, i.e. 81–101 dafb) and the final stage of fruit exponential growth (III, 102–124 dafb) for the nectarine cultivar considered in this study (cv 'Nectarlove'). For each period, we combined three different levels of water stress, namely a low, a medium and a high one. We thus derived a total of 27 irrigation scenarios (presented in Appendix C.1). Each water stress level was determined by a unique combination of maximum and minimum diurnal water potential at the root collar (Ψ, MPa), with the maximum assumed to happen before dawn, and the minimum at midday. Hourly values of water potential were then derived assuming a sinusoidal daily variation, with an amplitude determined by the minimum and maximum water potential. The values for the three levels were estimated (Table 3.1) with data from 2018 and 2019 experimental

seasons (data not shown).

Irrigation level	diurnal water potential (MPa)		
	minimum	maximum	mean
low stress (LS)	-0.8	-0.5	-0.65
moderate stress (MS)	-1.4	-0.7	-1.05
high stress (HS)	-2.0	-1.1	-1.55

Table 3.1 – Irrigation levels in each of the selected nectarine developmental periods and corresponding values of diurnal water potential.

To differentiate the irrigation scenarios in terms of water stress intensity, we used the water stress integral indicator WS_Ψ (Myers, 1988):

$$WS_\Psi = \mid \sum_{p=1:3} (\Psi_{min,p} - c) \cdot n_p \mid \tag{3.2}$$

where $\Psi_{min,p}$ (MPa) is the average value of minimum water potential at the root collar for each considered developmental period p, c (MPa) is the maximum of Ψ_{min} during the entire season (-0.8 in our case) and n_p is the number of days for each considered developmental period. The higher the value of the indicator is, the higher is the water stress to which tree is submitted during the simulation period. For crop load, expressed as the number of fruit left on the tree at the thinning date (N_f), we considered 41 levels from 200 to 600 fruits per tree (evolving by tens). The combinations of the different levels of crop load and irrigation scenarios resulted in 1107 agronomic scenarios.

For the post-harvest period, we considered 24 levels of average storage temperatures ($Temp_S$), 8 levels of average relative humidity values (RH_S) and 11 levels of storage duration ($t_{S,end}$). We assumed that, for each storage scenario, fruit were left for the first two days at 2 °C, in order to cool down the product. Management scenarios for the modeling framework were then constructed by considering each possible combination of pre-harvest practices and storage conditions (Table 3.2).

Management practice	Related variable			Range
Pre-harvest practices				
Irrigation	Water stress integral	WS_{Ψ}	MPa days	[0, 66]
Thinning	Number of fruit left on the tree at thinning	N_f	-	[200, 600]
Storage conditions				
Temperature	Mean daily temperature	$Temp_S$	°C	[2, 25]
Relative humidity	Mean daily relative humidity	RH_S	%	[60, 95]
Storage duration		$t_{S,end}$	days	[5, 15]

Table 3.2 – Pre-harvest practices and storage conditions considered in the study.

3.3.2 Model parameters and inputs

Model parameter values and inputs for the pre-harvest stage were retrieved from experimental data collected during the 2018 growing season in the INRAE Avignon (France) experimental orchard on nectarine (cultivar 'Nectarlove'). Full bloom was observed on 17 March and simulation start was set at the thinning date (66 days after full bloom, dafb). For tree architecture, we selected a tree representative of the training system of the orchard (double-Y training system, see Figure C.2 in Appendix C.2). The volume of the trunk, branches and stem were calculated considering them as conic-section structures. Volumes were then transformed into biomass using a wood-density value of 0.77 g cm^{-3}, as in Mirás-Avalos et al. (2011).

Some parameters concerning the carbon and water economy in QualiTree depend on the cultivar (Mirás-Avalos et al., 2011). They were thus specifically calibrated for the nectarine case. Some parameter values were estimated using different sub-models of QualiTree separately, while others were calibrated

directly through QualiTree simulations. The calibration procedures and the parameter values estimated for this study are presented in Appendix C.2.

Simulation inputs related to pre-harvest conditions were retrieved from experimental observations, except for the irrigation regime and the thinning intensity scenarios (Section 3.3.1) . The initial values for leafy shoot and fruit dry masses were randomly extracted from observations at the thinning date and distributed in the tree architecture (66 dafb), while for fruit sugar concentrations (sucrose, fructose, glucose, and sorbitol) we considered the average of observed values. Initial carbon reserves for tree organs were retrieved from Mirás-Avalos et al. (2011). The harvest date (t_H) was fixed as that of the observed commercial maturity in the orchard ($t_H = 124$ dafb). For meteorological variables, we used the 2018 values recorded daily by the INRAE meteorological station close to the experimental field. The same data were used to calculate the mean wetness duration in the week before harvest ($wd_{mean,h} = 3.26$ h at the considered harvest date), which is an input of the model of brown rot during storage. Another input of this sub-model is the prevalence of brown rot at harvest (I_H, %), calculated as the ratio between the fruit which at harvest show visual symptoms of brown rot and the total harvested fruit. This variable can be controlled by the fruit grower through fungicide treatments before harvest and also through agricultural practices (Bellingeri et al., 2018). However, we needed to fix the value of this variable because we did not find any explicit mathematical relationship expressing this control at the fruit scale. We fixed this value at the highest brown rot prevalence at harvest observed in 2018 ($I_H = 2.41$ %, see Chapter 2). For the sake of simplicity, we assumed that brown rot during the growing stage affected the fruit yield only at harvest. This means that a percentage of fruit equal to the brown rot prevalence at harvest was discarded at harvest. Starting from the hypotheses that the higher the surface area of cuticular crack is, the

higher the probability of infection is (Gibert et al., 2009), we discarded those fruit with the highest value of cuticular crack surface area at harvest.

Finally, for the post-harvest sub-model of fruit quality, we selected a daily average air velocity next to fruit surface during storage (v_S) of 0.4 m s^{-1}, which is generally the minimum threshold value detected by portable anemometers.

3.3.3 Performance criteria

From the modeling framework outputs, we defined six performance criteria related to fruit quality, fruit loss and net production per tree at the end of storage. In terms of fruit quality, we calculated the mean individual fruit mass $Q_{S,mass}$, (g) and sweetness index $Q_{S,sweet}$ (g kg^{-1}) at the end of storage. We considered the mean relative mass loss during storage $L_{S,mass}$ (%), i.e. the mean of individual mass losses relative to the fruit fresh mass at harvest. We also made the hypotheses that a loss of acceptance by consumers can take place under an excessive mass loss, which can lead to visual shriveling and excessive firmness loss (Ben-Yehoshua and Rodov, 2002). We used the threshold of 6% (Nunes and Emond, 2007) to reject a fruit as unmarketable because of excessive mass loss. We also calculated the percentage of cumulative fruit loss at the end of storage due to brown rot infections $L_{S,br}$ (%). We assumed that a fruit showed visual symptoms of brown rot infection when the expected time of visual infection was lower than the time since the beginning of storage ($\mu_i < t_s$). We thus calculated the criterion as the ratio between the number of cumulated infected fruit at the end of storage and the total number of harvested fruit.

The net production per tree was finally assessed as the total yield (Y_S) and the marketable yield (MY_S) at the end of storage. Y_S (kg $tree^{-1}$) was calculated on fruit without brown rot or excessive mass loss, and MY_S (kg $tree^{-1}$) was calculated as the previous one, but including only fruit of marketable size. Only the

fruit above the D grade and below the 4A grade were considered as marketable (based on personal communication, CTIFL).

3.3.4 Sensitivity analysis of performance criteria to pre-harvest practices and storage conditions

A sensitivity analysis was then performed to test the effect of the pre-harvest practices and storage conditions on the performance criteria calculated through the modeling framework. The brown rot prevalence at harvest (I_h) was added as a covariate as it can be influenced by agricultural practices and has a strong influence on the appearance of brown rot disease during storage (see Section 3.3.2).

The variance-based sensitivity indices were calculated using the extended FAST methodology (Saltelli et al., 1999), implemented in R via the 'fast99' function (from *sensitivity* package, Iooss et al. (2020)), using n=1500. For each performance criterion, the methodology calculates the proportion of output variance that is explained by the variation of each variable (main effect), as well as the interaction of the variable with the others (interaction effect). The first-order indices (S_j) measure the main effect of a covariate j on the output of interest. The sum of the main effect and the interaction effects ($S_{int,j}$) for each factor gives the total-order index ($S_{T,j}$), which identifies the total part of output variable in which the factor takes part (Qian and Mahdi, 2020; Makowski et al., 2006). A factor was considered to have an influential effect on the variance of a criterion when the total-order index was larger than 0.1 (Makowski et al., 2006). The boundaries of the management practices used in this analysis are presented in Table 3.2, while I_H was considered as ranging from 0 to 5%.

To visualize the effects of pre- and post-harvest factors on each performance

criterion and the direction of these effects beyond variance-based sensitivity indices, we then selected 4 levels for each of the factors presented in Table 3.2 and performed a total of 1024 simulations (combining all the selected level for each factor). I_H was not considered in this analysis.

3.3.5 Search for the combined pre- and post-harvest scenario offering the best compromise in terms of fruit quality and quantity at the end of storage

We assumed that fruit growers and packers (post-harvest actors) act as a unique actor, who aims to maximize the fruit marketable yield and quality at the end of storage. The identification of the scenarios of pre-harvest practices and storage conditions that meet these objectives can be seen as an optimization problem involving multiple antagonist objectives (multi-objective optimization problem). The hypothesis that fruit have a value that is determined by the quality criteria involved - in this case, fruit size and sweetness - could help to combine the quality-related objectives and the fruit yield into a unique score, and thus reduce the optimization problem to a single objective. This could be useful to obtain a formal solution. This value makes a lot of sense for fruit growers and wholesalers. It should be noted that it may vary according to the importance given by different types of consumers to the quality criteria (Bevacqua et al., 2019; Segura et al., 2020). Multiple quality criteria can be integrated by expressing the overall value of each unit of fruit (Segura et al., 2020) as a linear combination of the utility scores, which evaluate the degree of consumer satisfaction, and the importance (weight) assigned to each selected fruit quality criterion (Keeney and Raiffa, 1993). This firstly requires to define a utility function for each selected trait on a unitary scale, to express the fruit value associated to a

quality trait. The relationship $u(q)$ between a quality trait and fruit value was expressed through a logistic function as in Bevacqua et al. (2019):

$$u(q) = (1 + e^{\eta_q(\lambda_q - q)})^{-1} \tag{3.3}$$

where q is the fruit mass (m, g) or the sweetness index (s, g kg^{-1}), η_q is the consumer sensitivity to variable q, and λ_q is a semi-saturation value for variable q. Utility function parameters (Table 3.3) for fruit mass were calibrated using nectarine market data by the FranceAgriMer network for the 2018 fruit market in France (FranceAgriMer, 2019), considering a 50% satisfaction for B grade nectarines (105 g), 75% for A grade nectarines (135 g), and a complete satisfaction for 2A grade nectarines (180 g). For the sweetness index we considered the same utility values for sweetness indexes of 70 g kg^{-1}, 85 g kg^{-1} and 120 g kg^{-1} (Figure 3.2).

Quality related attribute (q)	**Parameters**	
	η_q	λ_q
Fruit mass m (g)	0.042	106
Fruit sweetness index s (g kg^{-1})	0.077	70

Table 3.3 – Utility function parameters for the fruit quality-related attributes.

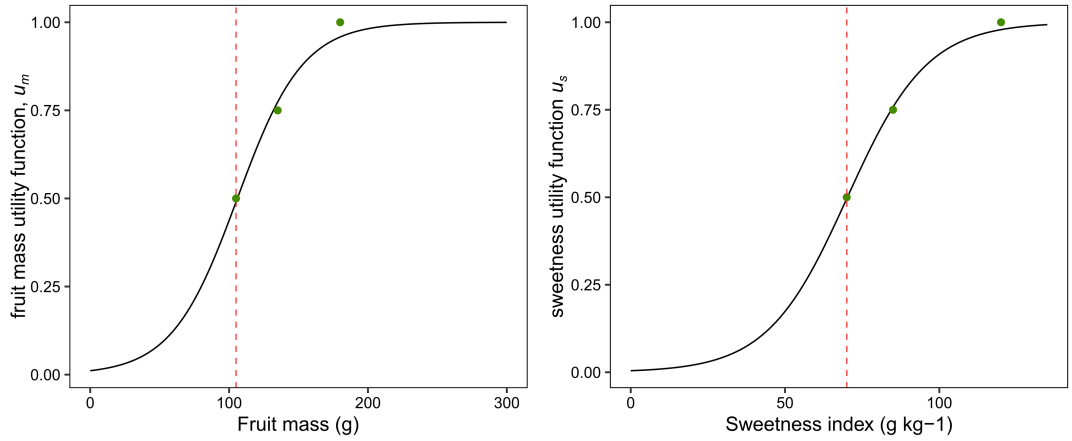

Figure 3.2 – Utility functions for fruit mass and sweetness used in this study. The red dashed lines represent the value of the fruit quality trait that correspond to a satisfaction of 50%. Points represent the couples of utility values and fruit traits used for parameter calibrations.

The relative importance of each quality-related attribute was expressed by the value of a weight ω_q, with $\sum_q \omega_q = 1$.

The value U_i (VU/kg, where VU is a value unit) for a singular fruit i was calculated at the end of storage as:

$$U_i(m, s) = u(m_i) \cdot \omega_m + u(s_i) \cdot \omega_s = u(m_i) \cdot \omega_m + u(s_i) \cdot (1 - \omega_m) \tag{3.4}$$

Finally the performance score at the tree scale under the combination of agricultural practices and storage condition PS (VU), for a certain storage duration $t_{S,end}$, was computed as:

$$PS(\, WS_\Psi, N_f, Temp_S, RH_S, \omega_s\,) = \sum_{i=1}^{N_f^*} (m_i \cdot 10^{-3}) \cdot U_i \tag{3.5}$$

where N_f^* identifies the fruit which are marketable at the end of storage. This includes the fruit of marketable fruit size minus the fruit loss due to the appearance of brown rot symptoms and the excessive mass loss during storage. 6% of individual fruit relative mass loss is a threshold above which fruit can show fruit shriveling and can reach an unacceptable firmness value (Crisosto and Day,

2012; Nunes and Emond, 2007), so that we used this threshold to reject a fruit as unmarketable for excessive mass loss.

In this study, we searched for the combination of agricultural practices and storage conditions that maximize the performance score, under three different storage durations: $t_{S,end}$={5, 10, 15 days}. Moreover, by using different values of ω_m (0.25, 0.50, 0.75, 1), we tested the effect of changes in the importance assigned to fruit mass and sweetness index on the performance score and on the choice of the optimal scenario. The optimization problems were solved through a genetic algorithm through the 'ga' function from the *GA* package (Scrucca, 2013), in R software, with a population of 50 solutions for a maximum of 150 iterations.

3.4 Results

3.4.1 Effects of pre-harvest practices and storage conditions on the performance criteria based on model outputs

The results of the sensitivity analysis of the six performance criteria based on model outputs highlighted the effects of interactions between pre-harvest and storage conditions on these performance criteria (Figure 3.3). The pre-harvest practices, and in particular the irrigation regime, influenced the most the variance of the mean fruit mass and sweetness at the end of storage. The cumulative main effects of irrigation and fruit load explained up to 92% of the variance of the mean fruit mass at the end of storage (without considering the interaction effects), while irrigation alone was able to explain almost 90% of the variance of the fruit sweetness index at the end of storage. When considering the in-

teraction effect, 97% of the variance of the mean fruit sweetness at the end of storage could be explained by a variation in irrigation scenario (S_{T,WS_Ψ}=0.97). The effects of storage conditions was thus negligible for these performance criteria. However, the mean relative mass loss during storage was mostly influenced by storage management variables (relative humidity, storage duration and temperature), showing a cumulative sensitivity index related to the main effect of about 82%, principally by relative humidity (31%) and storage duration (29%). Storage conditions showed also a major effect on the performance criteria related to fruit loss from brown rot disease during storage. The interactions terms of sensitivity indices were higher than those of the previous performance criteria, suggesting a high importance of the interactions between pre-harvest practices and storage conditions on fruit loss due to brown rot. For fruit loss related to the appearance of brown rot symptoms ($L_{S,mass}$), all the considered factors except the relative humidity were significant, in particular the prevalence of brown rot at harvest, the storage duration and the storage temperature. The interaction effects were important for all the significant variables (22%, on average). For the total yield at the end of storage (Y_S), all the considered pre-harvest and storage factors were significant, with the latter that turned out to be the most important factors. Storage duration was the most important factor (49%), followed by temperature (39%) and relative humidity (29%) during storage. Finally, for the marketable yield at the end of storage (MY_S), all the factors turned out to be significant, but in this case the irrigation regime was the most important variable (46%), followed by storage conditions.

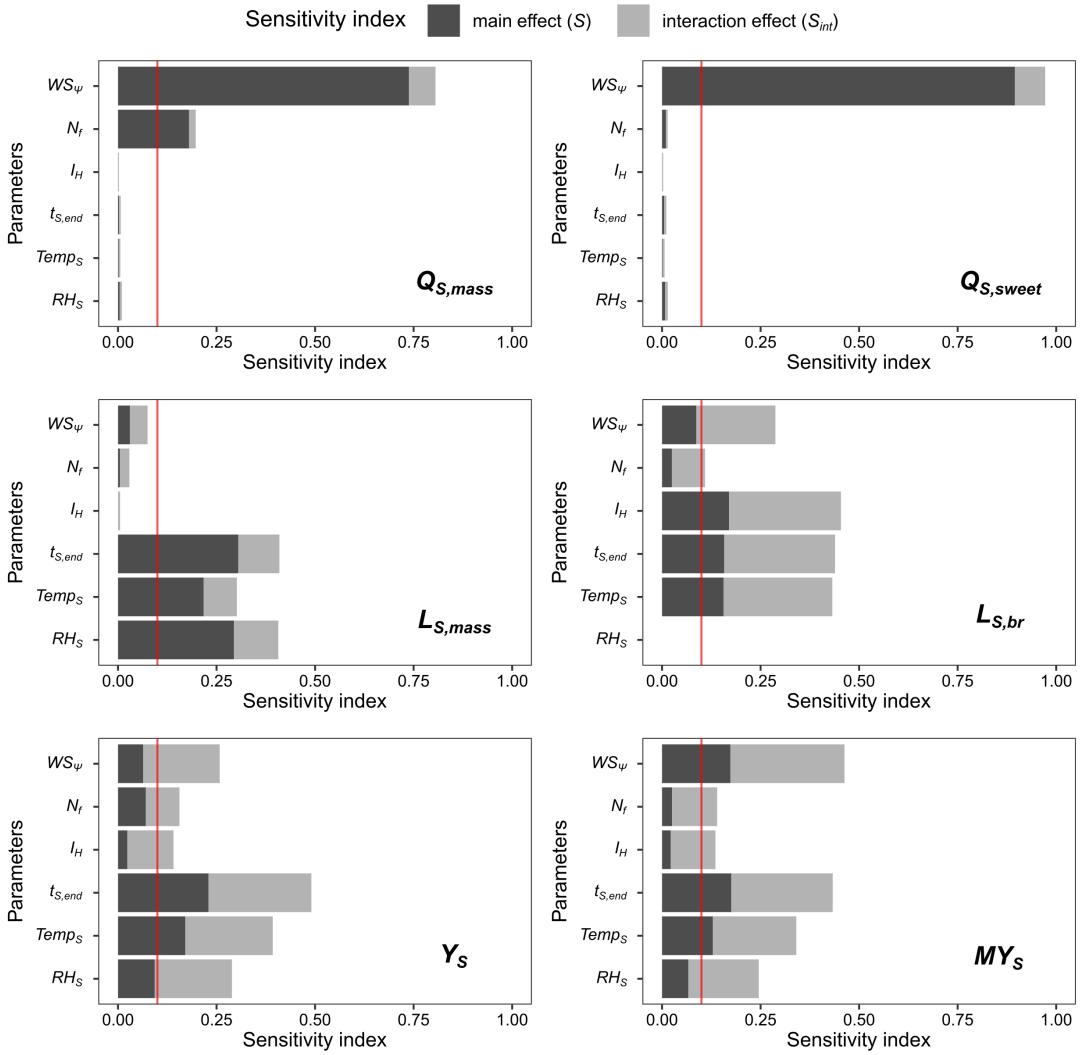

Figure 3.3 – Sensitivity index for the performance criteria based on model outputs, according to the five pre- and post-harvest management practices and the prevalence of brown rot at harvest (I_H). The performance criteria are referred to the end of storage and are the fruit mean mass ($Q_{S,mass}$), sweetness index ($Q_{S,sweet}$) and relative mass loss ($L_{S,mass}$), the fruit loss related to the appearance of brown rot symptoms ($L_{S,br}$), and the total (Y_S) and marketable yield (MY_S). The indices reflect the importance of each parameter on the variance of the considered output (main effect) and the strength of interaction with the other parameters (interaction). The red line identifies the threshold of the total effect index (S_T) above which a factor has significant influence on the variance of the considered performance criterion ($S_T > 0.1$).

For the model exploration (Figure 3.4), we selected only the factors that turned out to be influential in the sensitivity analysis ($S_T > 0.1$). The increase in water stress cumulated along the simulation period (increase in WS_Ψ) decreased, on average, the mean fruit mass and increased the mean fruit sweetness index at the end of storage (Figure 3.4a-b). However, this relationship was not uniform, but depended strongly on the intensity of the water stress in the last stage of fruit growth ($p = III$): specifically, a well-irrigated regime in this period (WS_Ψ=0 and 42 MPa, representative of the scenarios n° 1 and 9, detailed in Table C.1 in Appendix C.1) resulted in less sweet and bigger fruit with respect to the scenarios under the medium-stressed (WS_Ψ=21 MPa, scenario n° 11) and the high-stressed regime (WS_Ψ=57 MPa, scenario n° 26). A decrease in thinning intensity (increase in N_f) was instead related to a decrease in the mean fruit mass.

Storage conditions greatly influenced the relative mass loss during storage (Figure 3.4c), which increased when the mean storage temperature and storage duration increased, and decreased when the mean relative humidity during storage increased. Simulation results also showed that loss related to the appearance of brown rot visual symptoms during storage was the highest under well-irrigated conditions during the last stage of fruit growth (WS_Ψ=0 and 42 MPa) and strong fruit thinning, while also increasing when storage temperature and storage duration increased (Figure 3.4d).

Despite high losses due to excessive mass loss and to brown rot, simulations under the scenarios with no water stress in the last stage of fruit growth (WS_Ψ=0 and 42 MPa) showed a high yield (total and marketable, Figure 3.4e-f). The highest values for these performance criteria were also observed for low fruit thinning intensity and under low temperatures, high relative humidity and short storage duration. Moreover, the presence of water-stress in the stage I and II

of fruit growth (WS_{Ψ}=42 MPa, scenario n° 9) did not impact yield, which is not significantly different from that simulated in the case of good irrigation during these fruit growing stages (WS_{Ψ}=0 MPa, scenario n° 1).

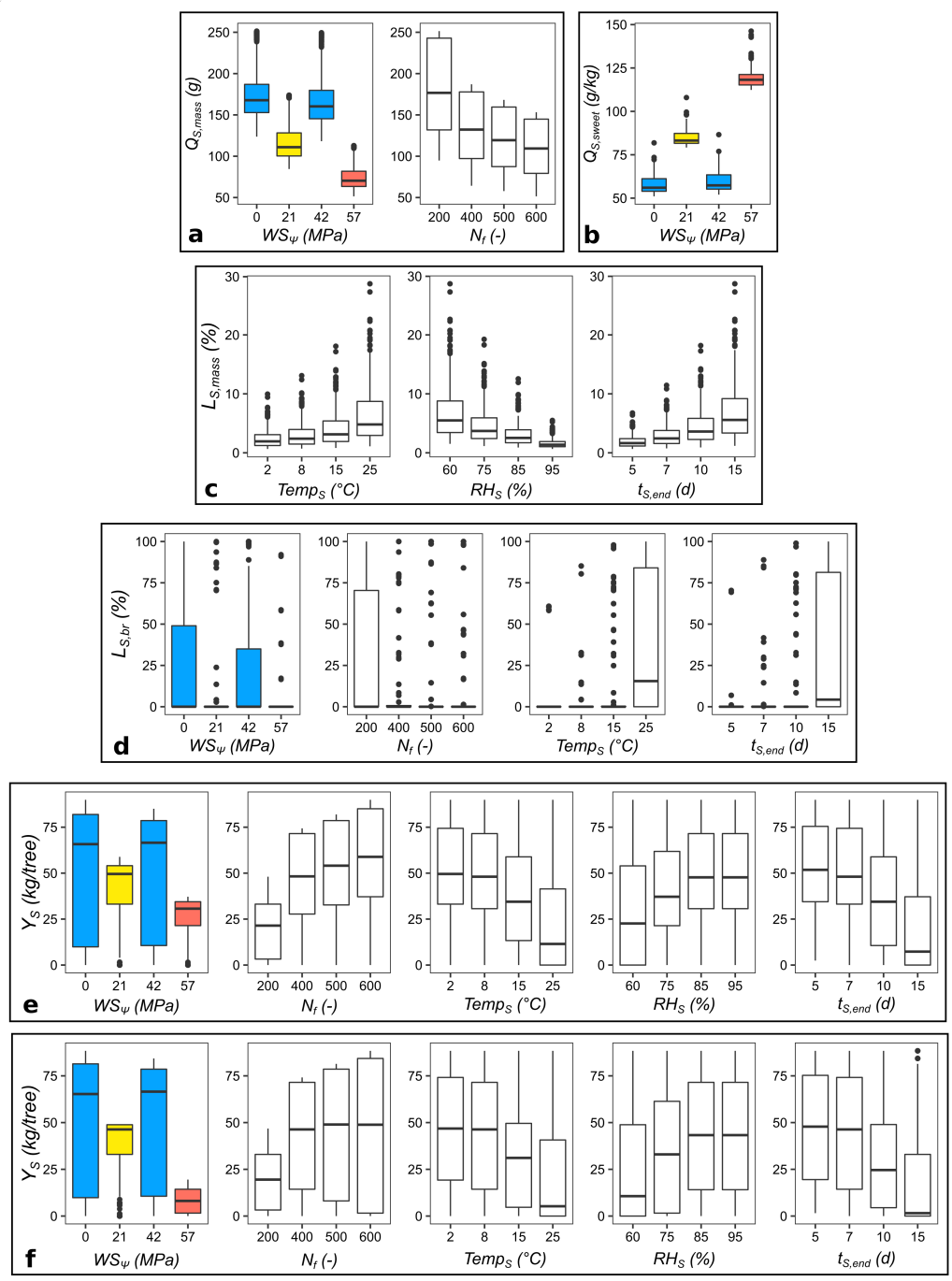

Figure 3.4 – Simulated effects of pre-harvest practices and storage conditions on the performance criteria based on model outputs. Boxes represent the first and third quantiles (25% and 75%) and the median of 256 simulated replicates of each treatment. The performance criteria are referred to the end of storage and are the fruit mean mass ($Q_{S,mass}$, a), sweetness index ($Q_{S,sweet}$, b), the relative mass loss ($L_{S,mass}$, c), the fruit loss related to the appearance of brown rot symptoms ($L_{S,br}$, d), and the total (Y_S, e) and marketable yield (MY_S, f). The water stress integral values correspond to the irrigation regime scenarios n° 1 (WS_Ψ=0), 11 (WS_Ψ=21), 9 (WS_Ψ=42) and 26 (WS_Ψ=57, Appendix C.1). Colours correspond to the simulated water regimes during the last stage of fruit growth ($p = III$): well-irrigated (blue), mid-stressed (yellow), and high-stressed (red).

3.4.2 Storage duration and importance of fruit quality criteria influence the pre- and post-harvest scenarios in terms of the optimal performance score

The scenarios of pre-harvest practices and storage conditions that maximized the performance score greatly varied with the storage duration and the relative importance of the fruit quality criteria (Table 3.4). In general, the optimization showed that an increase in storage duration needs to be supported by a decrease in storage temperature and an increase in relative humidity, in order to avoid fruit losses related to excessive mass loss and to prevent the appearance of brown rot symptoms.

When the importance of the fruit sweetness index was high (ω_s=1 and 0.75), the selected scenarios were characterized by a moderate water deficit in the last stage of the growing season ($\Psi_{min,III}$=-1.4 MPa, scenarios n° 10 and 12 in Table C.1) and a low to medium thinning intensity (from N_f=400 to 570 fruits per tree). The mean fruit sweetness was the highest (Q_{sweet}= 84.8 g kg^{-1}, on average), but at the expense of the value of mean fruit mass (Q_{mass}=107 g). In these cases, relative humidity values were the lowest, because these conditions enhanced fruit transpiration, which is responsible for the increase in sugar concentrations (and thus sweetness) inside the fruit pulp during storage. Consequently, the average marketable yield was the lowest one (MY_S=48.4 kg tree^{-1}), and the difference between the marketable and total yield was the highest one, due to the presence of more fruit which did not attain the marketable size. The aggregated performance of the best scenarios increased with an increase in storage duration, because sugars concentrate into fruit pulp due to fruit mass loss.

In the other cases (ω_m=0.50 and above), the selected scenarios were instead characterized by well-irrigated regimes in the last stage of fruit growing season

($\Psi_{min,III}$=-0.8, scenarios n° 1 and 3) and a very low fruit thinning intensity (from N_f=570 to 600 fruits per tree). Mean fruit mass was higher than in the previous cases (Q_{mass}=152 g), but at the expenses of sweetness (Q_{sweet}= 53.3 g kg^{-1} on average). These cases were marked by the lowest temperature (2 °C) and the highest relative humidity (95% RH) for all the considered storage durations. This is due to the fact that in these cases the objective was to minimize the fruit mass loss. When sweetness and fruit size had the same weight (ω_m=0.50 and ω_s=0.50), the best storage scenarios were characterized by an increasing relative humidity and a decreasing temperature when storage duration increased.

Storage duration (d)	Decision variables					Performance criteria					
	WS_Ψ (MPa days)	N_f (-)	$Temp_S$ (°C)	RH_S (%)	PS (VU)	Q_{mass} (g)	Q_{sweet} (g kg^{-1})	L_{mass} (%)	L_{br} (%)	Y_S (kg tree^{-1})	MY_S (kg tree^{-1})
ω_m=0, ω_s=1											
5	30 [12]	520	25	60	36.5	105.8	82.7	3.6	0	55.2	50
10	30 [12]	540	13	60	38.3	101.1	85.2	5.6	0	44.4	44.4
15	12 [10]	570	5	65	38.7	98.4	85.1	5.4	0	52.7	50.8
ω_m=0.25, ω_s=0.75											
5	30 [12]	400	25	60	35.2	121.3	84.6	3.9	0	49.8	47.3
10	12 [10]	490	14	65	35.9	107.6	85.1	5.4	0	50.1	48.7
15	30 [12]	480	7	70	36.2	108.6	86	5.4	0	52.1	49.3
ω_m=0.5, ω_s=0.5											
5	18 [3]	570	16	60	47.9	153.1	54	3.11	0	88	87
10	18 [3]	570	8	65	48.3	150	55.4	5	0	88	87
15	18 [3]	570	7	80	48.3	150.6	55.3	4.6	0	88	87
ω_m=0.75, ω_s=0.25											
5	0 [1]	600	2	95	62.3	153.3	52.2	0.8	0	90	88.4
10	0 [1]	600	2	95	62.3	152.8	52.6	1.1	0	90	88.4
15	0 [1]	600	2	95	62.3	152.3	52.9	1.4	0	90	88.4
ω_m=1, ω_s=0											
5	0 [1]	600	2	95	76.8	153.3	52.2	0.8	0	90	88.4
10	0 [1]	600	2	95	76.7	152.8	52.6	1.1	0	90	88.4
15	0 [1]	600	2	95	76.5	152.8	52.9	1.4	0	90	88.4

Table 3.4 – Pre-harvest practices (irrigation regime scenario in terms of water stress integral WS_Ψ and the number of fruit left on the tree at thinning N_f) and storage conditions (mean storage temperature $Temp_S$ and relative humidity RH_S) associated with the optimal scenarios in terms of the performance score PS, for different storage durations and relative importance accorded to fruit quality-related criteria (ω_m and ω_s, related to fruit mass and sweetness). For the irrigation regimes, the number of the associated irrigation scenario is also presented between squared brackets. For each optimal scenario, the values of the performance criteria are shown: the fruit mean mass ($Q_{S,mass}$), sweetness index ($Q_{S,sweet}$), the relative mass loss $L_{S,mass}$, the fruit loss related to the appearance of brown rot symptoms $L_{S,br}$, and the total (Y_S) and marketable (MY_S) yield at the end of storage.

3.5 Discussion

3.5.1 The modeling framework satisfactorily integrates the effects of pre-harvest practices and storage conditions on fruit quality development and fruit loss during storage

In this study, we designed a modeling framework to simulate, for each individual fruiting unit of a tree, the pre- and post-harvest temporal dynamics of fruit quality traits and the appearance of brown rot disease during storage, under the influence of pre-harvest practices and storage conditions. The model was conceived and calibrated for the case of nectarine, but it could be extended to the case of other fruits. To our knowledge, it is the first modeling framework facing these challenges.

The results from the sensitivity analysis and model exploration showed that fruit quality criteria at the end of the storage period are mainly influenced by pre-harvest practices, namely the irrigation regime during the growing season and the fruit load. A medium or high level of water stress in the last stage of fruit growth improved the mean fruit sweetness index, but at the expense of the fruit mean mass, as pointed out in several studies on peach (Crisosto, 1994; Alcobendas et al., 2012; Johnson and Handley, 2000). On the contrary, the application of water stress in the fruit growing stages that are not sensitive to water deprivation, such as the pit hardening one, did not impact the yield. This is in line with the findings on regulated deficit irrigation (Mirás-Avalos et al., 2016; Fereres and Soriano, 2007). The thinning intensity was shown instead to influence the mean fruit mass, probably by modifying the intensity of competition for carbon between fruit, as already pointed out by Grossman and DeJong

(1994) and Inglese et al. (2002) on peach, but it had no influence on the mean fruit sweetness at the end of storage. These results on pre-harvest practices were confirmed when searching for the pre- and post-harvest scenario offering the best compromise in terms of fruit quality and quantity. Water-stressed regimes and moderate fruit thinning were selected when the sweetness index was considered as the most important criterion, while the well-irrigated conditions during the last stage of fruit growth were preferred when fruit mass was the most important quality criterion.

The sensitivity analysis showed that pre-harvest practices, although they may change the fruit surface conductance to water vapour at harvest (Gibert et al., 2007), had no influence on the fruit mass loss during storage. This loss, which is a matter of concern since fruit could show signs of visual shriveling starting at 3-10% of mass loss (Ben-Yehoshua and Rodov, 2002), was principally related to storage conditions. The latter influence both the vapour pressure deficit, which is the main driver of fruit transpiration (Díaz-Pérez, 2019), and the fruit respiratory process (Xanthopoulos et al., 2017). In contrast, storage conditions had no influence on the mean sweetness of the fruit at the end of storage. However, during storage fruit sweetness can change under different storage conditions (Aubert et al., 2014; Brizzolara et al., 2018; Casagrande et al., 2021), but the effect of horticultural practices remained the most important factors in defining this quality trait.

The losses related to the appearance of brown rot during storage were particularly influenced by storage temperature, but also by the pre-harvest practices and the cumulative prevalence of brown rot at harvest. According to our simulations, all the fruit production can be lost under some temperature and storage duration conditions. The simulation results supported the important role of the interaction between storage temperature and duration in preventing brown rot

during post-harvest (Bernat et al., 2017b; Garcia-Benitez et al., 2020). They also stressed that the irrigation regime and fruit thinning should be considered to lower the incidence of brown rot during storage, since they can influence the magnitude of the fruit cracks, a major driver of the fruit sensitivity to brown rot (Gibert et al., 2009; Oliveira Lino et al., 2016) that was accounted for by a proxy, the fruit mass, in the brown rot model. The pre-harvest practices and meteorological conditions could also play a role in the spreading of brown rot infections during the growing season (Bellingeri et al., 2018; Mercier et al., 2008; Bannon et al., 2009), and their effects should thus be further included in the model.

The analysis of model outputs suggested that it can be important to take into account the interactions between pre-harvest practices and storage conditions to simulate the development of nectarine quality traits and of brown rot during storage. In additions, considering the harvest time, an important decision variable in relation to fruit maturity, would be a progress. Environmental conditions and pre-harvest practices are able to influence the timing and the velocity of fruit ripening process (Marini et al., 1991), and thus to modify the optimal harvest time. Moreover, fruit can show maturity differences inside the same tree. Then, fruit maturity affects the storage potential and the evolution of quality traits during storage (Shewfelt et al., 1987; Bonghi et al., 1999; Tijskens et al., 2007). These issues could be tackled with the inclusion of the concept of biological shift factor (Hertog, 2002), which can account for the difference in the developmental stage of each individual organism of a population, grown under different meteorological conditions, light, irrigation and other management issues, relative to an averaged development pattern typical for that particular species (Heuvelink and Marcelis, 1989).

3.5.2 Factors governing the choice of the optimal pre- and post-harvest scenarios in terms of fruit quality and quantity

The optimal scenarios - in terms of fruit quality and quantity – identified through the modeling framework varied according to the importance assigned to the quality criteria (weights). The optimization process pointed out the existence of a trade-off between the mean fruit sweetness and the fruit yield at the tree scale, which was already mentioned by Bevacqua et al. (2019) in a simulation study and is in line with experimental evidences (Marini, 2003; Kumar et al., 2010). This trade-off influenced the values of the performance criteria for the selected optimal scenarios. For example, we observed a small mean fruit mass when sweetness was the most important criterion, while the fruit sweetness was very low when fruit size was favoured. When sweetness was the most important criterion, the selected storage conditions consisted in high temperature and low relative humidity, which favoured fruit mass loss and thus the enhancement of sugar concentration in fruit pulp, while low temperature and high relative humidity, which minimize fruit mass loss, were selected when the fruit size was given high priority.

The value of the performance score was expressed on an arbitrary scale, but it can be further translated into monetary value, since monetary return is one of the major drivers of growers' and post-harvest actors' behavior (Zhao et al., 2017). This monetary value could consider the consumer's willingness to pay for quality criteria, which has however rarely been studied (e.g. for the US case: Parker et al. 1991; Parker 1993). Anyway, despite the consideration of quality criteria that are important for the consumers, the study reflected principally the vision of fruit growers and post-harvest actors, whom we assumed they aim at maximising

a performance score that was by construction highly dependent on fruit yield. The optimal performance scores were the highest when the importance of fruit mass was the highest, in line with the expectations of these actors of the fruit supply chain.

Finally, the performance scores obtained under different pre- and post-harvest conditions may also have been influenced by the utility functions associated to singular quality traits and their related parameters (Equation 3.3, for fruit mass and sweetness). These effects deserve further investigation, since consumers perception on fruit quality can depend on other factors such as fruit acidity and firmness (Hilaire, 2003; Crisosto and Day, 2012; Scandella and Roty, 2012).

3.6 Conclusions

In this study, we presented a new modeling framework able to simulate the interactions between the pre- and post-harvest processes, under the influence of several conditions in these two stages. The value of this work lies in its original approach, but to be used extensively, the model needs to be consolidated and tested in different situations, including different meteorological years.

Despite these limitations, the model showed its ability to integrate several eco-physiological and epidemiological processes in the pre- and post-harvest continuum for the nectarine case. Thus, it could be used to explore and to suggest targeted storage conditions for different combinations of pre- and post-harvest conditions, optimizing simultaneously fruit quality and yield, and aptitude to storage (avoid fruit loss). Moreover, this framework can help to design solutions that satisfy expectations from different actors in the fruit supply chain and it should be used as a tool for dialogue between these actors.

Supplementary Information

- **C.1** Water regime scenarios used in model simulations
- **C.2** Parametrization and initialization of the QualiTree model

General discussion and perspectives

Fruit quality development and brown rot infections are both influenced by pre-harvest and storage conditions, and these concerns are highly important for the fruit supply chain (Shewfelt, 1999; Bautista-Baños, 2014). However, there are no studies in the literature that integrate fruit quality and brown rot infections and their drivers on the two life stages of fruit. In addition, the consideration of ecophysiological, biochemical and epidemiological processes adds complexity to the integration. Understanding the levers of quality and infection requires thus considering the fruit and brown rot system characterised by these processes and their temporal variations. In this context, the use of mathematical modeling can help take into account the behavior of different parts of this complex system and exploring the whole (Thornley and France, 2007; Tijskens and Schouten, 2014). We thus proposed a modeling framework to simulate the dynamics of fruit quality traits during the growing season and the post-harvest stage, and the appearance of brown rot symptoms during storage, under the influence of agricultural practices and storage conditions. The processes and the experiments presented in the study refer to the nectarine case.

In the first chapter, we focused on the fruit quality development during the

pre and post-harvest stages. We built a model (called hereafter the quality model) that incorporated the effects of fruit growth and post-harvest storage conditions (temperature and relative humidity) on the nectarine quality development during these two stages. The quality model was composed of three sub-models, which simulated the time course of fruit surface conductance to water vapor during the growing season, the fruit mass loss during storage, and the sugar concentration dynamics in the fruit pulp during the growing season and storage. The sugar sub-model allowed us to calculate a fruit sweetness index and to evaluate its dynamics in both fruit life stages. To test the hypotheses underlying the processes described in the sub-models, we set up several experiments during 2018 and 2019, with different treatments in terms of horticultural practices (irrigation and fruit load) and storage conditions. We calibrated sub-model parameters using the results of these experiments. Despite the complexity of the processes described in the model and the few data available, the model simulations showed a satisfactory goodness of fit for all the described processes. The experimental results and model simulations under different pre-harvest and storage scenarios supported the well-known importance of horticultural practices on sweetness at harvest, as reviewed for the peach case by Minas et al. (2018). The sugar accumulations and concentrations during the growing season was principally influenced by irrigation regimes, with an observed increase under the water-stressed treatments, as already evoked in several literature studies on peach (Crisosto, 1994; Gelly et al., 2004; Mirás-Avalos et al., 2016). Thinning intensity was instead found to be not influential in sweetness development in the orchard, in contrast with findings by several authors (Marini, 2003; Kumar et al., 2010; Lopresti et al., 2014), probably because the thinning intensities used in the experiments were not enough contrasted. Fruit sugar concentrations were also subject to changes after harvest. These changes were influenced by the stor-

age temperature that altered sugar kinetics, as already suggested by (Lombardo et al., 2011; Aubert et al., 2014), and by water losses and fruit respiration, as observed on mangoes by Nordey et al. (2016). However, since only few studies on peach sugar dynamics under different storage conditions are available, the study pointed out that more attention should be paid to this subject, in particular for longer storage durations and different post-harvest scenarios.

Fruit mass loss during storage was correctly simulated by the respective submodel, which take into account transpiration and respiration. The latter were suggested to be both influential in this loss (Xanthopoulos et al., 2017). To describe these processes, we included both fruit intrinsic factors (such as fruit size and surface conductance to water vapour) and extrinsic ones (storage room temperature, relative humidity and air velocity) that have been cited as influential (Díaz-Pérez, 2019). In particular, the explicit consideration of fruit surface conductance to water vapour and of its control by growing conditions is quite novel compared to existing fruit mass loss models (Bovi et al., 2018). However, changes in fruit cuticle and surface conductance to water vapour during post-harvest were not dealt with in the study. This subject needs further investigation, since cuticular composition and properties may be subject to change with fruit ripening under different storage conditions (Lara et al., 2014; Díaz-Pérez, 2019; Lara et al., 2019).

Finally, the results from model simulations suggested that fruit sweetness increased with fruit mass loss during storage, both being enhanced by high temperature and low relative humidity. The simulation results also suggested that the choice of the harvest date, which determines the fruit sweetness and its level of maturity when fruit enters in storage, is important for obtaining a high sweetness index at the end of storage, as already observed on peach (Iglesias and Echeverría, 2009; Crisosto and Crisosto, 2005), mango (Joas et al., 2009)

and plum (Guerra and Casquero, 2008). The ripening processes, which are important in this respect, should be further included in the model, for example by considering the approach of Génard and Gouble (2005). In this regard, more attention should be paid to the effects of fruit maturity stage on the sugar dynamics during storage, as already suggested by Borsani et al. (2009).

In the second chapter we focused on the post-harvest infections by *Monilinia* spp. on nectarine, under the influence of different pre-harvest conditions and storage temperatures. We initially tested if sporulating infections by *Monilinia* spp. could be able to install secondary infections during storage on surrounding fruit by spore transmission between distant fruit (not by direct contact), which, to our knowledge, has never been reported before in the literature. Tian and Bertolini (1999) and Bernat et al. (2017b) argued that sporulation could lead to secondary inoculum infecting healthy fruit during storage. In contrast with these suggestions, we observed no symptoms of by spore transmission between distant fruit during our experiments. This should be confirmed by an analysis of the fruit skin surface, to test if spores generated by infected fruit can be found on the surface of surrounding fruit. If confirmed, this finding means that secondary infections may occur only by direct contact during storage. In this regard, it would be interesting to compare the disease patterns of fruit stored without direct contact (into alveoli) or into bin containers, where we can assume that the high level of direct contact enhances the risk of spreading the disease from fungal sporulation on fruit (Amorim et al., 2008).

We then observed experimentally the impact of several pre- and post-harvest conditions on the development of the brown rot disease during storage in 2018 and 2019. The results of these experiments showed that brown rot incidence increased with an increase in fruit mass at harvest, influenced by agricultural

practices, with a later harvest date, and with the storage temperature. These results are in line with previous experimental evidences. It is known that fruit mass relates with the fruit crack surfaces (Christensen, 1975; Gibert et al., 2007), which are the main entry sites for *Monilinia* spp. spores (Byrde and Willetts, 1977; Oliveira Lino et al., 2016). Moreover, fruit from later harvest dates are more prone to disease since fruit remain in contact with fruit spores in the orchard for a longer time, which can install latent infections that reveal during storage (Gell et al., 2008), and also because a maturity increase can enhance the infection process (Luo and Michailides, 2001; Xu et al., 2007). Storage temperatures are also known to influence the infection process by affecting decay, mycelium development and conidia survival (Bernat et al., 2017b, 2018; Garcia-Benitez et al., 2020). On these bases, we identified pre- and post-harvest candidate variables able to explain the brown rot progress during storage. We selected variables that were related to the meteorological, epidemiological and fruit physical characteristics at harvest, and to storage conditions. These variables concerned both the fruit population (epidemiological, meteorological and storage conditions) and the individual fruit (fruit mass). To our knowledge, the integration of these kind of variables in the explanation of brown rot infections during storage has never been tested before. We used these variables to build a survival model to estimate the probability of time-to-appearance of brown rot symptoms in nectarine during storage. The fruit mass and the prevalence of brown rot at harvest, the mean daily wetness duration in the week before harvest and the storage duration were selected as the best variables to explain the brown rot observed patterns during 2018 and 2019 experiments. The selected variables concerned the pre- and post-harvest stages, which points out the importance of interactions between the two stages for the brown rot incidence during storage. As an example, the use of the model indicates that fruit from water-stressed

or highly loaded trees (small fruit) can be stored at higher temperature than those from well-irrigated conditions (big fruit). The model could also be used to suggest possible scenarios of storage temperatures and storage duration to avoid brown rot development. However, despite its good adjustment quality, the model could benefit from the inclusion of more data from different years and harvest dates. We could set up experiments with fruit stored for a longer time, in order to reduce the effect of the high censoring rate found for the survival analysis (Perera and Dwivedi, 2020). Moreover, we could evaluate if the addition of variables related to the epidemiological state of the orchard at harvest, such as the *Monilinia* spp. spore concentration in the air (Luo et al., 2007; West and Kimber, 2015) and the number and timing of fungicide treatments before harvest, could improve the accuracy of the model. To use the model with other peach cultivars, it could be interesting to introduce the fruit crack surface area as a direct variable in the model, instead of the mass, even if it is difficult to measure in a rapid and effective way. As a matter of fact, cuticular deposition, which is implied in the sensitivity to fruit cracking (Lara et al., 2014), may vary according to the cultivars, which show different sensitivities to brown rot infections (Oliveira Lino et al., 2016). The model could also consider time-changing covariates (Petersen, 1986), notably the storage temperature, which could allow to test the effect of several "long" post-harvest scenarios (e.g. passing through transport, retail, consumer's home) on fruit rot. To do that, more data and research on *Monilinia* spp. infection process under dynamic post-harvest conditions are needed. In addition, this model was calibrated for the case of fruit that were not in direct contact. Nevertheless, peaches are generally stored in bins (Gross et al., 2016), where infections can easily spread. The model could give erroneous results if applied in this case. The use of proper epidemiological models that are able to account for the spread of the disease from fruit to fruit,

such as that presented by Dutot et al. (2013) on apple, could be more effective.

In the third, and last, chapter of the thesis we integrated in a modeling framework the quality and time-to-infection models, described previously, with the QualiTree model (Lescourret et al., 2001; Mirás-Avalos et al., 2011). The latter is a fruit crop model able to take explicitly into account the role of pre-harvest practices and meteorological conditions on the development of fruit characteristics during the growing season, for each individual fruiting unit at the tree scale. The integration of the QualiTree model overcame the limitation of the quality model, which was not able to consider explicitly the effects of pre-harvest practices on the development of quality traits during the growing season. Moreover, by articulating several sub-models through inputs and outputs, we followed a modular approach. As a matter of fact, sub-models can stand alone and they could be replaced, while new components could also be added to the modeling framework (Jones et al., 2001). With the resulting modeling framework, we were able to represent the development of fruit quality traits during the growing season and storage, the fruit yield build-up, the fruit mass loss and the appearance of brown rot infections during storage, and to consider explicitly the effects of pre-harvest practices and storage conditions on these processes. For the first time in a modelling exercise, objects of interest to different actors in the fruit value chain, i.e. fruit production (essential for the producers), fruit loss (post-harvest actors), and quality (consumers), were considered at the same time.
We initially tested the model behavior under different in silico scenarios of pre-harvest practices (water regimes during the growing season and fruit load) and storage conditions (temperature, relative humidity and storage duration). The results from the sensitivity analysis and the model exploration pointed out that fruit quality criteria were mainly influenced by pre-harvest practices. Irrigation

timing and intensity proved to be essential in defining mean fruit sweetness, fruit mass and fruit yield, in line with experimental evidences (Crisosto, 1994; Alcobendas et al., 2012; Johnson and Handley, 2000), while thinning intensity was found to impact fruit mass and yield, but not fruit sweetness. The latter is in contrast with some experimental findings (Wu et al., 2005; Lopresti et al., 2014). Further comparisons between model simulations and data obtained under various pre- and post-harvest scenarios are needed to investigate this point. Storage conditions were instead found to be important for quality and avoid fruit loss during storage. Low temperatures slowed down the epidemiological processes and the metabolic rates (Bernat et al., 2017b; Yahia et al., 2018), while high relative humidities and low temperatures slowed down the transpiration process (Díaz-Pérez, 2019). Pre-harvest practices were also found to be important in influencing the prevalence of brown rot during storage. However, pre-harvest practices and meteorological conditions could play a role in the spread of the brown rot during the growing season (Bannon et al., 2009; Bellingeri et al., 2018; Bevacqua et al., 2019), which should be further integrated into the modeling framework. Fruit yield at the end of storage (total and marketable) was found to be influenced by pre-harvest practices and storage conditions, due to possible fruit losses during storage. This is important, because attention on post-harvest is often only concentrated on fruit quality and fruit losses, which could generate communication problems between the pre- and post-harvest realm (Shewfelt, 1999; Tijskens and Schouten, 2014). In our study, we decided not to consider the effect of the harvest date, even if it is one of the more important decision variables in the fruit supply chain (Tijskens and van Kooten, 2006; Ahumada and Villalobos, 2011; González-Araya et al., 2015), since the processes related to peach ripening were not included in the modeling framework (as already pointed out before for the quality model). The stage of maturity at which fruit is har-

vested is crucial because it controls the fruit storage potential and its future acceptability by the post-harvest actors (Shewfelt et al., 1987; Bonghi et al., 1999; Tijskens et al., 2007).

We used the model in combination with an optimization algorithm, in order to retrieve the pre- and post-harvest scenarios that maximized fruit quality and quantity, aggregated into a unique performance score, for different storage durations and relative importance (weights) assigned to fruit quality criteria. We selected the fruit sweetness and the fruit size as the fruit quality criteria, which are among the most important criteria for peach consumer acceptance (Crisosto and Costa, 2008; Scandella and Roty, 2012). The identified optimal scenarios varied according to the importance assigned to the quality criteria. When fruit sweetness was selected as the most important criterion, the best scenarios consisted in applying a moderate water-stress during the last stage of fruit growth, along with balancing fruit size and number to maintain a high fruit yield. Moreover, storage conditions were chosen to allow the sugars to concentrate into fruit pulp, but also avoiding excessive mass loss due to transpiration and respiration. Conversely, when larger importance was given to fruit size, the tree was well-irrigated. The yield was higher than in the previous case, while the storage conditions focused on the minimization of fruit mass loss, with low temperature and high relative humidity values. These results pointed out the existence of a trade-off between fruit sweetness and fruit yield, which corresponds to a well-known potential conflict between fruit growers and consumers expectations (Shewfelt, 1999; Crisosto and Costa, 2008). The optimisation process, by making explicit this trade-off between fruit quantity and quality, highlighted that the model can help explore the choices that producers and post-harvest actors have to face to satisfy consumer preference. However, while it is relatively straightforward to assess the economic benefits associated with increasing fruit yield

and eliminating disorders that develop during storage of products, it is more difficult to assess the benefits associated by improving overall quality (Harker et al., 2003). This also reflects in the literature, where revenue maximization and post-harvest waste reduction are the main interests in the fresh produce supply chain studies, at the expense of consumer satisfaction (Shukla and Jharkharia, 2013). Consumer preference and willingness-to-pay for different quality criteria are not well assessed in the literature (e.g. Parker et al. 1991; Bi et al. 2012; Kelley et al. 2016; Zhou et al. 2018). Accordingly, utility functions for quality criteria were not easy to retrieve. Anyway, despite the consideration of quality criteria that are important for consumers, the performance score which we aimed at maximize reflected principally the vision of fruit growers, since by construction it was highly dependent on fruit yield. Further research is needed to better integrate the vision of consumers in the optimization procedure.

The modeling framework could also benefit from the introduction of processes related to the development of other fruit quality criteria, such as the fruit firmness and acidity. A high firmness value simplifies fruit shipping, storage and increases the retail market life potential (Crisosto and Costa, 2008), so this fruit property is sought after by transporters and retailers. Moreover, it also plays a central role in the choice of the product by consumers (Scandella and Roty, 2012; Crisosto and Day, 2012). The introduction of this variable could thus allow considering more food supply-chain actors in the framework (Gary and Tchamitchian, 2001). This variable, however, is not simple to simulate during the growing season (Tijskens and Schouten, 2014), but it generally varies during storage as a function of temperature (Schouten et al., 2007). Firmness is highly dependent on fruit maturity, which in turns depends on environmental conditions and on practices during the growing season (Marini et al., 1991), including in particular the choice of the harvest time (see above). Fruit acidity is instead

a component of fruit flavor, along with sweetness, and it can modify consumer's acceptance in the case of peach (Delgado et al., 2013; Hilaire, 2003).

Finally, several aspects of the modeling framework could be improved. First of all, we could ameliorate the integration of water dynamics in QualiTree. The latter considers as inputs the seasonal plant water status at the root collar, which does not allow to separate the effects of the rainfall and irrigation regimes. This implies, among other things, that it is not possible to calculate the amount of water used for irrigation during the growing season. This limitation could be overcome by integrating the soil water content dynamics and their interactions with the plant root system. Furthermore, lowering the energy consumed by storage is an issue of concern, since the top energy-consuming processes are those requiring cooling and refrigeration by cold storage refrigerating equipment (Latini et al., 2016). The impact of increasing storage temperatures on reducing energy could be calculated in the future by the modeling framework, if we manage to quantify the energy consumption during storage using an approach like those presented in Brito et al. (2014) and Duret et al. (2020). With such implementations, the model could be used to explore new scenarios to optimize, in addition to fruit quantity and quality, the use of water and the use of energy in face of climate change.

Perspectives

In addition to the above-mentioned areas of improvement, the modeling framework could gain in scope in several ways. First, it could be tested for other peach cultivars. For the empirical model predicting the time-to-appearance of brown rot during storage, this means collecting a lot of new experimental data, since this type of model can be considered valid only in the conditions explored by the data used for calibration (Gotelli, 2008). For the process-based qual-

ity models (QualiTree plus the post-harvest model of sugar dynamics and fruit mass loss), a sensitivity analysis would help to find the parameters to which the desired outputs are the most sensitive. The parameters related to the dry and the fresh mass accumulation, and to sugar dynamics in pre- and post-harvest, are probably concerned. This would help reduce the number of parameters to calibrate for a new cultivar, as demonstrated by Kanso et al. (2020). If the model is calibrated for several peach genotypes and if a significant variability in the parameter estimates is found, these parameters may reflect a genetic control of the concerned processes (Tardieu, 2003; Beauvoit et al., 2014). In this way, the variability could be used to search possible combinations of parameters that define fruit ideotypes, i.e. ideal fruit with respect to specific qualitative characteristics, e.g. high mass, high sweetness, under certain environment conditions (Constantinescu et al., 2016). This could be a means to add fruit breeders, who can contribute to improved consumers acceptance (Cirilli et al., 2016), to the supply chain actors already considered in our approach.

Second, the modeling framework could be adapted to other fruit species. On the one hand, this can be partly time consuming since there are strong differences between fruit species, notably regarding the sugar metabolism (different between apple and peach, for example) or the storage diseases – but the latter point is not critical except in terms of data availability, since the disease model is empirical. On the other hand, the recent study of Cakpo et al. (2020) who compared 10 fruit species using a coarse-grained model of primary metabolism shows that it is possible to adapt our model of sugar dynamics to make it generic. Moreover, the representation of the tree functioning in QualiTree is quite generic and this model has already been used on apple to simulate carbon allocation and organ growth variability in the tree (Pallas et al., 2016).

Eventually, broadening the range of criteria considered in the model, as sug-

gested before (fruit firmness, fruit acidity, water and energy consumed in the orchard and in the storage chamber, etc.), is a promising avenue. It would have the advantage of involving more actors and more actor's objectives. This would pave the way for the use of multi-objective analysis, which has been proven to be efficient when conflicting objectives are considered (Groot and Rossing, 2011; Grechi et al., 2012; Ould-Sidi and Lescourret, 2011). This method, provided that it is used in interaction with stakeholders and in conjunction with other decision support methods (Memmah et al., 2015), would help identify management policies that satisfy acceptable compromises between fruit growers, post-harvest actors, and consumers expectations.

Bibliography

Abate, D., Pastore, C., Gerin, D., De Miccolis Angelini, R. M., Rotolo, C., Pollastro, S., and Faretra, F. (2018). Characterization of monilinia spp. Populations on stone fruit in south italy. *Plant Disease*, 102(9):1708–1717.

Ahumada, O. and Villalobos, J. R. (2011). Operational model for planning the harvest and distribution of perishable agricultural products. *International Journal of Production Economics*, 133(2):677–687.

Alcobendas, R., Mirás-Avalos, J. M., Alarcón, J. J., and Nicolás, E. (2013). Effects of irrigation and fruit position on size, colour, firmness and sugar contents of fruits in a mid-late maturing peach cultivar. *Scientia Horticulturae*, 164:340–347.

Alcobendas, R., Mirás-Avalos, J. M., Alarcón, J. J., Pedrero, F., and Nicolás, E. (2012). Combined effects of irrigation, crop load and fruit position on size, color and firmness of fruits in an extra-early cultivar of peach. *Scientia Horticulturae*, 142:128–135.

Allen, M. T., Prusinkiewicz, P., and DeJong, T. M. (2005). Using L-systems for modeling source-sink interactions, architecture and physiology of growing trees: The L-PEACH model. *New Phytologist*, 166(3):869–880.

Allen, R. G., Pereira, L. S., Raes, D., and Smith, M., editors (1998). *Crop*

evapotranspiration - Guidelines for computing crop water requirements - FAO Irrigation and drainage paper 56. FAO - Food and Agriculture Organization of the United Nations.

Amorim, L., Martins, M. C., Lourenço, S. A., Gutierrez, A. S., Abreu, F. M., and Gonçalves, F. P. (2008). Stone fruit injuries and damage at the wholesale market of São Paulo, Brazil. *Postharvest Biology and Technology*, 47(3):353–357.

Aubert, C., Bony, P., Chalot, G., Landry, P., and Lurol, S. (2014). Effects of storage temperature, storage duration, and subsequent ripening on the physicochemical characteristics, volatile compounds, and phytochemicals of western red nectarine (Prunus persica L. Batsch). *Journal of Agricultural and Food Chemistry*, 62(20):4707–4724.

Baggio, J. S., Hau, B., and Amorim, L. (2017). Spatiotemporal analyses of rhizopus rot progress in peach fruit inoculated with Rhizopus stolonifer. *Plant Pathology*, 66(9):1452–1462.

Bannon, F., Gort, G., van Leeuwen, G., Holb, I., and Jeger, M. (2009). Diurnal patterns in dispersal of Monilinia fructigena conidia in an apple orchard in relation to weather factors. *Agricultural and Forest Meteorology*, 149(3-4):518–525.

Bautista-Baños, S., editor (2014). *Postharvest Decay: Control Strategies*. Academic Press, 1st edition.

Beauvoit, B. P., Colombié, S., Monier, A., Andrieu, M. H., Biais, B., Bénard, C., Chéniclet, C., Dieuaide-Noubhani, M., Nazaret, C., Mazat, J. P., and Gibon, Y. (2014). Model-assisted analysis of sugar metabolism throughout tomato

fruit development reveals enzyme and carrier properties in relation to vacuole expansion. *Plant Cell*, 26(8):3224–3242.

Bellingeri, M., Quilot-Turion, B., Oliveira Lino, L., and Bevacqua, D. (2018). The Crop Load Affects Brown Rot Progression in Fruit Orchards: High Fruit Densities Facilitate Fruit Exposure to Spores but Reduce the Infection Rate by Decreasing Fruit Growth and Cuticle Cracking. *Frontiers in Ecology and Evolution*, 5(January):1–7.

Ben-Yehoshua, S. and Rodov, V. (2002). Transpiration and Water Stress. In *Postharvest Physiology and Pathology of Vegetables*, pages 111–159. Marcel Dekker: New York, NY, USA.

Berman, M. E. and Dejong, T. M. (1996). Water stress and crop load effects on fruit fresh and dry weights in peach (Prunus persica). *Tree Physiology*, 16(10):859–864.

Berna, A. Z., Lammertyn, J., Buysens, S., Di Natale, C., and Nicolaï, B. M. (2005). Mapping consumer liking of tomatoes with fast aroma profiling techniques. *Postharvest Biology and Technology*, 38(2):115–127.

Bernat, M., Josep, U., Segarra, J., Casals, C., Teixidó, N., and Torres, R. (2017a). Relevance of the main postharvest handling operations on the development of brown rot disease on stone fruits. *Journal of the Science of Food and Agriculture*, 97(15):5319–5326.

Bernat, M., Segarra, J., Navas-Cortés, J. A., Casals, C., Torres, R., Teixidó, N., and Usall, J. (2018). Influence of temperature and humidity on the survival of Monilinia fructicola conidia on stone fruits and inert surfaces. *Annals of Applied Biology*, 173(1):63–70.

Bernat, M., Usall, J., Casals, C., Segarra, J., and Xu, X.-M. (2017b). Influence of temperature on decay, mycelium development and sporodochia production caused by Monilinia fructicola and M. laxa on stone fruits. *Food Microbiology*, 64:112–118.

Bevacqua, D., Génard, M., Lescourret, F., Martinetti, D., Vercambre, G., Valsesia, P., and Mirás-Avalos, J. M. (2019). Coupling epidemiological and tree growth models to control fungal diseases spread in fruit orchards. *Scientific Reports*, 9(1).

Bevacqua, D., Quilot-Turion, B., and Bolzoni, L. (2018). A Model for Temporal Dynamics of Brown Rot Spreading in Fruit Orchards. *Phytopathology*, 108(5):595–601.

Bi, X., House, L., Gao, Z., and Gmitter, F. (2012). Sensory evaluation and experimental auctions: Measuring willingness to pay for specific sensory attributes. *American Journal of Agricultural Economics*, 94(2):562–568.

Biggs, A. R. and Northover, J. (1988). Influence of Temperature and Wetness Duration on Infection of Peach and Sweet Cherry Fruits by Monilinia fructicola. *Phytopathology*, 78(10):1352–1356.

Bonghi, C., Ramina, A., Ruperti, B., Vidrih, R., and Tonutti, P. (1999). Peach fruit ripening and quality in relation to picking time, and hypoxic and high CO2 short-term postharvest treatments. *Postharvest Biology and Technology*, 16(3):213–222.

Borsani, J., Budde, C. O., Porrini, L., Lauxmann, M. A., Lombardo, V. A., Murray, R., Andreo, C. S., Drincovich, M. F., and Lara, M. V. (2009). Carbon metabolism of peach fruit after harvest: Changes in enzymes involved in

organic acid and sugar level modifications. *Journal of Experimental Botany*, 60(6):1823–1837.

Borve, J., Sekse, L., and Stensvand, A. (2000). Cuticular fractures promote postharvest fruit rot in sweet cherries. *Plant Disease*, 84(11):1180–1184.

Bovi, G. G., Caleb, O. J., Herppich, W. B., and Mahajan, P. V. (2018). Mechanisms and Modeling of Water Loss in Horticultural Products. In *Reference Module in Food Science*. Elsevier.

Bovi, G. G., Caleb, O. J., Linke, M., Rauh, C., and Mahajan, P. V. (2016). Transpiration and moisture evolution in packaged fresh horticultural produce and the role of integrated mathematical models: A review. *Biosystems Engineering*, 150:24–39.

Bradburn, M. J., Clark, T. G., Love, S. B., and Altman, D. G. (2003). Survival Analysis Part II: Multivariate data analysis- An introduction to concepts and methods. *British Journal of Cancer*, 89(3):431–436.

Brito, P., Lopes, P., Reis, P., and Alves, O. (2014). Simulation and optimization of energy consumption in cold storage chambers from the horticultural industry. *International Journal of Energy and Environmental Engineering*, 5(2-3):1–15.

Brizzolara, S., Hertog, M., Tosetti, R., Nicolai, B., and Tonutti, P. (2018). Metabolic responses to low temperature of three peach fruit cultivars differently sensitive to cold storage. *Frontiers in Plant Science*, 9.

Burnham, K. P. and Anderson, D. R. (2004). Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods and Research*, 33(2):261–304.

Bussières, P. (1994). Water import rate in tomato fruit: A resistance model. *Annals of Botany*, 73(1):75–82.

Byrde, R. J. W. and Willetts, H. J., editors (1977). *The Brown Rot Fungi of Fruit*. Elsevier, 1st edition.

Byrne, D. H., Nikolic, A. N., and Burns, E. E. (2019). Variability in Sugars, Acids, Firmness, and Color Characteristics of 12 Peach Genotypes. *Journal of the American Society for Horticultural Science*, 116(6):1004–1006.

Cakpo, C. B., Vercambre, G., Baldazzi, V., Roch, L., Dai, Z., Valsesia, P., Memah, M. M., Colombié, S., Moing, A., Gibon, Y., and Génard, M. (2020). Model-assisted comparison of sugar accumulation patterns in ten fleshy fruits highlights differences between herbaceous and woody species. *Annals of Botany*, 126(3):455–470.

Caleb, O. J., Herppich, W. B., and Mahajan, P. V. (2016). The Basics of Respiration for Horticultural Products. In *Reference Module in Food Science*. Elsevier.

Casagrande, E., Génard, M., Lurol, S., Charles, F., Plénet, D., and Lescourret, F. (2021). A process-based model of nectarine quality development during pre- and post-harvest. *Postharvest Biology and Technology*, 175:111458.

Casals, C., Griera, C., Vinas, I., Torres, R., and Usall, J. (2009). Effect of temperature and water activity on in vitro germination of Monilinia spp. *Journal of Applied Microbiology*, 108(1):47–54.

Chen, H. C., Kodell, R. L., Cheng, K. F., and Chen, J. J. (2012). Assessment of performance of survival prediction models for cancer prognosis. *BMC Medical Research Methodology*, 12(102).

Christensen, J. V. (1975). Cracking in Cherries: VII. Cracking Susceptibility in Relation to Fruit Size and Firmness. *Acta Agriculturae Scandinavica*, 25(1):11–13.

Cirilli, M., Bassi, D., and Ciacciulli, A. (2016). Sugars in peach fruit: A breeding perspective. *Horticulture Research*, 3:15067.

Clark, T. G., Bradburn, M. J., Love, S. B., and Altman, D. G. (2003). Survival analysis part I: basic concepts and first analyses. *British Journal of Cancer*, 89(2):232–238.

Collett, D. (2015). *Modelling survival data in medical research*. CRC press.

Constantinescu, D., Memmah, M. M., Vercambre, G., Génard, M., Baldazzi, V., Causse, M., Albert, E., Brunel, B., Valsesia, P., and Bertin, N. (2016). Model-assisted estimation of the genetic variability in physiological parameters related to tomato fruit growth under contrasted water conditions. *Frontiers in Plant Science*, 7:1841.

Crisosto, C. H. (1994). Stone fruit maturity indices: a descriptive review. *Postharvest News and Information*, 5(6):65N–68N.

Crisosto, C. H. (2002). How do we increase peach consumption? In *Acta Horticulturae*, volume 592, pages 601–605.

Crisosto, C. H. and Costa, G. (2008). Preharvest factors affecting peach quality. In Layne, D. and Bassi, D., editors, *The peach: botany, production and uses*, pages 536–549. CABI.

Crisosto, C. H. and Crisosto, G. M. (2005). Relationship between ripe soluble solids concentration (RSSC) and consumer acceptance of high and low

acid melting flesh peach and nectarine (Prunus persica (L.) Batsch) cultivars. *Postharvest Biology and Technology*, 38(3):239–246.

Crisosto, C. H. and Day, K. R. (2012). Stone Fruit. In *Crop Post-Harvest: Science and Technology: Perishables*, pages 212–225. Wiley-Blackwell.

DeJong, T. M. and Goudriaan, J. (1989). Modeling peach fruit growth and carbohydrate requirements: reevaluation of the double-sigmoid growth pattern. *Journal of the American Society for Horticultural Science*, 114(5):800–804.

Delgado, C., Crisosto, G. M., Heymann, H., and Crisosto, C. H. (2013). Determining the Primary Drivers of Liking to Predict Consumers' Acceptance of Fresh Nectarines and Peaches. *Journal of Food Science*, 78(4).

Díaz-Pérez, J. C. (2019). Transpiration. In *Postharvest Physiology and Biochemistry of Fruits and Vegetables*, pages 157–173. Elsevier.

Díaz Ricci, J. C., González-Candelas, L., Prusky, D. B., Moser, C., and Baraldi, E. (2020). Editorial: Interplay Between Fungal Pathogens and Fruit Ripening. *Frontiers in Plant Science*, 11:275.

Duret, S., Hamon, E., Hoang, H. M., Stahl, V., Derens-Bertheau, E., Delahaye, A., and Laguerre, O. (2020). Modelling methodology of temperature and energy consumption in food plant: Application to puff pastry. *International Journal of Refrigeration*, 115:28–38.

Dutot, M., Nelson, L. M., and Tyson, R. C. (2013). Predicting the spread of postharvest disease in stored fruit, with application to apples. *Postharvest Biology and Technology*, 85:45–56.

Emery, K. M., Michailides, T. J., and Scherm, H. (2000). Incidence of latent

infection of immature peach fruit by Monilinia fructicola and relationship to brown rot Georgia. *Plant Disease*, 84(8):853–857.

Exama, A., Arul, J., Lencki, R. W., Lee, L. Z., and Toupin, C. (1993). Suitability of Plastic Films for Modified Atmosphere Packaging of Fruits and Vegetables. *Journal of Food Science*, 58(6):1365–1370.

FAO (2021). Fruit and vegetables – your dietary essentials. Technical report, FAO.

Fearne, A., Barrow, S., and Schulenberg, D. (2006). Implanting the benefits of buyer-supplier collaboration in the soft fruit sector. *Supply Chain Management: An International Journal*, 11(1):3–5.

Fereres, E. and Soriano, M. A. (2007). Deficit irrigation for reducing agricultural water use. *Journal of Experimental Botany*, 58(2):147–159.

Fishman, S. and Génard, M. (1998). A biophysical model of fruit growth: Simulation of seasonal and diurnal dynamics of mass. *Plant, Cell and Environment*, 21(8):739–752.

Flaishman, M. A. and Kolattukudy, P. E. (1994). Timing of fungal invasion using host's ripening hormone as a signal. *Proceedings of the National Academy of Sciences of the United States of America*, 91(14):6579–6583.

FranceAgriMer (2019). La pêche et la nectarine en 2018.

Frare, G. F., Silva-Junior, G. J., Lanza, F. E., Bassanezi, R. B., Ramires, T. G., and Amorim, L. (2019). Sweet orange fruit age and inoculum concentration affect the expression of citrus black spot symptoms. *Plant Disease*, 103(5):913–921.

Galindo, F. G., Herppich, W., Gekas, V., and Sjöholm, I. (2004). Factors affecting quality and postharvest properties of vegetables: Integration of water relations and metabolism. *Critical Reviews in Food Science and Nutrition*, 44(3):139–154.

Garcia-Benitez, C., Casals, C., Usall, J., Sánchez-Ramos, I., Melgarejo, P., and De Cal, A. (2020). Impact of postharvest handling on preharvest latent infections caused by Monilinia spp. In nectarines. *Journal of Fungi*, 6(4):1–14.

Gary, C., Jones, J. W., and Tchamitchian, M. (1998). Crop modelling in horticulture: State of the art. *Scientia Horticulturae*, 74(1-2):3–20.

Gary, C. and Tchamitchian, M. (2001). Modelling and management of fruit production: the case of tomatoes. In *Food Process Modelling*, pages 201–229. CRC Press.

Gell, I., De Cal, A., Torres, R., Usall, J., and Melgarejo, P. (2008). Relationship between the incidence of latent infections caused by Monilinia spp. and the incidence of brown rot of peach fruit: Factors affecting latent infection. *European Journal of Plant Pathology*, 121(4):487–498.

Gell, I., De Cal, A., Torres, R., Usall, J., and Melgarejo, P. (2009). Conidial density of Monilinia spp. on peach fruit surfaces in relation to the incidences of latent infections and brown rot. *European Journal of Plant Pathology*, 123(4):415–424.

Gelly, M., Recasens, I., Girona, J., Mata, M., Arbones, A., Rufat, J., and Marsal, J. (2004). Effects of stage II and postharvest deficit irrigation on peach quality during maturation and after cold storage. *Journal of the Science of Food and Agriculture*, 84(6):561–568.

Génard, M. and Gouble, B. (2005). ETHY. A theory of fruit climacteric ethylene emission. *Plant Physiology*, 139(1):531–545.

Genard, M., Reich, M., Lobit, P., and Besset, J. (1999). Correlations between sugar and acid content and peach growth. *Journal of Horticultural Science and Biotechnology*, 74(6):772–776.

Génard, M. and Souty, M. (1996). Modeling the peach sugar contents in relation to fruit growth. *Journal of the American Society for Horticultural Science*, 121(6):1122–1131.

Gibert, C., Chadœuf, J., Nicot, P., Vercambre, G., Génard, M., and Lescourret, F. (2009). Modelling the effect of cuticular crack surface area and inoculum density on the probability of nectarine fruit infection by Monilinia laxa. *Plant Pathology*, 58(6):1021–1031.

Gibert, C., Chadœuf, J., Vercambre, G., Génard, M., and Lescourret, F. (2007). Cuticular Cracking on Nectarine Fruit Surface: Spatial Distribution and Development in Relation to Irrigation and Thinning. *Journal of the American Society for Horticultural Science*, 132(5):583–591.

Gibert, C., Génard, M., Vercambre, G., and Lescourret, F. (2010). Quantification and modelling of the stomatal, cuticular and crack components of peach fruit surface conductance. *Functional Plant Biology*, 37(3):264–274.

Gibert, C., Lescourret, F., Génard, M., Vercambre, G., and Pérez Pastor, A. (2005). Modelling the effect of fruit growth on surface conductance to water vapour diffusion. *Annals of Botany*, 95(4):673–683.

González-Araya, M. C., Soto-Silva, W. E., and Espejo, L. G. A. (2015). Harvest Planning in Apple Orchards Using an Optimization Model. *International Series in Operations Research and Management Science*, 224:79–105.

Gotelli, N. J. (2008). *A Primer of Ecology, 4th ed.* Oxford University Press Inc, second edition.

Grechi, I., Ould-Sidi, M. M., Hilgert, N., Senoussi, R., Sauphanor, B., and Lescourret, F. (2012). Designing integrated management scenarios using simulation-based and multi-objective optimization: Application to the peach tree-Myzus persicae aphid system. *Ecological Modelling*, 246(C):47–59.

Groot, J. C. and Rossing, W. A. (2011). Model-aided learning for adaptive management of natural resources: An evolutionary design perspective. *Methods in Ecology and Evolution*, 2(6):643–650.

Gross, K. C., Wang, C. Y., and Saltveit, M. E. (2016). The commercial storage of fruits, vegetables, and florist and nursery stocks. Technical Report 66, USDA.

Grossman, Y. L. and DeJong, T. M. (1994). Peach: A simulation-model of reproductive and vegetative growth in peach trees. *Tree Physiology*, 14(4):329–345.

Grossman, Y. L. and DeJong, T. M. (1995). Maximum fruit growth potential following resource limitation during peach growth. *Annals of Botany*, 75(6):561–567.

Guerra, M. and Casquero, P. A. (2008). Effect of harvest date on cold storage and postharvest quality of plum cv. Green Gage. *Postharvest Biology and Technology*, 47(3):325–332.

Harker, F. R., Gunson, F. A., and Jaeger, S. R. (2003). The case for fruit quality: An interpretive review of consumer attitudes, and preferences for apples. *Postharvest Biology and Technology*, 28(3):333–347.

Hertog, M. L. (2002). The impact of biological variation on postharvest population dynamics. *Postharvest Biology and Technology*, 26(3):253–263.

Hertog, M. L., Tijskens, L. M., and Hak, P. S. (1997). The effects of temperature and senescence on the accumulation of reducing sugars during storage of potato (Solanum tuberosum L.) tubers: A mathematical model. *Postharvest Biology and Technology*, 10(1):67–79.

Heuvelink, E. and Marcelis, L. (1989). Dry Matter Distribution in Tomato and Cucumber. *Acta Horticulturae*, (260):149–180.

Hilaire, C. (2003). The peach industry in France: state of the art, research and development. In Marra, F. and Sottile, F., editors, *Proceedings of the First Mediterranean Peach Symposium*, pages 27–34, Agrigento, Italy.

Hilaire, C., Mérendet, V., Ruesch, J., Roty, C., Annibal, S., and Nasri, L. (2013). Segmentation de l'offre pêche-nectarine: valoriser la diversité variétale selon la saveur (1re partie). *Infos CTIFL*, (290):32–37.

HLPE (2017). A report by the High Level Panel of Experts on Food Security and Nutrition of the Committee on World Food Security. Technical report, HLPE, Rome.

Holb, I. J. (2008). Monitoring conidial density of Monilinia fructigena in the air in relation to brown rot development in integrated and organic apple orchards. *European Journal of Plant Pathology*.

Hong, C., Holtz, B. A., Morgan, D. P., and Michailides, T. J. (1997). Significance of thinned fruit as a source of the secondary inoculum of Monilinia fructicola in California nectarine orchards. *Plant Disease*, 81(5):519–524.

Humplík, J. F., Dostál, J., Ugena, L., Spíchal, L., De Diego, N., Vencálek, O., and Fürst, T. (2020). Bayesian approach for analysis of time-to-event data in plant biology. *Plant Methods*, 16(1).

Iglesias, I. and Echeverría, G. (2009). Differential effect of cultivar and harvest date on nectarine colour, quality and consumer acceptance. *Scientia Horticulturae*, 120(1):41–50.

Inglese, P., Caruso, T., and Gugliuzza, G. (2002). Crop load and rootstock influence on dry matter partitioning in trees of early and late ripening peach cultivars. *Journal of the American Society for Horticultural Science*, 127(5):825–830.

Intrigliolo, D. S. and Castel, J. R. (2010). Response of plum trees to deficit irrigation under two crop levels: Tree growth, yield and fruit quality. *Irrigation Science*, 28(6):525–534.

Iooss, B., Janon, A., Pujol, G., Broto, B.-T., Boumhaout, K., Da Veiga, S., Delage, T., Fruth, J., Gilquin, L.-R., Guillaume, J., Le Gratiet, L., Lemaitre, P., Marrel, A., Mey-Naoui, A., Nelson, B. L., Monari, F.-I., Oomen, R., Rakovec, O., Ramos, B., Roustant, O., Song, E.-H., Staum, J., Sueur, R., Touati, T., and Weber, F. (2020). Package 'sensitivity': Global Sensitivity Analysis of Model Outputs. Technical report.

Joas, J., Caro, Y., and Lechaudel, M. (2009). Comparison of postharvest changes in mango (cv Cogshall) using a Ripening class index (Rci) for different carbon supplies and harvest dates. *Postharvest Biology and Technology*, 54(1):25–31.

Johnson, R. S. and Handley, D. F. (2000). Using water stress to control vegetative growth and productivity of temperate fruit trees. *HortScience*, 35(6):1048–1050.

Jones, J. W., Keating, B. A., and Porter, C. H. (2001). Approaches to modular model development. *Agricultural Systems*, 70(2-3):421–443.

Kader, A. A. (1999). Fruit maturity, ripening, and quality relationships. *Acta Horticulturae*, 485:203–208.

Kanso, H., Quilot-Turion, B., Memah, M. M., Bernard, O., Gouzé, J. L., and Baldazzi, V. (2020). Reducing a model of sugar metabolism in peach to catch different patterns among genotypes. *Mathematical Biosciences*, 321:108321.

Karabulut, O. A., Smilanick, J. L., Crisosto, C. H., and Palou, L. (2010). Control of brown rot of stone fruits by brief heated water immersion treatments. *Crop Protection*, 29(8):903–906.

Keeney, R. L. and Raiffa, H., editors (1993). *Decisions with Multiple Objectives*. Cambridge University Press.

Kelley, K. M., Primrose, R., Crassweller, R., Hayes, J. E., and Marini, R. (2016). Consumer peach preferences and purchasing behavior: A mixed methods study. *Journal of the Science of Food and Agriculture*, 96(7):2451–2461.

Koball, D. C., Wilcox, W. F., and Seem, R. C. (1997). Influence of incubation-period humidity on the development of brown rot blossom blight of sour cherry. *Phytopathology*, 87(1):42–49.

Kulp, K., Lorenz, K., and Stone, M. (1991). Functionality of carbohydrate ingredients in bakery products. *Food technology*, pages 136–142.

Kumar, M., Rawat, V., Rawat, J. M., and Tomar, Y. K. (2010). Effect of pruning intensity on peach yield and fruit quality. *Scientia Horticulturae*, 125(3):218–221.

Lara, I., Belge, B., and Goulao, L. F. (2014). The fruit cuticle as a modulator of postharvest quality. *Postharvest Biology and Technology*, 87:103–112.

Lara, I., Heredia, A., and Domínguez, E. (2019). Shelf life potential and the fruit cuticle: The unexpected player. *Frontiers in Plant Science*, 10.

Larena, I., Torres, R., De Cal, A., Liñán, M., Melgarejo, P., Domenichini, P., Bellini, A., Mandrin, J. F., Lichou, J., De Eribe, X. O., and Usall, J. (2005). Biological control of postharvest brown rot (Monilinia spp.) of peaches by field applications of Epicoccum nigrum. *Biological Control*, 32(2):305–310.

Latini, A., Campiotti, C. A., Pietrantonio, E., Viola, C., Peral, V., Fuentes-Pila, J., and Sagarna, J. (2016). Identifying Strategies for Energy Consumption Reduction and Energy Efficiency Improvement in Fruit and Vegetable Producing Cooperatives: A Case Study in the Frame of TESLA Project. *Agriculture and Agricultural Science Procedia*, 8:657–663.

Lee, D. R. (1990). A unidirectional water flux model of fruit growth. *Canadian Journal of Botany*, 68(6):1286–1290.

Lescourret, F., Ben Mimoun, M., and Génard, M. (1998). A simulation model of growth at the shoot-bearing fruit level I. Description and parameterization for peach. *European Journal of Agronomy*, 9(2-3):173–188.

Lescourret, F. and Génard, M. (2005). A virtual peach fruit model simulating changes in fruit quality during the final stage of fruit growth. *Tree Physiology*, 25(10):1303–1315.

Lescourret, F., Génard, M., Habib, R., and Fishman, S. (2001). Variation in surface conductance to water vapor diffusion in peach fruit and its effects on fruit growth assessed by a simulation model. *Tree Physiology*, 21(11):735–741.

Lescourret, F., Moitrier, N., Valsesia, P., and Génard, M. (2011). QualiTree, a virtual fruit tree to study the management of fruit quality. I. Model development. *Trees - Structure and Function*, 25(3):519–530.

Lill, R. E., O'Donoghue, E. M., and King, G. A. (1989). Postharvest Physiology of Peaches and Nectarines. In *Horticultural Reviews*, pages 413–452. Timber Press.

Lombardo, V. A., Osorio, S., Borsani, J., Lauxmann, M. A., Bustamante, C. A., Budde, C. O., Andreo, C. S., Lara, M. V., Fernie, A. R., and Drincovich, M. F. (2011). Metabolic profiling during peach fruit development and ripening reveals the metabolic networks that underpin each developmental stage. *Plant Physiology*, 157(4):1696–1710.

Lopez Camelo, A. (2004). Manual for the preparation and sale of fruits and vegetables : from field to market. Technical report, FAO, Rome.

Lopresti, J., Goodwin, I., McGlasson, B., Holford, P., and Golding, J. (2014). Variability in Size and Soluble Solids Concentration in Peaches and Nectarines. In *Horticultural Reviews: Volume 42*, pages 253–312. Wiley.

Lovell, D. J., Powers, S. J., Welham, S. J., and Parker, S. R. (2004). A perspective on the measurement of time in plant disease epidemiology. *Plant Pathology*, 53(6):705–712.

Luo, Y., Ma, Z., Reyes, H. C., Morgan, D., and Michailides, T. J. (2007). Quantification of airborne spores of Monilinia fructicola in stone fruit orchards of California using real-time PCR. *European Journal of Plant Pathology*, 118(2):145–154.

Luo, Y. and Michailides, T. J. (2001). Factors affecting latent infection of prune fruit by Monilinia fructicola. *Phytopathology*, 91(May):864–872.

Luo, Y. and Michailides, T. J. (2003). Threshold conditions that lead latent infection to prune fruit rot caused by Monilinia fructicola. *Phytopathology*, 93(1):102–111.

Lurie, S. and Crisosto, C. H. (2005). Chilling injury in peach and nectarine. *Postharvest Biology and Technology*, 37(3):195–208.

Madden, L. V., Hughes, G., and van den Bosch, F., editors (2017). *The Study of Plant Disease Epidemics*. American Phytopathological Society.

Maguire, K. M., Lang, A., Banks, N. H., Hall, A., Hopcroft, D., and Bennett, R. (1999). Relationship between water vapour permeance of apples and microcracking of the cuticle. *Postharvest Biology and Technology*, 17(2):89–96.

Makowski, D., Naud, C., Jeuffroy, M. H., Barbottin, A., and Monod, H. (2006). Global sensitivity analysis for calculating the contribution of genetic parameters to the variance of crop model prediction. *Reliability Engineering and System Safety*, 91(10-11):1142–1147.

Marcelis, L. F. M. and Heuvelink, E. (2007). Concepts of modelling carbon allocation among plant organs. *Functional-Structural Plant Modelling in Crop Production*, pages 103–111.

Mari, M., Casalini, L., Baraldi, E., Bertolini, P., and Pratella, G. C. (2003). Susceptibility of apricot and peach fruit to Monilinia laxa during phenological stages. *Postharvest Biology and Technology*, 30(1):105–109.

Marini, R. P. (2003). Peach fruit weight, yield, and crop value are affected by number of fruiting shoots per tree. *HortScience*, 38(4):512–514.

Marini, R. P., Sowers, D., and Marini, M. C. (1991). Peach Fruit Quality

Is Affected by Shade during Final Swell of Fruit Growth. *Journal of the American Society for Horticultural Science*, 116(3):383–389.

Martini, C. and Mari, M. (2014). Monilinia fructicola, Monilinia laxa (Monilinia Rot, Brown Rot). In *Postharvest Decay: Control Strategies*. Academic Press.

Memmah, M. M., Lescourret, F., Yao, X., and Lavigne, C. (2015). Metaheuristics for agricultural land use optimization. A review. *Agronomy for Sustainable Development*, 35(3):975–998.

Mercier, V., Bussi, C., Plenet, D., and Lescourret, F. (2008). Effects of limiting irrigation and of manual pruning on brown rot incidence in peach. *Crop Protection*, 27(3-5):678–688.

Michailides, T. J. and Manganaris, G. A. (2009). Harvesting and handling effects on postharvest decay. *Stewart Postharvest Review*, 5(2):1–7.

Minas, I. S., Tanou, G., and Molassiotis, A. (2018). Environmental and orchard bases of peach fruit quality. *Scientia Horticulturae*, 235(July 2017):307–322.

Mirás-Avalos, J. M., Egea, G., Nicolás, E., Génard, M., Vercambre, G., Moitrier, N., Valsesia, P., González-Real, M. M., Bussi, C., and Lescourret, F. (2011). QualiTree, a virtual fruit tree to study the management of fruit quality. II. Parameterisation for peach, analysis of growth-related processes and agronomic scenarios. *Trees - Structure and Function*, 25(5):785–799.

Mirás-Avalos, J. M., Pérez-Sarmiento, F., Alcobendas, R., Alarcón, J. J., Mounzer, O., and Nicolás, E. (2016). Using midday stem water potential for scheduling deficit irrigation in mid–late maturing peach trees under Mediterranean conditions. *Irrigation Science*, 34(2):161–173.

Muenchow, G. (1986). Ecological use of failure time analysis. *Ecology*, 67(1):246–250.

Myers, B. J. (1988). Water stress integral–a link between short-term stress and long-term growth. *Tree Physiology*, 4(4):315–323.

Newson, R. (2006). Confidence intervals for rank statistics: Somers' D and extensions. *Stata Journal*, 6(3):309–334.

Nordey, T., Léchaudel, M., Génard, M., and Joas, J. (2016). Factors affecting ethylene and carbon dioxide concentrations during ripening: Incidence on final dry matter, total soluble solids content and acidity of mango fruit. *Journal of Plant Physiology*, 196:70–78.

Nunes, C. A. (2012). Biological control of postharvest diseases of fruit. *European Journal of Plant Pathology*, 133(1):181–196.

Nunes, C. N. and Emond, J.-P. (2007). Relationship between Weight Loss and Visual Quality of Fruits and Vegetables. *Proc. Fla. State Hort. Soc*, 120(May):235–245.

Obi, V. I., Barriuso, J. J., and Gogorcena, Y. (2018). Peach brown rot: Still in search of an ideal management option. *Agriculture (Switzerland)*, 8(8):125.

OECD, editor (2010). *Peaches and Nectarines*.

Oliveira Lino, L., Pacheco, I., Mercier, V., Faoro, F., Bassi, D., Bornard, I., and Quilot-Turion, B. (2016). Brown Rot Strikes Prunus Fruit: An Ancient Fight Almost Always Lost. *Journal of Agricultural and Food Chemistry*, 64(20):4029–4047.

Opara, L. U., Studman, C. J., and Banks, N. H. (2010). Fruit Skin Splitting and Cracking. In *Horticultural Reviews*, pages 217–262. John Wiley & Sons, Inc.

Ould-Sidi, M. M. and Lescourret, F. (2011). Model-based design of integrated production systems: A review. *Agronomy for Sustainable Development*, 31(3):571–588.

Pallas, B., Da Silva, D., Valsesia, P., Yang, W., Guillaume, O., Lauri, P. E., Vercambre, G., Génard, M., and Costes, E. (2016). Simulation of carbon allocation and organ growth variability in apple tree by connecting architectural and source-sink models. *Annals of Botany*, 118(2):317–330.

Parajuli, R., Thoma, G., and Matlock, M. D. (2019). Environmental sustainability of fruit and vegetable production supply chains in the face of climate change: A review. *Science of the Total Environment*, 650:2863–2879.

Parker, D., Zilberman, D., and Moulton, K. (1991). How quality relates to price in California fresh peaches. *California Agriculture*, 45(2):14–16.

Parker, D. D. (1993). Retail price response to quality characteristics of fresh peaches by store type. *Agribusiness*, 9(3):205–215.

Perera, M. and Dwivedi, A. K. (2020). Statistical issues and methods in designing and analyzing survival studies. *Cancer Reports*, 3(4).

Petersen, T. (1986). Fitting Parametric Survival Models with Time-Dependent Covariates. *Applied Statistics*, 35(3):281.

Pethybridge, S. J., Ngugi, H. K., and Hay, F. S. (2010). Use of survival analysis to assess management options for ray blight in Australian pyrethrum fields. *Plant Pathology*, 59(3):480–491.

Plénet, D., Giauque, P., Navarro, E., Millan, M., Hilaire, C., Hostalnou, E., Lyoussoufi, A., and Samie, J. F. (2009). Using on-field data to develop the EFI© information system to characterise agronomic productivity and labour efficiency in peach (Prunus persica L. Batsch) orchards in France. *Agricultural Systems*, 100(1-3):1–10.

Porat, R., Lichter, A., Terry, L. A., Harker, R., and Buzby, J. (2018). Postharvest losses of fruit and vegetables during retail and in consumers' homes: Quantifications, causes, and means of prevention. *Postharvest Biology and Technology*, 139:135–149.

Prusky, D. (1996). Pathogen quiescence in postharvest diseases. *Annual Review of Phytopathology*, 34:413–434.

Qian, G. and Mahdi, A. (2020). Sensitivity analysis methods in the biomedical sciences. *Mathematical Biosciences*, 323:108306.

Rahmati, M., Mirás-Avalos, J. M., Valsesia, P., Lescourret, F., Génard, M., Davarynejad, G. H., Bannayan, M., Azizi, M., and Vercambre, G. (2018). Disentangling the effects of water stress on carbon acquisition, vegetative growth, and fruit quality of peach trees by means of the qualitree model. *Frontiers in Plant Science*, 9(January).

Ricklefs, R. E. and Scheuerlein, A. (2002). Biological implications of the Weibull and Gompertz models of aging. *Journals of Gerontology - Series A Biological Sciences and Medical Sciences*, 57(2):69–76.

Ripoll, J., Urban, L., Staudt, M., Lopez-Lauri, F., Bidel, L. P., and Bertin, N. (2014). Water shortage and quality of fleshy fruits-making the most of the unavoidable. *Journal of Experimental Botany*, 65(15):4097–4117.

Saltelli, A., Tarantola, S., and Chan, K. P. (1999). A quantitative model-independent method for global sensitivity analysis of model output. *Technometrics*, 41(1):39–56.

Scandella, D. and Roty, C., editors (2012). *Pêches et nectarines : perception des distributeurs et des consommateurs.* CTIFL, ctifl edition.

Scherm, H. and Ojiambo, P. S. (2004). Applications of survival analysis in botanical epidemiology. *Phytopathology*, 94(9):1022–1026.

Schouten, R. E., Huijben, T. P., Tijskens, L. M., and van Kooten, O. (2007). Modelling quality attributes of truss tomatoes: Linking colour and firmness maturity. *Postharvest Biology and Technology*, 45(3):298–306.

Schouten, R. E., Jongbloed, G., Tijskens, L. M., and Van Kooten, O. (2004). Batch variability and cultivar keeping quality of cucumber. *Postharvest Biology and Technology*, 32(3):299–310.

Scrucca, L. (2013). GA: A package for genetic algorithms in R. *Journal of Statistical Software*, 53(4):1–37.

Segura, M., Maroto, C., Segura, B., and Casas-Rosal, J. C. (2020). Improving food supply chain management by a sustainable approach to supplier evaluation. *Mathematics*, 8(11):1–23.

Shewfelt, R. L. (1999). What is quality? *Postharvest Biology and Technology*, 15(3):197–200.

Shewfelt, R. L., Meyers, S. C., Prussia, S. E., and Jordan, J. L. (1987). Quality of Fresh-Market Peaches Within the Postharvest Handling System. *Journal of Food Science*, 52(2):361–364.

Shukla, M. and Jharkharia, S. (2013). Agri-fresh produce supply chain management: A state-of-the-art literature review. *International Journal of Operations and Production Management*, 33(2):114–158.

Sloof, M., Tijskens, L. M., and Wilkinson, E. C. (1996). Concepts for modelling the quality of perishable products. *Trends in Food Science and Technology*, 7(5):165–171.

Soto-Silva, W. E., Nadal-Roig, E., González-Araya, M. C., and Pla-Aragones, L. M. (2016). Operational research models applied to the fresh fruit supply chain. *European Journal of Operational Research*, 251(2):345–355.

Sousa Gallagher, M. and Mahajan, P. (2011). The stability and shelf life of fruit and vegetables. In *Food and Beverage Stability and Shelf Life*, pages 641–656. Elsevier.

Spadoni, A., Neri, F., Bertolini, P., and Mari, M. (2013). Control of Monilinia rots on fruit naturally infected by hot water treatment in commercial trials. *Postharvest Biology and Technology*, 86:280–284.

Tamm, L. and Fluckiger, W. (1993). Influence of temperature and moisture on growth, spore production, and conidial germination of Monilinia laxa. *Phytopathology*, 83(12):1321–1326.

Tamm, L., Minder, C. E., and Fluckiger, W. (1995). Phenological analysis of brown rot blossom blight of sweet cherry caused by Monilinia laxa. *Phytopathology*, 85(4):401–408.

Tardieu, F. (2003). Virtual plants: Modelling as a tool for the genomics of tolerance to water deficit. *Trends in Plant Science*, 8(1):9–14.

Thornley, J. and France, J., editors (2007). *Mathematical models in agriculture: quantitative methods for the plant, animal and ecological sciences*. CABI, 2nd edition.

Tian, S. P. and Bertolini, P. (1999). Effect of temperature during conidial formation of Monilinia laxa on conidial size, germination and infection of stored nectarines. *Journal of Phytopathology*, 147(11-12):635–641.

Tijskens, L. M. and Polderdijk, J. J. (1996). A generic model for keeping quality of vegetable produce during storage and distribution. *Agricultural Systems*, 51(4):431–452.

Tijskens, L. M. and Schouten, R. E. (2014). Modeling Quality Attributes and Quality Related Product Properties. In *Postharvest Handling: A Systems Approach*, pages 411–448. Elsevier Inc.

Tijskens, L. M. and van Kooten, O. (2006). Theoretical considerations on generic modelling of harvest maturity, enzyme status and quality behaviour. *International Journal of Postharvest Technology and Innovation*, 1(1):106–120.

Tijskens, L. M., Zerbini, P. E., Schouten, R. E., Vanoli, M., Jacob, S., Grassi, M., Cubeddu, R., Spinelli, L., and Torricelli, A. (2007). Assessing harvest maturity in nectarines. *Postharvest Biology and Technology*, 45(2):204–213.

Tijskens, P. (2001). Introduction to The principles of modelling: fundamental approaches. In *Food Process Modelling*, pages 1–2. Elsevier.

Veraverbeke, E. A., Verboven, P., Van Oostveldt, P., and Nicolaï, B. M. (2003). Prediction of moisture loss across the cuticle of apple (Malus sylvestris subsp. mitis (Wallr.)) during storage Part 1. Model development and determination of diffusion coefficients. *Postharvest Biology and Technology*, 30(1):75–88.

Villarino, M., Melgarejo, P., Usall, J., Segarra, J., Lamarca, N., and de Cal, A. (2012). Secondary inoculum dynamics of Monilinia spp. and relationship to the incidence of postharvest brown rot in peaches and the weather conditions during the growing season. *European Journal of Plant Pathology*, 133(3):585–598.

Walcroft, A. S., Lescourret, F., Génard, M., Sinoquet, H., Le Roux, X., and Donès, N. (2004). Does variability in shoot carbon assimilation within the tree crown explain variability in peach fruit growth? *Tree Physiology*, 24(3):313–322.

Wallach, D., Makowski, D., Jones, J. W., and Brun, F., editors (2018). *Working with dynamic crop models: Methods, tools and examples for agriculture and environment*. Academic Press.

West, J. S. and Kimber, R. B. (2015). Innovations in air sampling to detect plant pathogens. *Annals of Applied Biology*, 166(1):4–17.

Wills, R. B. H., McGlasson, W. B., Graham, D., and Joyce, D. C., editors (2016). *Postharvest: an introduction to the physiology and handling of fruit and vegetables*. CABI, 6th edition.

Wu, B. H., Ben Mimoun, M., Génard, M., Lescourret, F., Besset, J., and Bussi, C. (2005). Peach fruit growth in relation to the leaf-to-fruit ratio, early fruit size and fruit position. *Journal of Horticultural Science and Biotechnology*, 80(3):340–345.

Xanthopoulos, G. T., Templalexis, C. G., Aleiferis, N. P., and Lentzou, D. I. (2017). The contribution of transpiration and respiration in water loss of perishable agricultural products: The case of pears. *Biosystems Engineering*, 158:76–85.

Xu, X. M., Bertone, C., and Berrie, A. (2007). Effects of wounding, fruit age and wetness duration on the development of cherry brown rot in the UK. *Plant Pathology*, 56(1):114–119.

Xu, X. M., Guerin, L., and Robinson, J. D. (2001). Effects of temperature and relative humidity on conidial germination and viability, colonization and sporulation of Monilinia fructigena. *Plant Pathology*, 50(5):561–568.

Yahia, E. M. and Carrillo-Lopez, A., editors (2018). *Postharvest physiology and biochemistry of fruits and vegetables*. Woodhead Publishing, 1st edition.

Yahia, E. M., Carrillo-López, A., and Bello-Perez, L. A. (2018). Carbohydrates. In *Postharvest Physiology and Biochemistry of Fruits and Vegetables*, pages 175–205. Elsevier.

Yu, F., Ni, Z., Shao, X., Yu, L., Liu, H., Xu, F., and Wang, H. (2015). Differences in sucrose metabolism in peach fruit stored at chilling stress versus nonchilling stress temperatures. *HortScience*, 50(10):1542–1548.

Zhang, P., Wei, Y., Xu, F., Wang, H., Chen, M., and Shao, X. (2020). Changes in the chlorophyll absorbance index (IAD) are related to peach fruit maturity. *New Zealand Journal of Crop and Horticultural Science*, 48(1):34–46.

Zhao, S., Yue, C., Luby, J., Gallardo, K., McCracken, V., McFerson, J., and Layne, D. R. (2017). U.S. peach producer preference and willingness to pay for fruit attributes. *HortScience*, 52(1):116–121.

Zhou, R., Yue, C., Zhao, S., Gallardo, R. K., McCracken, V., Luby, J. J., and McFerson, J. R. (2018). Using market segmentation analysis to identify consumer preferences for fresh peach attributes. *HortScience*, 53(11):1664–1668.

Ziosi, V., Noferini, M., Fiori, G., Tadiello, A., Trainotti, L., Casadoro, G., and Costa, G. (2008). A new index based on vis spectroscopy to characterize the progression of ripening in peach fruit. *Postharvest Biology and Technology*, 49(3):319–329.

Appendix A

Supplementary Information - Chapter 1

A.1 Sugar metabolism represented in sugar dynamics sub-models

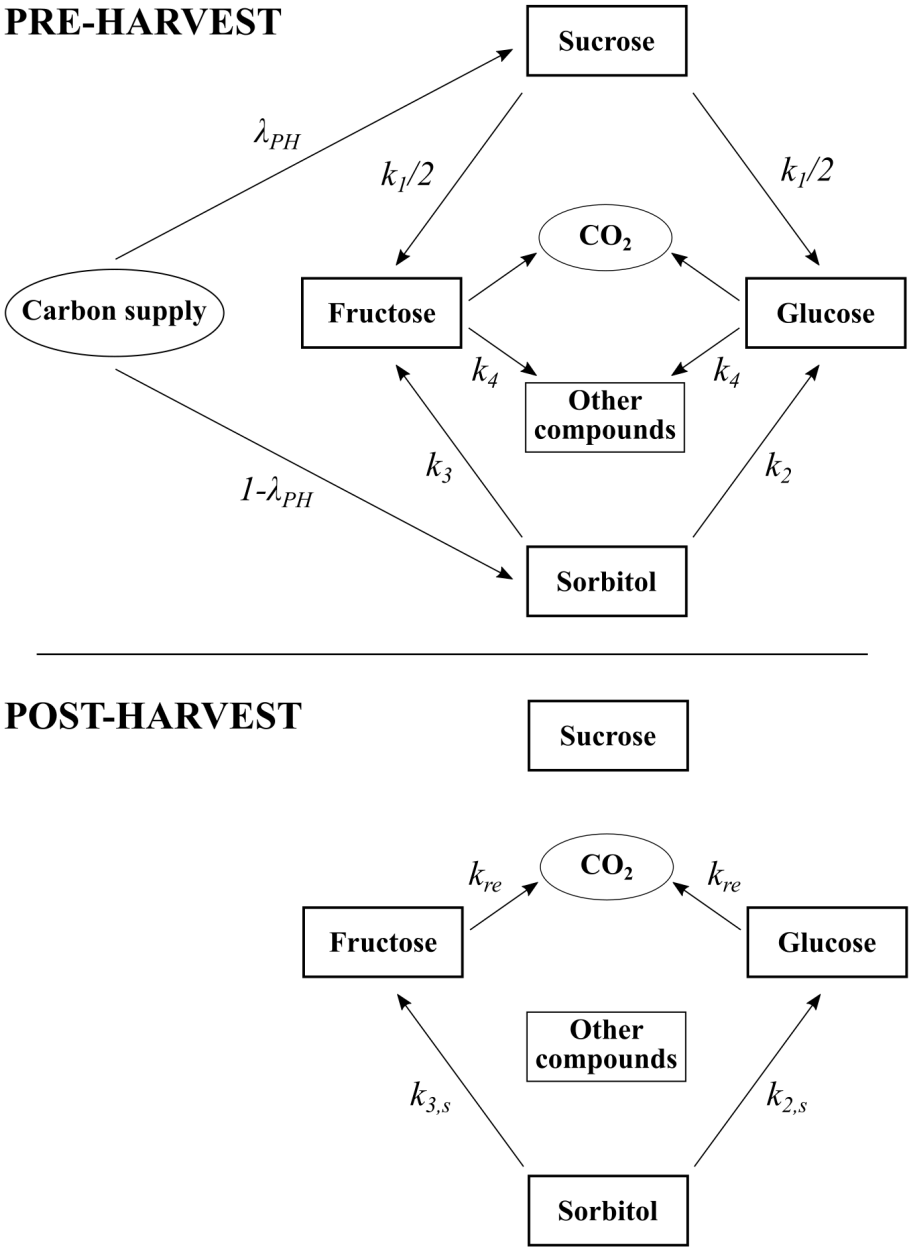

Figure A.1 – Carbon pathways assumed in the pre- and post-harvest sugar dynamics sub-models. Arrows and boxes represent carbon fluxes and carbon components included in the mathematical models, respectively. The ellipses represent carbon input (the tree) and loss by respiration. The proportion of sucrose in the phloem-sourced sugar pool (λ_{ph}) and the parameters sugar transformation are indicated next to each carbon flux to which they relate. In the post-harvest stage, 'sucrose' and 'other compounds' compartment do not participate in the carbon pathways.

A.2 Sub-model parameter and constant values taken from literature

Parameter	Meaning	Value	Unit	Source
n_{sto}	stomata number at the fruit anthesis	70 592	-	Gibert et al. (2010)
$q_{m,pre}$	maintenance respiration coefficient during growing stage	0.00144	g g^{-1} d^{-1}	Génard and Gouble (2005)
$q_{g,pre}$	growth respiration coefficient	0.0843	g g^{-1} d^{-1}	DeJong and Goudriaan (1989)
Q_{10}	temperature ratio of maintenance respiration	1.96	-	Grossman and DeJong (1994)
$q_{m,post}$	maintenance respiration coefficient during storage	0.0027	g g^{-1}	Caleb et al. (2016)
$E_{a,resp}$	activation energy for respiratory process	87600	J mol^{-1}	Exama et al. (1993)
σ_{fl}	carbon content in mesocarp dry mass	44.5	g g^{-1}	Génard and Souty (1996)
sr_{su}	sweetness rating of sucrose	1	-	Kulp et al. (1991)
sr_{so}	sweetness rating of sorbitol	0.6	-	Kulp et al. (1991)
sr_{gl}	sweetness rating of glucose	0.77	-	Kulp et al. (1991)
sr_{fr}	sweetness rating of fructose	1.75	-	Kulp et al. (1991)
c_{su}	carbon content of sucrose	0.421	g g^{-1}	
c_{so}	carbon content of sorbitol	0.395	g g^{-1}	
c_{gl}	carbon content of glucose	0.4	g g^{-1}	
c_{fr}	carbon content of fructose	0.4	g g^{-1}	

Table A.1 – Sub-model parameter values taken from literature and used in the models of pre- and post-harvest nectarine quality development

A.3 Measured and simulated fruit cuticular cracks surface area

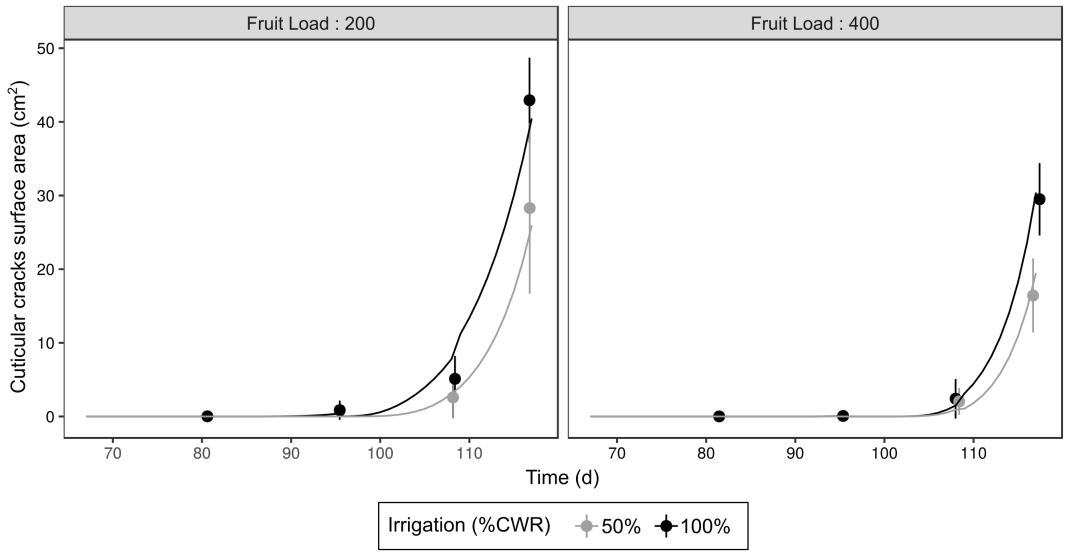

Figure A.2 – Average measured (points) and simulated (lines) values of fruit cuticular cracks surface area over the growing season, under the four experimental pre-harvest conditions of 2018. Bars stand for the standard errors. The time is in days after full bloom (17 March).

A.4 Simulated part of fruit mass loss due to respiration during storage

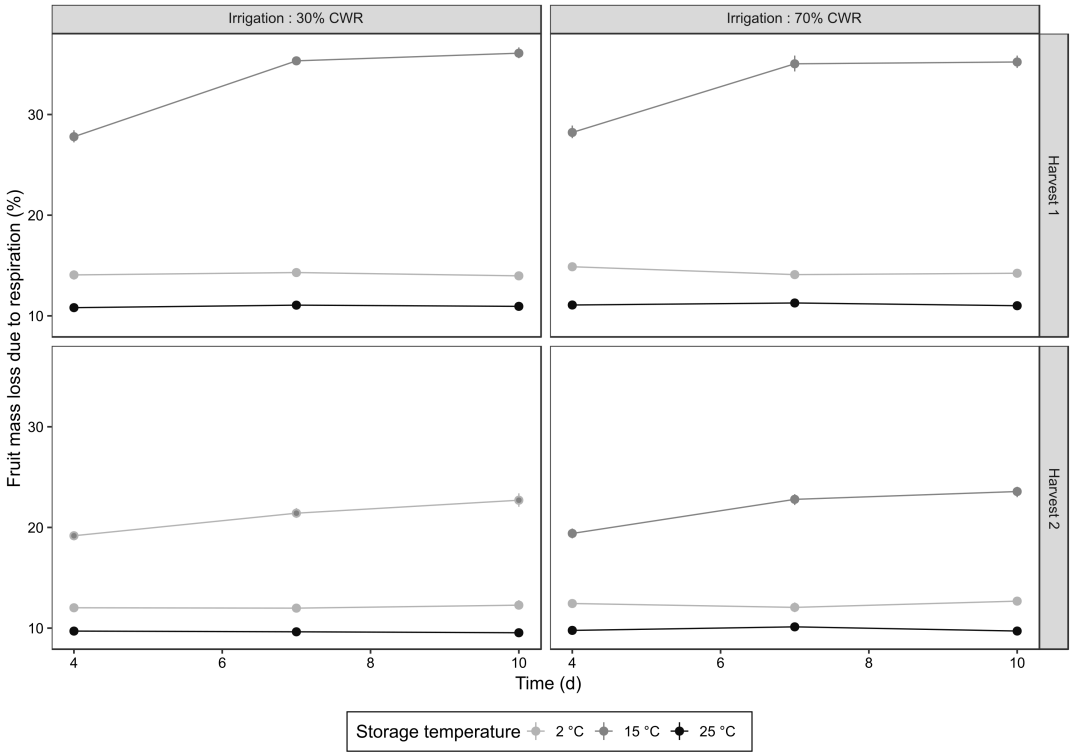

Figure A.3 – Simulated values of the part of fruit mass loss due to respiration, under the six experimental conditions of 2019 (Irrigation x Storage temperature), for two harvest dates (134 and 141 dafb). The time is in days after the beginning of storage.

Appendix B

Supplementary Information - Chapter 2

B.1 Results: brown rot secondary infections during storage

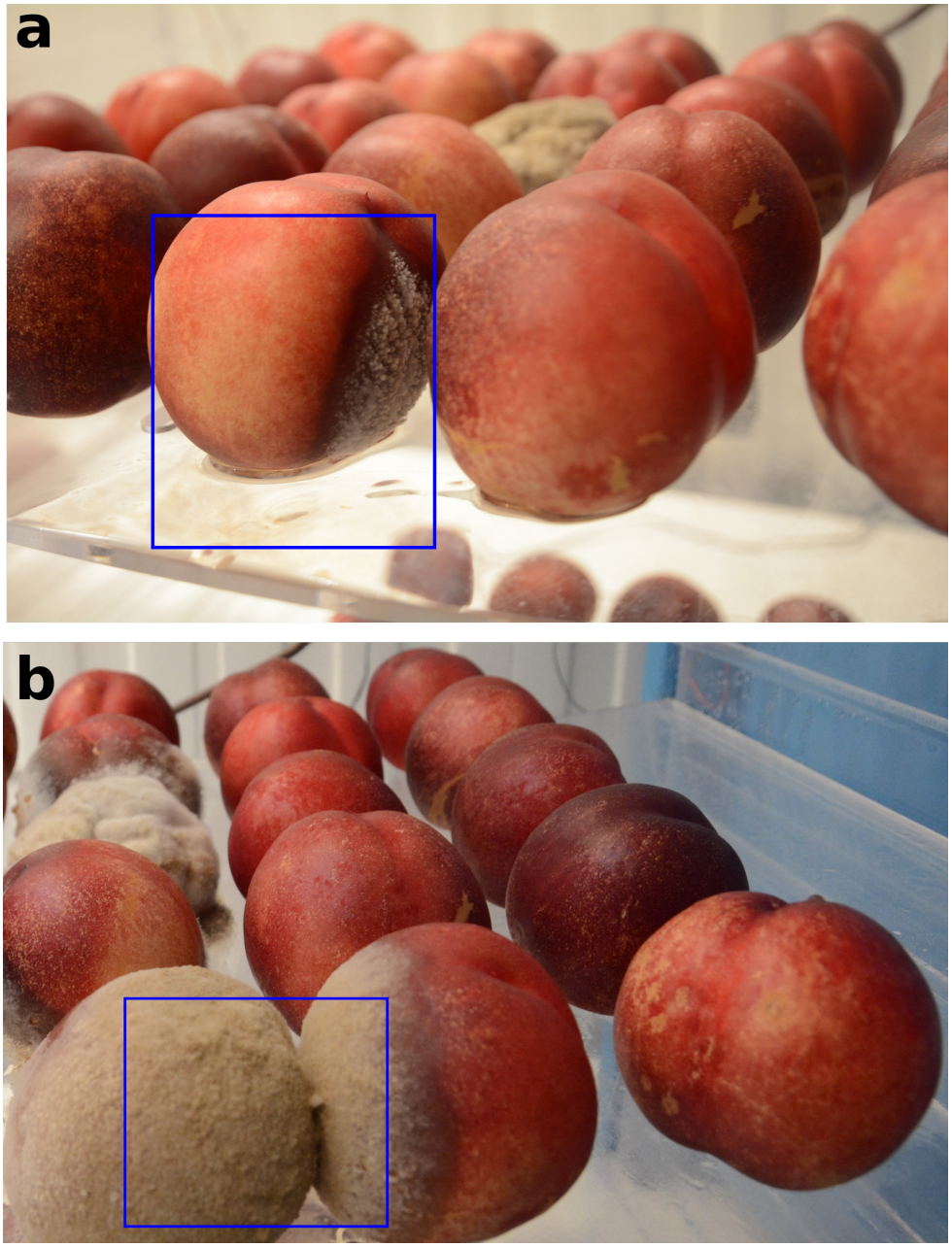

Figure B.1 – Spread of brown rot secondary infections on nectarine by contact with dripping juice from infected fruits (a) and from direct contact with infected fruits (b).

B.2 Results: cumulative incidence of brown rot disease at the end of storage, under different pre-harvest scenarios and storage conditions (2018-2019)

Harvest date (dafb)	Irrigation (% CWR)	Fruit Load	Fruit weight (g)	Follow up time (d)	Cumulative incidence (%)
117	100%	400	195.12±26 a	14	13.33
		200	207.95±23 b	14	20
	50%	400	150.90±25 c	14	3.33
		200	170.28±23 d	14	5.08
124	100%	400	166.02±30 a	14	32.20
		200	191.10±33 b	14	35.59
	50%	400	143.53±22 c	14	11.67
		200	148.38±21 c	14	18.33
132	100%	400	179.55±39 a	12	56.67
		200	208.04±35 b	12	83.33
	50%	400	164.16±34 a	12	30
		200	169.33±30 a	12	40

Table B.1 – Mean fruit mass (with standard deviation), maximum follow up time and cumulative incidence at the end of storage for brown rot visual assessment during storage in 2018, for each experimental treatment. Harvest dates are referred to full bloom date, which was on 17 March 2018. For fruit mass, comparisons between treatments were realised per harvest date, where means followed by the same letter do not significantly differ from each other (Tukey test with $\alpha = 0.01$).

Harvest date (dafb)	Irrigation (% CWR)	Storage temperature (°C)	Fruit mass (g)	Follow-up time (d)	Cumulative incidence (%)
134	70%	2	175.43±23 a	17	0
		15	180.43±26 a	17	12.5
		25	177.52±19 a	17	42.5
	30%	2	145.43±20 b	17	0
		15	141.55±22 b	17	12.5
		25	145.04±19 b	17	20
141	70%	2	144.16±20 a	21	0
		2	149.21±21 a	21	55
		2	151.30±20 a	21	95
	30%	2	125.17±25 b	21	0
		2	124.59±23 b	21	32.5
		2	126.74±23 b	21	91.25

Table B.2 – Mean fruit mass (with standard deviation), maximum follow up time and cumulative incidence at the end of storage for brown rot visual assessment during storage in 2019, for each experimental treatment. Harvest dates are referred to full bloom date, which was on 10 March 2019. For fruit mass, comparisons between treatments were realised per harvest date, where means followed by the same letter do not significantly differ from each other (Tukey test with $\alpha = 0.01$).

B.3 Survival analysis: model selection

Selected variables	Parameter number	Log-likelihood	BIC	D_{XY}
$T_{mean,s}$, w, $wd_{mean,h}$, I_h	6	-1589.013	3222.128	0.684
$T_{mean,s}$, w, $wd_{mean,h}$, I_h, $R_{sum,h}$	7	-1587.718	3226.889	0.689
$T_{mean,s}$, w, $wd_{mean,h}$, I_h, $T_{mean,h}$	7	-1587.729	3226.911	0.689
$T_{mean,s}$, w, $wd_{mean,h}$, I_h, GDD_h	7	-1588.099	3227.652	0.687
$T_{mean,s}$, w, $wd_{mean,h}$, GDD_h	6	-1593.896	3231.896	0.690

Table B.3 – Selected variables and number of estimated parameters for the best five Gompertz-shaped survival models in terms of the Bayesian Information Criterion (BIC).The value of the log-likelihood an the Somers' D_{XY} (%) statistic are presented.

Appendix C

Supplementary Information - Chapter 3

C.1 Water regime scenarios used in model simulations

Irrigation scenario number	$\Psi_{min,I}$	$\Psi_{min,II}$	$\Psi_{min,III}$	WS_{Ψ}
1	-0.8	-0.8	-0.8	0
2	-1.4	-0.8	-0.8	9
3	-2	-0.8	-0.8	18
4	-0.8	-1.4	-0.8	12
5	-1.4	-1.4	-0.8	21
6	-2	-1.4	-0.8	30
7	-0.8	-2	-0.8	24
8	-1.4	-2	-0.8	33
9	-2	-2	-0.8	42
10	-0.8	-0.8	-1.4	12
11	-1.4	-0.8	-1.4	21
12	-2	-0.8	-1.4	30
13	-0.8	-1.4	-1.4	24
14	-1.4	-1.4	-1.4	33
15	-2	-1.4	-1.4	42
16	-0.8	-2	-1.4	36
17	-1.4	-2	-1.4	45
18	-2	-2	-1.4	54
19	-0.8	-0.8	-2	24
20	-1.4	-0.8	-2	33
21	-2	-0.8	-2	42
22	-0.8	-1.4	-2	36
23	-1.4	-1.4	-2	45
24	-2	-1.4	-2	54
25	-0.8	-2	-2	48
26	-1.4	-2	-2	57
27	-2	-2	-2	66

Table C.1 – Irrigation regime scenarios, identified by the values of the root collar water potential at midday during the fruit growth period p ($\Psi_{min,p}$) and the water stress integral indicator (WS_{Ψ}, MPa days).

C.2 Parametrization and initialization of the QualiTree model

Experiments performed in 2018 in an orchard at INRAE Avignon (France) allowed to retrieve the input data for QualiTree and new parameters for the nectarine cultivar 'Nectarlove'.

Experimental and input data

Meteorological variables were recorded at a weather station located close to the orchard and they were used as model inputs. The trees of *Prunus persica var. nucipersica* (cv. 'Nectarlove') were planted in 2012. In 2018, full bloom occurred on 17 March and thinning took place 66 days after the full bloom (dafb). The experiments combined two irrigation treatments and two fruit loads. The irrigation scenarios were based on the crop water requirement (CWR), calculated as the difference between the potential evapotranspiration and the rainfall over the irrigation period (Allen et al., 1998). We tested a well-irrigated (100% CWR) and a water-stressed (50% CWR) scenario, which were differentiated at 93 dafb. The two fruit loads were a low load (200 fruit per tree) and a high load (400 fruit per tree), for a total of four pre-harvest treatment. Trees were subjected to commercial horticultural practices, including fertilization and pest control.
Measurements of fruit diameter and leafy shoots length, fruit allometry, dry matter and fresh mass were taken on 24 trees from the thinning date (66 dafb) since the last harvest (124 dafb). Cheek diameters (D, mm) from 30 random fruit per treatment were measured every seven days. These diameters were transformed into dry mass (M_{dry}, g) and fresh mass (M_{fresh}, g) using allometric relationships derived from experimental data. Leafy shoot length (m) was also measured on 15 random leafy shoots per treatment during fruit growth. Lengths were con-

verted to dry mass (g) using the allometric relationship of Walcroft et al. (2004). Finally, four trees in the orchard were selected after pruning as representative of the tree architecture, which is an input to the model. Diameters, lengths of the tree axes, insertion and phyllotaxic angles were measured in order to obtain a description of the tree architecture (example in Figure C.1). The volume of the trunk, branches and stem were calculated considering them as conic-section structures. Volumes were then transformed into biomass using a wood-density value of 0.77 g cm^{-3}, as in Mirás-Avalos et al. (2011). Carbon reserve for tree organs were retrieved from Mirás-Avalos et al. (2011). Initial values of leafy shoot and fruit dry masses, and fruit sugar concentrations (sucrose, fructose, glucose, and sorbitol) were taken from the experimental data at the start of the simulation (thinning data, 66 dafb). Fruit and leafy shoot numbers were allocated on the tree architecture, proportionally to the individual stem wood length.

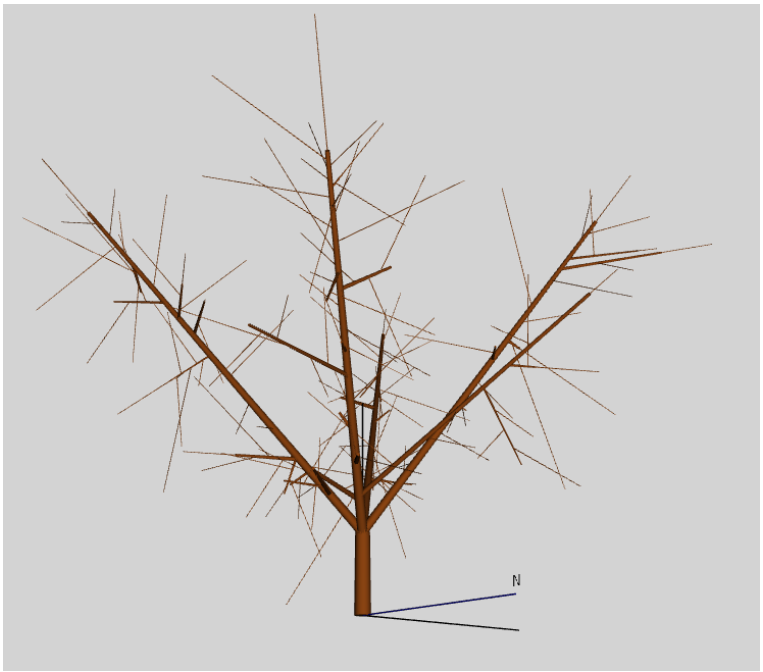

Figure C.1 – Example of tree architecture used as input in QualiTree simulations: 'Nectarlove' tree measured in 2019 after winter pruning at INRAE centre in Avignon (France).

Calibration of model parameters

New model parameters were calibrated for the nectarine cultivar 'Nectarlove' (Table C.2). More information on these parameters can be found in Lescourret et al. (2011), Mirás-Avalos et al. (2011), Fishman and Génard (1998) and Rahmati et al. (2018).

Potential fruit and leafy shoot growth parameters (in terms of dry mass), namely the initial relative growth rate (RGR_{ini}), maximal dry mass (DM_{max}), and minimum and maximum degree-days (dd_{min}, dd_{max}) were estimated by non-linear least square regressions using experimental data close to the potential growth (90 % quantile). These parameters were estimated by a stochastic search algorithm inspired by genetic evolution theory ('ga' function from *GA* package, in R version 4.0.3).

In the case of fruit dry mass, the growth equation is logistic, combined with a temporal component to account for the maturation process (Lescourret et al., 1998). However, for the considered cultivar we decided not take into consideration the temporal component of the maturation process, mostly because the observed dry mass did not reach a threshold value during the experimental season. A total of 8 parameters were calibrated globally by running the QualiTree model in two steps. In the first one, we calibrated six parameters related to the carbon economy: a global parameter (α, which express the distance effect in the carbon transport inside the whole tree), two parameters expressing the effect of water deficit on the leafy shoot growth limitation (Ψ_{min} and Ψ_{max}), and three related to the carbon growth demand of old roots, new roots and stem wood (RGR^{ow}_{ini}, RGR^{nr}_{ini}, RGR^{sw}_{ini}). The parameters were retrieved by minimizing the relative root mean squared error (RRMSE) between the average simulated and observed values of fruit and leafy shoot dry mass along the growing season (Wallach et al., 2018). The remaining two parameters related to fruit

water relationships (a_x, Y) were then retrieved by minimizing the RRMSE between the average observed values of fruit fresh mass along the growing season. The parameters governing the fruit sugar dynamics, the fruit surface conductance to water vapour and fruit cuticular crack development were retrieved from Casagrande et al. (2021). All the other parameters were retrieved from Grossman and DeJong (1994), Fishman and Génard (1998), Lescourret et al. (2011), Mirás-Avalos et al. (2011) and Rahmati et al. (2018).

After parameter calibration, the model well simulated the observed values in terms of dry (RRMSE=0.09, on average) and fresh mass (RRMSE=0.12) of fruit in the different experimental conditions, although model simulations overestimated the observed values of leafy shoots dry masses (RRMSE=0.2, Figure C.2).

Parameters	Definition	Value	Unit
Carbon growth demand for fruit			
DM_{max}^{fr}	fruit maximum potential dry mass	54.803	g
RGR_{ini}^{fr}	fruit initial relative growth rate	$4{\cdot}10^{-3}$	degree-day^{-1}
Carbon growth demand for leafy shoots			
DM_{max}^{ls}	leafy shoot maximum potential dry mass	17.4	g
RGR_{ini}^{ls}	leafy shoot initial relative growth rate	$7.5{\cdot}10^{-3}$	degree-day^{-1}
dd_{min}^{ls}	minimum degree-day value	275	g
dd_{max}^{ls}	maximum degree-day value	1186	g
Carbon growth demand for other tree entities			
RGR_{ini}^{ow}	old wood and coarse root initial relative growth rate	$2{\cdot}10^{-4}$	degree-day^{-1}
RGR_{ini}^{nr}	new root initial relative growth rate	$4{\cdot}10^{-3}$	degree-day^{-1}
RGR_{ini}^{sw}	stem wood initial relative growth rate	$5{\cdot}10^{-4}$	degree-day^{-1}
Water stress effects on vegetative growth			
Ψ_{min}	minimum threshold of leaf water potential	-2.68	MPa
Ψ_{max}	maximum threshold of leaf water potential	-1.59	MPa
Fruit water relationship parameters			
a_x	ratio of area of the composite membrane of the fruit area	0.077	-
Y	threshold value of hydrostatic pressure needed for growth	4	bar
Global parameters			
α	parameter expressing the effect of distance between organs on carbon exchange within the tree	0.01	-

Table C.2 – Parameter values concerning the carbon economy and water economy in QualiTree for 'Nectarlove' nectarine cultivar grown in France.

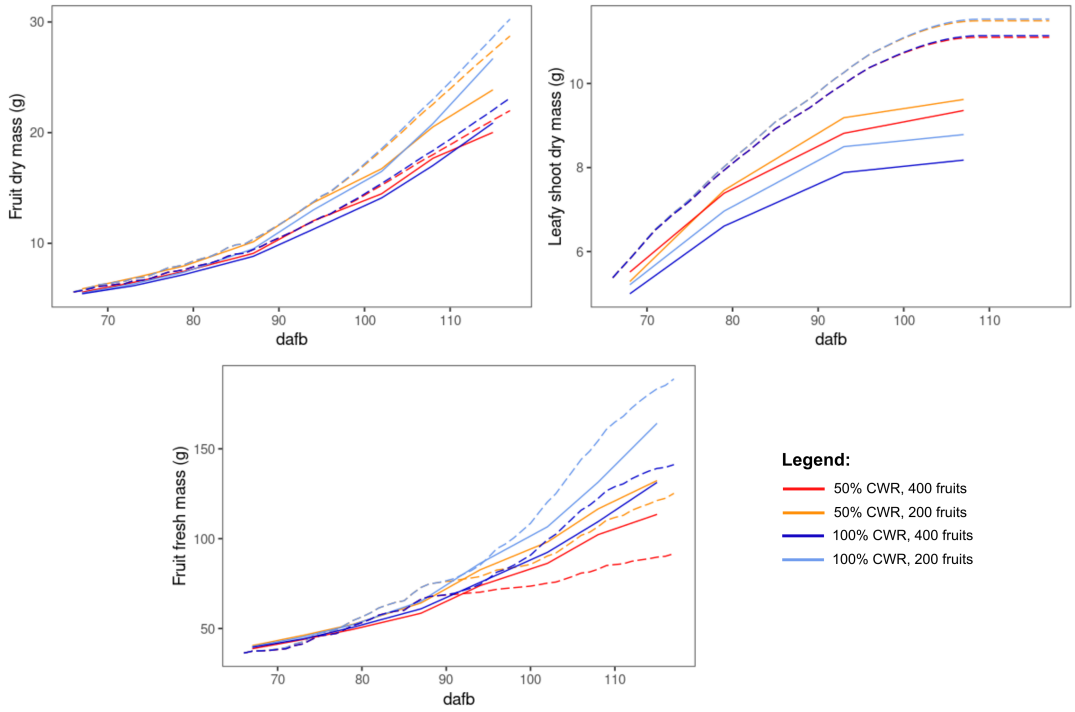

Figure C.2 – Average observed (continuous) and simulated (dashed) values of fruit and leafy shoot dry mass, and fruit fresh mass. The values refer to different experimental conditions (irrigation regime x fruit load) on nectarine 'Nectarlove' from the 2018 season (Avignon, France).

Équipe d'encadrement

Françoise Lescourret, Directrice de recherche, UR1115 PSH INRAE

Michel Génard, Directeur de recherche, UR1115 PSH INRAE

Sébastien Lurol, Ingénieur, CTIFL St-Rémy-de-Provence (unité CITAR)

Florence Charles, Maître de conférences, UMR Qualisud, Université d'Avignon

AVIGNON UNIVERSITÉ